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HISTORY OF NEUROSCIENCE

The Electrophysiological Work of Carlo Matteucci*†

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ABSTRACT: In 1964, Giuseppe Moruzzi (1910–1986), a prominent neurophysiologist of worldwide fame with a scholarly interest in the history of science, published an extensive and insightful analysis of the work and personality of Carlo Matteucci, a 19th century Professor of Physics at the University of Pisa who had worked on "animal electricity" in the great tradition of Galvani. By discovering fundamental phenomena such as the demarcation potential and action current in muscle and nerve, Matteucci paved the way for the development of modern electrophysiology. Being written in Italian and having appeared in a not easily available journal of history of science, Moruzzi's essay has been lost to most members of the international neuroscience community. An English translation of it is published here with two aims: first, to make known to a large audience of neuroscientists a fascinating account of the origins of electrophysiology as seen through a perceptive interpretation of the successes and failures of a brilliant scientist and passionate man; and second, to pay tribute to the memory of Giuseppe Moruzzi and his everlasting contributions to learning and science on the occasion of the 10th anniversary of his death.

KEY WORDS: History of neuroscience, Electrophysiology, Animal electricity, Demarcation currents, Action currents, Matteucci-du Bois Reymond controversy.

FOREWORD BY M. PICCOLINO

This article was originally in Italian and was published in 1964 ("L'opera elettrofisiologica di Carlo Matteucci." *Physis*, Vol. 6, pp. 101–140). It was written by Professor Moruzzi, after a lecture he gave in Pisa, in 1961, to celebrate the 150th anniversary of Carlo Matteucci's birth.

Giuseppe Moruzzi was an outstanding Italian physiologist, and his work on the neural mechanisms controlling the sleep–waking cycle in mammals still remains a milestone in the physiology of nerve centers. Besides being a great scientist, Prof. Moruzzi was a person of high cultural and human standards, and he left a profound impact on many of those who had the chance to meet him. History held a privileged position among his many cultural interests, already in his early youth. And, indeed, the young Moruzzi had planned to devote himself to the study of history, but later on he had to change his mind and turn to medicine, mainly for practical reasons. His inclination to history persisted, however, and, in the maturity years, it turned toward a specific interest for the historical aspects of physiology, clearly manifest in some of his review articles and on the notes he wrote on the life and activity of some 19th and 20th century scientists.

Moruzzi was convinced that science, even if it depends heavily on technical developments, is basically an intellectual activity, and that the most important scientific achievements are often due to the efforts of a single man. In his writings, he tries to point out particularly what is personal and individual in the scientific endeavour (what Cajal has indicated as *humano aroma*—"human flavor"). Another reason for Moruzzi's interest in history is to be found in his attachment to the books, considered as the long-lasting records of the outcomes of men, who contributed to the progress of knowledge with their work based on intelligence, creativity, emotion, men who were not, however, always immune from less noble passions. Through the books, all this human performance may escape the ravages of time and be transformed into one of the most perennial monument of human civilization. For Prof. Moruzzi, writing on the history of science was a way to render just consideration to scientists who had been disregarded or even unjustly dispraised during their life because of the misunderstanding of contemporaries or the envy of colleagues. His love for the history of science was also a way to revive the old books that he had collected, with enduring enthusiasm, in the magnificent physiological library, recreated in his Institute, after the disasters of the last war. The love for books is one of the most important legacy of Prof. Moruzzi and, by translating this article 10 years after his death, we hope to contribute in some way to keep viable this love.

MORUZZI'S ORIGINAL ENGLISH SUMMARY

1. The Nervous Control of the Electric Organs

Matteucci (1836) showed in torpedo that mechanical stimulation or injury of the electric lobes of the brain stem was followed by the discharge of the electric organs. In the following

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year (1837), he reported that the electric discharge was not produced by injury, nor prevented by ablation, of the cerebral hemispheres, the optic lobes, or the cerebellum. The critical factor was the injury or the ablation of the fourth lobe ("electric" lobes). In another paper (1838), he reported that galvanic stimulation of the electric lobes yielded the discharge of the electric organ, an effect which was abolished by cutting the nerves arising from the brain stem. In 1843 and 1844, Matteucci showed that the reflex electric discharge could no longer be produced by stimulating the body, following section of the spinal cord, nor by compressing the eyes, following section of the trigeminal nerves. The reflex activation of the electric organ through the electric lobes was thus established.

2. The Discovery of the Demarcation Currents

In 1842, Matteucci discovered the demarcation currents flowing between the intact and the cut surface of the striated muscles. Their existence was proved both with the galvanoscopic frog leg and with a galvanometer. With the latter instrument, he demonstrated that the direction of the current was such as would be expected if the cut muscle surface was negative relative to the intact surface.

3. The Discovery of the Action Currents

The discovery of the induced muscle twitch (1842) may be regarded as the first physiological evidence of the existence of the action currents. Becquerel (1842) gave the correct interpretation of the phenomenon, which, at first, was accepted by Matteucci (1844). A correct interpretation had been presented also in Müller's Handbook (1844), but Matteucci (1845) later refuted it. It is shown that the main reason for this attitude was Matteucci's reluctance to admit that an electric phenomenon (the demarcation current) could disappear as a consequence of muscle contraction. This fact had actually been first described by Matteucci himself (1838), but was rejected by him (1845). Hence, the discovery of the negative oscillation of the demarcation potential (1843) and, above all, the correct interpretation of the phenomenon (1848–49) should be attributed to du Bois-Reymond.

I. THE YOUTHFUL YEARS

The first electrophysiological paper of Matteucci appeared on 1 November 1830. The author, born in Forlí on 20 June 1811, was then only 19 years old and had just returned home after an 8 month period spent in Paris. He had graduated in Physics at the University of Bologna on 7 April 1828, when he was not yet 17 years old. His interest in the study of electricity was already documented by two publications in the field of meteorology which appeared in 1827 and 1828. The main biographer of Matteucci, Nicomede Bianchi (1874), notes that in Paris the young Italian physicist had already succeeded in earning the friendship and esteem of scientists like Arago and Becquerel.

The electrophysiological work to which Matteucci owes his imperishable fame begins in 1836. It can be divided into three parts: electrophysiological investigations on electric fish, studies of the demarcation potentials of muscle, and observations on muscle action potentials. All these will be dealt with in the present study, which ends with a historical account of the famous controversy between Matteucci and du Bois-Reymond, and with an attempt to evaluate the work and scientific personality of Carlo Matteucci.

II. INVESTIGATIONS ON ELECTRIC FISH

In 1836, Donné presented at the *Académie des Sciences de Paris* a communication by Matteucci in which he reported for the first time the first major discovery made by the Italian scientist: the identification of the nervous centers responsible for the discharge of the electric lobe of Torpedo (the electric ray). The main result of this paper follows (p. 431):

Lorsque la torpille a cessé de donner, quoique irritée, la décharge électrique, si l'on met son cerveau à découvert, et si l'on touche d'abord légèrement le dernier lobe du cerveau, celui qui donne les nerfs à l'organe, on a des décharges (trois ou quatre) plus fortes qu'à l'ordinaire, et qui ont la direction constante du dos au bas-ventre. Si au lieu de toucher simplement la surface du cerveau, on le blesse sans discrétion, alors des décharges très fortes se renouvellent.

[When the torpedo is no longer able to produce the electric discharge upon irritation, it is still possible to obtain some discharges (three or four), stronger than in ordinary conditions, and which have the constant direction from the back to the belly by exposing the brain and touching, delicately at the beginning, its last lobe, i.e., the one which innervates the electric organ. If one then pricks the brain surface vigorously, instead of simply touching it, strong discharges reappear.]

In 1837, Matteucci presented his fundamental memoir on the nervous mechanisms responsible for electric discharges in torpedoes at the *Académie des Sciences* (of Paris) (1837, pp. 502–503):

La ligature des nerfs détruit la décharge. Quant au cerveau, si l'on blesse les trois lobes supérieures, il n'y a pas la décharge, et l'on peut même les enlever sans que la décharge cesse. On peut couper la moelle allongée et la moelle épinière, et la décharge continue encore. Ce n'est que le quatrième lobe, qu'on peut appeler lobe électrique, qui ne peut être touché, sans qu'on ait la décharge, et une fois enlevé, tout phénomène électrique disparait.

Il faut observer pourtant que les nerfs de l'organe, même après qu'on l'a separé du cerveau, peuvent encore donner quelques décharges, si on les tiraille immédiatement après son enlèvement.

Lorsque la torpille est morte, quant à sa fonction électrique, on parvient encore à obtenir de très fortes décharges, même plus fortes qu'à l'ordinaire, si l'on touche le lobe électrique. L'action de ce lobe, dans ce cas, est directe, c'est-à-dire que si l'on touche la partie droite, c'est l'organe droit qui donne la décharge, et réciproquement: c'est de cette seule manière qu'on peut avoir la décharge d'un seul côté dans la torpille.

[Ligating the nerves abolishes the discharge. As regards the brain, there is no discharge if the three upper lobes are irritated, and they can even be removed without stopping the discharge. One can also cut the medulla oblongata and the spinal cord and the discharge still continues. It is only the fourth lobe, which can be called the electric lobe, which is important for the discharge. The discharge appears if it is touched, and when it is removed all electric phenomena disappear.

We should nevertheless consider that the nerves of the organ can still induce a few discharges after the organ has been separated from the brain if they are tugged immediately after its removal. When the torpedo is dead, as regards its electric function, it is still possible to obtain from it strong discharges, even stronger than under ordinary conditions, by touching the electric lobe. In this case, the action of this lobe is *direct,*[a] i.e., if one stimulates the right part, the discharge appears only in the right organ, and vice versa: this is the only way to obtain a discharge limited to a single side of the torpedo.]

The effect of nerve section had already been seen by Galvani, but the discovery of the electric lobe is due to Matteucci:

The Author concludes:

[a] "direct" here means evidently "oriented to" as opposed to "diffuse." (Translators' note)

Les conclusions principales sont les suivantes: 1°. Du dernier lobe du cerveau est produit et transmis dans l'organe, l'*élement* nécessaire à la décharge et à sa direction; 2°. ce n'est donc pas dans l'organe que cet *élement* est préparé; 3°. un courant électrique charge l'organe comme cet élement; 4°. il y a dans les nerfs une condition autre que celle de laisser passer le courant électrique, afin qu'il fonctionne.[b]

[The main conclusions are as follows: 1°. The *element* necessary for the discharge and for its direction is produced in the last lobe of the brain and is transmitted from there to the organ: 2°. it is not within the organ, therefore, that this *element* is prepared; 3°. an electric current charges this organ as does this element; 4°. there is in the nerves some condition other than simply permitting the electric current to pass, which is required for the functioning of the electric organ.[b]]

In this way, the localisation of the nervous structures responsible for the discharge of the electric lobe and their excitability to stimuli were demonstrated for the first time with a crystal-clear clarity.

In the November 6, 1837 session, chaired by Magendie, a Committee formed by the Academy members Breschet, Pouillet, and Becquerel reported on Matteucci's communication, stressing its importance and originality, and by an unanimous vote, proposed to include it in the "Recueil des Savans étrangers" ("Collection of Foreign Scholars").

The discussion of Becquerel's Report, held in Matteucci's presence, became somewhat harsh because of a priority question was raised against Matteucci by Linari, a scientist of Siena. It concerned a phenomenon of minor importance, the production of sparks by the torpedo. The Committee had recognised "que M. Matteucci a eu premier l'idée d'employer, à cet effect, l'appareil de l'extra-courant de Faraday, dont M. Linari n'a fait usage qu'après son compatriote lui en eût donné avis (1837b, p. 790). [that Mr. Matteucci was the first to have the idea to employ for this aim Faraday's extra-current apparatus, which M. Linari used only following the suggestion of his compatriot].

Only one member of the Academy, Libri,[1] an eminent mathematician of Italian origin, was against the Report's conclusion, claiming that the Committee did not have enough evidence to decide on the priority question. Moreover, he expressed himself against the decision to include the Memoir in the Recueil with these words (pp. 795–796):

M. Libri croit au contraire que il faut s'abstenir, dans ce cas, comme on s'est abstenu lorsque M. Matteucci a annoncé à l'Académie des découvertes encore plus éclatantes, découvertes qu'on n'a pas cru, faute de preuves, devoir publier dans le recueil des *Savans Étrangers*: car cette insertion est une marque de haute approbation, que perdrait beaucoup de son prix si elle était prodiguée, et non pas un moyen de publication. La publication a déjà eu lieu dans les *Comptes Rendus*, et la lettre de M. de Humboldt montre que les travaux de Matteucci, n'ont pas besoin de la tardive publicité des volumes des *Savans Étrangers*. D'ailleurs cette lettre sur laquelle on veut s'appuyer, prouve que M. de Humboldt lui-même n'a nullement vérifié le fait annoncé.

Dans cet état de choses, la Commission (qui n'a pas pu vérifier le fait principal ni se former une convinction) n'accordant pas son approbation au Mémoire de M. Matteucci, M. Libri pense q'il ne saurait y avoir lieu à le publier dans le recueil des *Savans Étrangers*.

[Mr. Libri believes that, on the contrary, one must abstain, in this case, as one also abstained when Mr. Matteucci communicated to the Academy even more striking discoveries which were not considered worthy of publication in the *Foreign Scholars* memoir collection in the absence of experimental verification by the Academy; indeed, the inclusion in this collection is a mark of high approval, which would lose much of its value if it were conceded without restriction, rather than being a method of publication. Publication has already occurred in the *Comptes Rendus*, and Mr. von Humboldt's letter shows that Mr. Matteucci's papers do not need the tardive publicity given by the *Foreign Scholars* volumes. On the other hand, the letter of Mr. von Humboldt, exhibited to support the proposal, shows that Mr. von Humboldt himself has in no way verified the fact communicated to the Academy.

In this state of things, Mr. Libri does not think that Mr. Matteucci's memoir should be published in the *Foreign Scholars* collection, since the Commission (which had been unable to verify the main finding communicated, and to form an opinion of it) does not grant approval of Mr. Matteucci's memoir.]

The response given by Arago (pp. 796–797) merits a complete citation. It represents the best homage to the work of the young scientist, then 26 years old.

M. Arago remarque, en répondant à M. Libri, q'il n'a point exprimé le désir que l'Académie *se prononçât* sur une question de priorité. Il n'a pas même demandé que les termes du rapport fussent modifiés. En émettant publiquement *son opinion personelle* sur un point de l'histoire de la science dont l'Académie s'était déjà occupée, il a désiré, autant que cela dépendait de lui, réparer le tort qu'il faisait à M. *Matteucci* quand il insérait dans le *Compte Rendu* de la séance du 11 juillet 1836, l'extrait d'une lettre de ce physicien, sans faire les parts, bien distinctes, de l'inventeur de l'expérience et de celui à qui il avait été donné de la réaliser le premier. Passant ensuite à la question de savoir s'il serait contraire aux usages, comme le pense M. Libri, de voter l'insertion dans le recueil des *Savans Étrangers*, d'un mémoire renfermant des expériences qui n'ont pas pu être vérifiées, M. Arago fait remarquer qu'en adoptant ce système, il n'arriverait presque jamais, dans les sciences d'observation du moins, que l'Académie dût approuver les travaux que lui sont soumis. Personne a-t-il prétendu imposer aux commissions académiques l'obligation de répéter, dans tous leur détails, les expériences délicates, difficiles, nombreuses, qui sont décrites dans les longs mémoires renvoyés à leur examen? *Quand elles le peuvent*, les commissions vérifient, ça et là, quelques points culminants; si cette vérification partielle réussit, elles admettent le reste, mais bien entendu, sous la responsabilité de l'auteur. Il y a plus, l'Académie adopte complétement, elle fait souvent insérer dans le recueil des *Savans Étrangers*, des mémoires dont on n'a pas été à même de vérifier un seul résultat. L'Académie exigea-t-elle, par exemple, de M. Arago, qu'il se transportât sur les sommités des Pyrénées, avant d'honorer de son suffrage le beau nivellement géodésique que M. Corabeuf a étendu le long de cette chaîne de montagnes, entre l'Océan et la Méditerranée? La Commission actuelle s'est conformée aux usages, elle a fait tout ce qu'on était en droit d'exiger. Ce qu'elle a pu vérifier, s'est trouvé exacte. L'expérience des lobes de la torpille, la plus simple, la plus facile peut-être de toutes celles que cite M. *Matteucci*, elle ne s'en est point occupée par la très bonne raison qu'il n'y a pas de torpilles a Paris. Eh bien! La Commission en avertit. A mon avis, dit M. Arago, c'est un excès de précaution: la facilité de cette observation particulière, l'exactitude constatée de toutes les autres, les succès que M. *Matteucci* a obtenus dans un grand nombre de recherches délicates étaient une garantie suffisante: ordinairement on n'en demand pas d'avantage.

