# Drawing a spark from darkness: John Walsh and electric fish

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**John Walsh's research on electric fish, carried out between 1772 and 1775, proved fundamental for demonstrating that electricity might be involved in animal physiology, and, moreover, in favouring a period of great progress in both the physiology and physics of electrical phenomena. However, Walsh is hardly known to modern neuroscientists and is largely neglected by science historians also. One of the reasons for this neglect is that he never published his 'crucial experiment', that is the production of a spark from a discharge of the electric eel.**

> 'It is with pleasure that I inform you that they have given me *an electric spark*, perceptible in its passage through a small gap or separation made in a tin lamina pasted on a glass. These fishes were in the air; since this experience has not succeeded in water; their electricity is very much stronger than that of the Torpedo, and there are some considerable differences in their electrical effects.'

These few lines, printed in 1776 in an important scientific journal published in Paris by Abbé François Rozier [1], are of great historical relevance, because they report the first successful attempt to obtain a visible spark from an electric fish, the eel of Surinam or *Gymnotus* (Fig. 1). The results of the experiment were never published by the researcher, John Walsh (1726–1795), fellow of the Royal Society and member of the English Parliament. Walsh, however, wrote to Jean-Baptiste Le Roy, who transcribed these lines in a correspondence published in Rozier's journal. The passage reported represents an 'abstract' of an experiment never to be published *in extenso*.

Walsh demonstrated the eel's spark experiment to colleagues and visitors in his London house in the summer of 1775 (and on later occasions). This peculiar way of publicizing scientific results (which often preceded the written report) depended, in part, on the necessity to have numerous and authoritative witnesses of scientific results, in the absence of other direct objective ways of documenting them. It was particularly necessary for a result that had been sought after unsuccessfully for so long. The production of a spark from the discharge of an electric fish was an event open to incredulity, because the idea that a fish shock was really electrical '...seemed, in some respects, to combat the general principles of electricity' [2], as we will explain.

This experiment addressed the issue of the identity between the common type of electric fluid (e.g. the electricity produced by electrical friction machines and accumulated in capacitors such as Leyden jars) and the 'fluid' involved in fish shock. Even though not published by Walsh, the news of his experiment spread to all the 'Republic of Letters' (learned community) of the time, mainly owing to the wide circulation of Rozier's journal, and the description of the experiment in contemporary scientific publications (see, for example, [3]). Together with the news of Walsh's previous experiments on the torpedo, it promoted a fresh interest in the possible involvement of electricity in 'animal economy' (animal physiology), and, probably, contributed to Luigi Galvani's decision to start his famous experiments on frog muscle contraction [4,5].

With time, however, memory of Walsh's experiment on the eel diminished gradually. Apparently, the experiment was unknown to Faraday, who repeated it in 1839 [6]. A few years before Faraday's experiment, Santi Linari and Carlo Matteucci succeeded in producing a spark from a torpedo [7,8], thus, concluding the phase of research into electric fish started by Walsh in 1772. Memory of Walsh's experiment on the eel was lost, at least partially, to science historians also. For example, Mary Brazier cast doubts on Walsh's achievement. In referring to Walsh and to the spark, she writes that 'later it was claimed that he had demonstrated this with the *Gymnotus*', and 'a discourse on the history of the electric properties of the torpedo, delivered in 1775 to the Royal Society by the eminent Sir John Pringle, mentioned no sparks' [9]. However, the discourse of Pringle, printed in 1775, was delivered on 30th November 1774 upon awarding Walsh the Copley medal (a kind of Nobel prize for the time) for his previous studies on the torpedo, and, thus, preceded Walsh's achievement with the eel [10]. Walsh himself seems destined to oblivion, notwithstanding all the important work that he did on the torpedo and all the further research he promoted directly or indirectly. Walsh's name is not listed in the *Dictionary of Scientific Biography*, or in recent editions of the *Encyclopedia Britannica*.

Among the witnesses to Walsh's experiment on the eel, Le Roy mentions more than 40 fellows of the Royal Society, and, from their report, we know that the shock could pass through a chain of 27 persons (all feeling it) and the experiment 'was repeated up to ten, twelve times'. The crucial importance of the event is attested by the sudden 'conversion' of William Henly, an eminent 'electrician' of the time. Shortly before the experiment, Henly outlined his scepticism about the electric nature of fish shock in an expressive way.

