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Visual Images in Luigi Galvani's Path to Animal Electricity

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The scientific endeavor that led Luigi Galvani to his hypothesis of "animal electricity," i.e., of an electricity present in a condition of disequilibrium between the interior and the exterior of excitable animal fibers, is reviewed here with particular emphasis to the role played by visual images in Galvani's path of discovery. In 1791 Galvani formulated his model of neuromuscular physiology on the base of the image of a muscle and a nerve fiber together as in a "minute animal Leyden jar." This was the last instance of a series of physical models that accompanied Galvani's experimental efforts in the search of a theory capable of accounting for the electric nature of nerve conduction in spite of the many objections formulated in the eighteenth century against a possible role of electricity in animal physiology.

Keywords Luigi Galvani, electrophysiology, animal electricity, history of neuroscience, 18th century

In 1791, after more than ten years of experimental research, Luigi Galvani announced his discovery of "animal electricity" in a famous memoir, *De viribus electricitatis in motu musculari*, published in the *Commentaries of the Institute and Academy of Sciences of Bologna*, the town in which he was born in 1737 and where he would spend all his life until his death in 1798. Galvani's discovery laid the grounds for electrophysiology, and, together with the nineteenth-century acquisitions on the microscopic organization of nervous system, it was probably the main founding stone of modern neurosciences. It is mainly through the work initiated by Galvani in 1780 and concluded in 1952 by Hodgkin and Huxley that we have deciphered the nature of the signals that unceasingly flow along the circuits of the brain (Hodgkin & Huxley, 1952a, 1952b, 1952c, 1952d; see Hodgkin, 1992). These signals are the elements of the "electric storm" alluded to by Charles Scott Sherrington in a famous book. They allow us to see a distant castle, the visage of a nearby friend, to hear a voice, to feel emotions, to speak, to think (Sherrington, 1951). Moreover, through the complex routes of scientific discovery, Galvani's achievement also opened the path to the invention of the electric battery by Alessandro Volta. It thus paved the way to the development of the physics and technology of electricity, with long-lasting consequences for humankind.

From his experiments Galvani came to conceive that an electric disequilibrium exists between the interior and the exterior of a single muscle fiber: a nerve fiber would penetrate inside it allowing for an electric flow similar to that which develops in a Leyden jar by

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connecting its internal and external coatings (Piccolino, 1998; Piccolino & Bresadola, 2003). This image of the neuromuscular system as a "minute animal Leyden jar" represented the last instance of a series of visual images that accompanied Galvani in his attempt to develop a physically coherent model of the involvement of electricity in neuromuscular physiology.

By relying mainly on Galvani's unpublished manuscripts (which are referred to as memoirs hereafter), I will try to outline the experimental and logical endeavors that led the scientist of Bologna to his discovery of animal electricity, giving particularly emphasis to the role of visual images and metaphors. Visual and metaphoric language is intrinsically ambiguous. It may thus be of particular importance for the scientist during the discovery process, when new hypotheses and theories emerge that are not totally justified by the existing evidence and thus may not be liable to formulation in a precise and abstract language. Scientists may aggregate the emerging bits of knowledge in coherent, although unstable, representations, rich of suggestions and capable of directing their further effort in the discovery process. For the historian, on the other hand, the study of visual images and metaphors may provide important clues to the crucial passages of the discovery path, a process that shares with the artistic creation a fundamental historical and psychological indeterminacy (Holton, 1978; Miller, 1984; Poincaré, 1908). My work is based on research on the early history of electrophysiology that I have been carrying out over the last ten years in collaboration with Marco Bresadola (see Piccolino, 1997 & 1998).

Electricity in the Natural Philosophy and Medicine of the Eighteenth Century

A great interest existed in the eighteenth century in electricity and in its possible applications (Heilbron, 1979). This was the consequence of various discoveries and technical advances, as well as of theoretical progress and, moreover, of some spectacular successes of the new electrical science (as, for instance, the demonstration of the electrical nature of lightning and thunder). On the technological side, besides the construction of new and powerful friction-type electrical machines and of the atypical electric generators (such as Alessandro Volta's "electrophore"), of particular importance was the invention of electric capacitors (such as the Leyden jar and the flat type "Franklin's square").

Starting from about the middle of the century, there was, moreover, a great concern for the possible therapeutic effects of electricity, and "electric fluid" was administered in different ways in a variety of diseases. However, after an initial phase in which electric medicine was considered as a kind of panacea, serious doubts emerged on the real efficacy of electric treatments (Rowbottom & Susskind, 1984; Bertucci, 2005).