Au surplus, en décidant, conformément à l'avis de la Commission, que le mémoire de M. *Matteucci* sera inseré dans le recueil des *Savans Étrangers*, l'Académie témoignera de son juste intérêt pour un travail qui touche à l'un des points les plus délicats de toute l'organisation animal: elle excitera les observateurs à diriger de ce côté leurs investi-

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[b] This "other property" is very probably the "excitability" of the nerve, the capacity to react to various stimuli, beside the electric one, and to elicit, as a consequence, the discharge of the electric organ. (Translators' note)

[1] Guglielmo Libri, an eminent historian of mathematics, was born in Florence in 1803. Appointed professor of physics at the University of Pisa in 1823, he emigrated to France in 1830 for political reasons. There he obtained, at the age of only 29, the chair of Mathematics at the *Collège de France* and was elected in 1833 as member of the *Académie des Sciences*. At the outbreak of the 1848 revolution, he repaired to England. He was afterwards sentenced by default, in France, for having taken possession of books belonging to public libraries. The sentence raised many polemics and was attributed to political hatred, since Libri had been a warm supporter of the July Monarchy. Nevertheless, the evidence of his innocence was never produced.

gations attentives; c'est là le rôle honorable que l'Académie s'est toujours donné, q'elle a constamment rempli dans des occasions pareilles et dont il est impossible quelle ait jamais à se repentir. Voici, au surplus, ajoute M. Arago, dans quels termes on parle des expériences de M. *Matteucci* de l'autre côté du Rhin: le passage que je vais lire se trouve dans une lettre de M. de Humboldt "ce qui m'a le plus remué dans ce derniers temps, est la grande découverte de M. Matteucci sur l'action du seul quatrième lobe du cerveau de la torpille!"

[In responding to Mr. Libri, Mr. Arago remarks that he did not express the wish that the Academy *adjudicate* questions of priority. Nor did he request that the terms of the report should be modified. In expressing publicly *his personal opinion* on a point of history of science, already considered by the Academy in a previous occasion, Mr. Arago wished, insofar as it depended on him, to rectify the wrong done to Mr. *Matteucci* by the Academy, when it included in the *Compte Rendu* of July 11, 1836 an excerpt of a letter of this physicist, without clearly distinguishing the person who planned the experiment from the person to whom Mr. Matteucci gave the possibility to carry out the experiment for the first time.

Moving then to the question to determine if it will be against the Academy policy, as Mr. Libri thinks, to vote for the inclusion in the *Foreign Scholars* collection of a memoir based on experiments that the Academy had no possibility of verifying, Mr. Arago notes that, were this system adopted, it would be then practically impossible, at least in observation-based experimental science, for the Academy to approve the papers submitted to it. Has somebody demanded that Academy Commissions should repeat, in all their details, experiments so delicate, difficult and numerous as those described in the long memoirs submitted to their scrutiny? *When they can*, the Commissions verify, here and there, certain fundamental points; if this partial verification succeeds, the Commissions take the remaining parts for granted, of course under the author's responsibility. What is more, the Academy completely accepts and often resolves to include in the *Foreign Scholars* collection some memoirs of which it could not verify even a single result. For instance, did the Academy require that Mr. Arago should transport himself to the Pyrenean peaks, before honouring with its approval the beautiful geodetic levelling made by Mr. Corabeuf along this mountain chain between the Ocean and the Mediterranean sea? The present Commission has followed the normal policy, it has done all that it was expected to require. What it could verify, it found to be correct. The experiment of the torpedo lobes, perhaps the simplest and easiest to do of all those cited by Mr. *Matteucci*, was not verified for the very good reason that there are no torpedoes in Paris. Well then! The Committee acknowledges it. In my opinion, said Mr. Arago, this is an excess of precaution: the ease of this particular observation, the ascertained precision of all the others, the success obtained by Mr. *Matteucci* in a great number of delicate experiments were a sufficient guarantee: normally one requires nothing further.

Moreover, if, following the advice of the Committee, the Academy were to decide to include Mr. *Matteucci*'s memoir in the *Foreign Scholars* collection, it will provide evidence of its interest in a work dealing with one of the most delicate aspects of animal organization: it will prompt scientists to direct their most careful investigations toward this topic; this is the most honorable role that the Academy has always given itself, the role it has habitually fulfilled in comparable situations, and which it will never regret. Besides, Mr. Arago says, these are the terms under which Mr. *Matteucci*'s experiments are considered on the other side of the Rhine, the passage I am going to read is from a letter of Mr. von Humboldt "What I have been most moved by recently is the great discovery made by Mr. Matteucci concerning the action of only the fourth lobe of the torpedo brain.]

At the end, the decision of the Academy was fully favourable to Matteucci (1837b, p. 737):

L'Académie adopte les conclusions du rapport. Le Mémoire de M. Matteucci sera imprimé dans le recueil des *Savans étrangers.*

[The Academy adopts the report conclusions. Mr. Matteucci's memoir will be included in the *Foreign Scholars* collection].

The unpleasant scene caused by Libri is described by Matteucci in a letter written from Paris to his Genevan friend, Auguste De la Rive,[2] as follows:

I will tell you about the scene at yesterday's session. What a shame my dear friend! The only Italian of the Academy, an old friend of mine, Guglielmo Libri, the miserable, the person who ten minutes before reading the Report had shaken my hand and spoken with me about the praise of my work recently expressed by von Humboldt, declared against me. It is impossible for you to imagine the sense of disgust felt by those present. You know how they normally vote. Well, this time all the members stood up, he alone remained seated.

But Libri was not the only one to remain insensitive to the enthusiasm of the *Académie des Sciences* and of Baron von Humboldt. In the fourth meeting of the Section of Physics of the first Congress of Italian Scientists, held in Pisa on October 9, 1839, we read (pp. 27–38):

Carlo Bonaparte, Prince of Musignano, asks the leave to speak and proposes the election of a Committee which should be present during the anatomical investigations concerning the fourth lobe of the brain he is going to carry out in torpedo. The Chairman delegates this task to Professors Orioli, Casari, Maiocchi, Zantedeschi, Belli, and Pacinotti, not for the purpose of passing judgment on those researches, but only to communicate the results to the Section. Afterwards, he closes the session.

Matteucci's name is not even recorded in the report of the second General Meeting made by the general secretary, Prof. F. Corridi. Although the Prince of Musignano[3] spoke at length of the ancients' notions about torpedoes, he probably did not mention Matteucci's researches to any significant extent, if the summary made by the general secretary is accurate:

The valuable things said by (abbé) Lambruschini were followed by news of great moment which the Prince of Musignano had presented in another memoir. After having recounted with high erudition what the ancients knew about the animal that in Italian we call *Torpedine*, he continued by expounding the properties he considered useful for illustrating and explaining the electric properties of this fish, utilizing the experiments of the famous Nobili and adding his own results. In this way, he called the attention of Physicists and Naturalists to this valuable aspect of electric science, and raised a lively desire that the letters addressed to him by Nobili on this subject, which were made even more precious by his new illustrations, could be published whenever possible. (p. XXVII)

Only at the end of the Secretary's report do we read:

As far as the works done by the physico-chemical Section about animal electricity are concerned, the Secretary reported that following the lead of the Prince of Musignano, investigations were begun on Torpedo to ascertain the new findings published by Matteucci; and that very accurate experiments were carried out on this topic by Professors Puccinotti and Pacinotti with the aim of clarifying whether an electrovital current exists in warm-blooded animals as well as in cold-blooded species, and these experiments, repeated at the presence of an especially elected Committee, were given high praise by that Committee. (p. XLV)

However, from the report we cannot infer whether the findings published by Matteucci were confirmed or not, and whether they were found to be of the same high quality as the experiments of Professors Puccinotti and Pacinotti.

[2] Auguste de La Rive (1801–1873), physicist and political man of Geneva, editor of the *Bibliothèque Universelle de Genève*. He was a relative of Cavour.

[3] Carlo Luciano Bonaparte, the son of Luciano Bonaparte, Prince of Canino and Musignano (1803–1857).

The third paper on torpedo was sent to the journal *La Bibliothèque Universelle de Genève*, edited by De la Rive.

In this paper, Matteucci showed that the discharge of the electric organs does not depend on blood circulation, and provided conclusive evidence that a galvanic current elicited, in the electric lobe and in the nerve originating from it, nervous impulses which were responsible for the discharge of the organ. It is worth reporting the exact words of Matteucci (1838a, p. 376), since they show how careful he was in checking a possible cause of experimental error constituted by the diffusion of the stimulus. This cause of error was too often neglected by physiologists even long after Matteucci's time:

Je prends une torpille vivante et j'en découvre le cerveau et les troncs nerveux qui vont à l'organe. Je pose le poisson ainsi préparé sur une lame de verre vernissée; je recouvre son organe avec des grenouilles préparées, et je met aussi les deux lames du galvanomètre, l'une sur le dos, l'autre sur le bas-ventre. Je porte alors les deux conducteurs en platine d'une petite pile à auges de 15 couples sur un des nerfs de l'organe, à la distance de deux à trois centimètres. A l'instant des fortes contractions ont lieu dans les grenouilles, et l'aiguille du galvanomètre dévie de 8° à 10°. Cette déviation est dans le sens de la décharge ordinaire. Je renverse la direction du courant, et les mêmes contractions, ainsi q'une déviation égale et dans le même sens, ont lieu. Toute autre partie de la torpille, tourmentée par le courant électrique, même plus près des grenouilles, ne produit aucun effet. On trouve aussi que les décharges obtenues par l'action du courant électrique sur un des nerfs de l'organe sont limitées à la portion de l'organe dans laquelle le nerf est répandu. Si le quatrième lobe est parcouru lui-même par le courant électrique, toute la surface de l'organe lance la décharge. Lorsque les nerfs sont liés, le passage du courant au-dessu de la ligature n'est plus capable d'exciter la décharge. Je rapporterais encore que si l'expérience est faite sur une torpille bien vive, on voit les signes de la décharge, même à l'instant où la circulation du fluide électrique cesse.

[I take a live torpedo and expose its brain and the nerve trunks which go to the (electric) organ. I lay down the fish thus prepared on a varnished glass surface, cover the organ with some prepared frogs, and put the two plates of the galvanometer on the fish, one on the back and the other on the belly. I put the two platinum wires of a small trough pile of 15 junctions on one of the nerves of the organ, at a distance of two to three centimeters. Suddenly strong contractions appear in the frogs, and the galvanometer needle deviates by 8 to 10°. The needle deflection is in the direction of the ordinary discharge. I reverse the current direction, and the same contractions take place, with the same deflection of the galvanometer and in the same direction. No effect is produced by challenging all other parts of the torpedo with the current, even quite close to the frogs. The discharges induced by the action of the electric current on one of the nerves of the organ are also found to be limited to the portion of the organ into which the nerve spreads. The entire surface of the organ generates the discharge if the fourth lobe is itself traversed by the electric current. When the nerves are tied, the passage of current along the nerve portion above the ligature is no longer able to excite the discharge. I will report, moreover, that the signs of the discharge can be seen even in the instant in which the current ends if the experiment is made in a lively animal.]

The last two lines report an observation which contains *in nuce* the phenomenon now known as *afterdischarge*.

The final conclusions of this paper are the most complete expression of the great scientific acumen of Matteucci. The parallelism, today universally accepted, between electric organ and striated muscle is expressed with crystal-clear clarity, and the same can be said about the nature of some reflexes of the electric lobe (1838a, pp. 377–378):

Je n'ai plus qu'à m'arrêter sur les conclusions qu'il est permis de tirer des expériences rapportées; j'espère qu'on trouvera qu'elles sont la conséquence nécessaire des faits découverts et qu'elles sont entièrement indépendentes de toute hypothèse... 1° Toute action extérieure ou irritation excercée sur le corps de la torpille vivante, et qui détermine la décharge électrique, est transmise par les nerfs du point irrité au quatriéme lobe du cerveau. 2° Toute irritation excercée sur le quatrième lobe, ou sur les nerfs qui en sortent et qui vont à l'organe, est suivie par une décharge électrique sans aucune espèce de contraction. 3° La liaison qui existe entre le quatrième lobe et les nerfs qui en sortent d'une part, et la substance de l'organe de l'autre, est précisement la même qui se trouve entre un nerf quelconque et les muscles dans lesquels il est ramifié. Dans le cas de la torpille, en agissant sur son quatrième lobe et sur ses nerfs, nous avons la décharge électrique; dans l'autre la contraction. Toutes les causes qui facilitent ou empêchent la contraction sont également celles qui favorisent ou détruisent la décharge de la torpille. L'action du courant électrique est aussi identique, et nous devons remarquer à ce propos que, tandis que toute action stimulante a deja cessé de déterminer la décharge de la torpille, le courant électrique a encore ce pouvoir. C'est la plus grande analogie que nous ayons entre la force inconnue des nerfs et l'électricité. En attendant nous pouvons enregistrer dans la science la conclusion suivante: *La force qui se développe et qui circule dans le système cérébral et nerveux, est transformée en électricité à l'aide d'une organization spéciale que la nature a disposée dans certains animaux; et le courant électrique est le seul agent extérieur dont l'action soit la plus puissante pour la décharge, et dont, par conséquent, l'analogie soit la plus grande avec l'agent nerveux.*

[I need now only to discuss the conclusions which can be drawn from the experiments I have reported; I hope that they will appear to be the necessary consequences of the facts I have discovered, and to be totally independent of any hypothesis... 1° All external actions or irritations exerted on the body of the live torpedo which produce the electric discharge are transmitted from the nerves of the irritated point to the fourth lobe of the brain. 2° Any irritation exerted on this fourth lobe, or on the nerves emerging from it and going to the organ, is followed by an electric discharge without any kind of contraction. 3° The link existing between the fourth lobe and the nerves emerging from it, on one side, and the substance of the organ, on the other side, is precisely the same which exists between any ordinary nerve and the muscles into which it ramifies. In the case of the torpedo, we obtain the electric discharge by acting on its fourth lobe or on the nerves issuing from it. All causes which induce or prevent the contraction are the same as those which favour or abolish the discharge of the torpedo. The action of the electric current is identical, and in this regard we must note that the electric current may still evoke a discharge when all other stimulating actions are no longer capable of doing so. This is the greatest possible analogy between the unknown force of nerves and electricity. Meanwhile, we can record for science the following conclusions: *The force which develops and circulates in the brain and nerve system is transformed into electricity by means of a special organization that nature has built up in certain animals; and the electric current is the external agent with the strongest action in evoking the discharge, and as a consequence, the one having the strongest analogy with the nervous agent.*]

In the last lines, the hypothesis of the electric nature of the nervous impulse is expressed with caution and clarity.