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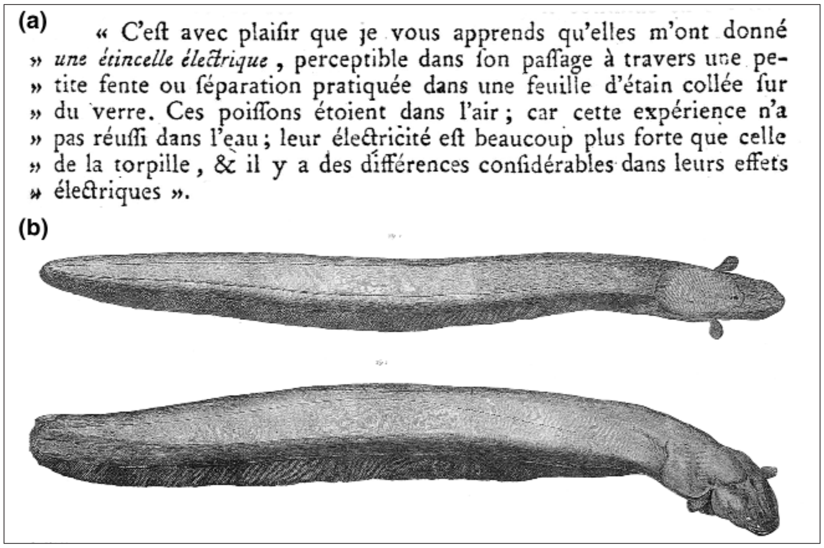


**Fig. 1.** (a) The passage of Walsh's letter describing his experiments on the spark produced by eels (reproduced from [1]). (b) A view of an electric eel (*Electrophorus electricus*) used by Walsh for his physiological experiments, and by Hunter for his anatomical observations (reproduced, with permission, from [30]).

> 'When a Gentleman can so give up his reason as to believe in the possibility of an accumulation of electricity among conductors sufficient to produce the effects ascribed to the Torpedo, he need not hesitate a moment to embrace as truths the greatest contradictions that can be laid before him.' [11]

However, after attending Walsh's experiment, he became enthusiastic and planned to determine the direction of the spark by using an apparatus built for this purpose [12]. Henly's original scepticism concerned the objections raised in the 18th century against the possibility that electricity could be accumulated in living tissues and involved in some physiological mechanisms, and, particularly, in nervous conduction. This possibility was challenged by Albrecht von Haller and his followers. Electricity, they argued, tends to diffuse from where it is in excess to where there is less if the two places are connected by conductive substances [13]. Because living tissues conduct electricity, no stable imbalance could exist inside animal bodies, and, consequently, the force required to move electricity through nerves for their function would not be present. Furthermore, it was difficult to envision how electric flux could be restricted to the specific nerve paths required by physiological needs. Were the nervous fluid of an electrical nature, argued Haller, we would move all the muscles of the foot when we wanted to move a single toe [14]. In the case of fish, a further difficulty arose from the conductive nature of their natural habitat; an 'electric fish' seemed a nonsense, somewhat like a charged Leyden jar plunged in water.

In spite of these difficulties, however, fish shock appeared to be similar to that produced by a Leyden jar (as noticed soon after the invention of this first electric capacitor). Moreover, it was transmitted by conductive bodies and arrested by insulating matters in a similar manner to the discharge of the Leyden jar. On the basis of such observations made on the 'torporific' eel of Guiana, Edward Bancroft questioned the mechanical interpretation of the torpedo discharge advocated by René-Antoine De Réaumur.

> '...it is self-evident that, either the mechanisms and properties of the Torpedo and those of the Torporific Eel are widely different, or that Mons. *De Réaumur* has amused the world with an imaginary hypothesis: and, from my own observations, as well as the information which I have been able to obtain on this subject, I am disposed to embrace the latter inference.' [15]

Encouraged by discussions with Benjamin Franklin, Walsh decided to verify Bancroft's assertion, and in 1772 he crossed the channel, convinced of the impossibility of obtaining live torpedoes in England (see, however, [16]). From June 26th to July 27th he carried out an extended series of experiments on torpedoes at La Rochelle and l'Isle de Ré that convinced him fully of the electrical nature of their discharge. These experiments were published in 1773 in the form of a letter to Benjamin Franklin, together with the anatomical observations performed by John Hunter on the same torpedoes used in physiological studies [2,17] (Fig. 2).