The century was also dominated by the interest in the possible involvement of electricity in nervous function and muscle excitability (see Duchesneau, 1982; Piccolino & Bresadola, 2003). In Bologna this possibility was supported by Tommaso Laghi, an influential member of the local scientific community, who considered "the electric effluvium as an emulus of animal spirits." In the classical system of Galen, animal spirits were entities of uncertain physical nature, derived from the "vital spirits" by the refinement process occurring in a vascular structure at the base of the brain (*rete mirabile*). They were supposed to flow through the internal hollow part of nerves to produce motion or sensation with relation to the final targets hit. As to their action on muscle contraction, the traditional view was that animal spirits made muscles stiff by inflating their fibers. This view was abandoned in the course of the seventeenth century, thanks to the work of scientists like William Croone, Niels Steensen, Thomas Willis, Francis Glisson, Giovanni Alfonso Borelli, and others, particularly when it became clear, that muscle volume does not increase during contraction. In post-Cartesian science, the prevailing idea was that animal spirits were a particular class of tenuous and greatly effective fluids, and that they produced muscle contraction by a chemical process akin to fermentation (see Clower, 1998; Ochs, 2004). A different view of nervous conduction was adopted by Newton who considered the phenomenon as a consequence of the vibratory motion of an æthereal medium penetrating the solid part of nerves. Indeed a development of Newton's suggestion led Stephen Hales to first conceive in 1733 the possibility that nervous conduction might be an electric phenomenon (Hales, 1733).

In the middle of the eighteenth century, the general conviction was that "animal spirits" was only a void expression useful to conceal the ignorance for such fundamental physiological processes as motion and sensation. The theory, which assumed the electric nature of the animal spirits ("neuroelectric theory"), was strongly criticized by the adherents to the doctrine of the "irritability" elaborated in 1753 by Albrecht von Haller, a prominent figure of eighteenth-century science. According to Haller, muscles possess an intrinsic capability to contract in response to physiological or experimental stimuli (or "irritability"). Nerves would bring about muscle contraction by putting into action this internal capability but they are not the effective agents of the contraction (as generally assumed in the neuroelectric theory and also in classical medicine) (Haller, 1756–1760; see Duchesneau, 1982; Cavazza, 1996; Piccolino & Bresadola, 2003).

Haller and his followers raised various objections to the neuroelectric theory, pointing to the presumed physical impossibility of the existence, inside animal body, of the electric disequilibrium required to move the electric fluid along nerve fibers. This was because of the presence inside animal tissues — they argued — of conductive humors capable of dissipating any electrical disequilibrium generated inside them. Moreover, and for a similar reason, an electric flow would not be restricted to specific groups of nerve fibers (as required by the physiological needs) thus leading to unwanted functional consequences. Another difficulty came from the different effects of nerve ligature on the propagation of nerve signals compared to electric conduction along nerve tissue: electric conduction persisted whereas the conduction of nerve signals was blocked.

The debate between the "hallerians" and the supporters of the neuroelectric theory was particularly harsh in the period 1755–1760, the formative scientific years for Luigi Galvani. In Bologna it was particularly intense, with Marc Antonio Caldani and Felice Fontana siding with Haller and supporting irritability, against Laghi and other members of the academic establishment generally backing the electric nature of nervous conduction and criticizing Haller. This debate helped to define the conditions that should be met by any electric theory of nervous conduction in order to be physically and physiologically plausible (Caldani, 1757; Fontana, 1757; Laghi, 1757; see Cavazza, 1997).

In the period 1772–1775, important evidence was being accumulated to support a possible role of electricity in animal economy. In intensive research carried out at La Rochelle in France in 1772, John Walsh demonstrated the electric nature of the shock caused by the torpedo fish. Three years later, in London, Walsh studied the strong shock produced by a strange eel imported from Guiana and arrived at a similar conclusion (Piccolino, 2003; Piccolino & Bresadola, 2002; Walsh, 1773). By the end of the 1770s the news of Walsh's achievements circulated throughout Europe, stimulating interest in the possibility that electricity might also be involved in the functions of less exceptional animals, and particularly in neuromuscular physiology (Piccolino & Bresadola, 2003).

By this time Galvani (who graduated in medicine and philosophy from the Bologna University in 1759) had become strongly interested in the mechanisms of muscular motion (see Bresadola, 1998). In 1772 he had read a dissertation on irritability at the

Istituto delle Science, a prestigious cultural institution of Bologna of which Galvani was a member since 1766. The *Istituto*, created in 1711 in order to face the apparently irreversible decline of the old University, promoted experimental investigation in specially designed laboratories and encouraged a modern way of teaching, mainly based on visual and experimental demonstration. The *Istituto* members, engaged in investigations in the more active fields of the contemporary science, such as electricity, optics, pneumatics, and chemistry (in addition to more traditional disciplines as natural history and anatomy), were requested to periodically demonstrate the results of their studies to their colleagues; this favored an interdisciplinary approach to scientific endeavor (Angelini, 1993; Cavazza, 1990).

Galvani's scientific development went on between the *Istituto* and the university: it concurred with the Bologna tradition for anatomy with the multidisciplinary and modern character of scientific endeavor at the *Istituto*. Also important was Galvani's practice of experimenting on living bodies acquired during his surgery apprenticeship in the town hospitals (Bresadola, 1998).