The proof that the reflex discharge of the electric organ occurs through supraspinal reflex centres was given only in 1843 (1843a, p. 313):

J'introduis dans l'estomac d'une torpille vivante plusieurs gouttes d'une solution aqueuse légèrement acidulée avec de l'acide chlorhydrique d'extrait de noix vomique. Quelques minutes après, en laissant toujours la torpille hors de l'eau, on lui voit donner spontanément la décharge, et au moindre contact de son corps la décharge a lieu. En coupant sur la torpille ainsi narcotisée la moelle épinière, les contacts de son corps qui ont lieu au-dessous du point coupé ne sont plus suivis de la décharge; ainsi la décharge est évidemment produite par un mouvement réfléchi par l'intermède de la moelle épinière. Les célèbres travaux de Hall, de Flourens, de Müller, ont prouvé que sur la grenouille narcotisée on produit des phénomènes semblables de contraction musculaire.

[I introduce into the stomach of a live torpedo several drops of an extract of *nux vomica* in an aqueous solution slightly acidified with hydrochloric acid. A few minutes later, while the torpedo remains out of the water all the time, discharges may appear spontaneously, and they also take place following the least contact with its body. If we cut the spinal cord in a torpedo thus narcotized, we don't get any discharge by touching its body below the cut point; therefore, the discharge is evidently produced by a movement reflected through the intermediation of the spinal cord. The famous works of Hall, Flourens, and Müller, have proved that it is possible to induce similar phenomena of muscular contraction in narcotized frogs.]

These experiments are developed and completed in the *Traité des Phénomènes Électrophysiologiques des Animaux*, published in 1844 (pp. 163–164).

A l'une de ces torpilles qui était réduite dans cet état, j'ai coupé à la moitié du dos la moelle épinière. Après cette opération, on pouvait toucher la partie du corps au-dessous du point coupé de la moelle sans avoir la décharge. En touchant au-dessus, la décharge avait lieu. Cette expérience suffit pour prouver que l'irritation extérieure était transmise du point touché au cerveau par la moelle épinière. C'est le cas de l'action réflechie découverte par Flourens et par Hall.

Parmi les causes extérieures qui influent sur la décharge électrique de la torpille, il faut mettre encore l'irritation qu'on produit en elle en la comprimant dans les différentes parties du corps. Le frottement sur les branchies est une des manières les plus sûres d'avoir la décharge, comme l'est encore la compression de l'organe dans le point qui correspond au passage des nerfs. La décharge a presque toujours lieu encore lorsque l'on plie le poisson de manière à ce que le bas-ventre devienne concave.

Enfin la compression des yeux et de la cavité qui est placée au-dessus du cerveau ne manque jamais de donner lieu à des fortes décharges électriques. Si les nerfs qui s'introduisent dans cette cavité et qui traversent les muscles de l'oeil sont liés ou coupés, cette compression ne produit plus la décharge.

[In one of the torpedoes thus prepared, I have cut the spinal cord halfway along the back. After the operation, one could touch the body region below the cut without eliciting the discharge. The discharge took place if the upper part was touched. This experiment suffices to prove that an external irritation was transmitted from the touched point to the brain through the spinal cord. This is an instance of the reflex action discovered by Flourens and Hall.

Among the external causes which influence the electric discharge of the torpedo, we must also include the irritation produced by compressing different parts of the torpedo's body. Rubbing its gills is one of the most reliable methods for obtaining the discharge, as is the compression of the organ at the point corresponding to the passage of the nerves. The discharge takes place almost always when the fish is bent in such a way that the lower ventral region becomes concave.

Finally the compression of the eyes and the cavity above the brain never fails to produce strong discharges. This compression no longer produces the discharge if the nerves which penetrate this cavity and pass across the eye muscles are tied or cut].

In the same treatise, Matteucci summarised the results of his researches in the following way (pp. 180–181):

1°. La décharge électrique de la torpille et la direction de cette décharge dépendent de la volonté de l'animal, qui, pour cette function, a son siège dans le lobe électrique de son cerveau.

2°. L'électricité est développée par cet organe de la torpille qu'on appelle ordinairement *électrique*, sous l'influence de la volonté.

3°. Toute action extérieure qui est portée sur le corps de la torpille vivante, et qui détermine la décharge, est transmise par les nerfs du point irrité au lobe électrique du cerveau.

4°. Toute irritation portée sur le quatrième lobe ou sur ses nerfs ne produit d'autres phénomènes que la décharge électrique. On peut donc appeler ce lobe et ses nerfs, *lobes et nerfs électriques*, comme on dit: *nerfs des sens, nerfs moteurs, nerfs de la vie organique*.

5°. Le courant électrique qui agit sur le lobe ou sur les nerfs électriques ne produit que la décharge de l'organe, et cette action du courant persiste plus longuement que celle de tous les autres stimulants.

6°. Toutes les circonstances qui modifient la fonction de l'organe électrique agissent également sur la fonction du muscle, cette-à-dire sur la contraction.

[1°. The torpedo's electric discharge and its direction depend on the animal's will, which, as regards this function, is situated in the electric lobe of the brain.

2°. The electricity is developed by this organ of torpedo, which is normally called electric, under the influence of voluntary control.

3°. Any discharge-producing external action directed to the body of the live torpedo is transmitted through the nerves from the irritated point to the electric lobe of the brain.

4°. Any irritation acting on the fourth lobe of the brain or on the electric nerves does not produce any other phenomenon than the electric discharge. We can therefore term this lobe *electric lobe* and its nerves *electric nerves*, in the same way as we say *sensory nerves, motor nerves, nerves of organic life*.

5°. The electric current which acts on the electric lobe or on the electric nerves produces only the discharge of the organ, and this action of the current persists for a longer time than that elicited by any other stimulating agent.

6°. All circumstances capable of modifying the function of the electric organ similarly act on the function of the muscle, i.e., the contraction.]

The attention that Matteucci, a physicist, devoted to the anatomical structures of the electric fish is admirable. In this study, he had become associated with a Pisan colleague, Paolo Savi, whose *Études Anatomiques sur le Système Nerveux et sur l'Organe Électrique de la Torpille* appeared in the same volume of the 1844 *Traité* (Figs. 1 and 2).

At that time Dr. Cesare Studiati, a young medical graduate, was a dissector in Savi's Institute. He was to become professor of physiology in the Faculty of Medicine in 1856. Matteucci scrupulously consulted the young and highly learned colleague on the anatomical details of electric fish. The letters of Matteucci to Professor Studiati, which we partially reproduce here by kind courtesy of his son Dr. Pietro Studiati, are interesting mainly for the epoch in which they were written. There are five letters which clearly belong to the period in which Matteucci was preparing the second edition of his *Traité*. They are undated, but must have been written between 1850 and 1854. There is mention of the period spent by Matteucci in Corliano. Referring to Matteucci's life and habits in the period which followed the disasters of 1849, Nicomede Bianchi writes (p. 204):

To spend a period in the countryside had therefore become almost a necessity for him. From 1850 to April 1854, Matteucci could satisfy this inclination by living in Corliano, an aristocratic villa situated at the foot of Pisan hills, within a 20-minute train journey from Pisa, and cheered by impressive views and the abundant greenery of century-old trees and fertile vineyards. In that peaceful countryside, Carlo carried out some of his most important scientific works.

Very near Corliano, in Molina di Quosa, there was Studiati's villa, and perhaps this proximity helped to tighten the bonds between the two scientists.

In a first letter from Pistoia, Matteucci wrote:

I need, but if possible do it quickly, that you provide me with a terse description—2–3 pages at most—of the electric organ of the gymnotus and the silurus of the Nile. You will understand that I cannot ask you to send a long paper, because I wish to have it right away, and because I cannot do otherwise, as I must devote myself to the second edition of the *Traité* I am preparing now.

He went on to say that he was interested to know "what is the central part of the nervous system which provides the nerves to the electric organ, what are the nerves of the organ, how the nerves

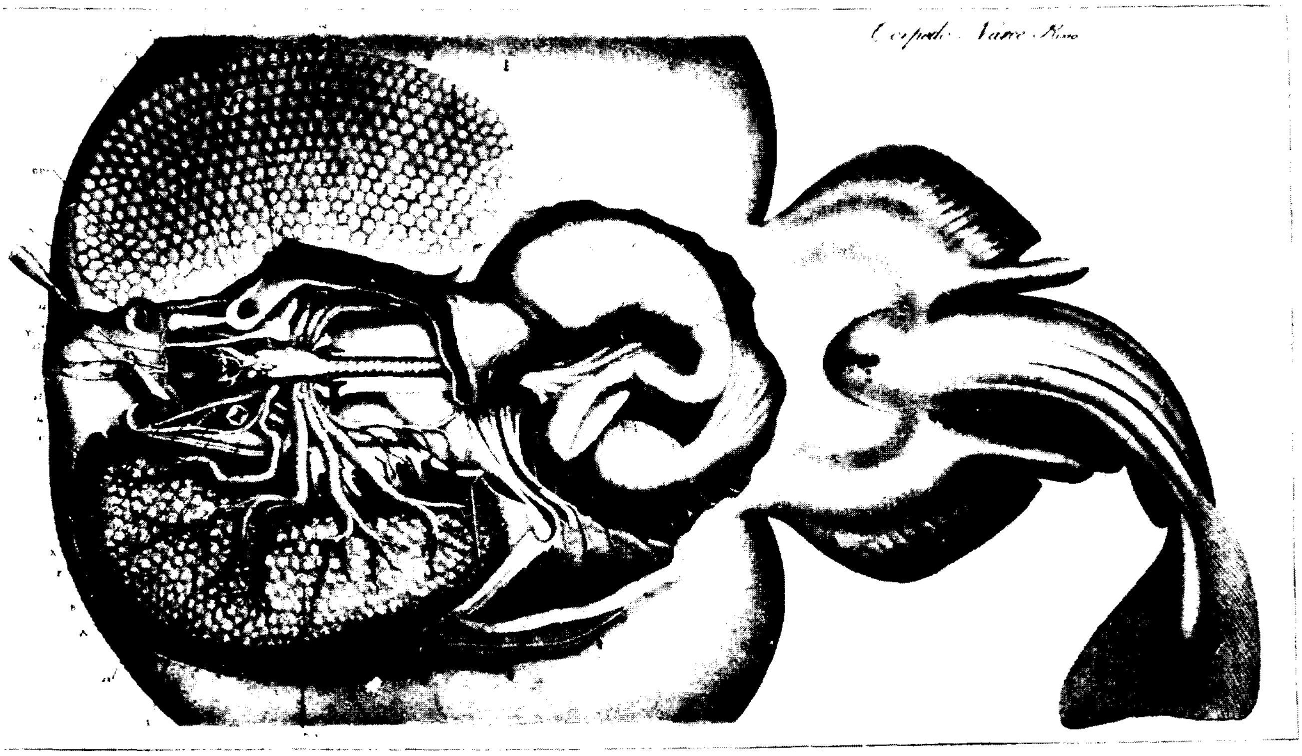

FIG. 1. Ventral view of *Torpedo marce* (Risso)—electric organs. Only the superficial part of the left electric lobe has been removed, and the entire inferior part of the left electric organ, to show the nerve trunk which distributes to it. (From P. Savi, Étude anatomiques sur le système nerveux et sur l'organe électrique de la torpille. Paris: Fortin, Masson et C.ie; 1844: Pl. II.)

end within the organ, which is the number of 'prisms,' their relative size." And he ended with a request which will arouse a sympathetic response in physicists who work in the field of biology: "I exhort you to tell me the basic things, the most certain and those which are of greatest interest to the physicist."

In a subsequent letter, perhaps answering Studiati's amicable complaints about the excessive hurry of his friend, Matteucci wrote:

Being in the business you must well know that it is not possible for me to hope to receive from you soon the information I am waiting for.

He continued by expressing the wish that Studiati could:

...compare the structures of the electric organ of *Torpedo* with those of the gymnotus and silurus... The information I asked for is necessary, as I think I have already written to you, for the preparation of a chapter on the structures of electric organs which on one hand could constitute a critical review of the work done by others. On the other hand, I would like this critical review to have a firm basis; and in the hope that you might find something new, I am thus pleased not to restrict you to summarise what others have done, but rather I would invite you to verify their work and study the subject anew. I allow you 15 days, at the end of which you will provide me with some definite facts. If you like this subject, if something comes out of it, I will wait for your help until you have finished your work. Don't lose sight of the questions or topics which I drew your attention to:

1. Are there any prisms in the Organ of silurus? Or any apparatus similar to that of torpedo and gymnotus?
2. Where are the extremities of these prisms in the silurus, i.e., those extremities which are represented by the ventral and dorsal aspects of the body in the torpedo, and by the head and tail in the gymnotus?
3. Is it true that the nervous filaments distribute themselves in the transverse septa of the prisms in a feather-like fashion, as found by Wagner[4] after Savi and now confirmed by everyone?
4. Is this termination of the nerves common to the organs of the three electric fishes we are considering?
5. Do the extremities of nervous filaments enter in the albuminous substance filling the globule and the space between adjacent septa? Or do all of them spread out and become part of the septa?
6. Make a comparison between the organs of the three fishes—torpedo, gymnotus, silurus—with respect to the arrangement of the cells and the space between the septa.
7. Are the nerves which go to the organ of electric fishes the same?
8. Is there something in the silurus and the gymnotus which corresponds to the electric lobe of the torpedo?

This incessant firing of questions gives us much a better idea of the personality of Matteucci than do his published writings. Nevertheless, in those years in which his talent and enthusiasm for research appeared so lively, the admirable creative impetus of his early youth had already vanished. The memoirs of 1847 and 1860 will not afford anything new to the physiology of electric fish. We will take up this problem again, after ascertaining that the electrophysiological researches on muscle which he did a few years later underwent a similar fate.

[4] The German physiologist Rudolph Wagner (1805–1864) carried out these researches in Pisa in the 1846–47 winter. The researches on the electric fishes are dealt with in the first 6 chapters of his book *Neurologische Untersuchungen*, Göttingen, G. H. Wigand, 1854, XVI+244 pp.

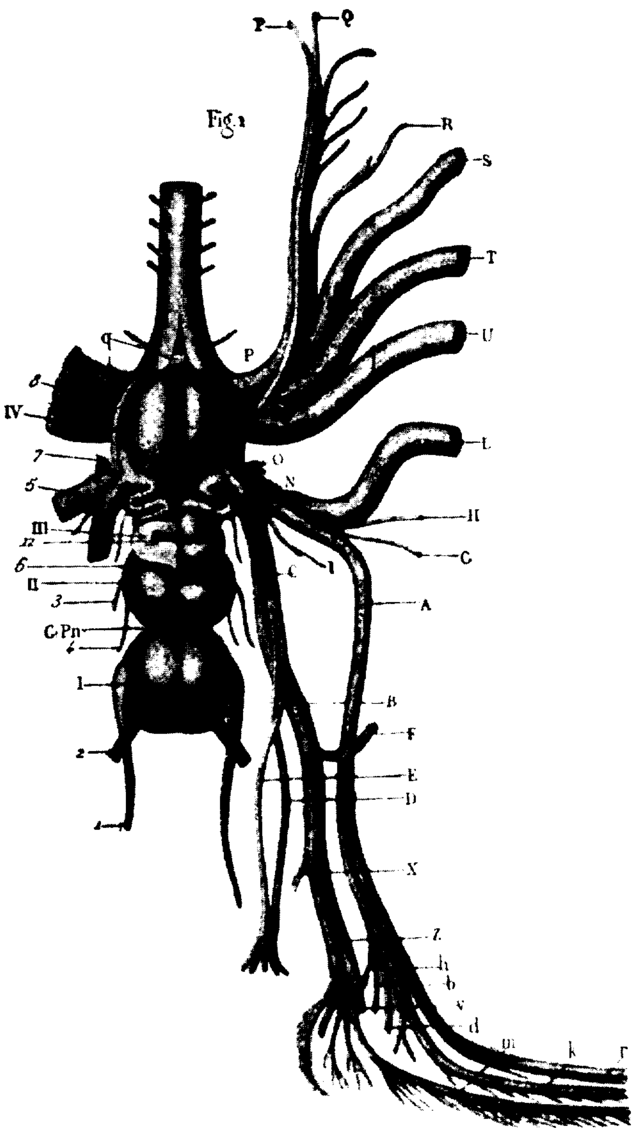

FIG. 2. Encephalon and encephalic nerves of *Torpedo galvani*. I: Brain and olfactory nerves (1). II: Optic lobes and optic nerves (2). III: Cerebellum. On the right, the superior part has been removed to show the cavity related to the IV ventricle. IV: Medulla oblongata and electric lobes. 3, 4, 5, 6: Nerves of the II, IV, V, and VI pair. 7: Acoustic nerve. 8: Pneumogastric nerve. G. Pn. Pineal gland. Branches of the trigeminal nerve (L) and pneumogastric nerve (P, Q, R, S, T, U) which innervate the electric organ. (From P. Savi, Étude anatomiques sur le système nerveux et sur l'organe électrique de la torpille. Paris: Fortin, Masson et C.ie; 1844: Pl. III.)