Walsh's investigations are reported also in a lively form in a 'journal of experiments' manuscript, also neglected by historians, in which a description of the progress of daily work is presented, together with 'reflections' and annotations of various natures [18]. Through these writings, we can follow, from a privileged point of view, a crucial phase of the scientific progress of the 18th century. The electric fish, for centuries an object of curiosities and legends, more suited for a *Wunderkammer* than for a laboratory [19,20], became the subject of a scientific investigation that, as Walsh anticipated, could open 'a large field for interesting enquiry, both to the electrician in his walk of physics, and to all who consider, particularly or generally, the animal economy' [2]. This passage may be considered, *a posteriori*, somewhat 'prophetic' if one considers that, through the work of Luigi Galvani, research on electric fish opened the path to modern electrophysiology [4,5] and, through the scientific endeavour of Alessandro Volta, led to the discovery of the laws of the capacitor and the invention of the electric battery [21] (Figs 3,4).

As in the case of Galvani and Volta, Walsh's research was characterized by a productive interchange of a physical and physiological disposition. Upon his arrival at La Rochelle, and before obtaining live torpedoes, Walsh interrogated local fishermen and noted:

> '...gave one of them a small Shock with the Leyden Phial and repeated it; he insisted that the Effect was precisely the same with that of the Torpedo.'

On June 30th, he experienced from 'a female Torpedo' his first shock, which reached, he said, '...half way of the part of my arm above the Elbow; both instantaneous in commencement, and ending precisely as an Electric shock'. A side-note testifies to Walsh's initial incredulity on the electrical nature of fish discharge.

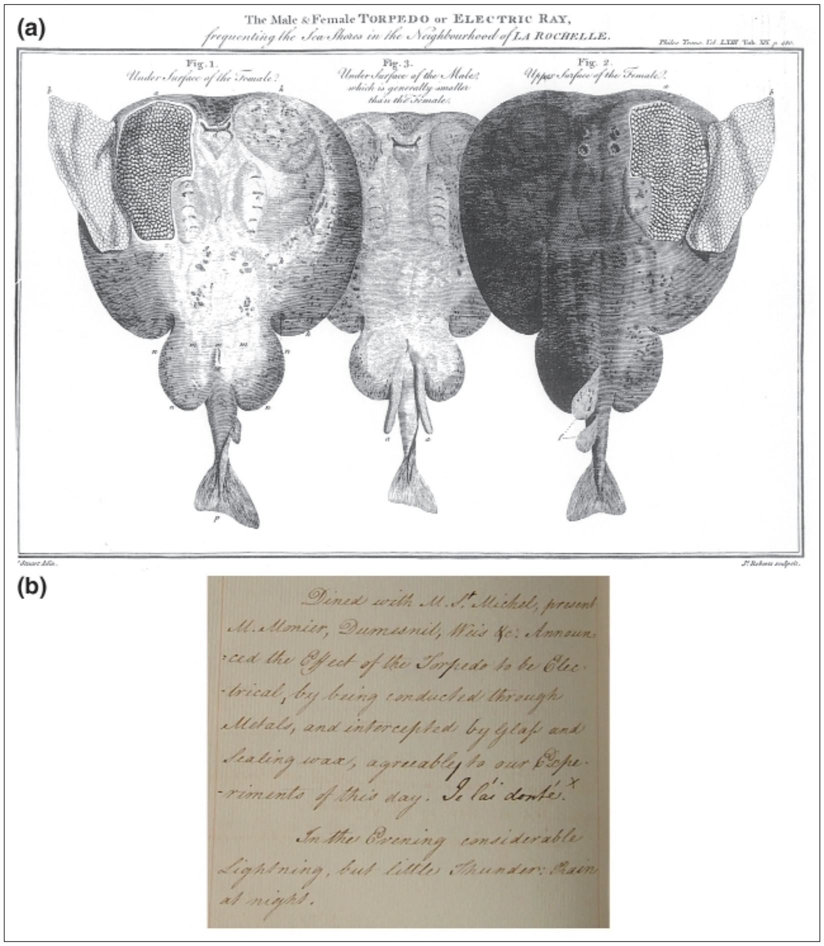


**Fig. 2.** (a) Torpedoes studied by Walsh in La Rochelle and used by Hunter for his anatomical investigations (reproduced from [17]). (b) The passage of Walsh's journal of experiments alluding to his first announcement of torpedo's electricity: 'Dined with M. St. Michel, present M. Monier, Dumesnil, Weis, &c. Announced the Effect of the Torpedo to be Electrical, by being conducted through Metals, and intercepted by Glass and sealing wax, agreeably to our Experiments of this day. *Je l'ai donté.*' (reproduced, by courtesy of the Royal Society, London, from [18]).

> 'On this my first experiment on the effect of the Torpedo, I exclaimed this certainly Electricity – but how?'

