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From an Ambiguous Torpedo to Animal and Physical Electricity

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Indicative of the fascinating unpredictability of scientific progress, the discovery path that in the last two centuries has brought about some fundamental developments in electrical science, was closely connected to studies leading to the demonstration of the physiological role of electricity in animal tissues. Both depended in an important way on the demonstration of the electrical nature of the shock of the torpedo fish provided by the English 'natural philosopher' John Walsh in the summer season of 1772. Until Walsh's time the painful shock produced by the torpedo and similar fish was considered to be the effect of a mechanical agency. This article briefly outlines some interesting aspects of the research path whereby the 'mechanical' torpedo turned out to be electrical in nature. It tries, moreover, to establish an ideal link that could relate the curious property of this singular fish with a major recent advance in the field of audiology. *Key words: electrophysiology, electrical fish, history of science, nerve signal, John Walsh, Luigi Galvani, Alessandro Volta, cochlear implant.*

INTRODUCTION

The modern world is dominated by electricity with an endless profusion of its technological applications. In medicine, and particularly in fields more or less connected to neurosciences (as audiology undoubtedly is), electricity is even more pervasive. This is because many branches of medicine involve electricity not only in its technological aspects (at both diagnostic and therapeutic levels), but also include, in a deeper way, the fundamental role of electric phenomena in nerve physiology. Sensory transduction, the elaboration of nervous information, sensory reflexes and reactions of various complexity, the programming and execution of movements and of language production are all based to a large extent on a crowd of minute electric signals which (as Charles Scott Sherrington reminded us half a century ago), continuously flow along the nerve fibres of our brain circuits or of the peripheral structures of our nervous system, like an incessant 'electric storm' (1). Consider for instance the device that so markedly epitomizes, at both scientific and therapeutic levels, the major advance in audiology of the last few decades – the cochlear implant. Here electricity is involved in the great sophistication of the electronic apparatus which converts sound waves into electric signals, filters them and extracts relevant auditory information so as to appropriately stimulate the peripheral structures of the auditory system. Eventually all of this results in a train of electrical impulses which carry sensory messages to the auditory centres of the brain, so that electricity is also involved in its physiological counterpart.

The great impetus that characterizes modern scientific endeavour forces scientists to look essentially forwards, and normally obliges them to restrict their historical view to the immediate past of their fields of narrow interest. Nevertheless, it is sometimes worthwhile enlarging our viewpoint and having a broader and extended perspective towards the historical development that lies behind our narrow views. Were we to do that in the field of electrical science, we would find out how closely related were, more than two centuries ago, the discoveries that prompted the great development of the physiological and technological aspects of electricity. We would learn, moreover, somewhat unexpectedly, of the decisive importance in this context of the studies that, in the second half of the 18th century, led to the demonstration of the electrical nature of the painful shock produced by some particular living creatures, and especially by the torpedo fish.

In this article I shall provide a rapid outline of the 18th century investigations into the involvement of electricity in animal physiology, giving particular emphasis to the research that led to the fundamental transition whereby the shock of the torpedo, traditionally believed to be due to a mechanical agency, was eventually shown to be an electrical phenomenon.

LUIGI GALVANI AND ANIMAL ELECTRICITY

The role of electricity in neurophysiology has emerged in the last two centuries, following the pioneer studies carried out by Luigi Galvani in Bologna in the second half of the eighteenth century. Galvani, who in the years of his scientific development investigated various aspects of anatomy and physiology (and studied, among others, the hearing system of birds (Figure 1), initiated, at the end of 1780, an investigation of the role of electricity in muscle and nerve function (2–4). After more than ten years of experimental work, in 1791 he reached the conclusion

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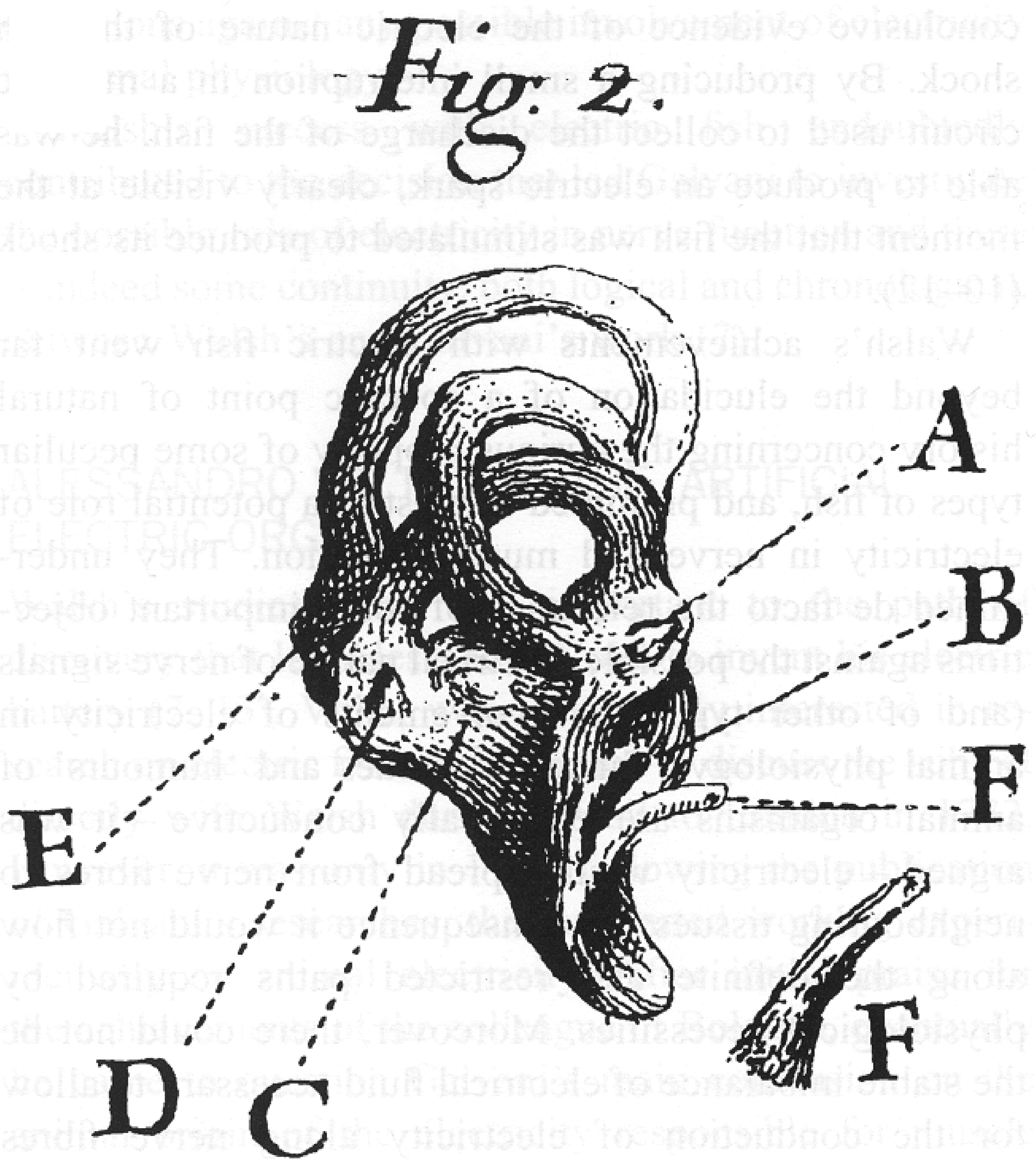