Among the interests of the *Istituto* were medical electricity and the possible role of electricity in neuromuscular physiology. Some of the main discussants in the debate on neuroelectric theory and on irritability, such as Laghi, Caldani, and Fontana, belonged to the *Istituto* as was the case for Giuseppe Veratti, who was charged in 1747 to verify the therapeutic efficacy of medical electricity (Veratti, 1748).

All this set the stage for Galvani's decision to investigate experimentally the possible role of electricity in animal physiology. Veratti's study had been limited almost exclusively to test the effects of electric treatments in various pathological conditions. Galvani aimed instead at a more ambitious task, in line of the ideal of "rational medicine" advocated in the seventeenth century by Marcello Malpighi, a significant reference for the Bolognese science and especially for the *Istituto*. For Malpighi, clinical medicine should be based on a deep investigation of animal anatomy and physiology and an effective and "rational" medical treatment could be established only through a comprehension of functioning of the "minute machines of the organism" (Malpighi, 1697; see Adelmann, 1966; Piccolino, 1999). In the spirit of Malpighi, Galvani was convinced that only by investigating the possible role of electricity in normal physiology could he formulate a valuable approach to medical electricity (Piccolino & Bresadola, 2003).

Also Galvani's decision to investigate the physiological role of electricity in a particular animal preparation was inspired to Malpighi who made his more important discovery (the blood capillaries) in a frog preparation. One of the important merits of Galvani is to transpose Malpighi's eminently anatomic approach in a more modern and dynamic context. In Galvani's electrophysiological research, the frog preparation is brought into a laboratory that is more similar to a *cabinet de physique* of a natural philosopher of the eighteenth century than to a classical dissection room (see Figure 1).

In addition to Walsh's achievements with electric fish, a triggering event for Galvani's decision to start his electrophysiological experiments around the end of 1780 might have been discussions that emerged during the public function of anatomy that Galvani was charged to perform in that year, in which he considered the possible involvement of electricity in motion and sensation.

The Early Phase of Galvani's Electrophysiological Research

The manuscripts still preserved at the *Istituto delle Scienze* of Bologna are important for trying to determine the complex path of discovery that eventually led Galvani in 1791 to formulate his final hypothesis of animal electricity (see Bresadola, 2003). Besides the

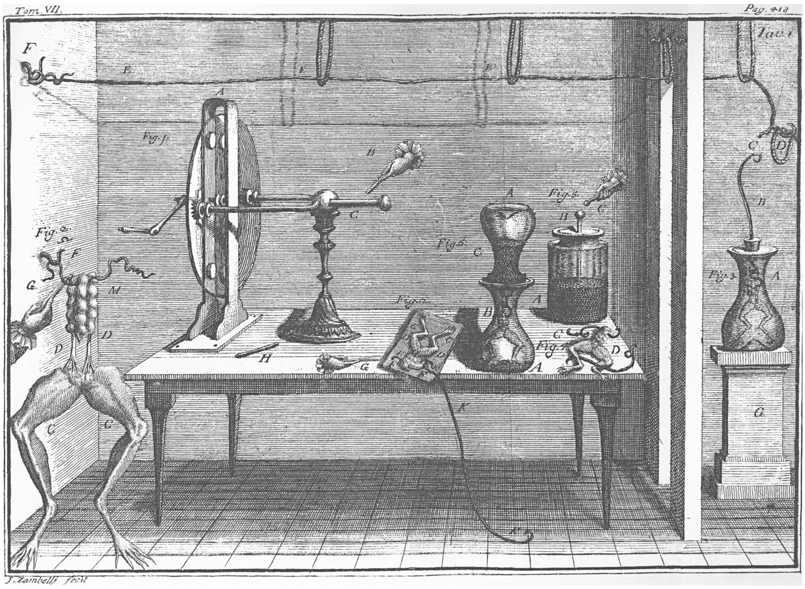

Figure 1. The first plate of the *De viribus electricitatis in motu musculari*. Beside various frog preparations and special devices designed by Galvani for his experiments, notice (respectively on the left and on the right side of the table) the presence of an electric machine and a Leyden jar (from Galvani, 1791).

protocols in which Galvani annotated the day-by-day progress of his experiments, among the manuscripts there are several attempts made, since 1782, to write a memoir aimed for publication. However, only in 1791, i.e., after more than ten years of electrophysiological research, was Galvani able to announce his theory in print. Of particular importance for the reconstruction of Galvani's path of discovery are two memoirs written in 1786 and in 1787 — a critical period for the conceptualization of his physiological hypothesis of neuromuscular system. In these memoirs it appears particularly clear the important role played by visual images in Galvani's scientific endeavor.

The protocols of electrophysiological experiments cover the period 1780–1787 with, a long interruption, between 1783 and 1786, when Galvani turned his interest to a series of physico-chemical investigations somewhat connected to his studies in neuromuscular physiology. We will limit our narration to a rapid outline of Galvani's investigations and we will concentrate on some particular aspects of his research that appear to be of particular relevance for illustrating his experimental and logical attitude.

