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HISTORY OF NEUROSCIENCE

Medicine and science in the life of Luigi Galvani (1737–1798)

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ABSTRACT: Together with its companion paper, dealing with the contribution of Luigi Galvani to the history of electrophysiology, this article provides a biographical sketch of the scientist of Bologna in the occasion of the bicentenary of his death. Studies on Galvani have focused mainly on his "discovery" of animal electricity, and on the controversy with Alessandro Volta. Much less is known about Galvani's life and activity as a teacher, physician, and researcher in the fields of comparative anatomy, physiology, and chemistry of life. Yet, a balanced assessment of the significance and the role of Galvani's research in the history of science will be possible only after a historical reconstruction of his entire activity. This should take into account aspects of Galvani's life that have been little studied up to now: Galvani's scientific background, the scientific context in which his interest for muscular physiology arose, the interplay between his activity as a researcher and as a physician, the origin and characteristics of his experimental approach to biological studies, and the development of his experimental research in the crucial period culminating in his electrophysiological explanation of muscular motion. The present article aims at offering a contribution in this direction. © 1998 Elsevier Science Inc.

KEY WORDS: Animal electricity, Electrophysiology, History of science, History of medicine, Biography.

GALVANI'S EDUCATION AND THE SCIENTIFIC CONTEXT OF BOLOGNA

Luigi Galvani (Fig. 1) was born in Bologna, Italy on 9 September 1737 from Domenico and Barbara Foschi. Our information on his life is rather scant and indeed a complete biography of Galvani is still to be written. In particular, very little is known about Galvani's family and youth. Galvani's father was a goldsmith and Barbara was his fourth wife. He had already had two children from his previous marriages and Luigi was the first of two more children he had with Barbara. The second child, Giacomo, was born in 1742 and was always very close to Luigi, whom he hosted in his house in the last years of his life. Even though Galvani's family did not belong to Bologna's aristocracy, and did not have a scholarly tradition, they were probably sufficiently well off to allow at least one of their sons to undertake a scholarly career. This decision

must not have been easy for Galvani, as he had shown a strong inclination for religious life since he was a child. When he was only 15 years old Luigi joined a religious institution, the *Oratorio dei Padri Filippini*, which was attended by some of the most illustrious people in Bologna. According to some biographers, he also considered taking his religious vows, but was discouraged from doing it. After his first studies of grammar and literature, in approximately 1755 Galvani entered the Faculty of Arts of the University of Bologna.

At that time the University of Bologna could boast a famous name and a long tradition, even if it was trying to emerge from a period of decline in both the number of students and the quality of teaching. The medicine course, which Galvani attended in the second half of the 1750s, lasted 4 years and was formally characterized by a bookish sort of teaching, dominated by the texts of Hippocrathes, Galen, and Avicenna. On the other hand, many of the university professors also gave lectures in their own houses, with the full backing of academic authorities. In such lectures they were markedly free both to teach modern authors and to impart a more practical slant to their teaching. One of these professors was Jacopo Bartolomeo Beccari (1682-1766), anatomicus emeritus of the University, who taught Galvani the first notions of medicine. Beccari's name is associated with the discovery that gluten is present not only in animal matter but also in wheat and other vegetables and to the study of the mechanism of phosphorescence. Beccari had an international reputation, and in 1728 he had even been elected fellow of the Royal Society of London. He taught Galvani not only the basic notions of medicine but also chemistry. As a matter of fact Beccari was the first professor of this latter discipline in an Italian university.

Even if the teaching of chemistry was associated to the University, Beccari gave his lectures at the *Istituto delle Scienze* (Institute of Sciences) of Bologna (Fig. 2). This institution had been founded by Count Luigi Ferdinando Marsili, with the purpose of introducing modern methods and new disciplines, such as chemistry, both in teaching and research, owing to the failure of attempts to reform the University. The Institute of Sciences, formed by a scientific and a literary academy, began its activity in 1714. The Academy of Sciences, in particular, was inspired by

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FIG. 1. The statue of Luigi Galvani erected in Piazza Galvani, in Bologna, facing the *Archiginnasio*, the old building of the University.

Baconian scientific ideals and was modeled on the *Académie des Sciences* of Paris. It became one of the main scientific and research institutions of the 18th century. The teaching activity that took place there was considered complementary to the courses held at the University. It was organized in *camere* (chambers), where the professors, generally the same who taught at the University, could take advantage of instruments and materials suitable for a practical and experimental teaching of their disciplines.

At the Institute of Sciences Galvani attended not only the chemistry course held by Beccari, but also the courses in natural history and in physics. The latter discipline was taught by Domenico Gusmano Galeazzi (1686-1775), who was also anatomicus emeritus of the University. For the experimental teaching of physics, Galeazzi used one of the best equipped laboratories in Italy, where he could illustrate by means of experiments, disciplines that had already obtained recognition, such as mechanics, as well as more recent ones such as electricity. Electricity was given a particular attention at the time when Galvani was a student. The discoveries of the first half of the 18th century, the invention of new instruments, such as the electrostatic machine and the Leyden jar, placed electricity at the top of many scientists' interests, and they made also electricity a discipline à la mode [34]. Around the half of the century Benjamin Franklin (1706-1790) published his researches on electricity, with his famous discoveries on the nature of lightning and thunder. According to Franklin, electrical phenomena could be explained by assuming the existence of a single fluid. A body became positively charged if it contained more than its "natural" amount of electricity, and became negative in the opposite case. Franklin's theory, which was spread in Italy especially through the work of Giambattista Beccaria (1716–1781), professor of experimental physics in Turin, had an immediate impact in Bologna. Galeazzi, but especially Laura Bassi (1711–1778) and her husband Giuseppe Veratti (1707–1793), became the main supporters of this theory and established direct contacts with Franklin himself and with Beccaria.

In those days, the Bologna scientific community was, therefore, well in the van of electrological research and could offer Galvani a sound formation in this field [35]. Even though Galvani was oriented toward medicine, he showed a continuous interest in electricity, and kept updated with the progress in the discipline through the most important works published in the field, which enriched his personal library [6]. Besides, he was particularly impressed by the personality and research work of the Verattis, with whom he started a relationship based on esteem and collaboration. It was to them, for example, that the young Galvani addressed his research on the kidney and ureter of birds, while he later collaborated with Veratti in important experiments of electrophysiology [18].

The usefulness for medicine of disciplines such as chemistry and physics was well accepted at the time. In Beccari's research work and teaching, for example, chemistry and medicine were closely connected. Beccari devoted himself mostly to the analysis of foods and of mineral waters, topics that were investigated and applied mainly to the therapeutic practice and to the problems concerning health. Galvani shared with Beccari the same view of the study of nature. Referring in particular to the discoveries in the fields of electricity and of pneumatics made in the third quarter of the 18th century, Galvani wondered: "what services doesn't physics render to medicine, . . . by which it can both preserve our health and can more assuredly win infirmity?" ([24] pp. 17–18).