Fig. 1. Image of the inner ear of birds from a plate of *De volatilium aure* of Galvani (Ref. 2, by courtesy of the Accademia Nazionale di Scienze, Lettere e Arti of Modena).

that nerve signals and muscle excitability depend on 'animal electricity', i.e. on an intrinsic form of electricity accumulated in a condition of imbalance between the internal and external compartments of excitable fibres (5) (Figure 2). Galvani's hypothesis was at the start of an intense phase of scientific progress in the field of electrophysiology. Throughout the nineteenth and twentieth centuries, it eventually culminated, in 1952, in the final elucidation, brought about by Alan Hodgkin and Andrew Huxley, of the mechanisms involved in the generation and propagation of nerve signals (6, 7).

Galvani's awareness of the possible role of electricity in nerve and muscle function had emerged as a result of the great interest in electrical phenomena of the eighteenth century, the electrical century par excellence. Many discoveries and practical applications, as well as great theoretical progress, put electricity on the centre stage of the science of the epoch. Among the main achievements we can record: the recognition that 'electric fluid' could propagate at fast speed and for long distances and the differentiation between conductive and non-conductive substances; the construction of new and powerful 'electrical machines', i.e. friction-type electric generators; the invention of the Leyden jar and of other kinds of electric capacitors; the discovery of the electrical nature of lightning and thunder (with the proud awareness that humans could subdue these tremendous manifestations of the energy of nature by means of their own artifices (8)).

There was, moreover, a great interest in the possibility that the 'electric fluid' might be useful for therapeutic purposes. Electricity, generated by electric machines or accumulated in Leyden jars, was administered in various