III. THE DISCOVERY OF THE DEMARCATION CURRENTS IN STRIATED MUSCLE

We are in 1792. Volta has for the first time taken a position against the theory of Galvani. According to him, the causal factor for the production of electricity is the contact between heterogeneous metals; animal tissues simply function as passive conductors and detectors (through muscle contraction) of the current passage. Galvani's reply to this is the discovery of the "*contrazione senza metallo*" (contraction without metal). The leg of a frog is immersed in a container full of water, while the stump of a cut sciatic nerve is immersed in another container. The contact between the two containers may be made with a piece of muscle or a moistened piece of paper. At the moment in which the contact is established, the leg contracts (Fig. 3).

But Volta objects that even if there is no metallic contact there is still heterogeneity of matter, and this can account for weak electric effects. In 1794, Galvani replies with his second experiment. The circuit is closed by the nerve itself, and still a muscle twitch appears whenever the surface of section comes into contact with the intact surface of the muscle (Fig. 4). Finally, in 1797, Galvani describes the fundamental experiment of electrophysiology in a letter to Spallanzani. As illustrated in Figure 5, at the moment in which the circuit is closed, so as to establish a contact between the cut surface of the second sciatic nerve with the intact surface of the first, both legs of the frog contract.

With this experiment, Galvani gave an irrefutable demonstration of the existence of animal electricity. The effect he discovered was due to the demarcation current of the nerve. As soon as the circuit is closed, a current passes through both nerves due to the difference of potential existing between the cut surface of one nerve and the intact surface of the other. It is this current which stimulates the nerve and generates the contraction. Galvani realised that his admirable experiment was sufficient to afford the definitive proof of the truth of the hypothesis of animal electricity. However, he did not understand that the critical element was represented by the contact between the *sectioned* and the *intact* surface of the nerve.

The experiment of von Humboldt (1799), in which the contraction of a frog gastrocnemius appears as soon as two points of the sciatic nerve are put into contact through a piece of muscle (Fig. 6), can be explained by the existence of a demarcation potential in the muscle itself, since it is likely that in this case the current flowed from the intact to the injured part of the tissue. Also here, however, the critical element which should have led

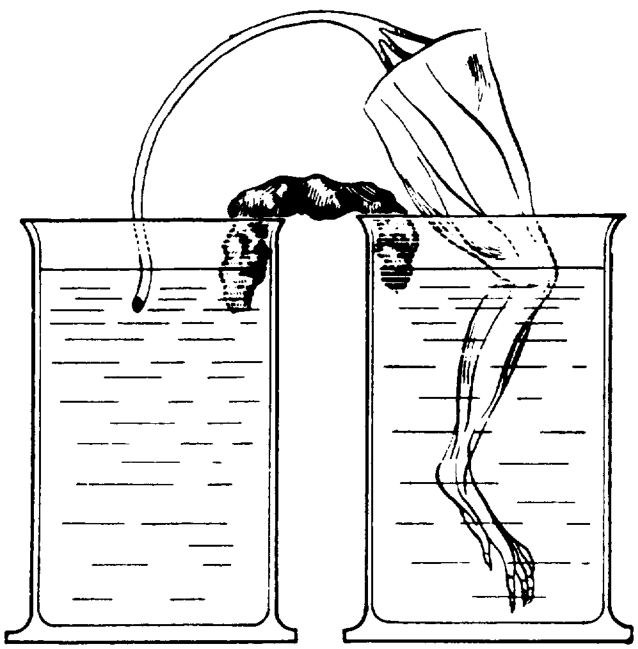

FIG. 3. The 1792 experiment of Galvani. When the circuit is closed with a piece of muscle or with wet paper, the leg contracts. (From Marc Sirol, Galvani et le Galvanisme—L'électricité animale. Paris: Vigòt Frères; 1939: Fig. 5.)

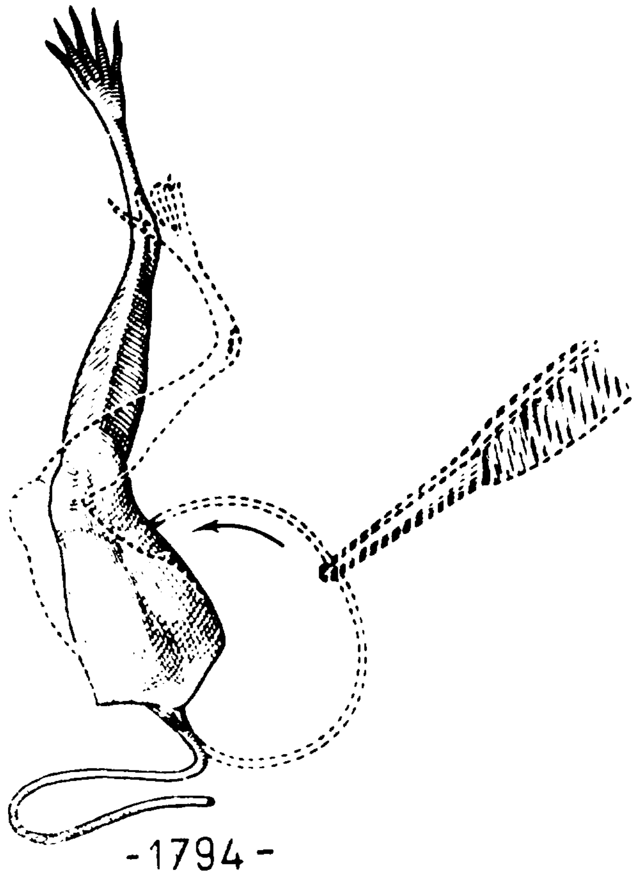

FIG. 4. The 1794 experiment of Galvani. When the surface of the sectioned nerve touches the muscle, the leg contracts. (From Marc Sirol, Galvani et le Galvanisme—L'électricité animale. Paris, Vigòt Frères; 1939: Fig. 6.)

to the discovery of the demarcation potential—i.e., the difference of potential between the intact and the injured surfaces—escaped the scientist's attention.

The third decisive step was to be initiated in 1827 by Leopoldo Nobili, who published his studies in 1828 and 1830. Nobili repeats Galvani's 1792 experiment by using the frog preparation of Galvani himself. Skinned limbs with intact muscle surface are immersed in a container of salted water; the lumbar plexuses are immersed with their cut surfaces in the other container. When the two containers are put into contact through moist cotton, a twitch is obtained, consistent with Galvani's description; if the moist cotton is removed, and the two containers are put into contact through the platinum extremities of the sensitive galvanometer built by Nobili himself, a current flow is observed. Nobili is thus the first scientist who replaced the galvanoscopic leg with a physical instrument, thus measuring what he called *courant de grénouille* or *courant propre* ("frog current" or "proper current"). We know the completely erroneous interpretation given by Nobili to this phenomenon, which he attributed to a thermoelectric effect from a differential cooling of nerve and muscle by evaporation. In fact, Nobili had probably measured the demarcation currents of the nerve since, in his experiment, the muscle, acting as a virtual electrode, indicated the potential existing on the intact surface of the nerve. Matteucci's schematic figure (1844) describing Nobili's experiment, which he con-

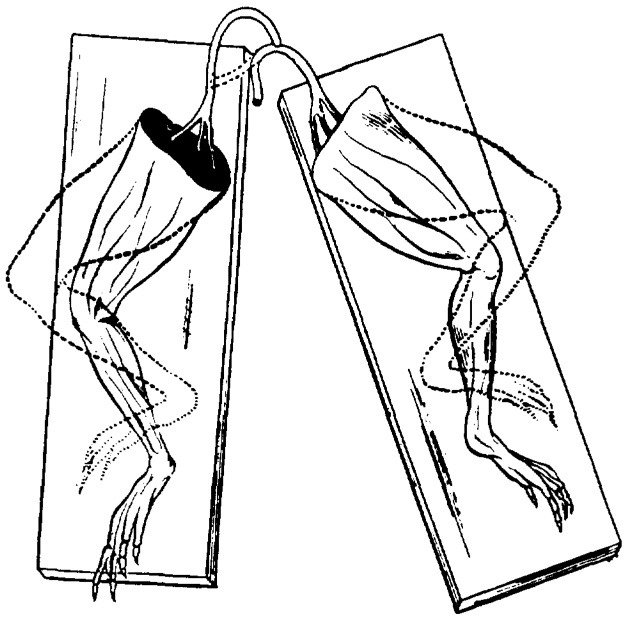

FIG. 5. The 1797 experiment of Galvani. When the surface of the sectioned right sciatic nerve touches the intact surface of the left sciatic nerve, both legs contract. (From Marc Sirol, Galvani et le Galvanisme—L'électricité animale. Paris, Vigòt Frères; 1939: Fig. 7.)

firmed (1838), leaves no doubt that the "proper" current is the demarcation current.

The first papers of Matteucci on this subject date back to 1838, when he had just been appointed director of the Hospital pharmacy in Ravenna. To appreciate the importance of Matteucci's

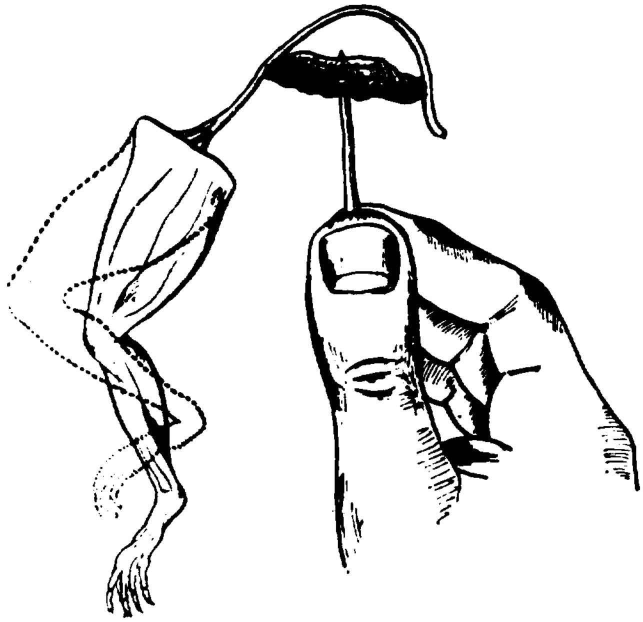

FIG. 6. The experiment of von Humboldt. The leg contracts when the intact surface of the nerve touches two different points of the muscle. (From Marc Sirol, Galvani et le Galvanisme—L'électricité animale. Paris: Vigòt Frères; 1939: Fig. 8.)

work on muscles, we need to place the times in which they were carried out in a proper historical context. The discovery of the pile had cast Galvani's researches into oblivion, because neither Galvani and Volta, nor any other scientist had realised that the conceptions of the two great antagonists could both be true. The triumph of Volta's conception had almost scared the scientists away from all kinds of electrophysiological hypotheses. The attitude held by Nobili toward his discovery, his tendency to refute the most plausible hypothesis by taking refuge under the possibility of an instrumental error, are precisely the expression of that reverential respect for widely accepted notions which often seizes one confronted with an entirely new path.

The researches on the proper currents of frogs are reported in a memoir of 1838 (1838b), in the *Essais* of 1840, and above all, in a memoir of 1842. They are finally summarised in the *Traité* of 1844. These dates are to be kept in mind in relation to the controversy with du Bois-Reymond, whose first preliminary note appeared in 1843.

Already in the 1838 paper, which stems from the researches of Nobili, there is a clear description of the existence in the dead frog of a difference of potential between a skinned but intact leg on one side, and the muscles of the thigh and the cut sciatic nerve on the other. The author stresses the fundamental fact that the potential is present when the anatomical connections between the two frogs are removed and replaced by moist cotton.

On peut encore observer au galvanomètre le courant de la grenouille, tout en détruisant la communication naturelle du nerf avec la jambe. Je coupe l'articulation qui réunit la jambe à la cuisse, je plonge dans une capsule la jambe, dans l'autre la cuisse avec son nerf, et c'est en réunissant, par une mêche de coton mouillée ou directement, les surfaces du membre coupé, que j'obtiens au galvanomètre une déviation très sensible et toujours dirigée dans le même sens (1838b, p. 161).

[The frog current can still be seen by the galvanometer even if one removes the natural communication of the nerve with the leg. I cut the joint between the leg and the thigh, I place the leg in one capsule, and the thigh with its nerves in another, and I obtain an evident deflection of the galvanometer needle, always pointing in the same direction, when I join the surfaces of the sectioned limb by means of a moistened cotton or directly.]

In the 1838 paper, it is clearly stated that the "proper current" of Nobili is not due to thermoelectric phenomena or electro-chemic actions independent of the life of muscle fibres (l.c., pp. 104–105). Matteucci correctly remarks (l.c., p. 105) that the action of muscle tetanus on the proper current (see below) was sufficient to show the biological nature of the phenomenon. However, it is only in 1842 that the fundamental concept of a current flow between the intact and cut surfaces of the muscle appears for the first time.

But before dealing with Matteucci's fundamental paper describing the discovery of what was later to be termed demarcation current, it is necessary to examine in some detail the communication presented at the 1839 Congress of Pisa by Luigi Pacinotti, professor of Physics in Pisa, and by Francesco Puccinotti, professor of Clinical Medicine at the same University, at a time when the work of Matteucci had already appeared. In the Proceedings of the Congress (p. 50) it is reported that "Professors Francesco Puccinotti[5] and Luigi Pacinotti[6] had repeated in the Cabinet of Physics the experiments on the vital electric current of warm-blooded animals, which they had discovered." And it is added that "those experiments had been honoured by the august presence of Her Imperial and Royal Highness Leopoldo II, Grand Duke of Tuscany. The Pisan clinician and physicist expressed a judgment on the work of Matteucci that was endorsed by an ad hoc Committee including Bufalini,[7] and summarised during the session of the Section on Medicine on October 14, 1839 as follows:

Such experiments were undertaken in June and in July 1839 in Pisa by Professors Pacinotti and Puccinotti. They were repeated by the last named in the Royal Museum of Florence. They were carried out again during the Congress of Scientists. It can be claimed without exaggeration that they are the first experiments in which it has been possible at last to obtain the current from the nervous and muscular tissues of living warm-blooded animals. The currents obtained by Donné and by Matteucci are electro-chemical, due to the products of acid and alkaline secretions of the skin, mucosae, and the hepatic surfaces sprinkled with bile. The neuro-muscular current is of a different nature, and is the only one deserving to be characterised as a proper current, or as a vital or discharge current. Matteucci in a last Memoir on the proper current of the Frog has written: "*The signs of the proper current are encountered not only in the Torpedo or in the Frog. I have done several experiments* on other recently killed animals, *and the current was evident in all of them and in the same direction* (See *Bibl. Univ. de Genève*, May and June 1838, p. 167). But apart from the differences in methodology revealed by this statement, given that we experimented on fully alive animals, Matteucci has never given a full account of these experiments; and a mere assertion can only have the value of assuring us, based solely on the word of the illustrious Physicist, that the currents were there; but nevertheless, one ought first to figure out a way to obtain them, and then obtain them (l.c., p. 258).