Another discipline that Galvani learned during his University years and that he practiced afterwards was surgery. His teacher in this field was Giovanni Antonio Galli (1708-1782) who, besides being professor ad lecturam chirurgiae at the University, in 1757 became the first professor of obstetrics of the Institute of Sciences. Galvani learned both the theory and practice of surgery by attending the lectures given at the hospital Santa Maria della Morte. Moreover, he also became Galli's assistant, and substituted for him in another hospital in Bologna during his absence. Galvani's apprenticeship and practice of surgery represent an important and yet neglected aspect of his training. In fact, along with anatomy, surgery contributed to Galvani's attainment of operative skills, to his great ability with lancets and scissors, necessary not only in the treatment of people and in the dissection of bodies, but also in experiments with animals. Moreover, it certainly contributed to familiarize Galvani with the manipulation of a living body, and represented a stimulus to intervene actively on the organism of experimental animals. In some way surgery was an important element of contrast vis à vis the static and pictorial approach to anatomy and the speculative attitude in physiology typical of traditional academic medicine. According to some historians, such aspects of surgery played a fundamental role in the birth of modern experimental physiology at the beginning of 19th century [43]. If we consider the case of Galvani, perhaps we could usefully apply a similar point of view to a previous period leading to modern life

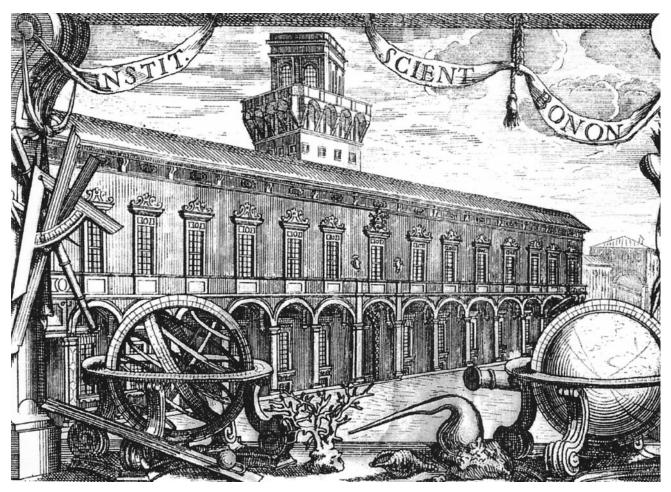


FIG. 2. The Istituto delle Scienze of Bologna at Galvani's days, as illustrated in the title page of the Commentarii of the Accademia delle Scienze.

GRADUATION AND EARLY CAREER

In 1759 Galvani graduated in both medicine and philosophy, according to an usual custom at the University of Bologna. Immediately he took his first steps to have access to the academic career, applying to the position of lecturer at the University. To this end, according to the University rules of the time, on 21 June 1761 he publicly defended a thesis on bones, taking advantage not only of his knowledge of anatomy, but also of his studies in chemistry and surgery [17]. In the following year Galvani was ascribed among the number of permanent anatomists (anatomici ordinari) of the University, and was appointed honorary (and unpaid) lecturer of surgery, as coadjutor of Gaetano Tacconi. During the 3 years in which he worked with Tacconi, Galvani had the possibility of perfecting his knowledge and technique of surgery.

The year 1766 was a very important one for Galvani's career. He was moved from the position of lecturer of surgery to that of theoretical anatomy, and, more importantly, he obtained an appointment at the Institute of Sciences as *custode e ostensore delle cere anatomiche* (curator and ostensor of anatomical waxes). At the Academy of Sciences of the Institute he had already read a few dissertations, based on researches involving comparative anatomy, physiology, and chemistry. He had dealt in particular with the kidney and ureter of birds, a topic already studied by Marcello Malpighi (1628–1694), one of the great scientific figures of Bo-

logna and a follower of the Galilean scientific method. In the tradition represented by Malpighi and by other anatomists of Bologna, the aim of comparative anatomy was not only to attain a greater knowledge of the human body, but also to establish the laws common to all living organisms. In order to study the composition and function of the kidney and the ureter, Galvani employed instruments such as the microscope, and new experimental techniques such as maceration and ligature of ureters. The latter technique, applied by Galvani to a living chicken, allowed him to restrain urine flow so that the kidney structure could be observed better than under normal conditions [18]. In these early researches, Galvani showed not only a great skill in dissection and observation, but also an attitude to intervene experimentally in order to obtain the best conditions for the investigation he was carrying out. These characteristics of Galvani's scientific practice will become quite evident in his electrophysiological research.

The new appointment at the Institute of Sciences consisted in the practical teaching of anatomy, which was conducted through human dissections and the use of the famous anatomical waxes made by the celebrated Ercole Lelli. It also meant a great advance in Galvani's professional status and financial conditions. Indeed, Galvani was elected in the number of the *accademici benedettini*, who were the paid members of the Academy of Sciences and constituted its scientific élite. Galvani's choice of anatomy as his teaching profession both at the Institute of Sciences and at the

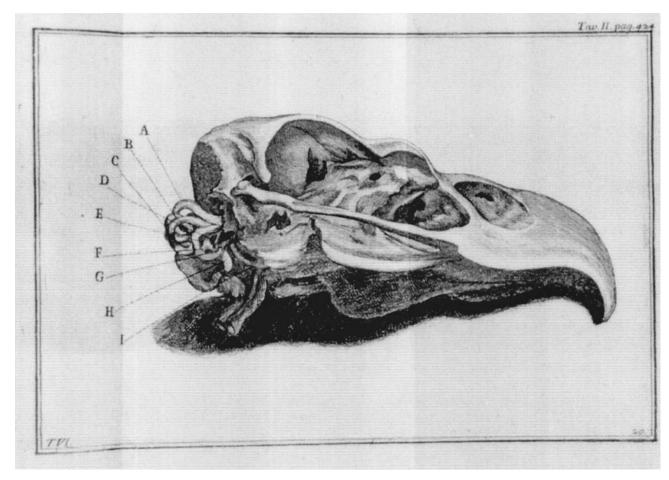


FIG. 3. Plate II of the De Volatilium Aure (from [19], courtesy of the library of the Department of Astronomy of the University of Bologna).

University depended on the indisputable prestige of this discipline, but also on more personal reasons. He was following the example of Gusmano Galeazzi, who had been not only his teacher, but had become his father-in-law some years before. In 1762 Galvani had married Galeazzi's daughter Lucia, and had moved to live at Galeazzi's house. Here he helped Galeazzi in his researches and probably took inspiration from him for his own investigations. In 1769 he became coadjutor of Galeazzi in the course of practical anatomy he gave to University students at his own house. When Galeazzi died in 1775, Galvani was appointed professor *ad lecturam anatomicam cum ostensione partium humani corporis domi* (of anatomy with demonstration of human anatomical parts at home) in Galeazzi's place.