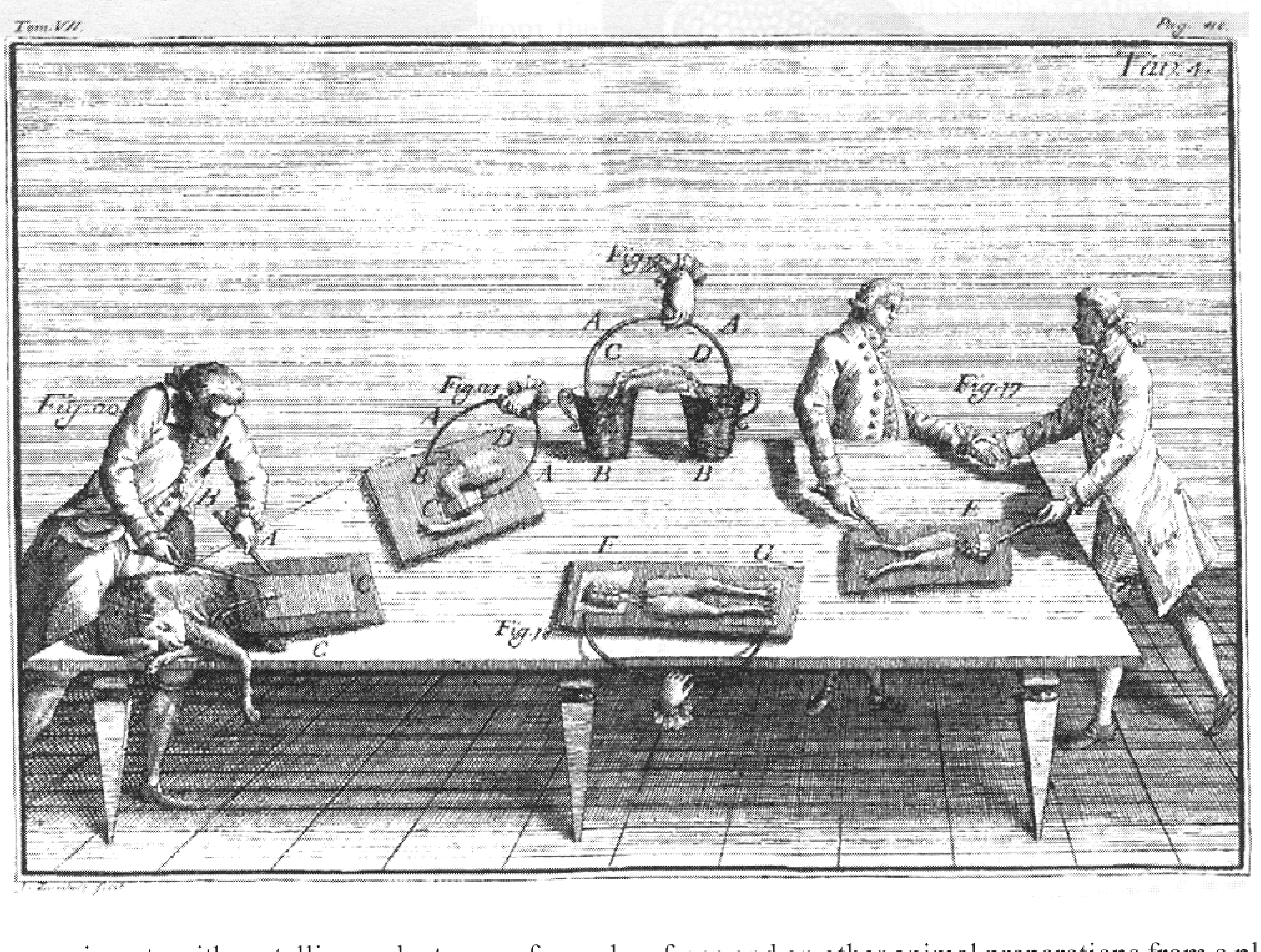

Fig. 2. Galvani's experiments with metallic conductors performed on frogs and on other animal preparations from a plate of *De viribus electritatis in motu musculari* (5).

ways with the hope of relieving a plethora of diseases, such as paralysis, apoplectic diseases, deafness, tinnitus, blindness, rheumatic affections, muscular and dental pain, gout, menstrual disorders, bleeding, and mental diseases (as Joseph Priestley recognized in his history of electricity published in various editions between 1767 and 1775 (9)).

JOHN WALSH, THE TORPEDO AND THE 'SPARKING' EEL

To an important extent, interest in a possible physiological role of electricity also derived from the demonstration, provided by the English amateur scientist John Walsh, of the electric nature of the shock produced by some particular fish, such as torpedo and the eel of Guiana. Walsh studied torpedoes in June–July 1772 at La Rochelle in France (Figure 3). He arrived at his conclusion as to the electrical nature of torpedo shock in a memorable day of intense experiments (9 July). On that day it was shown that the shock could circulate along a human chain if the persons of the chain established a mutual contact, either directly or through a metallic body, whereas it was intercepted if the contact was made through glass or sealing wax. Three years later in London, in experiments carried out on eels imported from Guiana, he obtained a further result which was considered to be conclusive evidence of the electric nature of the fish shock. By producing a small interruption in a metallic circuit used to collect the discharge of the fish, he was able to produce an electric spark, clearly visible at the moment that the fish was stimulated to produce its shock (10–12).

Walsh's achievements with electric fish went far beyond the elucidation of a specific point of natural history concerning the curious property of some peculiar types of fish, and prompted interest in a potential role of electricity in nerve and muscle function. They undermined de facto the relevance of some important objections against the possible electrical nature of nerve signals (and of other types of involvements of electricity in animal physiology). Since the tissues and 'humours' of animal organisms are electrically conductive – it was argued – electricity would spread from nerve fibres to neighbouring tissues; by consequence it would not flow along the definite and restricted paths required by physiological necessities. Moreover, there could not be the stable imbalance of electrical fluid necessary to allow for the conduction of electricity along nerve fibres between two distant sites of the animal's body, because any such imbalance would be rapidly dissipated due to the conductive nature of living substances. Despite all this, the torpedo and the eel of Guiana were able to produce an electric shock, and so undermined the basis of the