What was the nature of these experiments announced in such clamorous way and with so clearly polemical an attitude against Matteucci? One should read the report presented by the Session of Physics of the Congress (l.c., p. 50):

These experiments were carried out by inserting at the same time two platinum pointers connected with the ends of a galvanometric wire, one in the brain and the other in some muscle, the functions of these pointers being both to injure and irritate the animal, and to conduct the electricity. And it was observed that upon the insertion of these probes, a current arose which could attain 10 or 15 or more degrees of the galvanometer being used, and flew in the wire from brain to muscle. It was also observed, however, that *a current of a similar nature and direction of flow, though of a much smaller intensity, could be also induced in the dead animal*. . .[8] Therefore, even though the greater magnitude of the effects in the living animal tends to prove the truth of the deductions of the two talented investigators, we are left with the doubt that these effects could be due exclusively to physical and chemical actions arising from the tissues under investigation.

In the Physics session, there was a basically correct view of these experiments. Today, we could say that Pacinotti and Puccinotti produced a lesion in both brain and muscle, and that the constant direction of the current indicated that in these conditions the muscle became negative with respect to the brain, probably because of the symmetrical orientation of the muscle fibres. In other words, what Pacinotti and Puccinotti actually measured was not the current due to the difference of potential between an injured point and an intact point, but rather the current between two injured points. Their technique was thus clearly worse than the one used by Nobili.

[5] Francesco Puccinotti (1794–1872), from 1838 professor of Civil Medicine, and from 1840 director of the Medical Clinic, enjoyed in his times such a high consideration that, at his death, the Parliament decreed for his burial in the Church of Santa Croce in Florence (the place of the monumental burial of the great Italians).

[6] Luigi Pacinotti (1807–1889). Professor of Experimental Physics at the University of Pisa from 1831, and from 1841, professor of Technical Physics. He was Antonio Pacinotti's father.

[7] Maurizio Bufalini (1787–1875). Professor of Clinical Medicine at the Arcispedale of Florence.

[8] Italics is ours.

With the death of the animal, the membrane polarisation disappeared and obviously every physiological phenomenon ceased; hence, the currents which could still be observed proved the occurrence of a physical artifact in the measurements made by the Authors.

We might suppose that Pacinotti and Puccinotti had seen the action currents based on two assertions found in the report presented to the Section of Medicine (l.c., p. 259), in which it is stated that these currents "have an impulsive course *bearing some relation* to the twitch of the animal," and that "as the rapid jerks of the animal become stronger, stronger is the current measured in the first insertions." But it is clear that the struggling movements of the animal when the pointer was inserted into the brain would produce enormous artifacts. What the Authors actually observed was thus a mixture of phenomena depending on demarcation currents, physical artifacts and, probably, action currents as well.

While the section of Physics correctly expressed great caution with respect to the experiments of Pacinotti and Puccinotti, the reaction of the Section of Medicine was enthusiastic. It was chaired by a person famous at that time but now forgotten, the Professor of Clinical Medicine of Parma, Giacomo Tommasini.[9] The distinguished Committee "declared such experiments *true and extremely important*" invited the experimenters to publish them and to continue their work boldly (l.c., p. 261). Libri had then many ardent supporters in Italy and among the most famous persons of the time. It was thus a great fortune for Matteucci that in the following year the Grand Duke of Tuscany asked the advice of von Humboldt for appointing a professor to the chair of Physics, a position being vacant since the end of 1839 due to the death of professor Ranieri Gerli. "The illustrious Committee" appointed by the Sections of Physics and Medicine would surely have made a different decision.

During the four subsequent years, Matteucci completed these experiments and discovered the currents which will subsequently be termed demarcation currents. First, he notes (Fig. 7) that in order to obtain a contraction of the properly isolated galvanoscopic leg by putting the sciatic nerve into contact with any muscle, "it is necessary that the nerve touches the muscle in two parts, one of which has been injured." This is the first proof that the phenomenon observed by von Humboldt is due to a difference of potential between the two parts of the muscle. To quote Matteucci's words (1844, pp. 51–52):

FIG. 7. Method of the galvanoscopic leg. (From C. Matteucci, Traité des phénomènes électro-physiologiques des animaux. Paris: Fortin, Masson et C.ie; 1844: Pl. I, Fig. 4.)

[9] Giacomo Tommasini (1769–1846). Professor of Clinical Medicine in Bologna and, afterwards, in Parma.

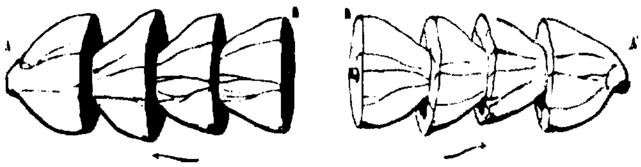

FIG. 8. "Pile" of half-thighs of frogs according to Matteucci. (From C. Matteucci, Traité des phénomènes électro-physiologiques des animaux, Paris, Fortin, Masson et C.ie, 1844: Pl. I, Fig. 3.)

Il y a une expérience très-simple et très facile à faire, qui prouve l'existence d'un courant électrique, développé en réunissant, avec un corps conducteur, des points différents d'une masse musculaire appartenant à un animal vivant, ou récemment tué. On prend pour cela la grenouille préparée que j'ai appelée grenouille galvanoscopique (Fig. 7); ensuite on coupe d'une manière quelconque le muscle d'un animal vivant, et on introduit dans la blessure, le nerf de la grenouille galvanoscopique. En se bornant à cela, il arrive souvent que la grenouille se contracte. Si l'on fait l'expérience avec soin, on découvre facilement, qu'afin de réussir il faut toucher, avec deux points différents du filament nerveux, deux points différents de la masse musculaire. C'est ainsi qu'en touchant avec le bout du nerf de la grenouille galvanoscopique le fond de la blessure, ou la surface du muscle, la grenouille se contracte constamment. Ceci prouve évidemment que c'est bien un courant électrique qui circule dans le nerf, puisqu'il faut former un arc dans lequel ce même nerf est compris. Que cette contraction de la grenouille soit excitée par un courant électrique dû aux points différents du muscle de l'animal vivant, c'est encore bien prouvé, quand on voit que quel que soit le liquide ou le corps conducteur avec lequel on touche deux points du nerf, on n'excite jamais de contraction. J'ai cru de quelque interêt de m'assurer que le sang tiré d'un animal vivant n'était, pas plus qu'un liquide conducteur, doué de cette proprieté. J'ai versé sur une lame de verre une grosse goutte de sang tiré d'un pigeon vivant. Avec le filament nerveux de la grenouille galvanoscopique, j'ai touché, sur deux points differents, la goutte de sang, et la grenouille la plus sensible ne m'a jamais donné le moindre signe de contraction.

[There is a very simple and very easily feasible experiment which proves the existence of an electric current which develops when two different points of a muscular mass of a living or recently killed animal are connected through a conducting body. To perform that experiment, we take the frog preparation which I called a galvanoscopic frog (Fig. 7); then, we make a cut into a muscle of a living animal by any method and introduce the nerve of the galvanoscopic frog into the wound. By simply doing so we often observe a contraction. By carefully doing the experiment, we easily discover that it succeeds only if one touches two different points of the muscular mass with two different points of the nerve filament. Thus, a contraction is constantly produced in the frog by touching the bottom of the wound or the muscle surface with the tip of the galvanoscopic frog nerve. This clearly shows that there is indeed an electric current circulating in the nerve, since it is necessary to create an arc which includes this same nerve. That this frog contraction is engendered by the electric current due to the different muscle points in the live animal is also well demonstrated by the fact that the contraction is never excited by touching two points of the nerve with any liquid or solid conducting material.

I thought it of some interest to verify that the blood taken from a live animal did not have the capacity of inducing the frog contraction more than any other liquid whatsoever. I poured onto a glass surface a big drop of blood taken from a live pigeon. I touched the drop of blood with the nerve filament of the galvanoscopic frog, and even the most excitable frog never exhibited the smallest sign of contraction.]

We said above that Nobili had been the first to measure what probably was the demarcation current of the nerve. But, the fact that one electrode was in contact with the intact surface of the muscle and the other with the sectioned surface of the nerve introduced a further complication in the experiment, namely the disparity between the two tissues. With the ingenious idea of the pile made by sectioned frog half thighs (Fig. 8), Matteucci succeeds in clearly showing the existence of a muscle demarcation current. He notices that the intensity of this current increases by increasing the number of the elements of the biological pile. Thus, he reproduces conditions similar to those present in the fish electric organs without being aware of it.

It does not escape Matteucci's attention that, in order to stimulate the nerve of the galvanoscopic leg, it is necessary to put the nerve into contact with the muscle in two points, one on a wound made in the muscle and the other on the intact part, so that the demarcation current can flow through the frog nerve.

Also, the constant direction of demarcation currents—the sectioned or injured surface being negative with respect to the intact surface—was discovered by Matteucci with the galvanometric method. The reader of the original papers can get confused by the fact that Matteucci refers always to the direction of current flow *through the muscle* and not through the galvanometer.

To quote from Matteucci 1842 work (1842, p. 331):

J'ai obtenu encore un courant bien distinct et quelquefois de 20 à 30 degrés en faisant une blessure dans le muscle de la poitrine ou de la cuisse d'un animal vivant (pigeon, lapin, brebis), *en plongeant une des lames dans l'intérieur de la blessure, et en posant l'autre sur la surface mise à nu du muscle blessé.*[10] Le courant était constamment dirigé, dans l'animal, de l'intérieur de la blessure à la surface extérieure du muscle. La constante direction de ces courants et les signes bien distincts que j'avais à mon galvanomètre auraient dû m'assurer qu'on ne devait les attribuer à aucune imperfection de l'expérience.

[I have also obtained a well evident current, sometimes of 20 to 30 degrees, by wounding the breast muscle or the thigh of a living animal (pigeon, rabbit, ewe) and then *plunging one of the plates within the interior of the wound and placing the other on the bare surface of the wounded muscle*.[10] The current was constantly directed, in the animal, from the inside of the wound to the external surface of the muscle. The constant direction of these currents and the very clear indications of my galvanometer made it certain that the currents were not due to any flaw of the experimental procedure.]

In the 1843 paper, Matteucci replicates these experiments and, without adding anything new, writes (1843, p. 432):

Toutes ces expériences, sans aucune exception, me conduisent à conclure, que toutes les fois que l'intérieur d'un muscle d'un animal quelconque récemment tué est, à l'aide d'un corps conducteur, mis en contact avec la surface de ce muscle, un courant électrique s'établit, lequel est toujours dirigé dans le muscle de son intérieur à la surface. Ce courant, dont l'intensité est variable dans les muscles des différents animaux, augmente proportionnellement au nombre des éléments musculaires qui sont disposés en pile.

[All these experiments, with no exception, lead me to the conclusion that an electric current is engendered whenever the interior of the muscle of any recently killed animal is put into contact with the surface of this muscle by means of conductors, the current being constantly directed in the muscle from the interior to the surface. This current, whose intensity is different in muscles of different animals, increases progressively in proportion to the number of muscle elements stacked together in the pile arrangement.]

The other researches of Matteucci have not led to results of a similar importance. I mention here the demonstration that the muscle currents are present after acute denervation, that they are not decreased by narcotics, and finally that they exist in all vertebrates with basically similar characteristics.

[10] Italics is ours.

Let us summarise. At the end of 1842, the existence of a difference of potential between the sectioned surface and the intact surface—the first being negative with respect to the second—could be considered as conclusively demonstrated by the work of Matteucci. It is fair, however, to recognise the presence of not a few uncertainties in the mind of the Italian physicist, the main one being the distinction he made between proper currents of the frog and muscle currents. The proper current, he says in his 1838 memoir (1838c, p. 96), can be obtained (by repeating the experiment of Nobili) even without lesioning any muscle in the frog:

...on peut se borner à lui enlever la peau tout entière, et à plonger les jambes dans une capsule, la tête et le dos dans l'autre; on voit alors s'établir un courant aussi intense que le courant obtenu avec les nerfs et le muscles, et toujours il est dirigé des pieds à la tête.

[It is sufficient to remove the entire skin, and to submerge the legs into a capsule, and the head and back into another, for generating a current which is as intense as that obtained with the nerves and muscles, and always directed from the feet to the head.]

It is extremely improbable that with the instruments available to him Matteucci could have succeeded in measuring the weak resting currents generated by the small differences of potential between two different points of the intact muscle surface. The effect he observed was more likely due to demarcation currents produced by muscle injuries inadvertently made while skinning the animal. This weak point will become a target aimed at by du Bois-Reymond, in the famous polemic.

In the following pages we will take for granted that the "proper" currents and the "muscle" currents studied by Matteucci were due to the same cause, i.e., what we now know to be the membrane polarisation of every muscle fibre.

IV. THE DISCOVERY OF THE ACTION CURRENT IN THE STRIATED MUSCLE

In 1838, Matteucci made an observation of capital importance, the significance of which, however, he missed completely. It is worth quoting his own words (1838b, p. 164):

Une autre cause qui modifie grandement le courant propre de la grenouille, c'est son état tétanique. Il arrive très souvent avec des individus vivaces, qu'en les préparant rapidement on le voit étendre leur jambes et les roidir de telle sorte qu'il devient impossible de les plier; on peut aussi, avec une solution de strichnine ou d'extrait de noix vomique déterminer en peu de secondes la convulsion tétanique. L'influence du tétanos est telle, que le courant propre manque toujours lorsque la grenouille en est attaquée. Nous n'avons plus des contractions, ni de signes au galvanomètre. Si l'animal a été tué par le poison, on ne réussit plus à en obtenir mais si, au contraire, le tétanos a été produit par l'irritation qu'on a donnée à la grenouille en la préparant, une fois que les convulsions sont passées, les signes du courant propre apparaissent encore.

[Another cause that strongly modifies the proper current of the frog is its tetanic state. It very often happens that rapidly prepared lively animals extend their legs and become so rigid that they cannot be bent; we can also induce a tetanic state with a strychnine solution or with an extract of *nux vomica* in a few seconds. The tetanus influence is such that the proper current is never present when it develops. We no longer have any contraction, nor any galvanometer sign. If the animal is killed by the poison, we will not see any of these phenomena, but if, on the contrary, the tetanus is produced by the irritation caused by the preparation procedure, the signs of the proper current reappear as the convulsions disappear.]

This observation, mentioned again in the 1840 *Essai*, was nothing less than the phenomenon of the "negative Schwankung" ("the negative oscillation") of the demarcation potential,

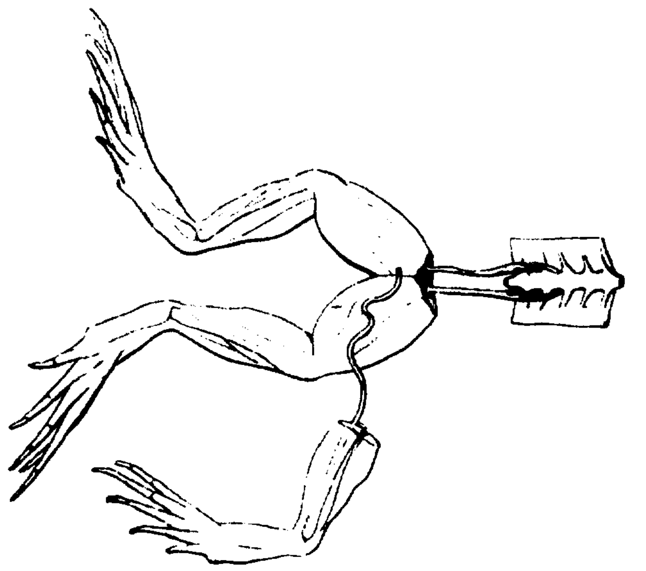

FIG. 9. The experiment of the induced twitch according to Matteucci. (From C. Matteucci, Traité des phénomènes électro-physiologiques des animaux. Paris: Fortin, Masson et C.ie; 1844: Pl. III, Fig. 24.)

the discovery of which (1848–49) is associated with the name of du Bois-Reymond. The negative oscillation can be easily interpreted today, since all muscle tissue becomes depolarized during the strychnine-induced tetanus and, thus, the difference of potential between the injured and the normal part of striated muscles disappears.