PROFESSIONAL ASCENT AND MEDICAL ACTIVITY

His election as a "Benedectine member" of the Academy of Sciences brought to Galvani not only financial advantages and great prestige, but also some commitments. The main one was to read at least one research paper every year at the Academy. Galvani always carried out this duty until his death. As a matter of fact, he always addressed his investigations primarily to his colleagues at the Academy, even in the case of his electrophysiological studies. This choice, which was shared by many other men of science in Bologna such as Beccari and Galeazzi, did not exclude a wider circulation of their scientific results. The *Commentarii* of

the Institute of Sciences (i.e., the periodical publication that collected a selection of the memoirs presented at the institution) were sent to the main scientific academies and institutions around the world, and were kept in great consideration by everyone interested in scientific matters. Unfortunately, the publication of the *Commentarii* was quite slow, so that it often happened that a research paper was made public long after its presentation and discussion within the Academy of Bologna. Some important investigations of Galvani underwent a similar delay, therefore causing an unpleasant debate on priority with Antonio Scarpa (1752–1832).

Between 1768 and 1772 Galvani delivered at the Academy of Sciences four papers on the hearing of birds, quadrupeds, and humans. He had discovered some structures in the ear of birds never detected before, such as the circular hole in the vestibule and a duct analogous to the aqueduct of Fallopius in humans (Fig. 3). Adopting a morphophysiological approach analogous to that used in his research on the kidney, Galvani described the functions performed by these structures. He also pointed out the analogies existing with the human ear, stressing the fact that they were much more numerous than it was commonly thought [19]. The ultimate aim of Galvani was to understand the functioning of the hearing apparatus in the general context of his long-standing research on the different senses. Indeed, he was probably planning a systematic physiological study of sense organs, but he abandoned the project after this research on hearing.

Among the reasons why he gave up this field of research was probably the fact that in 1772 Scarpa published his De Structura Finestrae Rotundae Auris, where were expounded many of the observations that Galvani had already announced but had not published yet. According to some evidence, Scarpa had attended Galvani's public dissertations, and he might have appropriated some of his discoveries, without acknowledging him. As a matter of fact the publication of Scarpa's work gave rise to a harsh debate on the priority of the discoveries, which involved not only the scientific community of Bologna and Modena, where Scarpa was professor of anatomy, but spread also to Padua and Pavia. As to Galvani, he probably kept a low profile, and when, in 1783, he finally published in the Commentarii of the Institute of Sciences a memoir containing some of his observations that Scarpa had not included in his work, he referred to him without any resentment ([19] pp. 90-91). This episode shows a side of Galvani's personality that all biographers have stressed. As one of them said, "... Even more admirable was [Galvani's] modesty, which accompanied and enriched his numerous merits . . . His face as well as his mind were characterized by the utmost decency and gravity...Even though he was very reserved and prudent when in public, he was far from being cold and apathetic . . ." ([50] p. 114).

The behavior of Galvani in the affair with Scarpa, and, as we shall see, in the controversy on animal electricity, his life entirely spent in Bologna, the lack of correspondence, which was one of the most widespread means of scientific communication of the time, all contribute to portray a rather reserved man, not very prone to public exposure, and reluctant to establish contacts beyond the circle of his friends and colleagues in Bologna.

The disillusionment Galvani must have felt in the episode with Scarpa was mitigated by a series of professional successes he obtained in the years around 1770. In 1768, Galvani successfully performed one of the major tasks for an anatomist in Bologna, the public function of anatomy. This was an official event that took place every year during the carnival, at the presence of the main city authorities, of lecturers and students of the University and also of laymen. Besides being an opportunity to celebrate the University, and a social event, the Anatomia represented a demonstration of skill, not only anatomical but also didactic and argumentative, for those who performed it. It consisted of a series of lectures—in Galvani's time there were 14 lectures—based on the illustration of the anatomy of a part of the human body, on the dispute (i.e., answers to questions and objections raised by attendants), and on the dissection and demonstration of the anatomical part being discussed. Even if the students had other and more effective ways of learning human anatomy, the public function was of fundamental importance for those who intended to start a career in the Faculty of Medicine [15]. In Galvani's case, performing the function successfully gained him a paid lectureship at the University, first in "practical medicine" and later in anatomy, as coadjutor of Galeazzi. He will hold the function three more times—in 1772, 1780, and 1786—exploiting also this opportunity to communicate the results of his researches.

In the 1770s Galvani continued his ascent in the scientific and medical élite of his hometown. In 1771 he was elected President of the Academy of Sciences, a not very demanding but a very prestigious appointment. Two years later he became *numerario* (i.e., a full-right member) of the College of Physicians. The College (which was composed by 15 members, with only 12 *numerari*) was the leading medical authority in Bologna and its region. The College of Physicians superintended the degrees in medicine, granted the licenses to practice medicine, and decided on the drugs that could be sold. It was, therefore, a very powerful and elitist institution; being one of its members meant being at the top of the medical hierarchy of the city [48]. Galvani belonged to

this body for 30 years and was its chief (*priore*) several times. He also performed many tasks connected to his position, such as promoting undergraduates in their final exams, inspecting pharmacies in the city and the countryside, and giving his advice on events related to public health as during an epizootic that broke out in 1775. Besides this public activity, Galvani practiced medicine both as a private doctor and as the physician of some religious confraternities in Bologna.

CONTEXT OF ELECTROPHYSIOLOGICAL RESEARCHES: MEDICAL ELECTRICITY AND HALLERISM

Galvani's medical practice, as well as his surgical apprenticeship, have often been neglected by historians. To the contrary, this is very important in order to give a fuller image of the scientist of Bologna and to understand the origin and context of his electrophysiological investigation. As a medical practitioner, Galvani soon took an interest in the therapeutical application of electricity, a field known at the time as "medical electricity." Medical electricity emerged at the middle of the 18th century following the electrical researches and the discovery of the effects of electricity on the human body (generally the investigator's own body): strong commotions of limbs, increase in perspiration, and acceleration in the heart beat. These observations pushed some doctors to apply electricity to the treatment of some diseases, which could not be cured by traditional remedies. The therapeutical application of electricity found in Bologna a very fertile field. In 1748 Giuseppe Veratti published a book in which he reported successful treatments of diseases such as paralysis, sciatic pain, deafness, and rheumatic afflictions [51]. Notwithstanding the positive results obtained with the new therapeutic technique, Veratti was cautious in assigning a universal validity to it, as done by other authors. Besides, he was aware that the therapeutical application of electricity needed a deeper understanding of the physiological mechanisms controlling body functions. This was the same opinion lately expressed by Galvani: "Since I wish to bring to a degree of usefulness those facts which came to be revealed about nerves and muscles through many experiments involving considerable endeavour, whereby their hidden properties may possibly be revealed and we may be able to treat their ailments with more safety . . .' ([27] p. 45).