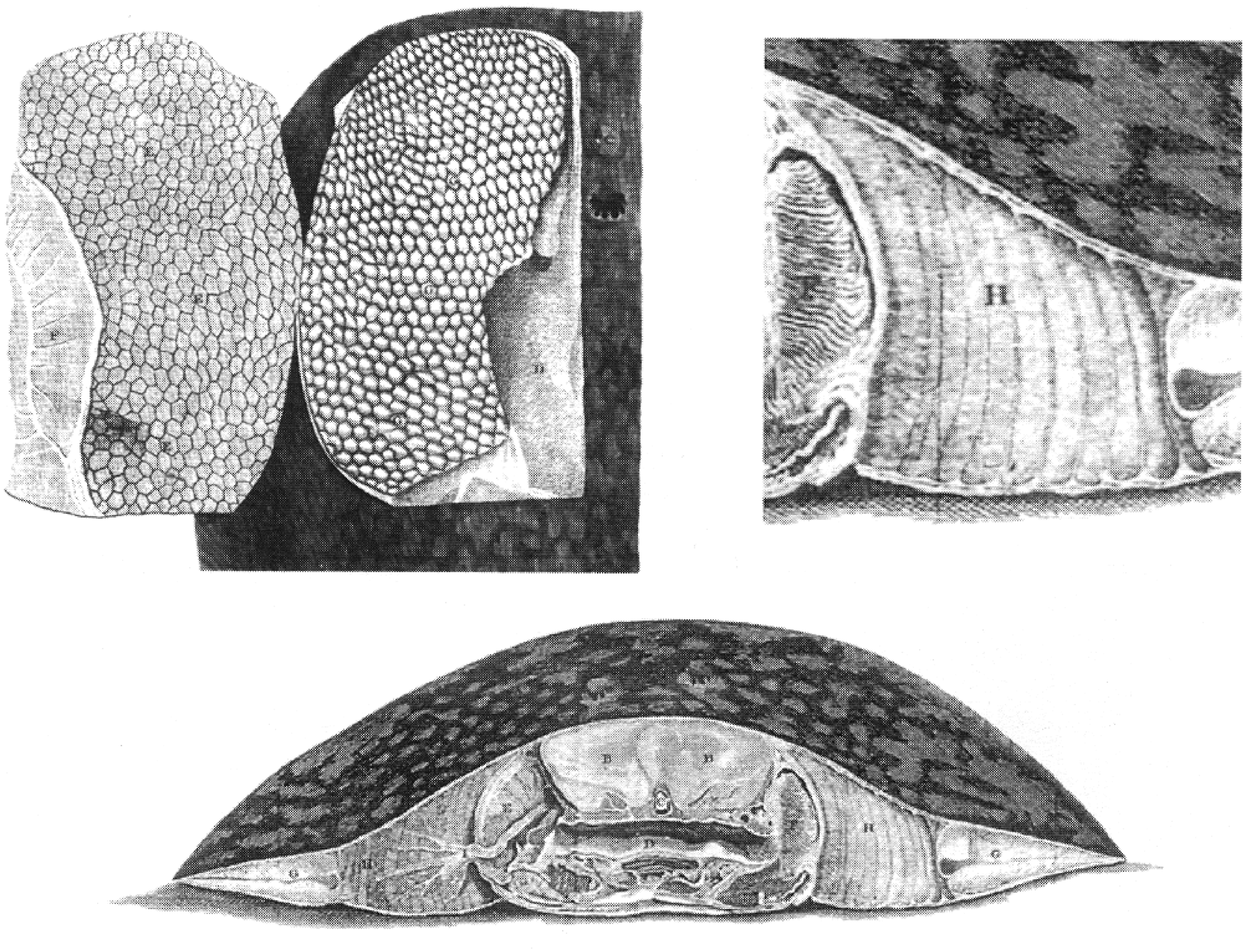

Fig. 3. A plate with the anatomical study performed by John Hunter on the torpedoes brought by Walsh from La Rochelle. Notice the appearance of the electrical organs in both the tangential and vertical views (22).

objections against any possible involvement of electricity in animal physiology.

Walsh's success with electric fish undoubtedly contributed to the decision that led Galvani to investigate the possible role of electricity in nerve function and there is indeed some continuity, both logical and chronological, between Walsh's and Galvani's work (7).

ALESSANDRO VOLTA AND THE 'ARTIFICIAL ELECTRIC ORGAN'

Walsh's studies were also important to the path of discovery that led Alessandro Volta to invent his electric battery (7, 13). Volta, who was greatly interested in research on electric fish, had occasion to discuss the subject directly with Walsh during a visit to London in 1782. However, it was only in 1792, following the publication of Galvani's researches, that he started working experimentally on animal electricity. After initial praise for the achievements of the colleague of Bologna, eventually he came to question Galvani's main conclusion on the animal origin of the electricity responsible for muscle contraction in his experiments. According to Volta, electricity originated from the metals used by Galvani to connect the nerve and muscle of frog legs (Figure 2). This objection led to an intense and fruitful controversy that, on one side, led Galvani, in the period 1794–1797, to produce muscle contractions by direct contact between animal tissues, in the absence of any metal and, on the other side, led Volta in 1796 to show, in a conclusive way, that a weak electromotive action would derive from the contact of two different metals, in the absence of any animal tissue. In the following years, Volta endeavoured to multiply this action by staking, one above the other, a series of bimetallic disks. The experiments were initially unsuccessful until the moment that, by a series of circumstances, his attention was directed to the special organs of the torpedo and electric eel. This organ, made of a stake-like assembly of organic disks (and thus apparently similar in its structure to his artificial device), was nonetheless capable of producing strong electrical effects. Eventually, from a consideration of the fish organ, Volta had, toward the end of 1799, an inspiration that represented the breakthrough in his effort to multiply metallic electricity – he interspersed humid disks between the metallic couples. In communicating his invention to Joseph Banks, president of the Royal Society of London in March 1800, Volta recognized his debt toward life in nature by calling his battery 'organ électrique artificiel', that is the artificial counterpart of the fish organ (14) (Figure 4).

The historical importance of Walsh's achievements with electric fish can hardly be overstated, since they represent a milestone in the research paths that led to revolutionary progress in two areas of electric science