Matteucci's priority was recognised by du Bois-Reymond with great fairness in his preliminary note of 1843, when the atmosphere was not yet embittered by the polemic. To quote du Bois-Reymond's words (1843, p. 12; see also 1849, p. 25):

Matteucci hatte in seinem *Essais sur les Phénomènes Électriques des Animaux*, Paris 1840. p. 81–82 angezeigt, dass im Tetanus der Froschstrom vorschwinde. Ich habe mich durch eine grosse Anzahl der sorgfältigsten Versuche, zu denen ich auf die unter beschriebene Art präparirte Gastrocnemien vom Frosch benutzte, welche ich nach Nobili's Angabe (*Ann. de Chim. et de Phys*. XLIV, p. 89) vom Nerven aus tetanisirte, und mich dabei der Methode der Compensation bediente, aufs bestimmteste überzeugt, dass in der That während heftiger und andauernder Zusammenziehungen der Strom zwar bei weitem nicht verschwindet, allein doch merklich an Intensität abnimmt.

[In his *Essai sur les Phénomènes Electriques des Animaux*, Paris 1840, pp. 81–82, Matteucci has claimed that the proper current of the frog disappears during the tetanus. I have performed a great number of the most accurate investigations using the frog gastrocnemius muscle preparation described below and tetanized through the nerve according to the indications of Nobili (*Ann. de Chim. et de Phys*. XLIV, p. 89). Based on the compensation method, I was totally convinced that during intense and prolonged contractions, the (proper) current does not disappear, but undergoes a measurable reduction in intensity].

It is fair to say that this early observation of Matteucci by no means obscures the glory of du Bois-Reymond who, in paragraphs IV, V, and VI of the seventh chapter of his *Untersuchungen über thierische Elektricität* (1848–49), has written on this subject 138 pages which remain among the monuments of the scientific literature of any time. But, it was destiny that both great adversaries should attain the peak of their scientific achievements with their investigations on the action potentials.

The discovery of the induced twitch was communicated by Matteucci on February 28, 1842 to the *Académie des Sciences* in a document under sealed cover which was read in the October 24 session in the presence of Matteucci. The words whereby the discovery was announced make it clear that those present were aware of witnessing a scientific event of the utmost significance:

M. Dumas demande a l'Académie la permission de l'entretenir d'experiences tellement remarquables, qu'elles lui semblent ouvrir une ère nouvelle aux recherches de la physiologie la plus délicate. Ces expériences se trouvent déjà rapportées dans un paquet cacheté déposé par M. Dumas, au nom de M. Matteucci, et dont l'auteur, présent à la séance, désire aujourd'hui l'ouverture. Voici comment s'exprime l'habile physicien de Pise, dans la Note que le paquet cacheté renferme:

Préparez rapidement la cuisse d'une grenouille, en y laissant le nerf attaché; placez ce nerf sur les cuisses d'une autre grenouille préparée à la manière ordinaire. Si alors vous obligez cette seconde grenouille à contracter ses muscles, soit au moyen d'une excitation électrique, soit par tout autre moyen, au moment où la contraction musculaire aura lieu, on verra se contracter également les muscles de la jambe de la première grenouille.

Si je ne me trompe, ajoute M. Dumas, c'est la première fois qu'on a vu la contraction des muscle d'un animal exercer une influence quelconque sur les nerfs d'un autre animal et déterminer la contraction; et si l'on ajoute que cette influence se transmet à travers une feuille de papier fin et sans colle interposée entre les deux animaux, tandis qu'elle est arrêtée par une lame d'or très mince, on comprendra tout ce qu'il y a de neuf dans cette classe de phénomènes découverts par M. Matteucci.

Cette experience, et quelques autres non moins nettes, ont été reproduites avec une précision singulière par M. Matteucci dans mon laboratoire, en présence de MM. de Humboldt, Kupfer, Valenciennes, etc. (1842a, p. 797).

[Mr. Dumas asks the Academie for the permission to entertain it with experiments so remarkable that they seem to him to open a new era in the most refined physiological investigations. These experiments are described in a document under sealed cover deposited by Mr. Dumas on behalf of Mr. Matteucci, who, being present at the session, would like it to be opened today. Here is what the skilled physicist of Pisa has stated in the Note contained in the sealed cover:

Prepare rapidly a frog thigh leaving its nerve connected; put this nerve on the thigh of another frog prepared in the usual way. If you force this second frog to contract its muscles, either by an electric excitation, or by any other method, at the moment in which the muscle contraction takes place, you will see that the leg of the first frog contracts as well.

If I am not wrong, Mr. Dumas continues, this is the first time that the contraction of the muscle of one animal has been shown to exert an influence on the nerves and to induce the contraction of another animal; and if we add that this influence is transmitted between the two animals through a sheet of fine paper, not containing any glue, whereas it is blocked by a very thin gold leaf, we can understand what is novel in the class of phenomena discovered by Mr. Matteucci.

This experiment, as well as others not less clear, have been reproduced with a notable accuracy in my laboratory by Mr. Matteucci, in the presence of Mr. von Humboldt, Kupfer, Valenciennes, etc. (1842a, p. 797).]

In the same year (1842), Matteucci published these results more extensively, and later devoted the whole chapter X of his *Traité* to them (see Fig. 9).

Becquerel (1842) immediately repeats these results, confirms them, and explains them correctly in the personal note to Matteucci reported below. This note can be considered as the description by a contemporary of the discovery of action currents (from Matteucci 1844, p. 134):

A l'instant où la grénouille se contracte, il y a une décharge électrique qui passe dans l'extrémité du nerf de la jambe, quand cette extremité pose sur le muscle, ou n'en est séparée que par une bande de papier humide; elle se décharge par la feuille d'or, attendu que celle-ci conduit mieux l'électricité que le nerf, fait analogue à celui qu'on observe en plaçant une torpille dans un étau de métal que l'on tient à la main. Dans ce cas, la décharge passe dans le métal et non dans la main; enfin, l'interposition d'une bande de papier glacé ou isolant doit empêcher le nerf de la jambe d'en être affecté.[c]

Tous ces effets ne peuvent donc être produits que par des courants dérivés; dès lors on est porté à admettre la production d'une décharge électrique à l'instant où le muscle se contracte.[11]

Si des expériences entreprises dans une autre direction viennent confirmer les conséquences que l'on tire du fait de M. Matteucci, ce physicien aura découvert une des propriétés les plus importantes des muscles sous l'empire de la vie, ou quelque temps après la mort.

[As soon as the frog contracts, there is an electric discharge which passes to the extremity of the leg nerve, when this extremity rests on the muscle, or is separated from it only by a sheet of moistened paper; the electricity is discharged by the gold leaf, since this conducts electricity better than the nerve, a finding similar to that observed when we put a torpedo in a metallic clamp held in our hand. In this case, the discharge passes through the metal rather than through the hand; finally, the interposition of a varnished or isolating paper must prevent the leg nerve from being affected by the discharge.

All these effects can only be produced by derived currents; as a consequence, one is led to acknowledge that an electric discharge is generated in the instant in which the muscle contracts.[11]

If other types of experiments will confirm the consequences which can be drawn from Mr. Matteucci's finding, this physicist will have discovered one of the most important properties of muscles under the empire of life, or some time after death.]

Matteucci soon tries to demonstrate the existence of an action current with the galvanometer. He utilises the technique of the frog pile (Fig. 10), and tries to see the effect of the contraction produced by the stimulation of the sciatic nerve on the proper current. Here is the account of these results in his own words (1844, pp. 137–138):

Un autre moyen auquel j'ai eu recours pour faire contracter les grenouilles d'une pile, a été l'application d'une solution alcaline sur leurs nerfs lombaires. J'attends, comme je l'ai déja dit, que l'aiguille soit fixe avant de toucher avec l'alcali les nerfs de la grenouille, et j'ai soins de ne pas toucher les deux grenouilles extrêmes, dans la crainte que l'alcali puisse parvenir jusqu'aux lames du galvanomètre. Les contractions qu'on obtient par ce procédé ne sont pas aussi violentes que celle obtenues par l'irritation mécanique de la moelle épinière, et elles persistent plus longuement. Voici ce que j'ai vu bien des fois: aussitôt l'alcali appliqué, les contractions commencent et l'aiguille, dans le même temps, s'avance de 5°, 6° et quelquefois de 10° au dela de l'angle où elle était fixée. Quelques secondes après les contractions cessent, et l'aiguille revient à sa position pour descendre ensuite lentement vers le zéro, comme elle l'aurait fait sans la déviation extraordinaire.

Il faut avouer que l'apparition de deux phénomènes, c'est-à-dire la production des contractions et la plus grande déviation de l'aiguille, se correspondent exactement.[12] Il faut dire encore que, si l'on touche les nerfs des grenouilles de la pile avec l'alcali pour une seconde ou troisième fois, les deux phénomènes ne reparaissent pas.

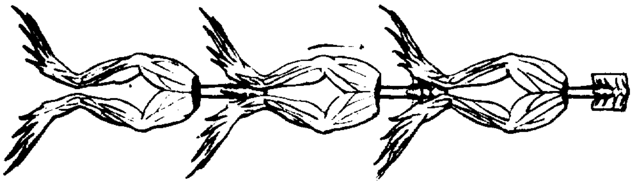

FIG. 10. "Pile" of frogs. (From C. Matteucci, Traité des phénomènes électro-physiologiques des animaux. Paris: Fortin, Masson et C.ie; 1844: Pl. II, Fig. 16.)

[Another method I have used for inducing the contraction in the stacks of frogs was the application of an alkaline solution to their lumbar nerves. As said above, I wait until the needle becomes stationary before touching the frog nerves with the alkali, and I am careful not to touch the frogs at the end of the stacks for fear that the alkali might reach the galvanometer plates. The contractions obtained by this procedure are not as violent as those obtained from the mechanical irritation of the spinal cord, and they persist for longer times. Here is what I have seen many times: as soon as the alkali is applied, the contractions begin and, at the same time, the needle deflects by 5°, 6°, and sometimes by 10° beyond its resting point. A few seconds later, the contractions terminate, and the needle moves in the opposite direction, slowly reaching the null position, as it would have done in the absence of the extraordinary deviation.

We must recognize that the appearance of the two phenomena, i.e., the production of contractions and the larger deviation of the needle, correspond to each other exactly.[12] We must also say that if we touch the nerves of the frog in the pile with the alkali a second or a third time, the two phenomena do not reappear again.]

These results seem to contradict completely those obtained in 1838, and Matteucci is therefore disconcerted. Nowadays, both observations would most probably be considered correct. But the chemical stimulation of nerves produced a contraction wave that did not invade all of the skeletal muscles in a quasi-synchronous way, as it occurs instead in the strychnine-induced tetanus. Thus, a difference of potential arose between the active and the resting zones of the muscle, and these EMFs added algebraically, in a completely unpredictable way, to the demarcation potentials produced by accidental injuries of muscle. The method of the frog pile was much less simple and far less precise than the method used by du Bois-Reymond in his investigations on the negative oscillation of the demarcation potential.

However, Matteucci considered his recent results as well as the discovery of the induced twitch manifestly incompatible with his old observations of 1838, notwithstanding the correct interpretation by du Bois-Reymond of the mechanism responsible for the induced twitch reported in the *Handbuch der Physiologie* of Johannes Müller, du Bois-Reymond's teacher. This interpretation was based on the observations made by Matteucci in 1838 and on those reported in du Bois-Reymond's note of 1843. Here is what Johannes Müller wrote about demarcation currents (1844, vol. I, p 558; see also du Bois-Reymond 1849, II, p. 27):

Dieser Strom wird durch die Contraction des Muskels selbst unterbrochen. Matteucci hat sein Aufhören beim Tetanus, du Bois- Reymond

[c] Since, out of context, the description of the effect of interposition of sheets of different materials between the muscle of one frog and the nerve of the the other may not be totally clear, we report here a passage from the memoir *On the Induced Contractions*, presented by Matteucci at the Royal Society of London (29 November 1845, communicated by W. Bowman, printed in *Electro-Physiological Researches by Signor Carlo Matteucci*, Taylor, London, 1845, p. 283): "I finally tried these experiments, introducing between the nerve of the galvanoscopic frog and the inducing muscular surface very fine laminae of different substances. A leaf of gold and a very fine nonconducting stratum of mica or of glazed paper being interposed prevented the phenomenon, that is to say, the induced contractions in the galvanoscopic frog failed to appear, while a stratum of fine paper soaked in water did not interrupt the induced contraction."

The induced contraction was prevented by the gold and mica laminae for different reasons: gold being a good conductor shunted the action current in the muscle of the first frog whereas, mica, being insulating, hindered the passage of the action potential from the muscle of the first frog to the nerve of the second one. The interposition of laminae of different materials between the muscle of one frog and the nerve of the other was used by Matteucci to differenciate between electric and mechanical influences as the cause of the induced contraction.

[11] Italics is ours.

[12] Italics is ours.

seine Schwächung oder Unterbrechung bei jeder Zuckung des Muskels beobachtet. Da die Contraction nicht die leitende Verbindung aufhebt, so muss die Unterbrechung von einem Aufhören der elektrischen Polarität selbst während der Contraction abhängen. Bis so weit berechtigen die Elektricitätsphänomene an den Muskeln und Nerven noch nicht zu einer Identificirung des Nervenprincips und der Elektricität. Mehr scheint hiefür der Versuch Matteucci's zu sprechen, dass, wenn auf den Muskel A. der Nerve eines zweiten Muskelpräparates B. gelegt wird, und der Nerve des Muskels A. mechanisch oder galvanisch gereizt wird, zugleich der Muskels B. zuckt. Indessen lässt sich dieser Erfolg nach du Bois-Reymond auf andere Art erklären. Da nämlich der Muskelstrom des Muskels A. durch seine Contraction unterbrochen wird, so muss diese Unterbrechung eine Gleichgewichtsstörung in dem zweiten berührenden Nerven und daher Contraction des Muskels B. hervorrufen.

[This current is interrupted by the contraction of the muscle itself. Matteucci has observed that the current ceases during the tetanus, while du Bois-Reymond has observed that it is decreased or interrupted by each twitch of the muscle. Since the contraction does not remove the conducting connection, the interruption must depend on a disappearance of the electric polarity during the contraction. Until now, the electric phenomena of the muscles and nerves do not allow the identification of the principles of nerve functioning and electricity. At this point, it is more appropriate to discuss Matteucci's finding that when one connects to a muscle A the nerve of a second muscle B and stimulates the nerve of muscle A mechanically or galvanically, muscle B twitches at the same time (as muscle A). However, du Bois-Reymond suggests another explanation of this phenomenon: Since the muscle current of muscle A is interrupted by its contraction, this interruption must bring about a disturbance in the equilibrium of the resting second nerve and, as a result, a contraction of muscle B.]

Using modern words, we would say that a depolarization at a point A created a difference of potential if the muscle was intact, or destroyed it if there was a demarcation current, thus reproducing the conditions created by the closure or by the opening of a continuous current circuit. The induced twitch was the consequence of such an event. This explanation was not accepted by Matteucci who could not conceive that an increase of muscle activity could be associated with a decrease of electric signal.