Like Veratti, Galvani believed that medical therapy should be strictly connected to anatomy and physiology. His interest in electrical medicine was one of the factors that directed his attention towards neurophysiology. In 1772, Galvani read at the Academy of Sciences a paper entitled "On Hallerian Irritability," which unfortunately is lost. The title of the paper referred to the researches made public by the great Swiss physiologist Albrecht von Haller (1708-1777) approximately 20 years earlier. On the basis of a long series of experiments, Haller had located in the animal body two different properties: "irritability" and "sensibility." Irritability was the property typical of muscle fibers to contract when stimulated; sensibility, on the other hand, depended on nerves and consisted of the painful sensation produced by a stimulus in some parts of the body [33]. Through the distinction between irritability and sensibility, and the assignment of the former to muscles, Haller denied the fundamental role traditionally played by nerves in muscular motion. Before Haller, the prevailing view implied the existence of a fluid matter, named "animal spirits" or "nervous fluid," which was produced in the brain. Animal spirits flew from the brain through nerves to produce muscular contractions and, therefore, animal motion, and they flew the opposite way (i.e., from muscles to the brain) to produce sensations. In the Hallerian system the matter contained in nerves was no longer the "efficient" cause of muscular motion. Instead, it was a stimulus, like the prick

of a needle, which activated a specific property of the muscle, irritability, on which contraction and motion really depended.

Haller's theory aroused great interest all over Europe, and caused a great debate during the 1750s, particularly in Bologna [14]. Haller's experiments were confirmed by some investigators, in particular by two young Italian scientists, Leopoldo Marc' Antonio Caldani (1725–1813) and Felice Fontana (1730–1805), who became the main supporters of Hallerian irritability in Italy. But in the scientific community of Bologna not everyone was willing to abandon the traditional animal spirits in favor of the new theory. Tommaso Laghi (1709-1764), an anatomist of the University and a very influential figure in the medical establishment, was among the most convinced and explicit critics of the Hallerian theory of muscular motion. Laghi assumed that muscular contractions were brought about by a fluid flowing through nerves and having an electrical nature [42]. This hypothesis somewhat combined the traditional theory of animal spirits with the achievements of the electrical researches of the time. On the basis of some conjectures proposed by Isaac Newton in the "Queries" of his Opticks, some authors had already suggested that electricity played an important role in the phenomena of life, and particularly in the mechanism of muscular motion. In 1733 Stephen Hales (1677-1761), who made fundamental researches on blood pressure, conceived the possibility that muscular motion, "this wonderful and hitherto inexplicable mystery of nature," depended on an "energy" that acted "along the surfaces [of nerves] like electrical powers . . ." ([32] p. 58-59). Two decades later Giambattista Beccaria devoted one chapter of his popular treatise on electricity to "electricity referred to vegetables, animals, and metals." In this chapter Beccaria described an experiment in which he electrified the leg muscles of a living cock. He reported several other observations and arguments, including the success obtained by Veratti and others in medical electricity, to support a role of electricity in muscular motion ([1] pp. 124, 186). Notwithstanding these suggestions, the neuroelectrical theory maintained by Laghi was vague and ill-founded. Laghi could oppose only occasional observations and indemonstrable conjectures to the enormous experimental apparatus of the Hallerians. Haller and his supporters, therefore, put forward some objections that Laghi was not able to solve [40]. Two of them were especially important. The first one concerned the different effects of a ligature applied to nerves on the conduction of nervous signal and of electricity [47]. The second objection was based on the electrical properties of nerves (see later).

During the following two decades the Hallerian system won increasing approval and put the neuroelectrical theory in the shadow. Anyway, the latter theory was not completely removed from the scientific arena, and was reproposed with strength during the 1770s, after the researches on "electric fishes." The investigations of John Walsh (1725-1795), John Hunter (1728-1793), Henry Cavendish (1731–1810), and others demonstrated convincingly that the shock produced by some fishes such as the *Torpedo* and the Gymnotus was an electrical phenomenon [9]. This showed that some animals in nature were endowed with an intrinsic electricity. Although these were special animals, their properties suggested that an electrical fluid might be present and have a function in every animal. Among those who proposed again a neuroelectrical explanation of muscular motion there was Galvani [36,41]. After the presentation of the paper on Hallerian irritability in 1772, Galvani made some researches on the motion of the heart, discovering that the irritation of the spinal cord could cause a heart arrest, and on frog nerves. Unfortunately very few documents about these investigations still exist today. The first known mention by Galvani of the neuroelectrical theory of motion dates back to 1780. At the beginning of that year Galvani performed the public function of anatomy for the third time. In the final lecture "on bones," while considering death from a physiological point of view, he wondered: "Where [has gone] that most noble electrical fluid on which motion, sensation, blood circulation, even life itself, seem to depend?" Further on Galvani supposed that death derived from the cessation of blood circulation and of "its friction on the brain and nerves which produces the electrical fluid" ([28] pp. 135–137). The hypothesis proposed by Galvani on this occasion was analogous to the one already expressed by Laghi. Unlike Laghi and other adherents to the neuroelectrical theory, however, Galvani did not simply propose conjectures, but began a systematic investigation on frogs and other animals. This lasted for the rest of his life and led him to write in 1791 his most famous work, the *De Viribus Electricitatis in Motu Musculari Commentarius*.

In the *Commentarius* Galvani gave his personal, retrospective account on how he became interested in the study of electrical phenomena in animals and how he progressed in his investigations. On the other hand, a different and more direct insight into the progress of his studies in this field can be gained from his numerous laboratory notes, and also some memoirs he wrote before the *Commentarius* and left unpublished [25]. Although relatively poorly studied until now, Galvani's laboratory notes are a precious source of information in order to understand the development of his electrophysiological experiments and also the basis of his scientific practice [37,38].

ORIGINS AND FUNDAMENTS OF GALVANI'S EXPERIMENTAL PRACTICE

The experimental approach of Galvani, as well as his conception of muscular motion, was undoubtedly influenced by the researches carried out in the context of the debate over the Hallerian system. Most of those who took part in the debate claimed that the location in the animal of "sensible" and "irritable" parts could be established only by experiments. One should isolate completely the part under scrutiny—nerves, muscles, ligaments, tendons, etc.—and should act on it by using heat, the lancet, or chemical irritants (such as "vitriolic oil"). If the part so treated contracted without a general reaction of the animal, it was considered irritable and not sensible; if, on the contrary, the animal reacted showing pain-related behavior, the part was considered sensible. The experiment could provide univocal results only if great care was used both in preparing the animal and in applying the stimulus. Only investigators very experienced in anatomy and capable in the use of dissecting and surgical instruments could perform the experiment quite assuredly. As Leopoldo Caldani stated: "If physicists cannot decide on our problem without using the lancet and without the habit of sectioning living animals, metaphysicians, who are much less used to these instruments, will be much farther from succeeding" ([8] p. 346).