On this point, however, Walsh passes rapidly from scepticism to enthusiasm. This occurred particularly on July 9th, during a long series of experiments in which Walsh and his nephew Arthur, forming a circuit with the fish, showed that the shock is transmitted by a metal, whereas it is arrested by glass and sealing wax. These experiments, varied and repeated many times, are reported in short notes that convey the idea of a rapid crescendo, as, for example, when comparing the conductive properties of different materials.

> 'Touched the upper and lower sides of the same flank with Spoons; Shock, twice.
> Repeated it with Spoons; a Shock.
> With sealing Wax; nothing.
> Repeated it with spoons; Six times.
> With sealing wax, twice; nothing.'

In the evening, Walsh announced publicly the electrical nature of the torpedo, and in his journal the pride of the discovery is manifested by a note in French – '*Je l'ai donté*' (i.e. '*dompté*', 'I have tamed it'; Fig. 2) – alluding to a verse of the Latin poet Claudian, 'Who did not hear of the untamed art of the wonderful Torpedo?'. The announcement was made to eminent personalities of La Rochelle, some of whom, as members of the local *Académie,* were involved directly in these experiments. Three days later, Walsh sent a letter to Franklin (included in the 1773 paper), to communicate 'with particular satisfaction…that the effect of the Torpedo is absolutely electrical', and asked him 'to acquaint Dr. Bancroft of our having confirmed his suspicion concerning the torpedo'.

During his last days at La Rochelle, Walsh gave public exhibitions of the 'electric power of the Torpedo', which were reported in the *Gazette de France*, thanks to a correspondence of the Academy secretary and Mayor of the town, Monsieur Seignette, who confirmed that the commotion experienced by various persons connected in a circle '…differed in nothing from that of the Leyden experiment' [2]. A ramification of these demonstrations was the exhibition of the torpedo's shock requested of the *Académie* by the Austrian Emperor Joseph II, who, in 1775, experienced the shock personally [22].

However, in spite of similar characteristics between the torpedo's effects and artificial electricity, differences also 'were remarked by the Company', who noticed that fish shock 'was attended with neither Spark nor Sound, that it occasioned no Attraction and Repulsion'. Before voltaic batteries, electricity was produced commonly with friction-type electric machines, thus, resulting in electric performances involving tiny charges and very high tensions (more that 10 000 V). Attraction and repulsion, sparks and sounds were, in these circumstances, landmarks of genuine electrical phenomena. Indeed, Walsh had tried, without success, to obtain these 'typical' electrical signs from the torpedo with 'a narrow strip of Tinfoil being pasted on a stick of sealing wax, and a very minute interstice made in the Tinfoil, by only drawing the edge of a sharp knife across it'. A similar method was to be effective in 1775 with the eel, due to the larger potential of the shock of this fish (up to 600 V) compared with that of the torpedo (~50 V).

Thus, torpedo electricity and genuine electricity did not appear to be identical. As for the absence of attraction and repulsion, Walsh could assume easily that the production of electricity by the fish was an instantaneous process, too rapid to produce any mechanical effect. It was more difficult to account for the absence of sparks and sounds, and for the inability of the shock to pass across 'the minutest separation possible made in Tinfoil'. These difficulties could not be dismissed by saying that torpedo electricity was weak. 'The Torpedo' – Walsh notes – 'often gives severe Shocks, his Electricity therefore cannot be deemed weak'.

It is precisely in what seemed to be the most serious difficulties against the identity between 'torpedinal' and electrical fluid, that the research started by Walsh proved to be of fundamental importance for the understanding of the physical laws involved in electric phenomena, as he had anticipated during his public exhibition at La Rochelle.

> '…as artificial Electricity had led to a discovery of some of the operations of the Animal, the Animal if

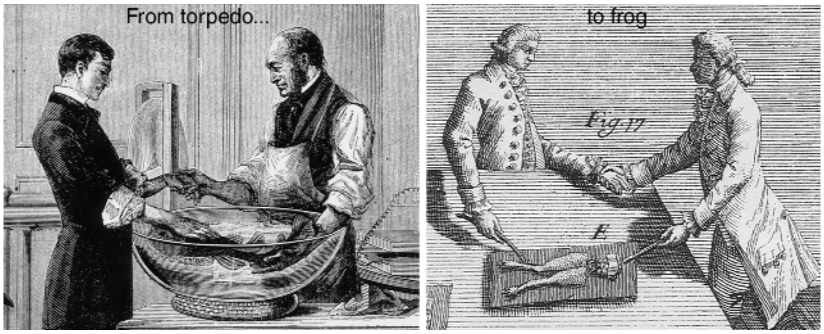


**Fig. 3.** Analogy of Galvani's experiments on muscular motion with the experiments showing the electric nature of torpedo's discharge. On the left, two investigators forming a circuit experience the shock of a torpedo when they touch the dorsal and ventral surface of the fish, respectively (from an end of the 18th century illustration, signed B. N/J-L. Charmet, by courtesy of P. Moller). On the right, frog's muscles contract when the two investigators touch each other and establish a contact with the frog's muscular and nervous tissue, respectively (reproduced from [31]).