From the outset it must be said that the overall view that emerges from the study of Galvani's writings is completely different from the received image of Galvani still present in a certain historiographic tradition and in popular imagery: a scientist of the *ancien régime*, largely ignorant of physics, incurring by chance in some unexpected phenomenon but incapable of interpreting it correctly, whose merit would be only that of opening the way to more acute scientific explorers (such as, in particular, Alessandro Volta, the inventor of the "voltaic" battery whose story is largely connected to that of animal electricity). (For a discussion on Galvani's historiographic stereotypes, see Piccolino and Bresadola, 2003.)

Galvani appears instead to be a genuine and highly competent scientist, endowed with many of the characteristics of the ingenuous experimentalist. He was capable of pursuing with the force of "modern" science a research plan toward its successful end, eventually producing in the physiology of the eighteenth century a revolution that, for his epoch, was compared to that caused in the previous century by Harvey's discovery of blood circulation.

In his scientific endeavor Galvani aims at obtaining a coherent hypothesis on the involvement of electricity in neuromuscular function that, in addition to be physiological and physical plausibility, should face all the objections formulated against the neuroelectric theory. He develops his investigation through a series of well-planned experiments, showing an extreme attention to the experimental setup that he designs and varies carefully with relation to the specific questions investigated. He shows a particular ability of learning from his experiments how to proceed further. This can result from conscious reflection on the results obtained but can also be a form of unconscious training whereby he progressively improves his ability in designing and modifying the conditions of the experiment. Often it is a subtle and unconscious form of apprenticeship whereby previous events or decisions (or even linguistic choices) may progressively influence the further progress of his experimentation.

The presence on the experimental stage of a particular instrument (for instance Franklin's capacitor or the Leyden jar) useful initially just as a convenient source of electricity may eventually contribute to a conceptual shift whereby the animal preparation is perceived as similar, in its shape or experimental behavior, to the instrument. Even the application of metallic wires and hooks to the nerves or muscles of the frog preparation (useful for administering electricity) contributes to envisioning specific parts of the animal organism as components of identifiable electric circuits. The use of the notation "conductor" for these metallic tools applied to the animal preparation (first appearing in the protocols of February 1781) might seem obvious for an object designed to "conduct" electricity. "Conductor" was, however, the term normally used to indicate the metallic rod by which a Leyden jar (or the electric machine) could be discharged, and this eventually contributed to his envisioning the that neuromuscular system could behave as an "animal Leyden jar" (see Figure 1 and also Figure 4).

An important aspect of Galvani's scientific attitude is his freedom from dogmatic commitments. In spite of the fact that he is, from the outset, verifying the involvement of electricity in neuromuscular physiology and keeping a constant reference to the neuroelectric theory, he maintains a liberal attitude toward any theory. As we shall see, he would take advantage also of the antagonist "irritability" theory, both as a perceptual filter useful to capture unexpected events in the course of his experiments, and as a conceptual paradigm for interpreting his results.

The first cycle of Galvani's experiments concerned the effect of "artificial electricity," i.e., the friction electricity produced by electrical machines and accumulated in capacitors like the Franklin's square or the Leyden jar. Another device capable of producing and maintaining an electric power that appears in Galvani's laboratory is Volta's electrophore, whose presence is first recorded in the protocol of February 7, 1781. In his first experiments Galvani also uses metallic "arcs," i.e., the tools normally used to induce the discharge of the machines or the capacitors (Galvani, 1937).

The importance of the discussions on the neuroelectric theory and on irritability soon appears clear during Galvani's first investigations. In the experiment of November 22, 1780, for instance, he applies the electric stimulus to a frog in which one crural nerve has been ligated and the other is free, with the evident aim of verifying Haller's objection on the effects of ligature on nerve conduction. On November 25th he performs the first of a series of experiments with the purpose of testing the electric conductive properties of nerves. He concludes that nerves can conduct electricity but not in such a free way as metals; a finding fitting to one of the hypothesis developed by the supporters of the neuro-electric theory in order to face another objection of the hallerians: electricity is able to flow along nerves but it has a strong affinity for the "nervous fluid" and thus is retained inside nerve fibers without escaping outside.

On January 26, 1781, something unexpected happened: a frog preparation contracts when one of Galvani's assistants extracts the spark from an electrical machine situated far apart from the frog and *not connected* to the electric source by any conductor whatsoever. Since it appears unlikely that the effect the "electric atmosphere" associated with the spark could be strong enough to directly cause the contraction, this experiment leads Galvani to suppose (within the irritability framework) that contractions are due to the excitation of some principle internal to the animal. Contractions occur only if, in correspondence with the spark, somebody touches the nervous tissues with a conductive body, whereas nothing happens with an insulating body. Contractions are less easily produced by putting the conductor in contact with muscles, a finding hard to reconcile with the irritability theory (which assigns to the muscle rather than to nerves the internal principle responsible for the contractile response to external stimuli).

