Maxwell's Current in Mitochondria and Nerve, Version 3

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Abstract

Maxwell defined a ‘true’ or ‘total’ current in a way not widely used today. He said that “... true electric current ... is not the same thing as the current of conduction but that the time-variation of the electric displacement must be taken into account in estimating the total movement of electricity”. We show that the true or total current is a universal property of electrodynamics independent of the properties of matter, shown using mathematics without the approximation of a dielectric constant. The resulting Maxwell Current Law is a generalization of the Kirchhoff Law of Conduction Current used in circuit analysis, that also includes the displacement current. Engineers often introduce the displacement current through supplementary circuit elements, called ‘stray capacitances’.

The Maxwell Current Law does not require currents to be confined to circuits. It can be applied to three dimensional systems like the electron transport system of mitochondria and the signaling system of nerve cells. The Maxwell Current Law clarifies the flow of electrons, protons, and ions in mitochondria that generate ATP, the molecule used to store chemical energy throughout life. The currents are globally coupled because mitochondria are short. The Maxwell Current Law approach reinterprets the classical chemiosmotic hypothesis of ATP production. The conduction current of protons in mitochondria is driven by the protonmotive force including its component electrical potential, just as in the classical chemiosmotic hypothesis. The conduction current is, however, just a part of the true current analyzed by Maxwell. Maxwell’s current does not accumulate, in contrast to the conduction current of protons which does accumulate. Details of the accumulation do not have to be considered in the analysis of true current.

The treatment here allows the chemiosmotic hypothesis to take advantage of the knowledge of current flow in the physical and engineering sciences, particularly Kirchhoff and Maxwell Current Laws. That knowledge has been helpful in understanding action potentials in biology, and in technology in general. Knowing the current means knowing an important part of the mechanism of ATP synthesis.

Most scientists today are unaware of Maxwell's definition [1] of the 'true' current needed to estimate "the total movement of electricity":

> *"One of the chief peculiarities of this treatise is the doctrine which it asserts, that the true electric current, that on which the electromagnetic phenomena depend, is not the same thing as the current of conduction, but that the time-variation of the electric displacement, must be considered in estimating the total movement of electricity, so that we must write, [the sum] .... as an equation of true currents."*
>
> Note that '*peculiarities*' is a Victorian word (in formal 19th Century English) equivalent to *'characteristics'* or *'features'* in modern scientific American/English.
>
> The text is from Vol. 2, Section 610, p. 232. The *'equation of true currents'* is in, eq H, Vol.2, Sect 610, p. 233 of [1]. Maxwell uses the name *'Total current'* throughout his analysis 327-341 of Vol 1. This paper uses the names interchangeably, as defined in eq. (2).

Maxwell's definition is esthetically appealing because of its author, and its generality. It involves no adjustable parameters, beyond the electric and magnetic constants. It is numerically beautiful and helpful [2, 3]. It applies to systems that involve three dimensions, like stray capacitances of circuits, and mitochondria of biological cells. Maxwell's current is used to design important parts of our daily lives. Maxwell's current flows in the circuits that bring light and information (and power, voices, and images) to our homes and businesses. Circuit laws like eq. (2) and (5) are used to build these circuits.

It is interesting to compare Maxwell's idea of true current with the idea of current used in many papers and textbooks of electrodynamics. Many define current as the conduction current and do not discuss 'true' current explicitly, with little emphasis on displacement current. They certainly do not take the approach that the "*that the time-variation of the electric displacement, must be considered in estimating the total movement of electricity".*

Engineers, on the other hand, include the displacement current when they analyze real circuits. They define current as the conduction current, but they introduce supplementary circuit elements, called 'stray' or 'parasitic' capacitances into their idealized (branched) one-dimensional circuits to deal with the displacement currents of real systems that occur in three dimensions and involve coupling to nearby systems. Feynman has a particularly clear discussion of this practice in [4], Vol 2, Section 22-23.

This paper looks for a way to use Maxwell's idea of true current in a modern context useful in biology, as stray capacitances and displacement current have been useful in engineering. We show that the idea of true current casts a useful light on the role of sodium and potassium fluxes in the action potential of nerve and muscle cells [5-7].

We show that the idea of total or true current is needed if we want to estimate the '*total movement of electricity'* in mitochondria. There the total movement of electricity involves sodium Na^+ and potassium K^+ ions, hydrogen ions, and, of course, electrons. We show in particular that the movement of protons is coupled to the movement of all charges by the current laws eq. (2) & (5). The word 'proton' in the relevant biological literature is shorthand for the positively charged form of water, which can take on many chemical forms [8-11], depending on the context. Proton movement is not controlled by just proton 'concentration'. Current laws couple the protonmotive force to the electric field, and thus to the movement of all charges and membrane currents. This chemiosmotic flow of electrons and protons [12-20] is an essential biological system that generates ATP. [16-18, 20-24] ATP stores chemical energy throughout living systems. The hydrolysis of ATP provides most of the energy of life.