Frogs, which had been used in the study of anatomy and physiology since antiquity, were among the thousands of animals—dogs, cats, sheep, calves—sacrificed to test the Hallerian system. Besides being easy to find, frogs offered useful characteristics for physiological research on the mechanism of contractions, since, for instance, their muscles kept on contracting for a long time after death [39]. Caldani and Fontana prepared frogs in a way very similar to that adopted by Galvani afterwards, and which was called *alla maniera di Galvani* (in Galvani's way). They also carried out some experiments on frogs in Laura Bassi's laboratory, with the collaboration of Giuseppe Veratti. In a decapitated frog they uncovered the crural nerves and brought an electrified rod near them: the limb muscles contracted, even when any other stimulus had become ineffective. Caldani, therefore, concluded that electricity was the most effective stimulus to put in action

muscle's irritability, but denied that it was the "efficient" cause of muscular contractions, as supposed by Laghi ([7], p. 332).

These electrophysiological experiments were an important point of reference for Galvani's investigation, both for the choice and preparation of the animal, and for the use of electricity as a stimulus to obtain muscular contractions. Moreover, as discussed in the companion paper by Piccolino [47], Haller's theory represented an important conceptual framework for Galvani, particularly through the conceptual elaborations of Felice Fontana.

On the basis of his previous researches on birds, Galvani shared the conviction that animal experimentation was fundamental to understand the physiological mechanisms underlying the processes of organisms, humans included. Furthermore, as already mentioned, his surgical and anatomical training made him very skillful in manipulating various animal body parts such as nerves and muscles. He added to this ability a good knowledge of electrical phenomena and of the experimental investigation done in this field. In the laboratory he built in his own house there were all the main instruments of electrical research of the time: electrostatic machines, various types of condensers-Leyden jar, Franklin square, and Aepinus' condenser-and many other research instruments, some of which had been recently invented, such as the electrophorus and "Volta pistol." Having a private laboratory up to the needs of the most advanced research must have been quite a rare occurrence in the scientific panorama of the 18th century, also because of the high cost of many instruments.

EARLY ELECTROPHYSIOLOGICAL INVESTIGATION

Galvani's approach to the study of neuromuscular physiology combined the Hallerian experimentation on living beings and the electrological one in a particularly successful synthesis. The laboratory notes of his electrophysiological experiments show quite clearly: i) the care he used in preparing the experiment, so as to exclude all accidental circumstances of a phenomenon; ii) the method displayed to explore all the possible variants of an experiment; iii) the ability in devising the most suitable experimental conditions (Fig. 4). These aspects of Galvani's experimental practice stand out even more if we consider that Galvani was moving in an almost unknown domain. Moreover, and importantly, even though he started his investigation to verify a particular hypothesis (i.e., the neuroelectrical hypothesis), from the laboratory notes Galvani appears to be open-minded and ready to change his views depending on the results of his experiments. On several occasions he considers alternative explanations for what he is observing and seems ready to abandon his initial interpretation. Sometimes an experimental result appears to contradict his expectations and forces him to change the explicative model and the direction of research. An explanation rejected after a series of experiments could rise again after another series. An experiment designed to solve an anomaly in the explanatory model produced new problems. Certainly, the investigative pathway that eventually led Galvani to his discovery of animal electricity appears more tortuous and intricate from the laboratory notes, than it may seem from the retrospective reconstruction offered by Galvani himself in the Commentarius. The broad mental attitude of Galvani in his investigations on animal electricity contrasts with the restricted mind of many of the scientists in both the Hallerian and anti-Hallerian field. As a matter of fact, the theory of animal electricity Galvani eventually proposed on the basis of his researches seems to incorporate conceptual elements of both the neuroelectrical hypothesis (advocated mainly by anti-Hallerians), and of the Hallerian views on irritability that, as already mentioned, situated in the muscle itself the fundamental mechanism of animal motion [47].

From many points of views Galvani's electrophysiological

experimentation strikes us for its modernity, particularly if we compare it with other works on animal electricity published in the same period. An example is provided below.

In 1780, the same year of the first known laboratory notes of Galvani, the Academy of Lyon awarded a prize on medical electricity. There were two winners: Pierre Bertholon (1741–1800), a French physician already known for some electrical researches, and Giuseppe Gardini (1740-1816), a Piedmontese physician associated to the Academy of Turin [3,30]. The works of both Bertholon and Gardini became important points of reference for those who were studying medical electricity and electrophysiology. Galvani himself quoted them with admiration in the Commentarius, and acknowledged Bertholon as the inventor of the term animalis electricitas. Both Gardini and Bertholon claimed the existence of an electricity proper to animal and human bodies, and affirmed the identity of nervous and electrical fluids. But these conjectures were in no way elaborated in an explicative model about the mechanism of muscular motion. Besides, they did not describe any electrophysiological experiment to support these conjectures, but reported only some scant phenomena and observations, sometimes of uncertain origin and meaning: effects of lightning on living beings, contractions of muscle and increased perspiration induced by electrical stimulation, experiments that seemed to demonstrate a faster growth of "electrified" plants, researches on electric fishes, electrical manifestations of cat's coat or some people's dresses when rubbed, the particular nervous irritability of some aristocrat lady in days of dry climate, and a multitude of amazing anectodes on the electrical power of some animals and humans. It was an enriched and updated account compared to that offered by authors such as Laghi and Beccaria 30 years before, but it did not produce any substantial advancement in the neuroelectrical theory.

Neither Gardini nor Bertholon felt the need to give an answer to the objections Haller and his supporters had moved against the neuroelectrical theory or, when they tried, they did not succeed. This was the case of the objection on the electrical properties of nerves, which Bertholon considered briefly in the enlarged edition of his work. As already mentioned, the widely accepted Franklin's theory stipulated that all bodies contained a specific natural quantity of "electrical fluid," being divided in conductive (also called "deferent") and nonconductive bodies. The electrical fluid manifested itself through peculiar signs-sparks, attraction of light bodies, muscular contraction—only if some cause intervened to change the equilibrium with which it was diffused in the space. There could be no disequilibrium between two conductive bodies if they were in reciprocal contact. Given this theory, Hallerians (and particularly Felice Fontana) wondered how nerves could conduct the electrical fluid into the muscles and cause contractions. If nerves (as well as muscles and surrounding tissues) were conductive, there could be no electrical disequilibrium, and consequently no muscular contraction could be produced. If, on the other hand, nerves were nonconductive, they would have stopped the flow of the electrical fluid, therefore preventing its action on muscles ([16] p. 207). The solution proposed by Bertholon to this objection consisted in conjecturing that "the electrical fluid had a stronger affinity with nerves than with conductive matter," so that it could be confined to nerves without spreading into surrounding tissues ([4], p. xxii). Perhaps this was a new theory—a théorie nouvelle according to Bertholon's-but it did not have any experimental ground and could not offer a valuable solution to the objection of Hallerians.