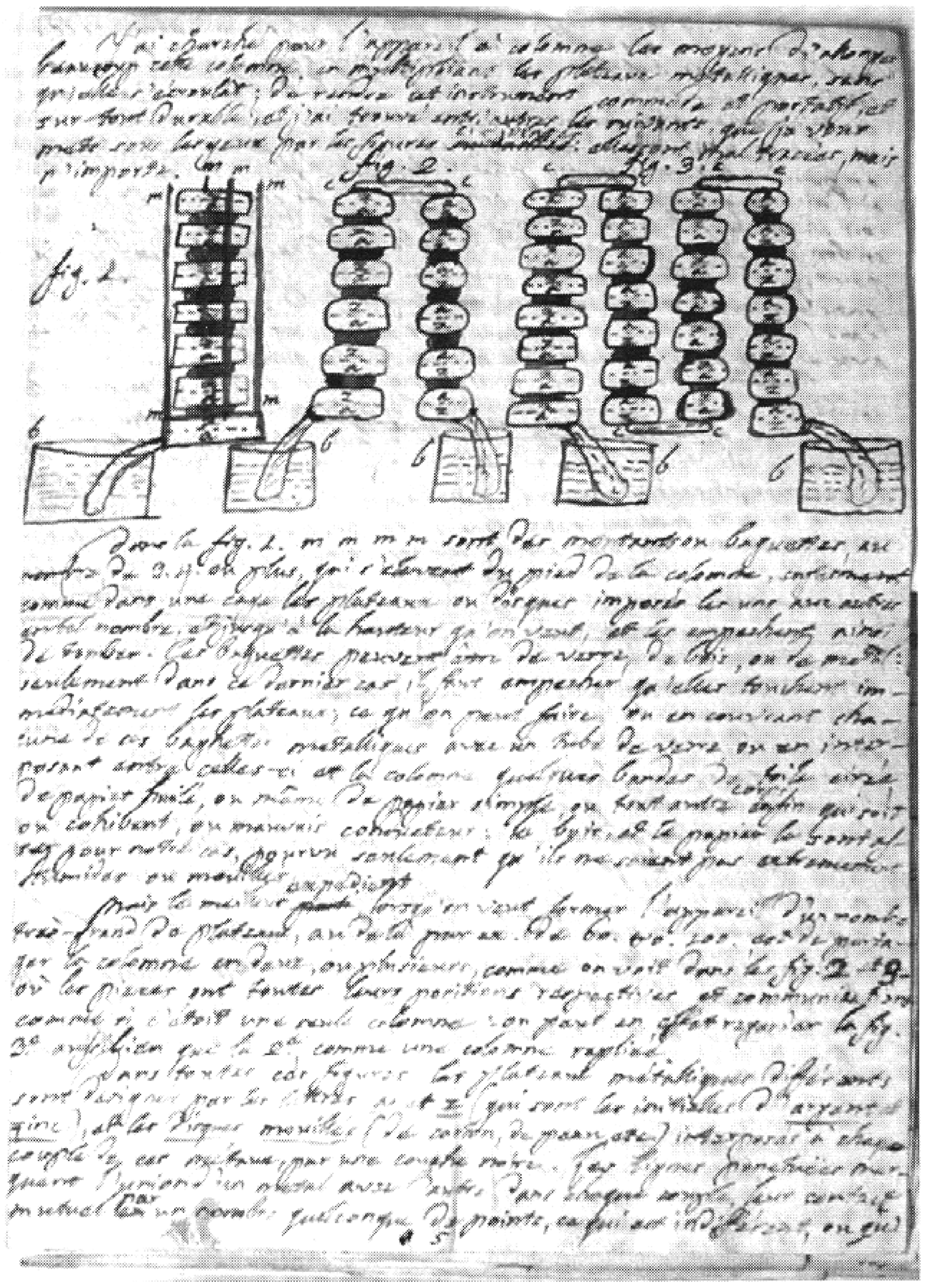

Fig. 4. A page of Volta's letter dated 20 March 1800 announcing the invention of the battery, the 'organe électrique artificiel' By courtesy of the Royal Society, © The Royal Society.

over the last two centuries, on the physiological and physical sides, both of paramount importance for medicine.

THE ELECTRIC VERSUS MECHANICAL SHOCK: A PARADIGM SHIFT?

There is another interesting element which lies behind the story of Walsh and of his electric fish that I would like to consider here, because it illustrates how revolutionary was the recognition of the electric nature of fish shock, and, moreover, it makes clear how complex scientific progress can be and how difficult its interpretation can sometimes be.

In his studies on torpedoes at La Rochelle, Walsh had been particularly attentive to ascertain if fish shock was accompanied by some obvious movement of the fish's body, particularly in the region of the electric organs. The conclusion, reached after an intense series of experiments, was that, although sometimes the shock could be preceded by some small movement in the preparatory phase (particularly a sudden winking of eyes), there was usually no visible movement of the organs. As a consequence, he excluded the possibility that the shock might be, at least in part, the effect of a mechanical agency. This conclusion, consistent as it was with his electric hypothesis of torpedo's shock, stood, on the other hand, in overt contrast to the opinion that was dominating the science of the time which was based on a mechanical hypothesis.

The mechanical hypothesis had emerged with the studies carried out in the second half of the 17th century by the adherents of the new science inspired by the mechanical principles of the Galilean revolution. It was formulated in an explicit way by Stefano Lorenzini, a pupil of Francesco Redi, one of the members of the famous Accademia del Cimento. Redi attributed a muscular nature to the strange fish organs and called them '*musculi [or muscoli] falcati*' (15). On Redi's suggestion, Lorenzini (the discoverer of the ampullar electroreceptors bearing his name) performed a thorough study of torpedoes caught on the coast of Tuscany (16) (Figure 5). By explicit reference to Galilean physiological conceptions, he postulated that, at the moment of the shock, the fish emitted, with great violence, a multitude of minute corpuscles ('*corpicciuoli*'). These corpuscles would produce the commotion and the numbing effect by penetrating deeply into the tissues of any prey (or of the experimenter) and by hitting their nerves.

In 1714 the great French naturalist Réné-Antoine Ferchault de Réaumur also advocated a mechanical explanation, which did not, however, involve anything like the '*corpicciuoli*' of Lorenzini (17) (Figure 6). Réaumur assumed instead that the torpedo's shock was the consequence of a direct and rapid percussion of nerve trunks similar to that produced in the forearm by the action of a sharp body hitting the elbow region. According to this view, the shock would be produced by the fish at the moment that its dorsal surface (normally flat or even concave in the preparatory phase), became suddenly convex as a consequence of a contraction of the '*musculi falcati*'. The effect of this contraction is described by Réaumur in such a way as to defy any attempt at falsification ('a movement so rapid that even the most attentive eyes could not perceive it').