Fundamental Equations of Electricity. The partial differential equations introduced by Maxwell, summarized in [25], have been used for more than a century to describe the properties of electricity and its dynamics, in the form given in Feynman [4]. We start with the Ampere-Maxwell partial differential equation that describes how the magnetic field **B** is created by changes in the electric field $\mathbf{E}$ and the conduction current $\mathbf{J}$.

The charge and current are parsed in an unconventional manner here for reasons discussed below, immediately after variables are defined. The Ampere Maxwell equation is written here without the dielectric constant ε_r, more formally called the 'relative permittivity'. Dielectric currents are included in $\mathbf{J}$.

Ampere-Maxwell Equation $\quad \frac{\mathbf{1}}{\boldsymbol{\mu_0}} \mathbf{curl\ B} = \mathbf{J}_{\boldsymbol{true}} = \mathbf{J} + \varepsilon_0\, \partial \mathbf{E}/\partial t \quad$ $\mathbf{J}$ is zero in a vacuum (1)

$\mathbf{J}_{\boldsymbol{true}}$ is Maxwell's 'true current' (defined above in words) displayed prominently as eq. A, p. 465, 480 of [25]. ε_0 is the electrical constant. μ_0 is the magnetic constant. The parsing used here allows the fundamental eq. (1) to be independent of all other parameters. No properties of matter are included in this version of the Ampere-Maxwell equation.

The conduction current of charge ρ with mass is described by $\mathbf{J}$, however brief, small, or transient its flux. The conduction current $\mathbf{J}$ does not include the displacement current $\varepsilon_0\, \partial \mathbf{E}/\partial t$ found throughout space. The conduction current $\mathbf{J}$ does include the polarization current and the dielectric current $\varepsilon_0(\varepsilon_r - 1)$ of an ideal capacitor. In a vacuum, the only current $\mathbf{J}_{\boldsymbol{true}}$ is the displacement current $\varepsilon_0\, \partial \mathbf{E}/\partial t$. That vacuum displacement current $\varepsilon_0\, \partial \mathbf{E}/\partial t$ allows radiation like light to propagate in the space between the earth and the sun, which is nearly a vacuum.

Note that Maxwell's original statement of displacement current differs from that used here. Maxwell's original treatment included two components of displacement current. One of Maxwell's components was the displacement current of our eq. (1) $\varepsilon_0\, \partial \mathbf{E}/\partial t$ that is universal and has no adjustable parameters. The other component Maxwell used $(\varepsilon_\mathrm{r} - 1)\varepsilon_0\, \partial \mathbf{E}/\partial t$ depends on properties of materials. The material displacement current uses adjustable parameters and models to describe how material charge changes when the electric field changes. Maxwell's original treatment of displacement current can be reinstated from our equations in two steps. First, (1) by replacing $\varepsilon_0\, \partial \mathbf{E}/\partial t$ in our equations with $\varepsilon_\mathrm{r}\varepsilon_0\, \partial \mathbf{E}/\partial t$ and then (2) by changing the

definition of charge and conduction current correspondingly so displacement currents are not counted twice.

Current is parsed this way here so the Ampere-Maxwell equation (1) can be written as a universal law without explicit reference to the properties of matter. Eq. (1) has no adjustable parameters, beyond the electrical and magnetic constants. Without this rewriting, the fundamental field equations become constitutive, not universal laws, with the properties of matter—in all its diversity, with all its difficulties of measurement—embedded in its very definition of variables. This problem is widely recognized [26] Vol. 2, S 13-4, and the traditional formulation is strongly criticized [27], p. 500-507. A parsing as done here to resolve the problem is not proposed by those authors, or in general use.

The properties of charge and current in the approach used here do not appear in the Ampere-Maxwell equation itself eq. (1), and equations derived from it. Rather the properties of charge and current need to be described by a separate conjoined theory [28-30] that shows how charge and current vary with conditions, just as the compressibility of matter must be included as a separate conjoined theory in fluid mechanics. Treating matter, charge, and electric/magnetic fields this way does not add significant difficulties to analysis. The conjoined theory is analyzed with existing methods [28-30]. The difficulties involved arise from the complexities of the material displacement currents, including polarization currents [27], not from the mathematics.

The classical form of the Ampere-Maxwell equation (1) involves the dielectric constant as an adjustable parameter. It is limiting for biological applications because those involve an enormous range of concentrations of ions and dielectric properties of liquids depend on concentration.[31-36] The approximation of a dielectric constant is a useful teaching tool and a necessary part of first investigations in ionic solutions and thus living systems.[32-35] But the approximation is not very accurate and is too restrictive to use in investigations of many systems of practical importance, in my view [36]. Biological systems like enzymes [37], binding proteins, and channels contain a large range of concentrations of ions, up to tens of molar, and dielectric properties vary importantly in that range.[31]

The approximation of a single dielectric constant fails altogether when dealing with the remarkably diverse (and specific) dielectric properties of organic molecules revealed by their spectra, e.g., their infrared spectra. The spectroscopic properties of organics are so specific that they are used as fingerprints to separate and identify individual chemical species [38-40]. The relation of dielectric and spectroscopic measures is explained by Parsegian [41] p. 241-275. In essence, dielectric and spectroscopic measures are different ways of measuring the same polarization currents. The different methods were originally used in different bands of frequency, but that constraint comes from the measurement technology and does not reflect different properties of molecular polarization.