Galvani cannot draw definite evidence on the electric nature of the internal principle involved in muscle contraction elicited by external stimuli in spite of his efforts during an intense series of experiments as it appears clearly from an unpublished memoir that he writes at the end 1782 (see Piccolino & Bresadola, 2003).

The Experiments with Metals

Galvani interrupted his electrophysiological research in February 1783 and came back to them again in April 1786. Meanwhile he carried out a series of physico-chemical researches on animal tissues, and particularly on nerves, whose results would be important, as we shall see, for his elaboration of the animal electricity model (see Seligardi, 1999).

The initial experiments of the second phase of electrophysiological research concerned the effects of the atmospheric electricity associated with the discharge of thunder and lightning. The table illustrating these experiments in the *De viribus*, with long wires connected to the frog and pointing toward the sky is famous also because it has inspired various cinematographic version of *Frankenstein* (see Figure 2). Galvani could prove that the electricity of stormy weather produced muscle contraction in a very similar way to the artificial one.

The experiments initiated in September 1786 began with a famous chance observation made in the course of investigations aimed at ascertaining the effect of the atmospheric electricity of a calm day. The prepared frog, collocated on the iron fence of the balcony and with a metallic hook inserted in its spinal cord, remained quiet until it was manipulated: brisk contractions were then evoked by pushing the metallic hooks toward the iron bars of the railing. Further experiments showed that to produce contractions it sufficed to connect muscle and nervous tissue through conductive bodies and particularly through metals, whereas nothing happened with insulating materials. These experiments, repeated and varied in numerous ways, led Galvani to suspect the presence, between nerves and the muscles, of "a flow of an extremely tenuous nervous fluid [. . .] similar to the electric circuit which develops in a Leyden jar" (Galvani, 1791, p. 378).

It appeared unlikely to Galvani that this electric flow could be induced by some property of the metals used to connect nerve and muscle; it seemed thus plausible to assume that nerves and muscles were the site of an electric disequilibrium.

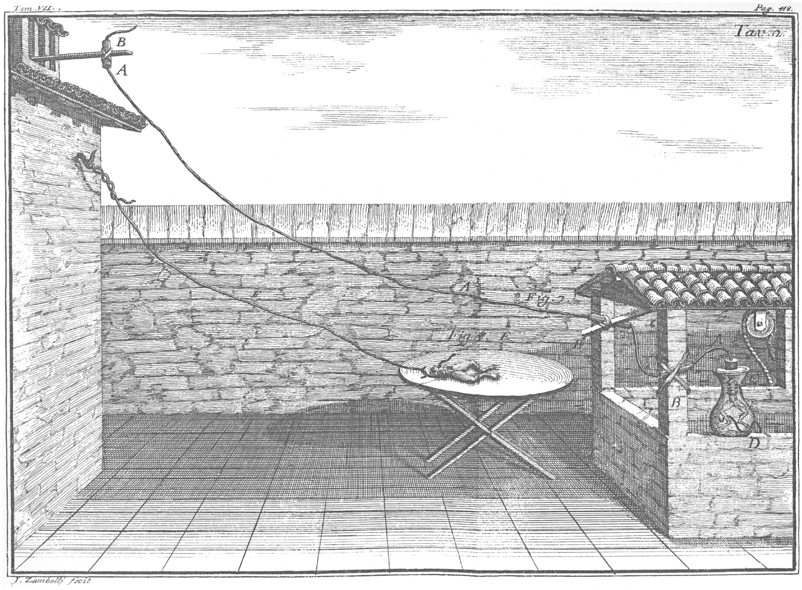

Figure 2. Galvani experiments with the atmospheric electricity of a stormy day as illustrated in the second plate of the *De viribus electricitatis in motu musculari* (from Galvani, 1791).

The mention of the Leyden jar, as a convenient mental tool to represent the hypothetical electric circuit between nerve and muscle, appears in a memoir written at the end of October 1786, i.e., a few months after his first experiments with metals. In the physical Leyden jar the electric circuit is due to the presence of two distinct forms of electricity, respectively in the inner and outer metallic plates (or armatures) of the jar. Galvani investigated which could be the site of this "double and opposite electricity, i.e. positive, as it is said, and negative" and concluded that "no doubt can subsist that, of the said two forms of electricity, one is situated in muscle and the other in nerve" (see Galvani, 1967, p. 176).

In spite of the importance of this conclusion, Galvani declined, however, to publish his memoir: because it did not lead to a physiologically and physically plausible model of the functioning of neuromuscular system, the target that he was eagerly aiming to address.