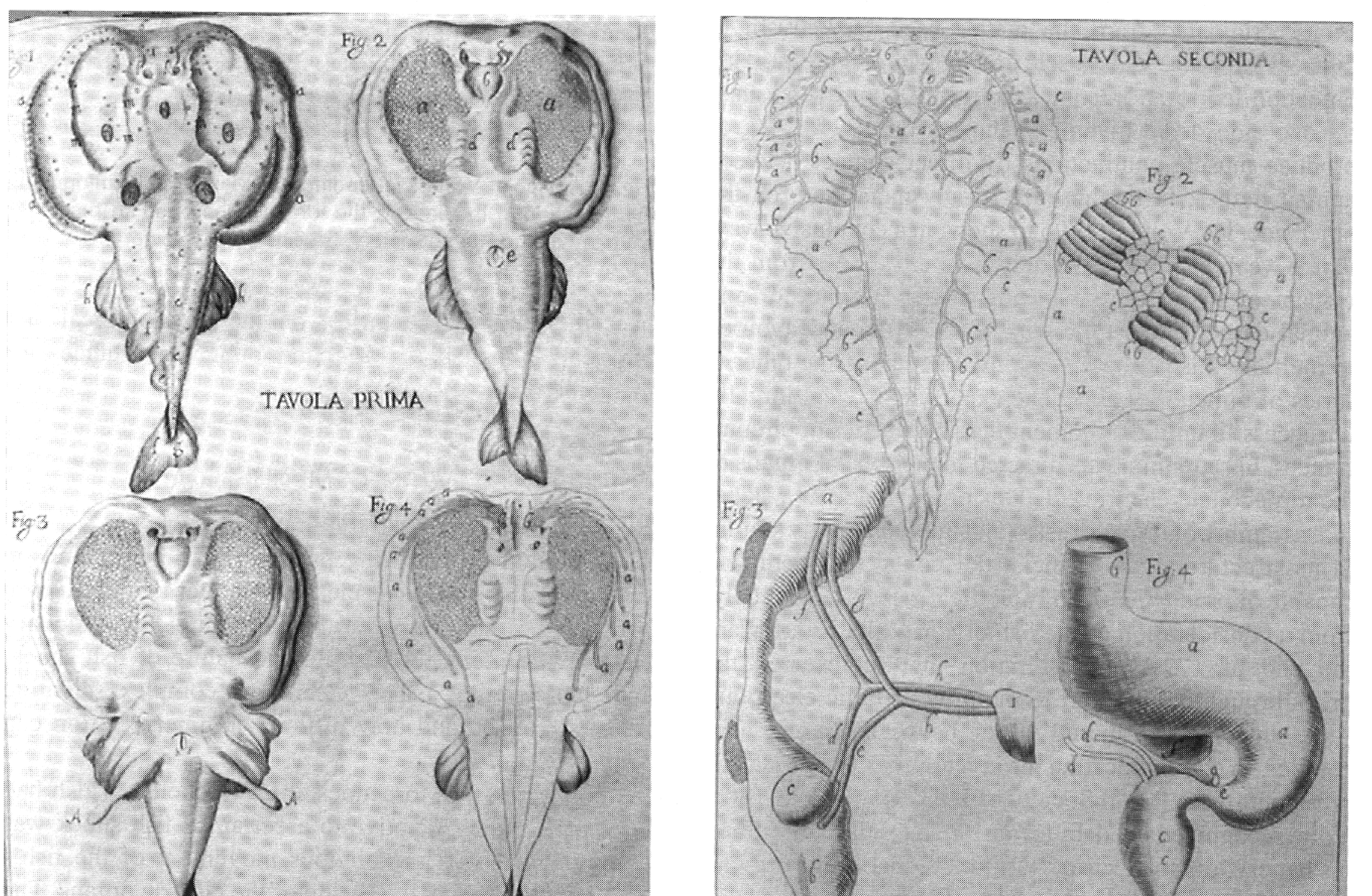

Fig. 5. Two plates on the Torpedo from Lorenzini 1678 (16).