In his letter to Dumas of September 1845 (1845a, pp. 69–70), Matteucci's uneasiness appears clearly:

Je ne dirai plus qu'un mot au sujet de la contraction induite à propos de l'explication que M. du Bois-Reymond en a donnée. Ce physiologiste pense que le courant musculaire est interrompu par la contraction, et que cette interruption doit déterminer une *rupture d'équilibre* dans le nerf de la seconde préparation, et par conséquent, amener à la contraction du second muscle. Ce sont le mêmes expressions avec lesquelles M. Müller rapporte l'hypothèse de M. du Bois-Reymond, faite pour expliquer la contraction induite. Il m'a été impossible de me faire une idée de la valeur physique de ces expressions. Il paraît que M. du Bois-Reymond admet que le courant musculaire ou propre s'affaiblit ou s'interrompt pendant la contraction musculaire; mais il n'y a aucun fait qui vient à l'appui de cette idée. Galvani avait bien vu que les signes des contractions propres s'affaiblissent ou disparaissent dans la grenouille prise de tétanos: moi-même j'ai bien confirmé ce fait; mais il faut remarquer que cet affaiblissement se montre, parce qu'on prend pour indication du courant propre la contraction de la grenouille, même en repliant sa jambe sur les nerfs lombaires. Mais on ne trouve pas cela en mesurant le courant propre ou le musculaire avec le galvanomètre. La différence est donc due à l'état d'excitation du nerf dans l'animal tétanisé. Ce n'est que dans un cas, que j'ai noté dans mes premiers travaux et que j'ai vérifié après, qu'on pourrait trouver la preuve du principe admis par M. du Bois-Reymond. J'ai trouvé que les grenouilles prises dans l'état de surexcitation développé par l'emploi de la noix vomique, preparées à la manière ordinaire et disposées en pile, donnent un courant propre plus faible que celui que l'on obtient en agissant sur des grenouilles qui n'ont pas subi l'action de la noix vomique. Mais, si l'on réflechit que les contractions ne persistent pas dans les grenouilles préparées et disposées en pile, on ne pourra pas voir, dans ce fait unique, la demonstration du principe invoqué par M. du Bois-Reymond. Du reste, il est difficile de concevoir comment les actions chimiques doivent s'affaiblir dans un muscle par le fait de sa contraction.

Si j'ai bien saisi l'idée du jeune physiologiste de Berlin, émise dans son Memoire dejà cité, il me semble qu'il devrait admettre que le muscle qui entre en contraction, en diminuant de longuer et en augmentant en largeur, devient par le courant, moins resistant,[13] et de là la rupture d'équilibre qui donne, selon lui, la contraction induite. Mais on ne sait pas de quel courant il parle; le courant musculaire et le courant propre circulent dans les masses musculaires seulement dans le cas où ces masses seraient coupées et préparées. Et, après tout, je viens de démontrer, par des expériences, que la contraction induite ne peut jamais être produite par une action électrique, ou directe, ou d'induction. Je le répète, la contraction induite est le premier fait d'une action à distance, ou plus proprement, d'induction qui est excercée par un muscle en contraction sur un nerf. Je pense que ce principe aura de l'importance dans la physique du système nerveux.

[I will say no more than one word on the subject of the induced contraction in relation to Mr. du Bois-Reymond's explanation of it. This physiologist believes that the muscle current is interrupted by the contraction, and that this contraction should cause a *break of equilibrium* ("rupture d'équilibre") in the nerves of the second preparation and, as a consequence, produce the contraction in the second muscle. These are the same statements by which Mr. Müller reports the hypothesis of Mr. du Bois-Reymond to explain the induced contraction. It has been impossible for me to imagine the physical meaning of these statements. It seems that Mr. du Bois-Reymond admits that the muscle or proper current weakens or stops during muscle contraction; but there is no fact to support this idea. Galvani had already obeserved that the signs of intrinsic contractions weaken or disappear in the frog seized by tetanus: I have also confirmed this finding myself; but we must acknowledge that this weakening manifests itself if we take the contraction of the frog, even by bending its leg onto lumbar nerves, as an index of the proper current. But, we don't see this weakening if we measure the proper or the muscle current with the galvanometer. The difference is thus due to the state of excitability of the nerve in the tetanized animal. It is only in one case, that I have noticed in my first papers and confirmed later, that it is possible to find the proof of the principle envisaged by Mr. du Bois-Reymond. I have found that frogs in a condition of over-excitation induced by *nux vomica*, prepared in the ordinary way and arranged in a pile, produce a current weaker than that of frogs not submitted to the treatment with *nux vomica*. But, if we consider that the contractions do not persist in frogs prepared and arranged in a stack, we cannot see in this single fact the demonstration of the principle invoked by Mr. du Bois-Reymond. Moreover, it is difficult to conceive how a chemical action could be reduced in a muscle as a consequence of its contraction.

If I have fully understood the idea of the young physiologist of Berlin, presented in the previously quoted Memoir, it seems to me that we should admit that the muscle which contracts becomes less resistant to the current because it decreases in length and increases in width,[13] and from this follows the break of the equilibrium which according to him causes the induced contraction. But, one doesn't understand which current he is speaking of: the muscle current and the proper current circulate in the muscular masses only when the latter are cut and prepared. And, after all, I have just demonstrated experimentally that the induced contraction can never be induced by an electric action, either direct or inductive. I repeat, the induced twitch is the first expression of a distant action, or more appropriately, of an induction which is exerted by a contracting muscle on a nerve. I believe that this principle will have importance in the physics of the nervous system.]

In such a way Matteucci disclaimed the value of his 1838 discoveries. The reaction of du Bois-Reymond is not worthy of

[13] This was the completely erroneous interpretation that du Bois-Reymond gave in 1843 (p. 19) of the phenomenon of the weakening of muscle current during contraction. It was in overt contrast with the explanation given in the Müller's treatise (1844), and this fact also contributed to Matteucci's uneasiness.

a great scientist (1848, II, p. 29). "Matteucci hat mir durch diese Bemerkungen, ohne sein Wissen, einen wahren Freundschaftsdienst geleistet." [With his observations Matteucci has done me, without knowing it, a real friend's service].

The discovery of the induced twitch (1842) marks the highest moment of the electrophysiological work of Matteucci, who was then only 31 years old. Unfortunately, it also marks the start of his decline. Matteucci will continue to work and publish very actively until his death, but he will never succeed in overcoming the initial disorientation produced in him by du Bois-Reymond's discovery of the negative oscillation. Pressed by the adversary, who was 7 years his junior, treated in an ungenerous and unjust way, perhaps betrayed by the lesser sensitivity of his galvanometers, he takes the wrong way and firmly denies the existence of the negative oscillation. His subsequent papers on the induced twitch—and particularly the five memoirs published in the "Philosophical Transactions" of the Royal Society, and reproduced afterwards in a French version in the "*Annales de Chimie et de Physique*"—have now merely a historical value. They attest to the impossible situation in which Matteucci found himself when he tried to explain the phenomenon of the induced twitch without accepting du Bois-Reymond's discovery of the negative oscillation.

History must attribute to Matteucci the discovery of the action current, which was demonstrated for the first time with the experiment of the induced twitch (1842). The impartial historian must also recognize that he was the first to observe the effects of the depolarisation associated with muscle contraction by using the galvanometer, in 1838 and in 1842. It is certain, nevertheless, that modern electrophysiology begins with du Bois-Reymond's discovery (1848–49) of the "negative Schwankung," which Matteucci had accidentally observed in 1838, but was unable to interpret correctly.

V. THE CONTROVERSY BETWEEN MATTEUCCI AND DU BOIS-REYMOND

In the introduction to his treatise, *Untersuchungen über thierische Elektricität*, Emil du Bois-Reymond recounts how, in the spring of 1842, Johannes Müller lent him a newly published (1840) book of Matteucci, *Essai sur les Phénomènes Électriques des Animaux*, advising him to repeat and continue those investigations. In January 1843, du Bois-Reymond published, in the "*Poggendorff's Annalen*," his first preliminary note, in which he largely confirmed all Matteucci's observations on the muscle demarcation current and on the tendency of this current to disappear when the muscle contracts. This last observation was seminal to the discovery of the negative oscillation of the demarcation current, which would appear in his classical formulation in the 1848–49 treatise. The results of du Bois-Reymond were later summarized in 1844 in a simpler and clearer way in the *Handbuch der Physiologie* of Johannes Müller.

To understand the controversy between du Bois-Reymond and Matteucci, we need to examine carefully the preliminary note, undoubtedly somewhat prolix and not altogether clear, published by the German physiologist in 1843. Very objectively, du Bois-Reymond quoted, in paragraph 19 of his note, several whole sentences taken from Matteucci's papers, in which it appeared that Matteucci had clearly perceived the existence of a difference of potential between the intact and the sectioned surface of the muscle. Moreover, in paragraph 32, du Bois-Reymond mentioned the 1838 experiments of Matteucci, also reported in Matteucci's *Traité* of 1840, on the disappearance of what today we would term a demarcation potential during muscle contraction; and also, in this case, he fully confirmed the conclusions of the Italian scientist.

We have already mentioned that Matteucci did not realise that the action potential was the negative oscillation of the demarcation potential, and we have also said that the discovery of this phenomenon is undoubtedly to be ascribed to du Bois-Reymond, who clearly showed and correctly interpreted it. It is fair, however, to state that the discovery of the "negative Schwankung" is described clearly for the first time in du Bois-Reymond's treatise of 1848–49. In the 1843 preliminary note, we cannot find a demonstration (at least a convincing one) of the phenomenon of the negative oscillation. Moreover, in this note du Bois-Reymond gives a completely wrong interpretation of the electric phenomena occurring during muscle contraction. It is worth reporting this strange interpretation, even though it is exclusively of a historical interest now, because it contributed to Matteucci's confusion. Here is what du Bois-Reymond wrote in 1843 (§49, p. 19).

Die Abnahme des Muskelstroms im Tetanus erklärt sich dann vielleicht so, dass, da die ganze Masse des Muskels Nebenschliessung für den Strom jedes einzelnen Primitiv-Muskelbündels bildet, diese Masse aber in Tetanus an Querschnitt zu-, an Länge ab-, folglich an Leitungswiderstand abnimmt, der Stromarm in dem leitenden Bogen an Intensität abnehmen muss.

[The abolition of the muscle current during the tetanus can perhaps be explained as follows: the whole mass of the muscle functions as a conductor for the current of each single bundle constituting the muscle; since, during the tetanus, the section of the mass increases and its length decreases, its resistance is bound to diminish accordingly, so that the intensity of the current flowing through the measuring device must also diminish].

We have seen that the correct interpretation of the phenomenon was given in the following year by du Bois-Reymond in Müller's treatise (1844). However, the treatise did not say that the first interpretation of du Bois-Reymond was wrong; in fact, that interpretation was not mentioned at all. Only in the second volume of du Bois-Reymond's treatise, published in 1849, do we find the formal recognition that "the decrease in the muscle current during muscle contraction was not due to a variation of the proper resistance of the muscle" (pp. 73–85).

When Matteucci started the controversy in 1845, he was unaware of the monumental construction represented by du Bois-Reymond's treatise, but was only aware of a preliminary note in which du Bois-Reymond himself acknowledged (through plentiful quotations) Matteucci's priority and gave a manifestly erroneous explanation of the electric phenomena associated with muscle contraction, an explanation which must have appeared not altogether convincing even to the author himself (see du Bois-Reymond 1848–49; vol. II, p. 74).

In September 1845, the first polemical article of Matteucci appeared in the form of a letter addressed to Dumas and published in the "*Annales de Chimie et de Physique*."

There is no doubt that what du Bois-Reymond without false modesty termed "The law of muscle current," i.e., the ensemble of notions generally accepted today about demarcation currents, had been already presented in the papers published by Matteucci in 1838 and in 1842, as mentioned above in the first part of the present article. But, Matteucci certainly overstepped all limits when he wrote (1845a, p. 66):

Je ne puis pas m'expliquer comment le célèbre physiologiste de Berlin, M. Müller, peut dire, dans son *Manuel de Physiologie*, que l'on vient de découvrir en Allemagne les principes généraux qui peuvent expliquer les faits que j'ai découverts. Ces principes généraux se réduisent à ceux-ci:

"Un courant électrique se produit lorsque la coupe transversale d'un muscle vient à être mise en communication par un arc avec sa coupe longitudinale." Plutôt qu'un principe général, il me semble qu'il n'y a là qu'une formule brute et incomplète de mes phénomènes.

[I cannot comprehend how the celebrated Berlin physiologist, Mr. Müller, can say, in his *Physiological Manual*, that the general principles which explain the findings I discovered have just been discovered in Germany. These general principles reduce to this: "An electric current is produced when the cross section of a muscle is put into contact through an arc with its longitudinal section." It seems to me that rather than general principles, these are only a rough and incomplete formulation of my phenomena.]

It is certain that the data of du Bois-Reymond, and especially their systematization, were much more than a rough and incomplete formulation of the phenomena discovered by Matteucci, and would be even more so after the publication of his great treatise. As far as the negative oscillation of demarcation currents is concerned, nobody fails to recognise that it is one of the cardinal phenomena of electrophysiology. These acknowledgements are obvious to us, who have in our hands the 1848–49 treatise. We must recognise, however, that in 1845, when the available material was represented by a preliminary note in the "*Poggendorff's Annalen*," and by two pages of the Müller's treatise, an erroneous evaluation of it was readily excusable. We will see below that Matteucci himself later made generous amends for his careless judgment.

The polemic riposte of du Bois-Reymond cannot be read without a deep sorrow; it is hard to believe that a great scientist could have written such things. It consists of tens of pages inspired by a real and true parossysmic hatred of Matteucci, full of brutal attacks on his person and even on his scientific integrity. The above-mentioned weak points of Matteucci's work, the contradictions in which the Author falls, are pointed out mercilessly, as if it were a matter of a court trial rather than of a scientific debate. The poorly systematic way in which Matteucci wrote his works, the incomplete bibliography, the hurried style, and (at least at the beginning) an incomplete mastery of the French language,[14] all helped in this demolishing action. There is no doubt, moreover, that the dissemination of experimental results through preliminary notes, academic memoirs, and treatises, and the not infrequent repetitions, make a first-hand knowledge of the scientific work of Matteucci difficult. His adversary was undoubtedly vigorous and incisive; and, at the same time, he was systematic in his exposition and had a perfect knowledge of the literature. According to Rosenthal (1896), his writings belong to the best of German prose, even though French was the language spoken in the family in which du Bois-Reymond had grown up. Only one thing did du Bois-Reymond concede to Matteucci: the discovery of the induced twitch. And, for many, Matteucci has remained exclusively the physiologist of the induced twitch.

Matteucci abstained from following du Bois-Reymond along the sad path of personal insults—not a small credit for a man of lively temperament, as he was.

The controversy revived in 1850 when du Bois-Reymond presented his Treatise at the *Académie des Sciences* of Paris, with a brief note where he speaks of his "*loi du courant musculaire*" ("law of muscular current"), without any mention of Matteucci. A second note was essentially devoted to the repetition (with a full confirmation) of the experiments on the induced twitch and tetanus of Matteucci, who was mentioned only at the end of the note with these words (1850a, p 408):

Je terminerai en faisant observer que ces expériences contiennent l'explication du phénomène que M. Matteucci a découvert en 1842, qu'il nomme contraction induite, et au sujet duquel il a hasardé tant d'hypothèses.

[I will end by saying that these experiments contain the explanation of the phenomenon that Mr. Matteucci discovered in 1842, which he calls induced twitch, and on which he has hazarded so many hypotheses.]

In a note of less than two pages, Matteucci (1850) stated that the fundamental facts of the law of muscle current had been already observed by him. The reply of du Bois-Reymond, summarized in two notes (1850b,c) does not bring any new fact which could refute this claim. It points out mainly the contradictions and obscurities in Matteucci's thinking we have already mentioned. Perhaps out of regard for the Academy, or because of the natural abatement of passion, the language used in the treatise is fortunately completely abandoned in this note of du Bois-Reymond. The controversy has a bitter flavor, but formal appearances are respected and personal attacks are completely absent.

The reply of Matteucci (1850a) is clear, correct, and logically cogent as far as the demarcation potentials are concerned, but declines in scientific level, without losing dignity, when the author comes to grips with the negative oscillation of du Bois-Reymond. Manifestly, it is the concept of negative oscillation itself which is not clear to Matteucci's mind: one could say that Matteucci's spirit repulses it.