A fundamental requisite of the sought-for model was that it should explain how an electric disequilibrium could be present inside an animal organism, in spite of the conductive nature of body tissues (an argument, as we know, of Haller's objections to the neuroelectric theory). Indeed, the impossibility that an electrical disequilibrium could exist inside a conductive body was invoked by Galvani himself in his 1786 memoir to exclude that the supposed double electricity could be located in the metals used to connect nerve and muscle. In discussing this point he was aware, however, of a possible exception to this rule, because the presence, inside a conductive body, "of a double polarity, one positive and the other negative, this was a fact — as he wrote — that the physicists admit for tourmaline" (Galvani, 1967, p. 167).

In searching for a plausible localization of the electric disequilibrium responsible for muscle contractions, Galvani conjectured it might be localized inside the muscle tissue. This appeared likely, since — as he wrote "there is in muscles a big quantity of substance, which for its nature, may be apt to develop and hold electricity, in spite of the presence inside it of conductive matter." And added:

> [T]his is not unlike what we saw happening in electrophores which are made of analogous substances. If that would appear it would be perhaps justified to call muscle *animal electrophores*. (Galvani, 1967, p. 169)

The possibility that electricity could be generated inside muscle tissue according to a mechanism analogous to that operating in the electrophore was, however, simply alluded to by Galvani in the 1786 memoir. He kept to his main conclusion of the localization to nerve and muscle tissue of the two forms of electricity and did not further elaborate on the electrophore model. In the course of his experiments with metals he had discovered that contractions were stronger if muscle and nerve were wrapped with thin laminas of different metals (tin, silver, brass, gold). There was no simple way to conceive, with reference to the electrophore, how the physiological effects of the animal electricity could be made stronger by these metallic laminas.

In the 1787 memoir, Galvani amply discusses the problem of the localization of the two forms of intrinsic electricity within animal tissues. An electrical tool, alluded to *en passant* in the 1786 writing, now becomes central in this context: the tourmaline. The property of this stone to produce signs of double electricity upon heating had been brought to the attention of the science of the epoch by Franz Ulrich Aepinus (1756). Among other characteristics, Aepinus demonstrated that, upon breaking a tourmaline crystal, the property of generating a double electric pole was present in every fragment.

In comparing neuromuscular system to tourmaline Galvani wrote:

> Our electricity has much in common with that of tourmaline stone, for what concerns its localization, distribution, and property of parts. In this stone we observe indeed a double matter, transparent and reddish the first one, opaque and colourless the other; this second one is arranged in stripes. Nobody can ignore that nerves are laid down between the layers of muscular fibres, and when these ones are devoid of blood they are transparent, while nerves are opaque. In tourmaline the poles of the double electricity appear to be situated on the same opaque line; so it is in muscles in the same direction. The double electricity of tourmaline does not belong only to the entire stone, but to every fragment. Similarly, in muscles, the admitted double electricity does not belong only to the entire muscle body, but to every part of it. (Galvani, 1967, p. 194)

As it occurred with the "animal electrophore" model alluded to in the 1786 memoir, the analogy between neuromuscular system and tourmaline was both mechanistic and visual. In his path of discovery, Galvani was indeed very sensible to visual suggestions. To Galvani's eye the visual similarity between muscle and tourmaline consisted mainly in the striated and heterogeneous pattern common to both bodies. The mechanistic similarity suggested that muscle electricity might arise in the contact between a muscle fiber and a nerve fiber. Galvani was thus able to keep his previous idea of muscle and nerve as the site of the double electricity but his attention moved from the macroscopic to the microscopic level (Figure 3).

As in the case of the electrophore, Galvani also eventually abandoned the "tourmaline model": in spite of his visual attractiveness, it did not lead to his envisioning a plausible way for the involvement of electricity in neuromuscular function. Moreover, also in the case of the tourmaline model, it was difficult to account for the intensification of animal electricity produced by thin metallic laminas.

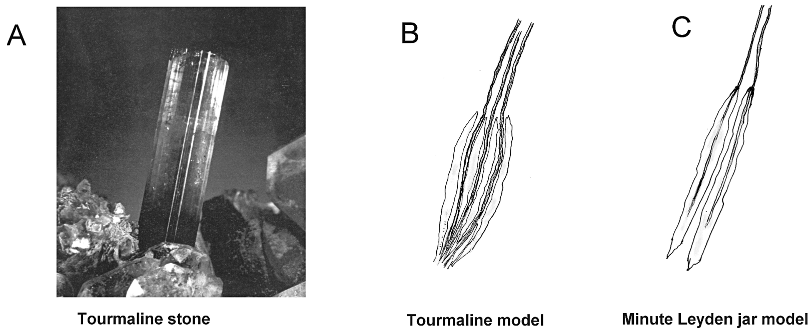

Figure 3. Tourmaline stone (A), a modern reconstruction of Galvani's model of the neuromuscular system as conceived in his unpublished essay of 1787 (B), and in the final version of the "minute animal Leyden jar" (C). In B, the nerve fibers are situated in between the muscle fibers, while in C a single nerve fiber penetrates inside a single muscle fiber (from Piccolino & Bresadola, 2003).