> well considered would lead to a discovery of some truths in artificial Electricity which were at present unknown and perhaps unsuspected.'

As Walsh elaborated upon his return from France, the fish shock, with regards to both the 'positive signs' of electrical nature (commotion and passage through conductive bodies) and 'negative phenomena' (i.e. absence of attraction, repulsion, sparks and sounds) 'may be imitated by art' with purely physical devices [2]. Through a pneumatic analogy, Walsh assumed that electric effects do not depend exclusively on the quantity of electricity involved, but, also, on the 'dense or rare state' that electric matter might assume. If a given quantity of electricity is 'condensed', as it occurs in a 'highly charged', 'small Phial', then it will be 'capable of forcing a passage through an inch of air, and afford the phenomena of light, sound, attraction, and repulsion'. If the same quantity of electricity is made 'rare' by communicating it to large Leyden jars, then 'it will not now pass the hundredth part of that inch of air', and yet it could produce sensible effects. This last condition imitates the electrical state responsible for torpedo's shock, and Walsh mentions that 'Mr. Cavendish' has, indeed, succeeded in showing 'that a shock could be received from a charge which is unable to force the passage through the least space of air'.

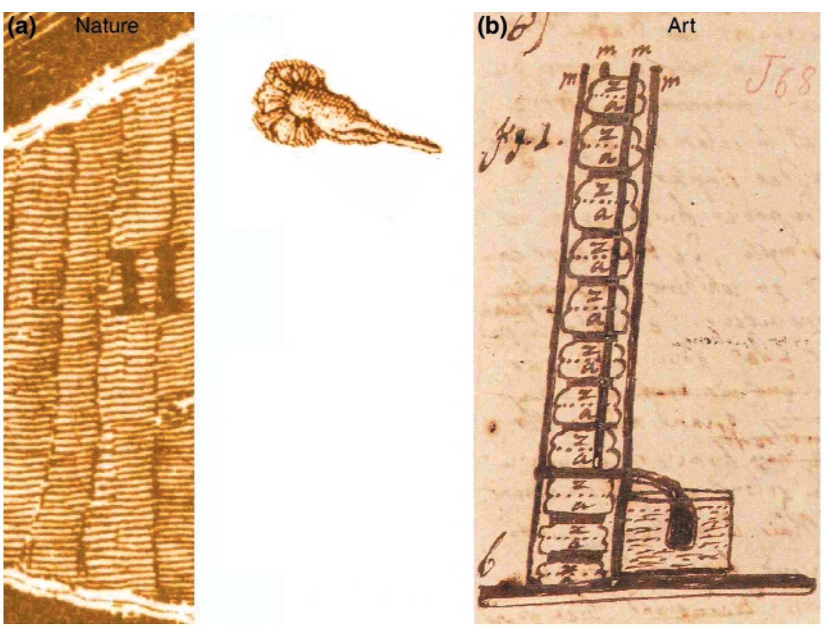


**Fig. 4.** The structure of the electric organ of fish, with its columns of membranous disks, inspired Alessandro Volta to assemble, in a stack-like manner, several disks of two different metals and a humid element, thus, leading to the invention of the electric battery. (A, modified from [17]; B, drawing from Volta's draft of the communication of battery invention, by courtesy of the Istituto Lombardo, Accademia di Scienze e Lettere, Milan.)

**Fig. 5.** Vertical section of one of the torpedoes studied by Walsh in his experiments in France and used by Hunter for his anatomical investigations, showing the structure of the electric organ and its rich innervation (reproduced from [17]).

Here, Walsh alludes to the experiments that led Henry Cavendish to build up an 'artificial torpedo' capable of imitating a natural torpedo, in producing strong shocks and lacking attraction, repulsion and visible sparks, and in the inability 'to pass through the least sensible space of air'. Like the natural fish, the artificial torpedo could also produce commotion even when immersed in water, if powered by many Leyden jars charged to a low degree. Cavendish gave public demonstrations of his device, and, in 1776, he published an important paper in which he identified the 'degree of electrification' and the 'quantity of electric fluid' as the determining factors responsible for electric effects. In some way, Cavendish anticipated Volta in the elaboration of the concepts of tension and charge and of the laws of the capacitor [23].