The controversy between Galvani and Volta is rightly referred to as a model of lofty scientific discussion, and is often mentioned to show how a disagreement between scientists can result in a progress of Science. Unfortunately, this happens rarely, as the controversy between Matteucci and du Bois-Reymond clearly shows. It was not only devoid of scientific fruits, but perhaps was even detrimental to Science since it pushed Matteucci to refuse the concept of negative oscillation.

In a letter to Matteucci of March 3, 1853, Faraday expressed himself as follows:[d]

...I knew from matters reported in the Comptes Rendus & otherwise, that you and du Bois-Reymond were antagonistically placed; a thing much to be regretted which, however, often happens among the highest men in many departments of Science, and more often when there are two or three only that really pursue the subject, than when there are many.

Being entirely unacquainted with German I do not know what either du Bois-Reymond or Dr. Muller may have said controversially; but I concluded you had borne with the work of the latter with that patience which most men of eminence have to practice. For who has not to put up with the inconsistencies or misrepresentations in the accounts of his proceedings given by others, leaving for the time the present injustice which is often unintentional and often originates in the hasty of temper,

[14] See the letter of Auguste de La Rive published by Bianchi (1874, p. 69).

[d] The original of this letter was not available to Prof. Moruzzi when he wrote this article, and he resigned to quote from the translation made by Nicomede Bianchi, although he was aware of the possibility that this translation was not correct (among other things the letter was incorrectly dated by Bianchi 27 September instead of 3 November). A draft of Faraday's letter was found in Faradays's correspondence at the Royal Society due to the effort and courtesy of Mitchell Glickstein, to whom we express our deep gratitude. The occasion of the letter was the publication by H. Bence Jones of the book *On Animal Electricity: Being an Abstract of the Discoveries of Emil Du Bois-Reymond* (Churchill, London, 1852).

and committing his force of character to the judgement of the men of his own and future time.

I see that that moves you which would move me most namely the imputation of want of good faith; and therefore I cordially sympathize with any one who is so charged unjustly. Such cases have seemed to me almost the only ones for which it is worth while entering into controversy. I have felt myself not unfrequently misunderstood, often misrepresented, sometimes passed by; as in the case of specific induction capacity, the magnetoelectric currents, definite electrolytic actions; but it is only in the cases where moral turpitude has been implied that I have felt called upon to enter the subject in reply.

...

These polemics of the scientific world are very unfortunate things; they form the great storm to which the beautiful edifice of scientific truth is subject: *are they unavoidable?* They certainly cannot belong to science itself but to something in our fallen natures. How earnestly I wish in all such cases that the two champions were friends yet I suppose I may not hope that you and du Bois-Reymond may some day become so. Well, let me be your friend at all events and with the kindest remembrance to Madame Matteucci and yourself believe me my dear my dear Matteucci ever very truly yours,
M. Faraday

Perhaps these concepts were present in Matteucci's mind when, in 1856, he wrote these noble words in his preface to the *Course of Electrophysiology*.

More serious and well-founded surely appear the accusations of the kind that du Bois-Reymond has cast on me many times and, unfortunately, with such a liveliness and solemnity that there is no scientist who ignores them and who does not know the arguments I raised in my defence. By comparing the years in which my memoirs on the frog current, on the muscle current and on the induced twitch were published [1841 and 1842] with the date [1843] of his first electrophysiological memoir, nobody has ever doubted who was the true author of these discoveries. Two years had elapsed since the publication of my first memoirs, I had already shown my experiments to a great number of French and German scientists and, among others and many times, to the Baron von Humboldt. I had repeated them in front of the British Society of Sciences in a meeting held in York, and still I was unaware of the existence of the memoir of Mr. du Bois-Reymond, as I must suppose was the case for the scientists I have alluded to. I was kept in this ignorance by a letter of Müller received at that time, in which the famous Physiologist of Berlin mentions my experiments with great benevolence, and informs me that the work on animal Electricity of du Bois-Reymond, about which I asked information, was in press. Shortly thereafter, I discovered the existence of du Bois-Reymond's memoir from a passage in Müller's Physiology. At that moment, as well as many other times afterwards, reading that memoir, which lacks a detailed exposition of the instruments and of the experimental method used by the Author, in which many of the results, perhaps the main ones, are not demonstrated with sufficient clearness or are contradicted by others, where the Author lets himself go to generalise and to explain, instead of deducing rigorously from the facts; that reading, I do say, unfortunately led me to conclude, without much basis, that du Bois-Reymond's investigations had not added anything important to the results of my experiments. The confidence I was acquiring more and more on my methods, the passion for the results I achieved, kept me in this error, from which originated my unjust criticisms that I published then on du Bois-Reymond's experiments.

The controversy having arisen, the subsequent publications of du Bois-Reymond have given me the desired opportunity to recognise and to confess my error, and I am glad to say that among the reasons which encouraged me to publish this Course, not the least was to have an opportunity to put in the true light the services rendered to Electro-physiology by that person whom I would like henceforth to call my old adversary.

VI. AN ATTEMPT TO EVALUATE THE ELECTROPHYSIOLOGICAL WORK OF MATTEUCCI

About one hundred years after his death, which occurred in 1868, it is not difficult for an impartial historian to express in a synthetic way what electrophysiology owes to Carlo Matteucci. He discovered the nervous structures responsible for the discharge of the electric organ in torpedo, demonstrated their excitability to mechanical and galvanic stimulation, and revealed their involvement in the reflex discharge of the electric organ. Matteucci was the first to demonstrate the existence of an difference of electric potential between the sectioned surface and the intact surface of a muscle; he revealed the law governing this current and, in particular, its constant polarity, by using the galvanoscopic leg and the galvanometer. He, thus, discovered the demarcation potential, which we know to be due to the resting polarisation of muscle membrane. Finally, Matteucci carried out the first galvanometric measurement of the action potential and, with the induced twitch experiment, provided the first evidence for the existence of these potentials.

Each of these three research topics would suffice to assure a perennial fame to a physiologist. But, we are even more bewildered when we consider that the person who made these discoveries, dead at the age of only 58 years, was also a physicist of merit; that, finally, as a political man of high stature in the fight for Italian independence, as a senator in the Royal Parliament and as Minister of Public Instruction, he achieved an eminent position in the public life of his Country.

That is not all. What is enduring in his physiological work was done in not more than 8 years: in the four years spent in Ravenna (1836–1840) and in the first four years in Pisa (1840–1844). At the age of 33, Matteucci had already carried out all the researches whereby his name has passed into history.

Faced with such a man, the historian is led to investigate on that prodigious youth and on the reasons responsible for the early exhaustion of such creative power.

Youth fills the soul with an admiring bewilderment. Born in 1811, graduated in physics when he was not yet 17, Matteucci goes to Paris to study in 1829, and at the age of 18 he earns the friendship of men like Arago and Becquerel. To Matteucci, a young man of 22, Faraday writes, on October 1 1833, these truly prophetic words:[15]

I.X.1833
Royal Institution
Being convinced that you cannot refrain from pursuing science by experiment, I need not express a hope that you will do so successfully. No man of judgment can work without succeeding and you are not likely to leave a cause which has already made your name known through the European Continent.

In 1837, the famous session of the *Académie des Sciences* devoted to the memoir on electric fish takes place. It is the great moment in Matteucci's life; it is also the undisputed success, a success that Libri's jealousy can only emphasize. Some time later, on 9 January 1838, von Humboldt writes these words to the Italian physicist, then 27 (retranslated from Bianchi, 1874, pp. 66):

Your name has reached such a high reputation in Germany, and particularly at the Academy of Berlin, that Mr. Poggendorff will soon translate your important works... I have been very happy to hear that the expres-

[15] This letter was left by Senator Nicomede Bianchi to the Municipal Library of Reggio Emilia (Mss. Reggio 210/11). Bianchi (1874) published an Italian translation with many inaccuracies.

sions of my high regard, and some words on the fourth lobe in a letter of mine to Mr. Arago, turned out to be useful in a discussion raised about your works.

Alexander von Humboldt (1769–1859) the famous naturalist, the friend of Goethe,[16] was at that time one of the highest scientific authorities in the field of Natural Sciences. From a biography written by the chemist Francesco Selmi (1862), when Matteucci was still alive, we learn that it was the mention of von Humboldt, who had been informed by Arago of the vacancy of the Chair of Physics in Pisa, that convinced Leopoldo II to appoint a young man only 29 years old to that important position.

But the ascent continues and the highest peak is reached with the discovery of the induced twitch, which Matteucci repeats in Paris in front of von Humboldt, Dumas, and Becquerel. Once more, the *Académie des Sciences* gives the official sanction to an immense success.

The obscurity and the economic difficulties will belong henceforth to the past. In the same year, Matteucci will be awarded, together with Longet, the prize of the *Académie des Sciences*, of which he will become foreign member in 1857 in the place left vacant by Melloni. The Grand Duke of Tuscany will provide Matteucci with the means to build up the best Institute of Physics in Italy. In those same years, the creative impetus of Matteucci seems to decline.

It has been stated that Matteucci abandoned electrophysiology for political activity, which he had embraced with enthusiasm due to his libertarian and patriotic ideals. This explanation is not convincing, however. Firstly, the papers on the induced twitch presented at the Royal Society appeared before 1848, and it is clear to the reader that Matteucci had already abandoned the correct path. We know furthermore that Matteucci devoted himself again completely to scientific studies in the decade 1849–1859, and published several notes and memoirs. Finally, the letters to Studiati, which belong to that period, show clearly the highest enthusiasm and the vigor of his talent in those years. The man was, moreover, capable of a prodigious activity. He took advantage of the period spent in Turin as a senator to give a course of electrophysiology at that University (1861). Deadly tired and seriously ill, he still sent, a few months before his death, a communication to the *Académie des Sciences* (1868).

The reasons of the decline must therefore be profound. There is in the life of many great scientists a blessed period, when everything seems to succeed easily, discovery follows discovery, as if nature were yielding its secrets to an irresistible force. Afterwards, at a certain moment, this creative power seems to vanish, or perhaps it has required an effort so painful that the scientist almost refuses to sustain it further. Scientific production comes to an end, or becomes qualitatively of a much lower level compared to the years of fortune. Public cares and academic duties are normally considered to deprive Science of its best men—wrongly, perhaps, because they are very often the consequence, not the cause, of a deep change in the scientist's spirit. The last 40 years of Newton's life poses this problem to the historian, in a manner that the greatness of the man makes almost dramatic.

Extrinsic factors can speed up the moment of decline: the pressing of younger energies, the deep feeling to be unable to follow the rhythm of time, sometimes trivial errors of a methodological nature. The person who has meditated on the work of Matteucci, who has perceived his tragic uneasiness at the precise moment in which fortune gave him, with the discovery of the induced twitch, the keys to modern electrophysiology, is led to wonder if among these factors are also to be sought the reasons of the rapid fall, and at such young age, of an impetus that had brought to such a high level the Italian scientist.

[16] On 11 December 1826, Eckermann in his *Gespräche mit Goethe* writes:
"Ich fand Goethe in einer sehr heiter aufgeregten Stimmung. 'Alexander von Humboldt ist diesen Morgen einige Stunden bei mir gewesen,' sagte er mir sehr belebt entgegen. 'Was ist das für ein Mann!—Ich kenne ihn so lange, und doch bin ich von neuem über ihn in Erstaunen. Man kann sagen, er hat an Kenntnissen und lebendigem Wissen nicht seinesgleichen. Und eine Vielseitigkeit, wie sie mir gleichfalls noch nicht vorgekommen ist! Wohin man rührt, er ist überall zu Hause und überschüttet uns mit geistigen Schätzen. Er gleicht einem Brunnen mit vielen Röhren, wo man überall nur Gefässe unterzuhalten braucht und wo es uns immer erquicklich und unerschöpflich entgegenströmt.' "
["I found Goethe in a very excited and happy mood. 'This morning Alexander von Humboldt spent a few hours with me' he told me with great panache. 'What a man! I have known him for so long, and yet he always surprises me. One can say that he has an erudition and a lively knowledge without comparison. And a versatility which I have never seen before. Whatever topic one touches, he is at home and showers us with spiritual treasures. He is like a fountain with many spouts under which one can always hold his vessels to be refreshed by an inexaustible stream.' "]

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APPENDIX

Translation of the enclosed letter, written by Matteucci (at the age of 17) to A. De La Rive (Reproduced by courtesy of the Biblioteca Municipale of Reggio Emilia):

Although I have not had the honor of meeting you personally, but know you only through your excellent works on Physics, I dare to send you two booklets of mine on Meteorology. Enclosed with my paper on the Storm, you will find two short memoirs that I would like you to publish in your Journal of the Universal Library (*La Bibliothèque Universelle de Genève*). As to the first one about the calorific currents, that you published already on invitation by Signor Cavaliere Nobili, and which I wished then to include in this journal that is nowadays the only one dealing with such interesting subjects.

Hoping that you will forgive me and looking forward to your reply, with the expression of my high esteem and respect, eminent Signor Professore,

I remain your humble and devote servant
From Forlì, July 3, 1828
Carlo Matteucci

Transcription of the enclosed letter from Faraday to Matteucci. (Reproduced by courtesy of the Biblioteca Municipale of Reggio Emilia):

Royal Institution London
1 October 1833
Sir

I am very much your debtor for your kindness in sending me your papers and for your good opinion. All such notes of good will are stimuli to me urging me still onward in the course which has obtained such commendation.

I have been very much gratified in reading your papers and think it a high compliment that such men as yourself are induced to touch a subject which I had the good fortune to start. I continue fully occupied with Electricity and expect soon to have the *fourth* and *fifth* series of my researches printed. If I knew how to send them to you, I should be happy in so doing to acknowledge your kindness.

Being convinced that you cannot refrain from pursuing science by experiment, I need not express a hope that you will do so successfully. No man of judgment can work without succeeding, and you are not likely to leave a cause which has already made your name known throughout the European Continent.

M. Matteucci — Ever Your Obedient Servant
& & & — M. Faraday

N° 1

Chiarissimo Sig.r Professore

1

Benchè non abbia l'onore di conoscerla personalmente, [illegible] per le tante Sue bellissime opere di Fisica, pure ardisco spedirle due de' miei opuscoli di Meteorologia. Ella troverà poi unite all'opuscolo sul Temporale due mie picole memorie, che desiderarei Ella mi pubblicasse nel Suo Giornale della Biblioteca Universale. Riguardo alla prima sulle correnti calorifiche la quale pubblicò anche per invito del Signor Cav.re Nobili, e che ho desiderato poi d'inserire in questo Giornale per essere ormai l'unico, che s'occupi di sì interessanti materie.

Credo che vorrà scusarmi, e pregandola di un suo riscontro con tutta stima e rispetto mi sottoscrivo

Di Lei chiarissimo Sig.r Professore

Di Forlì il dì 3 Luglio 1828.

umilissimo devotissimo Servitore
Carlo Matteucci

No. 1

Royal Institution
London
7 October 1833

Sir

I am very much your debtor for your kindness in sending me your papers and for your good opinion all such marks of good will are stimuli to me urging me still onward in the course which has obtained such commendation

I have been very much gratified in reading your papers and think it a high compliment that such men as yourself are induced to touch a subject which I had the good fortune to start. — I continue fully occupied on Electricity & expect soon to have the fourth & fifth series of my researches printed. If I knew how to send them to you I should be happy in so doing to acknowledge your kindness.

Being convinced you cannot refrain from pursuing such experiment I need not express a hope that you will do so successfully. A man of judgment cannot work without succeeding and you are not likely to leave a course which has already made your name known throughout the European Continent.

Your Very Obdt Servt
M Faraday

M. Matteucci
&c &c &c

Carlo Matteucci (1811–1868)

Giuseppe Moruzzi (1910–1986)