The power of metallic laminas directed the attention toward another electric device that Galvani had used extensively in his experiments: the Leyden jar. This device had been invoked in both the 1786 and 1787 memoirs as an analogical representation of the electric flow between nerve and muscle, but was not initially considered as a convenient model of neuromuscular physiology. In the 1787 memoir there is, however, an important indication to suggest that Galvani's attention was shifting in a more on less unconscious way toward the Leyden jar. The action of metallic sheets is diffusely described in both the 1786 and 1787 memoirs. However, although in the first memoir the metallic sheets are indicated exclusively as laminas or foils (*lamine* or *fogli*), in the second memoir they are indicated as "armatures." In the electric terminology of the epoch, "armature" was commonly used to designate the thin laminas coating the internal and external glass surface of the Leyden jar.

Eventually the Leyden jar had started to exert on Galvani a strong suggestion as a possible visual and mechanistic model for the involvement of electricity in neuromuscular function. The visual character of the analogy between the preparation and the physical device would be explicitly recognized by Galvani in 1794, when he considered justified to call the muscle "an animal Leyden jar" and this "because of a certain similarity that the muscle united to its nerve seems to have with a Leyden jar rather than with any other electric machinery whatsoever" (in Galvani, 1841, p. 206, see Figure 4).

The passage from the tourmaline model alluded to in 1787 to the final "minute Leyden jar" represents the conclusive phase of Galvani's elaboration. It can be subdivided in three logical steps.

The first step illustrates the powerful interchange, in Galvani's conceptualization, between visual and mechanistic suggestions. In the Leyden jar, the discharge was normally obtained through a contact between the outer armature and the "conductor" (i.e., the metallic wire connected to the inner armature and protruding outside the jar mouth); however, the double electricity was not accumulated between the conductor and the outer armature, but between this and the internal one. If the analogy was also operational (as suggested by the armature effect), then the two forms of electricity in their entirety should be accumulated inside the muscle rather than *between* the muscle and the nerve (as initially assumed), as he explicitly recognizes in the *De viribus* (Galvani, 1791, p. 196).

It remained to be conceived how an *insulating* substance could exist in muscle analogous to the glass of the jar. This problem, already alluded to in the 1786 memoir, is