In his paper, Cavendish makes frequent allusions to Walsh's studies on the torpedo, and, in particular, he mentions that, according to him, the shock produced by many weakly charged Leyden jars resembles the shock of the natural torpedo more than that produced by a strongly charged small jar does. Both Walsh and Cavendish assumed that the torpedo could accommodate a great quantity of electric fluid, in an uncompressed state, in the large surface of the staked membranous elements that make up the structures denoted as 'electric organs' by Walsh himself. At the end of the century, a reflection of the electric organs was to be of importance for Volta's invention of the electric battery. Volta would call it an '*organe eléctrique artificiel*', not only for its similar shape but, also, because, in his opinion, the battery resembled the natural organ in being capable of producing electricity by the 'mere contact of conductive substances' [24] (Fig. 4).

The electric organs of fish were the subject of accurate anatomical studies by John Hunter (Fig. 5), whose association with Walsh and Cavendish in electric fish research seems to prefigure the

**Box 1. The discharge mechanisms of electric organs, by Richard D. Keynes.**

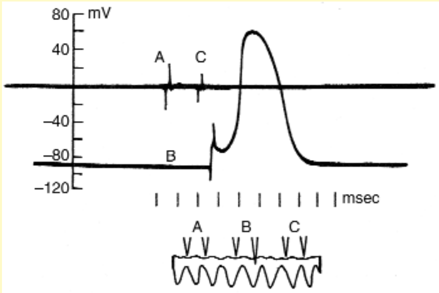


**Fig. I.** Membrane potentials recorded from an electroplate in a specimen of *Electrophorus*, with two electrodes connected differentially approaching through the nervous face. Record B shows that the signal recorded across the nervous face reverses the potential at its peak. Similar records made with the electroplate inverted showed that the potential across the non-nervous face remained constant during the discharge. Reproduced, with permission, from [2].

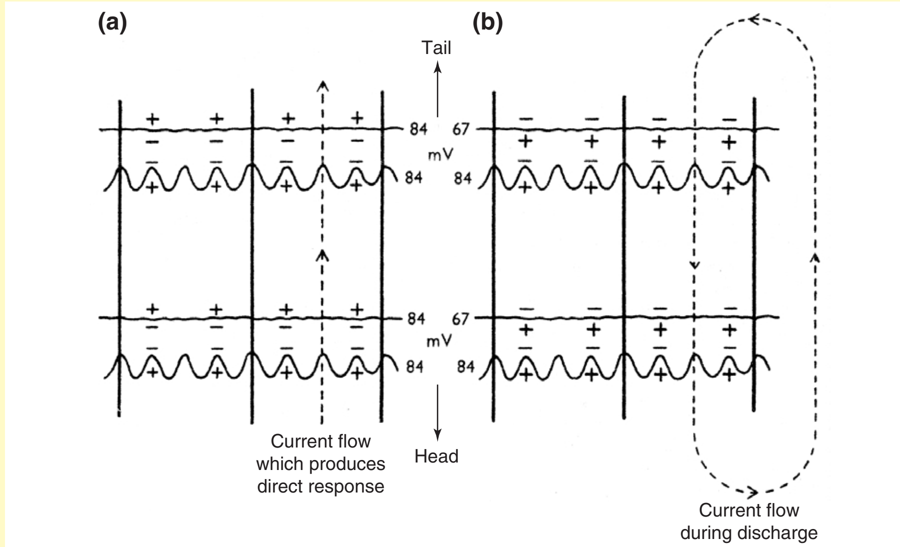


**Fig. II.** Diagram illustrating the additive discharge of the electroplates in Electrophorus. At rest (a) there is no net potential across the stack of electroplates, but at the peak of the spike (b) all the potentials are in series, and the head of the eel becomes positive with respect to its tail. Reproduced, with permission, from [2].