Galvani's attitude in examining this objection was quite different. This was one of his main worries during the winter of 1780–1781 (i.e., in the first experiments recorded in the known laboratory notes). In one experiment, for example, Galvani isolated

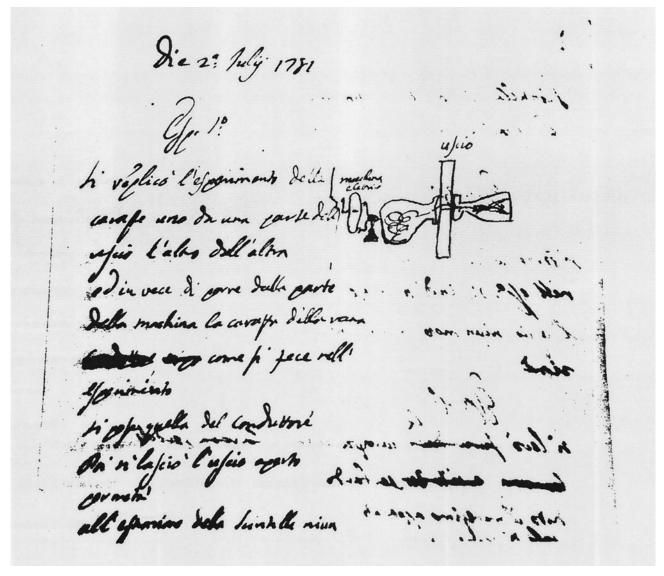


FIG. 4. A sample of the original laboratory notes written by Luigi Galvani: the log of the experiment of 2 July 1781 (by courtesy of the Accademia delle Scienze of Bologna).

a prepared frog on a glass panel, covered spinal cord and crural nerves with insulating material, then applied an electrical shock to the spinal cord. Leg muscles contracted, therefore suggesting that nerves were conductors through their intimate substance. This experiment answered to part of the objection of the Hallerians ("whether nerves were conductive"). Although the experiment left unsolved the problem of how nerves could conduct electricity along restricted paths without spreading it to surrounding tissues, the answer to the second part in the Hallerian dilemma will be at hands some years later. In his following experiments Galvani will find that nerves contain a great proportion of "oily matter," and he will suppose that this matter could provide an insulating surface to nerve fibers. Eventually, he will conceive that nerves conduct electricity through an internal "medullary" core insulated from the exterior by a nonconductive sheath (a hypothesis fully elaborated in the Commentarius, see later). Galvani's attitude, therefore, represented an effective progress compared to the discussion of Bertholon and others who had considered the same objection.

Between the end of 1780 and the beginning of 1782, Galvani's experimental activity in the laboratory was rather continuous and intense. Galvani performed experiments approximately twice a week. Considering his many other commitments—teaching, practicing medicine, public tasks in health-care—it was an intensive pace. During this period, on 26 January 1781 Galvani performed the famous experiment on the contractions of a frog's limbs elicited by a distant spark that opened the Commentarius and which has been defined as Galvani's "first experiment" ([25] p. 254; [45,47]). In February of the following year, Galvani's laboratory notes, and therefore presumably also his experimental activity, stopped. The most likely reason to explain this interruption was a turn in the academic career of Galvani. On 13 February 1782 Giovanni Antonio Galli, who had taught Galvani surgery and who was the professor of obstetrics at the Institute of Sciences of Bologna, died. Galvani was chosen to take Galli's place and to move from the anatomy to the obstetrics chair at the Institute, while continuing his anatomical lectures at the University. Galva-

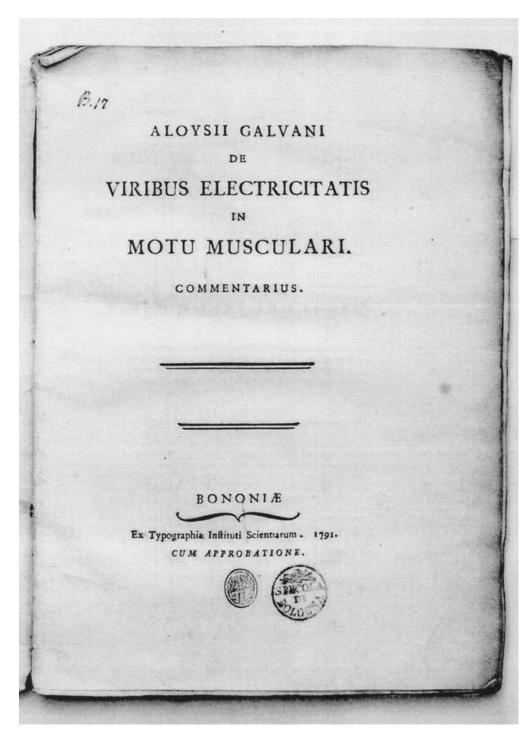


FIG. 5. Title page of the *De Viribus Electricitatis in Motu Musculari Commentarius*. This is one of the few copies printed in 1791 that Galvani sent to some colleagues, including Alessandro Volta (by courtesy of the library of the Department of Astronomy of the University of Bologna).

ni's appointment was on 26 February 1782, the last laboratory note is dated 17 February. Apparently Galvani devoted all his time and energy to the new duty, leaving aside his experimental program.

Galvani taught obstetrics for 16 years both to medical students and to midwives. He considered the training of midwives very important, as they were the main actors of childbirth at the time, particularly in the countryside. His annual course lasted 2 months. Special attention was given to the anatomical description of the female genital apparatus, to the clinical aspects of delivery, to the use of forceps, a rather new and debated instrument, and to cesarean section, which was not yet accepted by many authors. In his teaching of obstetrics Galvani took advantage of the obstetric

models built by Galli to which he added some of his own design. Among the authors most often quoted in his lectures there were two of the main obstetricians of the time, André Levret (1703–1780) and Jean Louis Baudelocque (1748–1810) [29]. In obstetrics, as well as in the other fields of his interest such as electricity, anatomy, and physiology, Galvani, therefore, displayed a solid background and an updated knowledge.