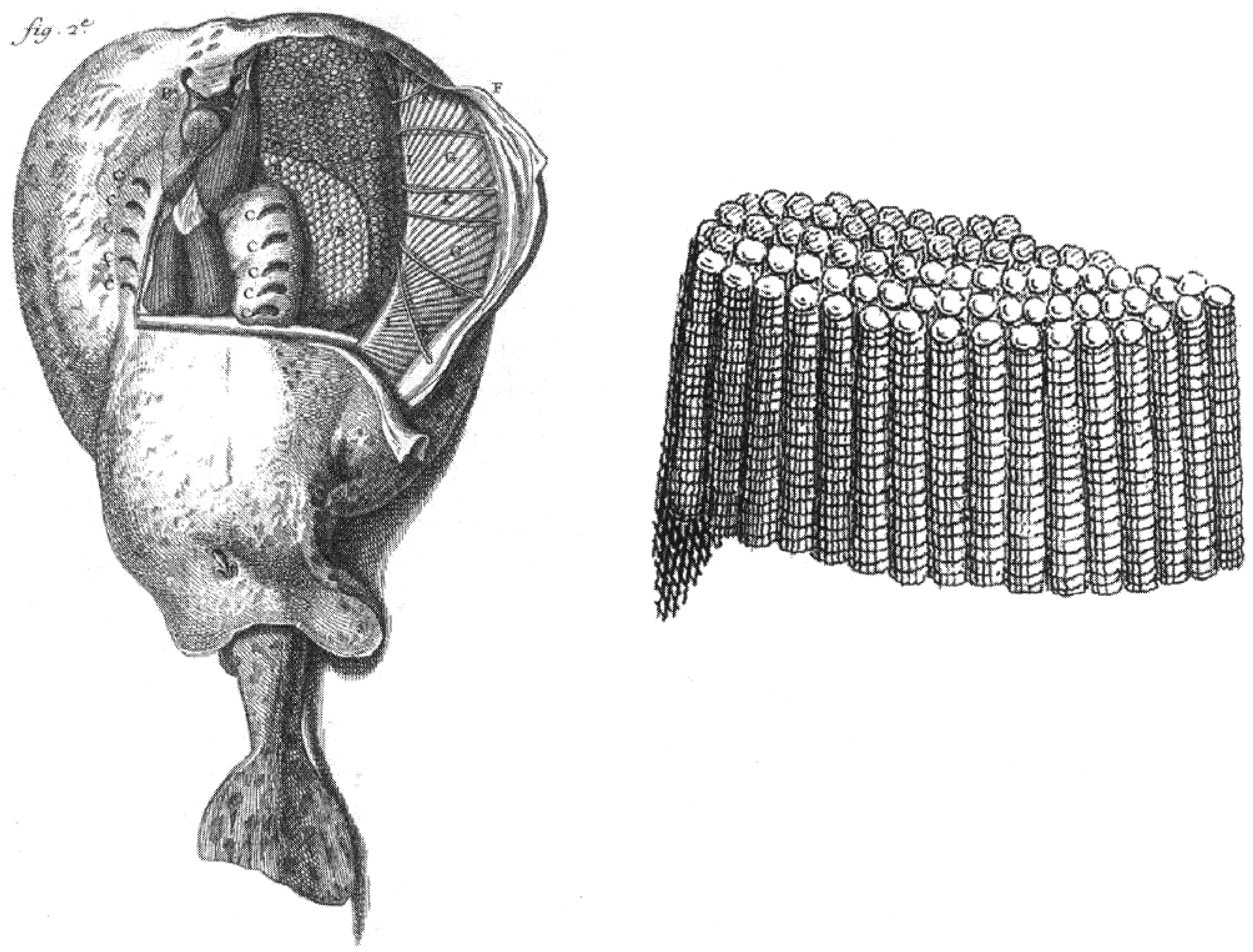

Fig. 6. A plate on the Torpedo from Réaumur with the detail of the structure of the electric organs (Ref. 17, modified; by courtesy of the Accademia Nazionale di Scienze, Lettere e Arti of Modena).

Since we now know that there is no mechanical component in the torpedo's shock it may be difficult at first view to account for the movements 'seen' by Lorenzini and Réaumur in their studies of the shock produced by the fish.

However, on the basis of modern views of the philosophy of science (which stress the importance, also in scientific observation, of subjective attitudes, or 'paradigms', resulting from a variety of conditioning influences), the case of Réaumur can be easily discounted as due to the influence of a mechanical 'system' leading him to see what he expected to see. Alternatively, it can be considered that the French scientist was interpreting equivocal evidence supportive of his views and, possibly, presenting under the form of an observation what was instead only a somewhat plausible hypothesis.

The situation is rather different with Lorenzini, because in his work the description of the movements of '*muscoli falcati*' is not limited to a passing allusion, but is repeated in an insistent way, with a clear assertive character and a richness of visual details. After describing the numbing and painful sensation ('intormentimento') produced by the fish shock he writes:

> It must be remarked in first place that when I made these trials, I felt pain and numbness only when I squeezed those two bodies, or muscoli falcate, and the fibres, they are made of, did contract; while I did not feel any kind of alteration when they did not contract and remained in their natural state (16, p.108).

He is even more explicit in a further passage, in which he attempts to establish a somewhat quantitative relationship between the intensity of the perceived shock and the strength of the contraction in the fibres of the *muscoli falcati*:

> It must be noted that the numbness varies in accordance with the contraction of the fibres: in such a way that, when the fibres contract in a vigorous way, then the torpor is very strong, and affects not only the hand, but also the entire forearm up to the elbow; when the fibres do not contract so intensively, but a little more slowly, then one only feels something like a fourmillement or creeping in the entire hand; and, when they contract very slowly, then one feels in the finger something like a convulsive motion, which comes back again when the fibres contract, whereas no alteration occurs in the hand that touches, when the fibres do not contract at all; as a consequence, the cause of torpor or numbness is the contraction of the fibres making up the muscoli falcati; which will be manifest to anybody wishing to perform this trial. (pp. 108–9).

These bold assertions of Lorenzini stand in sharp contrast with what the celebrated Italian naturalist and physiologist, Lazzaro Spallanzani, wrote about one century later, in a period in which, following Walsh's experiments, the electrical hypothesis had been firmly established. Spallanzani carried out a study of the torpedo during two journeys on the Mediterranean coast, made respectively in 1782 in various parts of the Adriatic region, and in 1783 at Portovenere, on the Riviera not far from Genoa. On this second occasion, profiting from the availability of a large number of living fish, he addressed with particular attention the problem of possible movements in the electrical bodies at the moment of the shock. Here is how he summarizes the conclusions of these experiments on the torpedoes in a letter published in 1784 and addressed to his famous correspondent, the Genevian naturalist and philosopher Charles Bonnet:

> By profiting of the occasion of these new experiences I wished to test them [the fish] with more heavy trials. You will hear in how many and many different ways I tormented them with the sharp metal, to see if the electrical shot was preceded or accompanied by some tremor or commotion, or shaking or contraction of the parts composing the organs: or, in short, to ascertain which was the material mutation underwent by these organs. Nor I left aside to explore them even with the microscope at the moment that preceded, accompanied or followed the shock. But I must tell you with the purest candour that I could never perceive even the smallest movements of the parts, except for that universal agitation of the body, companion, although inconstant of the electrical shot. I will tell you, moreover, that, having tormented the electrical organs with diverse and powerful stimuli, they never manifested that property which characterizes the living muscle. (18, p. 655)

By comparing Spallanzani's words with those written by Lorenzini one century before, and by considering that, in between, the prevailing scientific paradigm in interpreting the phenomena of living organisms had shifted from the mechanicism of the post-Galilean era to the electricism of the 18th century, one would easily endorse the opinion expressed by Thomas Kuhn in his celebrated essay 'The structure of scientific revolutions': 'with the mutation of the prevailing paradigm that characterizes scientific revolutions, scientists see new and different things even when they look with the same traditional instruments in the same directions where they had looked before' (19, p. 110). On this basis, the case of Lorenzini could be classified as a typical instance of an observation strongly influenced by subjective attitudes, or, as modern philosophers of science say, an observation 'laden' with an *a priori* theories.