Electric organs of widely varying sizes and anatomy have evolved independently in different families of fishes of both fresh and sea water, and are almost all derived embryologically from muscle fibres. These fishes generate electricity through membrane processes that are similar to those involved in electric phenomena of other animals, but, unlike them, these fishes can produce large potential differences at their body surface, and thus affect other animals living in their habitat [1]. Normally this occurs because the individual cells in the stacks of electroplates are asymmetrical, maintaining a constant resting potential across one face (normally not innervated), while a command from the CNS generates a brief electrical response in the other face, which receives a strong innervation (nervous face). This was first explained in experiments carried out on the electrical eel, *Electrophorus electricus*, just 50 years ago, soon after intracellular recording electrodes had become available [2]. In *Electrophorus*, this response is a normal $Na^+$-dependant reversal of the membrane potential, so that on open circuit, each electroplate contributes about 150 mV at the peak of the spike (Figs I,II). In *Torpedo* the innervated face of the electroplate behaves differently because it consists in effect of a closely packed mass of motor end plates, and responds to the release of acetylcholine from the nerve terminals with a non-selective increase in membrane permeability, without generating action potentials. The potential across the non-innervated face remains at its resting level, so that each *Torpedo* electroplate contributes about 80 mV to the total discharge. Another powerful electric organ is that of African electric catfish, *Malapterurus*. It is again derived from muscle, and depends on an asymmetrical $Na^+$-dependant action-potential discharge, but the internal anatomy of the individual electroplates is complicated by an arrangement that delays the discharges to compensate exactly for the conduction time in the command signal from the single neuron that controls each half of the electric organ, and thus neatly synchronizes all of them [3]. The electric organs of the small gymnotid and mormyrid fishes of South America and Africa that are equipped with electric direction-finding systems generate relatively low-voltage signals, and can be modified to enable them to discharge at a specially high frequency. The electric organ of the gymnotid fish *Apteronotus* is peculiar in that it is derived from myelinated nerve fibres instead of muscle fibres.

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interdisciplinary character of modern science. Hunter underlined the rich innervation of the electrical organs, supposing that it '…must on reflection appear as extraordinary as the phenomena they afford'. With reference to the electrical nature of torpedo shock, Hunter supposed that nerves might be '…subservient to the formation, collection, or management of the electric fluid' and concluded, in a manner that appears to anticipate the importance of electric fish studies for the development of neurophysiology (Box 1):

> 'How far this may be connected with the power of the nerves in general, and how far it may lead to an explanation of their operations, times and future discoveries alone can fully determine.' [17]

In spite of the evidence provided by Walsh and Cavendish, the apparent inability to draw a spark from the torpedo appeared to many as an expression of some essential difference between common electrical phenomena and fish shock. This explains the 'crucial' importance that the scientists of those

**Box 2. Nerve cells and electricity: from Galvani to Hodgkin**

Although Walsh demonstrated experimentally that animals can be 'electric', he did not account for how electricity could be stored in tissues made up of conductive matter (see text). This problem was central to the logical elaboration of Luigi Galvani of Bologna, who, in 1791, provided firm experimental evidence for the involvement of electricity in neuromuscular function. According to Galvani, an electric disequilibrium exists between the interior and exterior of muscle fibers, and it does not dissipate because of the insulating property of the delimiting surface between the two compartments. Galvani supposed that a nerve fiber penetrates inside a single muscle fiber, thus, allowing for electrical flow between the interior and exterior of the muscle fiber when required by physiological needs. This is similar to what occurs in a Leyden jar, where a metallic conductor serves to connect the internal and external coatings to discharge the accumulated electricity. To appreciate the far-sightedness of Galvani's conception we should consider that, in his days, the cellular theory had yet to be formulated.

Galvani's theory was somewhat revived more than a century later by Julius Bernstein, who elaborated the 'membrane hypothesis' of bioelectric potentials; an electrical potential arises across a plasma membrane because of the ionic concentration differences existing between the intra and extracellular compartments [a,b]. Specifically, membrane potential would depend on potassium ions because, at rest, the membrane is selectively permeable to these ions. In Bernstein's hypothesis, an electrical disequilibrium exists, and does not dissipate, in spite of membrane permeability to electrically charged particles, because it contributes to the maintenance of an overall electrochemical equilibrium across the plasma membrane. If positive charges enter into the cell because of the intracellular negative potential, potassium ions diffuse outward owing to the concentration gradient and, thus, re-establish the equilibrium.

In Galvani's conception, nerve conduction was a passive phenomenon, similar to electric flow along metallic cables, and depended on the electrical disequilibrium existing across the muscle-fiber membrane. However, during the 19th century, it became clear that an electrical disequilibrium exists also in nerve cells, and that nerve conduction differs from passive electric conduction along a cable. Bernstein proposed that the nerve signal comprised a sudden disappearance of the resting potential owing to an increase in membrane permeability to all ionic species; and that it was propagated along the fiber by local current fluxes from the excited region to the region ahead, as envisioned initially by Ludimar Hermann [c].