PHYSICO-CHEMICAL INVESTIGATION OF THE ORGANISM

At the end of 1782 Galvani took up again the experimental activity, moving from electrophysiology to the physico-chemical study of life. In the following years he carried out a long series of experiments on "airs," the term used in the 18th century for gaseous matter. The study of airs was at the core of scientific investigation in the 1780s, after the discovery that air was not a simple substance, as previously believed. Within a short period of time and thanks to the researches of men such as Joseph Black (1728–1799), Joseph Priestley (1733–1804), Carl Wilhelm Sheele (1742-1786), and Alessandro Volta (1745-1827), new airs such as hydrogen, oxygen, methane, nitrogen were isolated and their properties studied. These investigations culminated in the discovery of the composition of water and in the explanation of combustion and respiration made by Antoine-Laurent Lavoisier (1743–1794), milestones in the revolutionary process leading to modern chemistry [11,31]. The researches on airs had a strong echo in Bologna, where Giuseppe Veratti began a thorough experimental investigation in this field. Probably Veratti, who had already influenced Galvani in medical electricity and who had performed some electrophysiological experiments with him, introduced Galvani to these new researches.

Among the studies on airs made by Galvani in the early 1780s, those on the airs released by animal solids and fluids were particularly important. Following a path opened by Priestley, Galvani aimed at determining the role of airs in the composition of organism and in its physiological functions. In his experiments, he took a given amount of organic material (e.g., blood, bile, urine, bones, tendons, nerves, muscles) and exposed it to fire. He then measured the quantity and examined the quality of the air released in the process of heating. Galvani obtained from nerves an amount of "inflammable air" (a term that could indicate either hydrogen or methane) much greater than from any other animal body part, and found that this air developed a particularly vivid flame. From this observation Galvani concluded that nerves were partially formed by an oily matter, that was electrically insulating, and this offered a ground to the idea that nerves could confine electrical fluid and limit its spreading. Combining this observation with the previous one on the conductive properties of nerve matter, derived from the electrophysiological experiments of 1780, Galvani could, therefore, propose a sound solution to the Hallerian objection on the electrical properties of nerves, which he will present in the Commentarius ([27] p. 76).

RETURN TO ELECTROPHYSIOLOGY AND THE PUBLICATION OF THE COMMENTARIUS

In the second half of the 1780s Galvani devoted himself mainly to his electrophysiological research, carrying out the experiments on the effects of "atmospheric electricity" (i.e., the electricity produced by lightning) on muscular motion and those with conductive arcs, which will constitute the central part of his *Commentarius*. While carrying out these experiments Galvani conceived the analogy between the muscle and the Leyden jar. These experiments aroused an enormous interest and triggered off the controversy on animal electricity. However, the contemporary readers of

the *Commentarius* perceived not only the "great and marvelous discovery" of a form of electricity intrinsic to the organism, but also the fact that it could represent "the most productive of very useful applications to Medicine, both practically and theoretically." ([52] pp. 24–25). In fact the last part of the *Commentarius* was devoted to the theory of muscular motion that Galvani had perfected through his experiments and the therapeutical applications of the discovery of animal electricity.

After over 10 years of research, the De Viribus Electricitatis in Motu Musculari was published in the seventh volume of the Commentarii of the Institute of Sciences of Bologna [20] (Fig. 5). Although this volume was dated 1791, it was actually published at the beginning of 1792, due to the usual delays in publication [2]. The news of Galvani's research spread immediately through various channels: copies of the Commentarii were sent to all the main scientific centers in Italy and abroad, an extract of the memoir was circulated, even if in a limited number of copies, and descriptions of it, made by those colleagues of Galvani in Bologna who supported animal electricity, were posted to their correspondents. Galvani's memoir caused a sensation everywhere, also beyond the Alps, and many investigators repeated his experiments in order to check his results [2,49]. Galvani's achievements were considered revolutionary and the discovery of animal electricity "a honour to the whole of Italy," as Bassiano Carminati, an important physicist of Pavia, wrote in a letter addressed to Galvani. But not everybody shared this enthusiasm: in Bologna, for example, some of the main representatives of the scientific community who supported Hallerian irritability realized that animal electricity could endanger Haller's system, and they immediately started to question it. One of them was Leopoldo Caldani, who in the meantime had moved to Padua and had become one of the major defenders of Hallerism. Caldani pointed out that the theory expounded by Galvani was basically a more sophisticated version of Laghi's neuroelectrical theory, which had already been refuted [2].

In order to satisfy the pressing requests for a copy of Galvani's memoir, which was getting progressively more difficult to find, Galvani's nephew, Giovanni Aldini (1762–1834), prepared a second edition of the *Commentarius*, which was published in Modena in the autumn of 1792 [21]. This edition contained an introduction and several notes, written by Aldini most probably under the supervision of Galvani, which replied to the attacks moved to the theory of animal electricity and tried to situate Galvani's research in the context of contemporary science.

Alessandro Volta was among the first scientists who repeated and checked Galvani's experiments. After enthusiastically embracing animal electricity, the scientist from Como, who was professor of physics in Pavia, started to doubt the fact that contractions were caused by a form of specific electricity intrinsic to animals. Volta proposed that contractions depended instead on an electricity that was already known and was put into motion by the metals used by Galvani to connect nerves and muscles in his experiments. The debate between the different explanations put forward by Volta and Galvani is well known and has been widely studied [2,10,12, 45]. The terms of the controversy are discussed by Piccolino in the companion article [47]. Here we wish only to outline Galvani's attitude in it.

GALVANI'S ATTITUDE IN THE CONTROVERSY ON ANIMAL ELECTRICITY

Even if he believed in the importance of his achievements, Galvani probably did not expect that the *Commentarius* would create such a sensation. His reaction, opposite to Volta's but coherent with his reserved character and confined life style, was to keep a low profile in the controversy that followed. This behavior

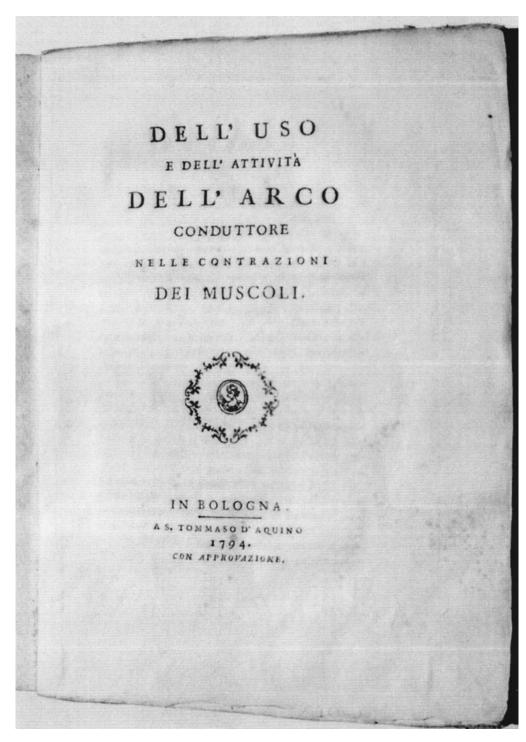


FIG. 6. Title page of the *Trattato dell'Arco Conduttore* (from [22], courtesy of the library of the Department of Astronomy of the University of Bologna).

was induced also by reasons depending on his age and on personal circumstances. In the early 1790s, Galvani was a man approaching old age, with declining health, unable to continue all the activities and all the charges involved in his profession as a physician and teacher. In 1790 he had been appointed *anatomicus emeritus* at the University of Bologna. In the same year he asked to be relieved

from performing the public function of anatomy and was granted the permission to hold his anatomy course only in his own house, while he kept his teaching position in obstetrics at the Institute of Sciences. Moreover, a series of family misfortunes had befallen him, undermining his health and his spirits, in particular the death of his beloved wife Lucia.