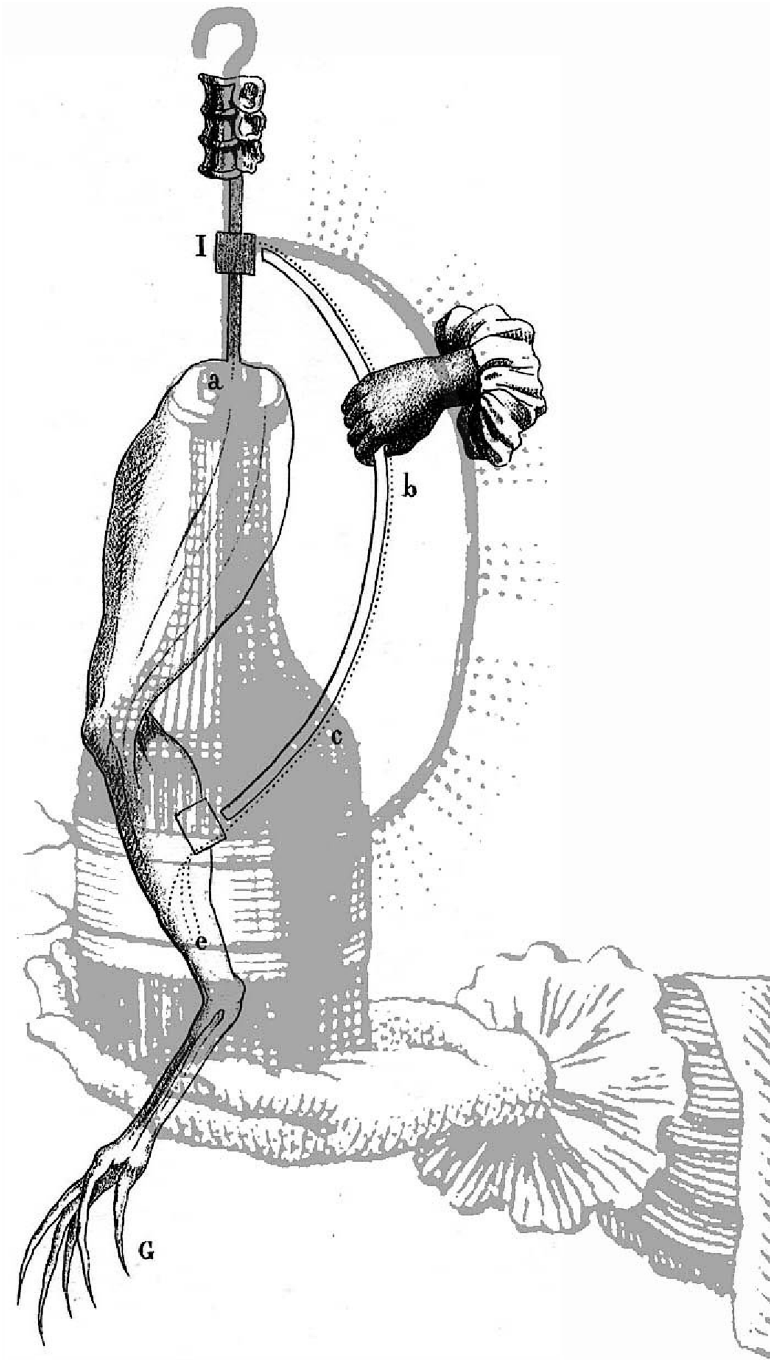

Figure 4. Galvani's visual suggestion of the neuromuscular preparation as a "animal Leyden jar" in a reconstruction due to the courtesy of Prof. Nicholas Wade. The Leyden jar image is from Nollet, 1746, while the frog leg preparation is from Galvani's *Memorie sull'elettricità animale* reprinted in Galvani's collected works published in 1841; notice, in both the physical and the animal device, the presence of metallic "armatures".

considered in a new way in the *De viribus*, where Galvani suggests that the insulating substance might be at the interface between the interior and the exterior of every muscle fiber:

> It is even more difficult that the existence of a duplex electricity in every muscular fibre itself could be denied if one thinks not difficult, nor far from truth, to admit that the fibre itself has two surfaces, opposite one to the other; and this from consideration of the cavity that not a few admit in it, or because of the diversity of substances, which we said the fibre is composed of, diversity which necessarily implies the presence of various small cavities, and thus of surfaces. (Galvani, 1791, p. 196)

With this bold conjecture Galvani is able to face the main objection against the role of electricity in animal physiology. In some way he anticipates a fundamental aspect of modern understanding of the localization of bioelectric potentials; he does it in a period in which the cell theory is still beyond the horizons and the fiber is the only available approximation to the microscopic constitution of living tissues.

The next step is to assume that the nerve fiber penetrates inside the muscle fiber like the conductor enters inside the Leyden jar, such as to allow for a possible flow of electricity between the internal and external armatures. This is apparently just a small rearrangement of the mutual relation of nerve and muscle fiber with respect to the tourmaline stone model (where a nerve fiber was put aside to the muscle fiber, see Figure 3). However, it allows Galvani to envision how muscle electricity might flow outside, when requested by physiological needs, in spite of the insulating character of the surface delimiting the muscle fiber (see Figure 4).

The final step concerns the way in which electric flow could be restricted to individual nerve fibers in spite of the conductive character of body humors. To this purpose Galvani makes reference to his previous physico-chemical studies showing a particular richness of “oily matter” inside the nervous tissue. In order to reconcile this finding with the conductive character of nerves that emerged in his physiological experiments, he assumes that the nerve fiber is made up by a central conductive core wrapped by the insulating matter. With this conjecture he can circumvent another fundamental objection against the neuroelectric theory, enunciated explicitly in *De viribus* in the form of a dilemma:

> As a matter of fact, either nerves are of an idioelectric [i.e., insulating] nature, as many admit, and they could not then behave as conductors; or they are conductors, and were this the case, how could they contain inside them an electric fluid, which would not spread and diffuse to nearby parts, with a sure detriment of muscle contractions. (Galvani, 1791, pp. 398–399).

The response to this dilemma is given in the immediately subsequent passage of the *De viribus*:

> But this difficulty can be easily faced by supposing that nerves are hollow in their internal part, or at least made up of matter apt to the passage of electric fluid, and exteriorly of an oily substance or of another matter capable of hindering the passage and the dispersion of the electric fluid which flows inside them. (p. 399)

The muscle fiber delimited by a nonconductive substance separating the two forms of electricity, the nerve fiber penetrating inside it and made of an inner conductive core and an insulating wrapping: this is the final model of the "minute animal Leyden jar" by which, more than two centuries ago, Galvani laid down the foundation of electrophysiology. Although this model differs in many respects from the modern understanding of neuromuscular physiology, the publication of the *De viribus* represented a fundamental revolutionary passage in eighteenth-century science. With Galvani's endeavor, after a millennium of presence, "animal spirits" were definitely exiled and electricity entered forever in nerve physiology. We can now fully acknowledge Galvani's merits and justify his pride in announcing in 1791 his discovery of the "electric nature of animal spirits":

> [T]he electric nature of animal spirits, until now unknown and for long time uselessly investigated, perhaps will appear in a clear way. Thus being the things, after our experiments, certainly nobody would, in my opinion, cast doubt on the electric nature of such spirits [. . .] and still we could never suppose that fortune were to be so friendly to us, such as to allow us to be perhaps the first in handling, as it were, the electricity concealed in nerves, in extracting it from nerves, and, in some way, in putting it under everyone's eyes. (Galvani, 1791, p. 402)

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