Particularly relevant for understanding the mechanism of nerve conduction was the idea that the nerve signal regenerates during its propagation, using energy accumulated along the fiber membrane, in a manner formally similar to firing progression along a gun-powder track. This idea emerged from the work of Keith Lucas and Edgar Douglas Adrian at the beginning of the 20th century [d,e]. The complete elucidation of the mechanism of nerve conduction had to await the work started by Alan Hodgkin in approximately 1934. In 1939, Hodgkin and Huxley showed that the nerve action potential involves a polarity-inversion phase, unaccountable for in Bernstein's hypothesis [f]. The subsequent experiments of Hodgkin, Huxley and Katz, culminating in a series of fundamental papers published in 1952 [g–k], demonstrated that the upstroke of the action potential is due to an influx of sodium ions along their electrochemical gradient. This results from a regenerative increase of membrane sodium permeability; membrane depolarization increases sodium permeability, and this, in turn, leads to further membrane depolarization as a consequence of the resulting sodium influx. This process accounts for electric signal regeneration along the fiber at the expense of the local electrochemical energy gradient accumulated across the plasma membrane. The necessity for such a complex mechanism depends on the physical difficulties of conducting electricity in thin fibers made up of materials that, contrary to the supposition of 18th century physiologists, are poorly conductive compared with metals. Hodgkin calculated that the longitudinal resistance of a long, thin nerve fiber could be of the same order of magnitude of that of an ordinary electric cable extending several times the distance between the earth and the planet Saturn [l].

After Hodgkin, membrane electrophysiology has been dominated by the notion of ionic channels, the molecular structures that allow for ionic fluxes across the membrane in a manner that might depend on membrane potential, the action of ligands and various physico-chemical influences. An epochal event for studies of ionic channels was the introduction by Erwin Neher and Bert Sakmann of the patch-clamp technique, which makes it possible to record the elementary current across a single channel with a time resolution that has no counterpart in the study of other molecular structures [m,n]. But this is contemporary history.

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days attributed to Walsh's achievement with the eel, an importance commented on by Tiberio Cavallo in 1795 with these words:

'The subject of Animal Electricity was considerably advanced by the discovery of the spark, with which the shock of the *Gymnotus* was attended; for, notwithstanding the previous discoveries relating to the torpedo, and the actual possibility of imitating the effects of that animal's extraordinary power by means of a large battery weakly charged with artificial electricity, yet the scrupulous philosopher still suspected that the power of the torpedo might be something different from electricity, since the two principal characteristics of Electricity, namely the spark and attractions, had never been discovered in the torpedo.'[25]

By demonstrating that electricity could serve a physiological process, the eel's spark undermined Haller's objections against the electrical nature of 'nervous fluid'. With regard to the principle responsible for neuromuscular functions, Felice Fontana, one of the strongest supporters of Haller's conceptions, wrote in 1781:

> '...that principle, if it be not common electricity, may be something, however, very analogous to it. The electrical *Gymnotus* and torpedo…make it at least possible, and this principle may be believed to follow the most common laws of electricity.'[26]

In 1780, Galvani had indeed started the experiments that led him eventually to discover the existence of an intrinsic 'animal electricity', analogous to that of electric fish, in the nerves and muscles of common animals (Box 2; Fig. 3). At the time, Volta was interested also in electric fish research, and in 1782 he gave an account of Walsh's experiment, containing some noteworthy details based on a personal conversation with Walsh [27]. In particular, Volta wrote:

> 'Mr Walsh...has discovered in the said eel what can rightly be called an *electric sense*. If one puts in the water tub where the eel is, one, two, or more good conductors, but separated, the animal does not seem to be affected at all; but, as soon as a communication is established between two of these plunged conductors so as to complete the circuit, and the parts of the conductors that are outside the tub are also reunited, the animal becomes agitated, and rushes to them, and brings the extremity of its head to one end of this *conductive arc* as if he would like to smell it, he provokes the electric discharge, which hits the intermediate person or persons, assuming that these create the chain linking the two conductors.'

Even this aspect of Walsh's work (mentioned also by other scientists of the time) has been largely ignored. In particular, it was unknown to those who tried to explain why some fish endowed with electric organs could avoid obstacles or localize prey in complete darkness. Possibly, this might explain why electroreception was discovered only about two centuries after Walsh [20].

### Concluding remarks

Buried in the dark side of scientific development, other important observations might be lost forever. The evolution of scientific knowledge from the past to the present might appear as sharp as the clear-cut profile of a bridge arch viewed from a distance. In Italo Calvino's *Invisible Cities*, Marco Polo remarks, however, that a bridge arch cannot exist without its constitutive stones [28]. John Walsh is one of the foundation stones of neurophysiology, and his scientific endeavour should be of interest, at least, to those who contribute now to the progress of this science.

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