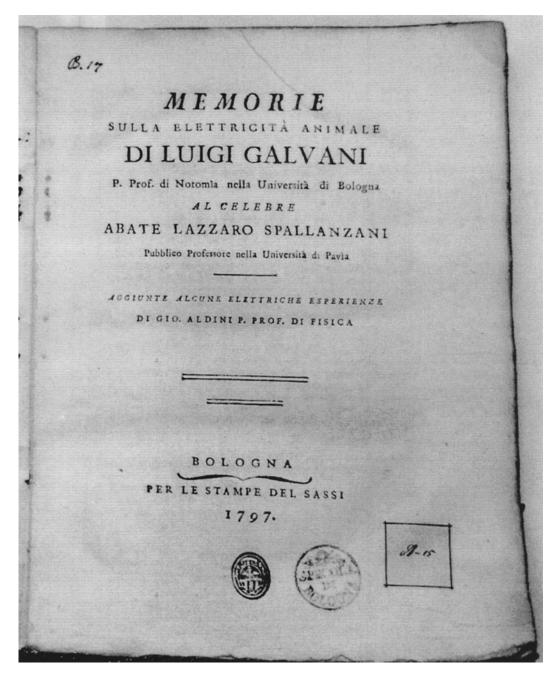


FIG. 7. Title page of the *Memorie Sull'Elettricità Animale* (from [23], courtesy of the library of the Department of Astronomy of the University of Bologna).

Galvani's reluctance to intervene directly in the controversy induced him to entrust his nephew Aldini with the task of performing as the main defender of the theory of animal electricity. When in 1794 Galvani published his second important work on animal electricity, the *Trattato dell'Arco Conduttore* (Treatise on the Conducting Arc), he did so anonymously, as if he wanted to underline that he felt extraneous to the scientific debate he himself had triggered (Fig. 6). As he told Heinrich Pfaff who visited him in Bologna in 1795 to discuss his electrophysiological research, his old age forced him to leave the research and the development of his discovery to a younger generation [46]. However, he had not

given up at all his investigations on frogs and other animals. The *Trattato*, which contained many new experiments, including the one on muscular contractions produced without metals, was soon followed by a *Supplemento* [22,47]. In 1795, Galvani, who probably had never traveled outside Bologna, went to the Adriatic coast. Here he could obtain some torpedoes, one of the most used electric fishes at the time, in order to find further experimental confirmation to his theory of animal electricity [26]. The results of the experiments performed during this scientific journey were included in a new work published in 1797, the five *Memorie Sulla Elettricità Animale* (Memoirs on Animal Electricity) (Fig. 7). The

second one of the *Memorie* contained the description of the famous experiment on the contractions produced by the contact between homogenous substances, that afterwards has been considered crucial for the science of electrophysiology [23,47]. Galvani dedicated this last work to Lazzaro Spallanzani (1729–1799), one of the most influential men of science at the time. Spallanzani accepted enthusiastically Galvani's theory of animal electricity from the beginning. His constant support of Galvani constituted an important encouragement for Galvani to carry on with his electrophysiological investigation and to sustain Volta's criticism.

DEATH AND LEGACY

Galvani continued to actively investigate animal electricity until the end of his life. In July 1798, just a few months before his death, he wrote some notes about what, according to him, the experiments had demonstrated and what remained to be proven. Unfortunately the time did not allow him to develop these research programs. In this period Galvani had to face one of the worst humiliations a person like him could suffer. The newly born Cisalpine Republic, which was founded by the French after their occupation of Northern Italy, Bologna included, imposed to every university professor to swear loyalty to the new authority. Galvani, who disagreed with the social and political confusion brought by the French in Bologna, and who felt this oath of allegiance contrasted with his religious belief, refused, along with a few other colleagues. The new authority decided to deprive him of all his academic and public positions, taking every financial support away. What had been his entire world for all his life crashed on him. Luigi Galvani died in Bologna, in his brother's house, on 4 December 1798.

Galvani's death deprived Volta of the major opponent to his theory and probably represented, together with the invention of the battery, one the main reasons of Volta's success at his time [44]. The pace of research on animal electricity slowed down for almost three decades after Galvani, and new achievements were to be obtained only with the researches of Nobili and Matteucci in the first half of the 19th century [47]. A new biological discipline emerged, electrophysiology, which was to fully confirm the validity of Galvani's hypothesis according to which electricity is involved in nervous conduction and muscle contraction. However, in spite of the importance of Galvani's research and theory, the received view of the scholar of Bologna is that of a pioneer of the studies of electricity on animals who was largely wrong in the interpretation of his experiments and whose scientific stature was clearly inferior to that of his competitor, Alessandro Volta. To a great extent this view was probably influenced by the account of early stages of research on animal electricity given by Emile du Bois-Reymond in 1849 [13]. Even though he was an estimator of Galvani, du Bois-Reymond undervalued the importance of Galvani's achievements in order to present himself as the real founder of the science of electrophysiology, the one who had succeeded in showing the electrical nature of the animal spirits of classical science. In some way many historians have uncritically relied on this interpretation, both because Volta and the rise of the physics of electricity have received more attention than Galvani and the beginning of electrophysiology, and because of a wider knowledge of physics compared to physiology among the large majority of those who have studied this period of science history. The distinction between physical and biological perspective is rather unfortunate and somewhat misleading in the case of Galvani. As we have seen, in his investigation Galvani remarkably combined biological and physico-chemical approaches, and he succeeded in accounting for some fundamental aspects of life processes on the basis of models that took advantage of physical notions of his

times. As Niels Bohr so efficaciously claimed in 1937, "the immortal work of Galvani which inaugurated a new epoch in the whole field of science, is a most brilliant illustration of the extreme fruitfulness of an intimate combination of the exploration of the laws of inanimate nature with the study of the properties of living organisms" ([5], p. 68).

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