What, perhaps, would remain to be ascertained is whether, in Lorenzini's case, the mechanistic paradigm influences the act of seeing in its primitive sensory meaning; or, alternatively, whether it affects seeing as an act of judgement on sensory appearances that did not really change between him and Spallanzani (and Walsh). In a great number of languages there is indeed a large superposition between the semantic area of the vision and that of the understanding. In English, for instance, when one says: 'I see the problem', it may actually mean that one understands what the problem is. It might also be surmised that Lorenzini's description is not an actual observation, but a theory which is visualized by its author and made real through some kind of literary artifice: as a consequence, what is described would not be the phenomenon truly observed, but what one assumes should occur, on the basis of his own explicative model.

Without denying the role of subjective influences in various phases of the process leading to scientific knowledge, I propose here a different view of the matter: in the case of Lorenzini and Spallanzani; the phenomenon visually observed would be truly different, and not simply the way the two observers looked at it.

Spallanzani utilized a variety of methods in order to stimulate the shock of torpedo, and, particularly in the experiments aimed at verifying the presence of movements in the organs, he did not usually directly touch the fish with his hand but used a metallic object to both provoke and feel it. In his case, Lorenzini, in order to produce the shock, usually established an immediate contact with the fish, and in most cases he squeezed or held tightly its body.

If one tries to reproduce this last condition, what happens is that the electric shock of the fish, *per se* independent on any movement of the organs, stimulates the hand keeping the fish and induces in it a tremor which continues as long as the fish repeats its discharge and the observer keeps his hold. The tremor would be stronger and would diffuse to a larger portion of the observer arm when the fish gives a stronger shock. Under all these circumstances, however, if (as Lorenzini did), the experimenter keeps hold of the fish during the observation (in spite of the unpleasant sensation felt), its hand transmits the tremor to the fish. As a consequence, the fish's body actually moves. In other words, under the circumstances of Lorenzini's experiments, the organs of the fish, or *muscoli falcati* would really move, even though this movement, far from being the cause of the shock, is actually its effect (and indeed a secondary and mediated effect).

Besides doing some justice to Lorenzini (who should thus not be considered some kind of a visionary, or a scientist incapable of distinguishing facts from theories, even though his mechanical hypothesis would not stand the test of time), this conclusion should encourage caution in philosophers of science so as not to uncritically overestimate the importance of subjective factors and conceptual structures in scientific observation. Although Lorenzini was very probably influenced by the mechanical concept, this paradigm might not have been the only reason for him to see movements associated with the torpedo's shock. There are linguistic considerations relevant in this context. In various languages torpedo or other electrical fish (electrical eel and electric catfish) are indicated with common names alluding to their 'trembling' capability (tremola, tremula, tremolo, tremble, trembleur, tremielga, trembladora, tremoló, tremolosa, trembladeira, Zitterrochen, anguille tremblante, trembling eel, Zitter-Aal, Zitter-Wels etc.) and it very unlikely that these names were attributed to them by people under the influence of mechanical concepts. Very probably they are the results of a cause-effect substitution, as in the case of Lorenzini's observation (according to our interpretation).

CONCLUDING REMARKS

Aware as we are of the involvement of electricity in important aspects of animal physiology (and notably in nerve and muscle physiology), we may perhaps have difficulty in realizing how hard it was, more than two centuries ago, to arrive at the conclusion that electricity might have any role whatsoever in living organisms. In his manuscript journal of the experiments at La Rochelle, Walsh expressed this kind of difficulty, by writing, on his first experience of torpedo's shock: 'this is certainly Electricity, but how?' (10, p. 7) (12). Besides the objections already considered (and based on the electrical conductive nature of animal tissues), for the case of a fish there was the additional difficulty represented by the conductive nature of the liquid habitat of the animals: electricity generated in a fish by a physiological mechanism would be rapidly dissipated by the medium surrounding its body.

For the science of the epoch, an 'electric fish' seemed a nonsense, something like a charged electrical device (a Leyden jar for instance) plunged in water. However, in spite of apparently sound theoretical difficulties, eventually it emerged that the fish shock was really electrical. Since the period of Isaac Newton, one of the important *regulae philosophandi* of the new science was that evidence obtained from experimental work should be considered more valuable than any opposing theoretical hypothesis (20, p. 389). The experimental nature of the acquisition of scientific knowledge had been indeed one of the characterizing aspects of the scientific revolution of the 17th century. This was why Walsh's results with electric fish were so important for the further development of electrical research on the involvement of electricity in animal physiology. The fact that they played also an important role in the discovery of the electric battery, is one of the unpredictable and fascinating events of the history of science.

At the beginning of this article we considered the cochlear implant as an example of the importance of electricity in audiology in both its technological and physiological aspects. Before the introduction of this device in audiological practice, many (and sound) objections were raised against the possibility that a cochlear implant could be of some value in restoring hearing in deaf patients (five important ones are discussed by Grahame Clark in a chapter of a recent textbook of audiology (21). Tracing an ideal link from 18th century electrical science to modern medicine, we could thus perhaps conclude that another characteristic of science, particularly prominent at the moment of great discoveries and of important inventions, is its unpredictability and the challenge it sometimes issues against 'commonsense'.

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