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Luigi Galvani's path to animal electricity

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Abstract

In spite of the historical importance of the research that, in the second half of the 18th century, led Luigi Galvani (1737–1798) to lay down the foundation of modern electrophysiology, his scientific personality is largely misrepresented in science history and in popular imagery. He is still considered as a pioneer that by chance incurred some surprising experimental observations and was incapable of pursuing his research in a coherent way. In contrast with these views, Galvani was a high-standard scientist who succeeded, with the strength of experimental science, in demonstrating, in animals, electricity in a condition of disequilibrium between the interior and the exterior of excitable fibres. This electricity, called 'animal electricity', was deemed responsible for nerve conduction. By studying the scientific endeavours of Galvani, through his published and unpublished material, and by situating them in the historical context of the physiology of the Enlightenment, this paper attempts to trace the elusive and complex path that led Galvani to his extraordinary discovery. ***To cite this article: M. Piccolino, C. R. Biologies 329 (2006).***

Résumé

Le cheminement de Luigi Galvani vers l'électricité animale. La figure de Luigi Galvani (1737–1798) est souvent malmenée dans l'histoire des sciences et l'imagerie populaire, malgré ses recherches menées durant la seconde moitié du XVIII^{e} siècle, d'importance historique, puisqu'elles aboutirent à fonder l'électrophysiologie moderne. Il est encore considéré comme un pionnier ayant par hasard réalisé des observations, sans pouvoir poursuivre sa recherche d'une manière cohérente. Cependant, Galvani était un scientifique hors pair, qui parvint, par une approche expérimentale, à démontrer l'électricité animale comme une condition de déséquilibre entre l'intérieur et l'extérieur des fibres excitables, et donc comme étant à la base de la conduction nerveuse. En étudiant les résultats scientifiques de Galvani, publiés ou non, ainsi qu'en le situant dans le contexte de la physiologie des Lumières, cet article tente de retracer les voies insaisissables et complexes qui amenèrent Galvani à réaliser son extraordinaire découverte. ***Pour citer cet article : M. Piccolino, C. R. Biologies 329 (2006).***

Keywords: Luigi Galvani; History of science; Animal electricity; Electrophysiology

Mots-clés : Luigi Galvani ; Histoire des science ; Électricité animale ; Électrophysiologie

1. Galvani, the story, the legend and the *images reçues*

Among the main achievements of the 18th century science is the demonstration made in 1791 by the scientist of Bologna, Luigi Galvani, of the presence in liv-

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ing tissues of an intrinsic form of electricity involved in nerve conduction and muscle contraction. Galvani's discovery laid the grounds for electrophysiology. Moreover, and unexpectedly, it also opened the path to the invention of the electric battery, by Alessandro Volta, thus paving the way to the development of the physics and technology of electricity, with long-lasting consequences for humankind.

According to Galvani, electricity is mainly accumulated between the interior and the exterior of a single muscle fibre: a nerve fibre penetrates inside it allowing, in either physiological or experimental conditions, "the flow of an extremely tenuous nervous fluid [...] similar to the electric circuit which develops in a Leyden jar" [1 (p. 378)]. With the nerve fibre penetrating into its interior, the muscle fibre represented a "minute animal Leyden jar" for Galvani, and by this image he communicated the discovery of animal electricity in an epoch-making memoir in 1791, *De viribus electricitatis in motu musculari* [1].

In spite of the importance of his research, Galvani's figure is still largely seen as that of a physician of the *Ancien Régime*, incurring by chance an unexpected observation (a dead frog preparation jumping when a light suddenly sparked off from a distant electric machine), a man who meandered aimlessly in interpreting his further experiments until the physicists of Pavia, Alessandro Volta, entered the field [2,3]. With his own research, Volta would be able to claim that the electricity responsible of frog muscle contraction in Galvani's experiments was not intrinsic to nerve and muscle tissues, but derived from the metals used by the scientist of Bologna to connect nerve and muscle in accordance with his idea of the neuromuscular preparation as a Leyden jar [4,5].

In order to demolish the 'legend' of the doctor of Bologna and of his frogs still dominating historiography as well popular imagery, it is necessary to combine an accurate study of Galvani's original sources with an analysis of the historical context and of the scientific problems he was investigating. It is also been essential to evaluate Galvani's experiments and results in the light of modern knowledge on the physiology of nerve conduction.

In this article I shall present the scientific stature of Galvani and his electrophysiological prior to the formulation (in 1791) of his hypothesis of animal electricity. This work is largely based on the research that I have been carrying out over the last ten years in collaboration with Marco Bresadola [6–10].

2. Electricity in the 18th-century natural philosophy and medicine

Electricity was undoubtedly at the centre stage of the scientific interest of the *Grand Siècle*, the electrical century *par excellence*, as a consequence of many discoveries, theories and practical applications [11].

There was, in particular, a great interest in the possibility that the electric fluid might have therapeutic effects. Electricity, provided by electric machines or accumulated in Leyden jars, was administered with the aim of relieving a plethora of diseases. New systems of 'electric medicine' were proposed where diseases were considered as due to an excess or to a lack of 'electric fire', and thus liable to different electric remedies. Enthusiasm was gradually transmuted into deception, as it became increasingly clear that many of the presumed successful medical applications of electricity were such only in the hands of a few practitioners, and could not be easily and constantly replicated by established scientists and physicians [12–14].

Physiologically, the century was dominated by interest in the possible involvement of electricity in nervous function and muscle excitability [10,15,16]. The prevailing view among the supporters of the 'neuroelectric' theory was that an electric fluid propagates along nerves, producing sensations or movements according to the final targets eventually hit, i.e., the central regions of the nervous system or muscular tissue. On this respect, electricity was a possible replacement for 'animal spirits', the elusive entities considered in classical science as messengers of soul for sensation and will [17, 18].

Even if electricity appeared to be a powerful agent for stimulating nerves and muscles, the idea that the nervous agent could be of an electrical nature encountered fierce opposition among many reputed members of the scientific establishment. This was particularly the case for the followers of the doctrine of 'irritability', elaborated by Albrecht von Haller, a dominating figure of the 18th-century science. According to his doctrine, muscles contract in response to physiological (or experimental) stimuli, because they are provided with an intrinsic capability to contract (or 'irritability'), which depends on their intimate substance and organisation, and is not simply a passive outcome of an external agency. Nerves would act on muscles just as stimulating or exciting factors, capable of putting into action intrinsic muscle irritability [10,16,19].

For 'Hallerians' it was difficult to accept the electric theory of nervous conduction, because it implied the electric fluid of nerves as the effective agent of muscle