The approximation of a single dielectric constant (a real number) was developed when measurements were confined to low frequencies, say < 100 Hz, as they were in Maxwell's time. Modern data shows that polarization currents vary in a complex multi-dispersion way with frequency, type, and concentration of ions. All types of ions, not just the main charge carrier, change the dispersions.[31-36] Thus, a dispersion in a physiological salt solution will depend on many species, perhaps some in small concentrations and not on the main constituents (typically

Na^+ ions outside cells, and K^+ ions inside cells). The polarization current of an ideal dielectric, with a single dielectric constant—that is assumed in the classical Maxwell equations—cannot describe these properties.

It is interesting history that Maxwell anticipated the complexity of dielectric polarization quite explicitly [1]: Vol. 1, p. 381. He was concerned that it might resemble electrochemical polarization, which modern experimentation confirms is the case.[32-35]

The difficulties with the dielectric approximation are not confined to liquids. The approximation is barely adequate [42, 43] even for crystalline solids like the silicon of our modern semiconductors. Currents in modern circuits operate at frequencies $> 10^8$ Hz in which bits of information might last 10^{-9} seconds. It is not reasonable to expect an approximation derived for frequencies $< 10^2$ Hz to work well at $> 10^8$ Hz. A single dielectric constant is often not good enough to allow design of new devices on the 10^{-9} second time scale, although it may be an adequate description of existing devices under some circumstances [44-50] and it is certainly an important teaching tool, and a necessary component of first investigations using 'toy' models. Later investigations require measurement and description of the properties of dielectrics and polarization currents under all conditions of interest.

Current Laws. The Ampere-Maxwell equation (1) can be converted into a current law valid under the same conditions that the Ampere-Maxwell equation is valid. Take the divergence of $\mathbf{curl\ B}$ and use the general mathematical result that divergence of the curl of a vector field is zero.

Maxwell Current Law
$$\mathbf{div}\ \mathbf{J}_{true} = \mathbf{div\ curl\ B} = \mathbf{0} \tag{2}$$

Equation (2) needs a name of its own because of its generality and so it is called the Maxwell Current Law in this paper. Equation (2) says in mathematics what Maxwell said in words. True current does not accumulate. The fact that true current never accumulates allows understanding of important systems in biology. One example is the propagation of an action potential signal in nerve cells that traditionally use circuits and current laws eq. (2) & (5). Another example is the transport of electrons, protons, and ions in mitochondria, in which circuits and current laws are not so traditional.

True Current and Incompressible Fluids. True current behaves like the flow of a perfectly incompressible fluid that Maxwell called the aether (sometimes called the absolute ether). It is customary to avoid discussions of the aether and to deal with the current flow of the aether $\varepsilon_0\, \partial\mathbf{E}/\partial t$, not the aether itself. The Michelson-Morley experiment convinced physicists that the movement of the aether could not be detected mechanically [19], Vol 1, Section 15-3. The motion of the aether can be seen as light from the sun because of the displacement current it creates. The displacement current $\varepsilon_0\, \partial\mathbf{E}/\partial t$ allows electrodynamic waves to propagate through the near vacuum of space.

Maxwell's True Current is a property of the fields of electrodynamics and has useful properties that are independent of the properties of matter because the true current is incompressible with $\mathbf{div}\ \mathbf{J}_{true} = \mathbf{0}$. Other kinds of current—like the conduction current $\mathbf{J}$—are not incompressible. Those currents $\mathbf{J}$ depend on the properties of charge density and matter (through the continuity eq. (4)) as well as the properties of electrodynamic fields.

Many properties of any incompressible fluid flow are determined simply by the fact that it is incompressible [51, 52]. That is probably why Maxwell called the total current a "true" current and emphasized that definition in [25] as his first equation, eq. A, p. 465, 480.

It is not clear why Maxwell's focus on displacement current has fallen into disuse—with the notable exception of Landauer [53]. True current is hardly mentioned in the modern literature, despite his statement of its central role in electrodynamics. Maxwell called true current, displacement current (and time dependence) *"chief peculiarities"* of his work.

Maxwell's *"chief peculiarities"* have proven to be ephemeral in the literature of physics, perhaps because they are aethereal in their essence, existing as they do in a vacuum that contains no charges. But the *"chief peculiarities"* allow the propagation of light in a vacuum. The peculiar importance of the phrase 'displacement current' evidently did not survive the paradigm shift to relativity that converted Maxwell's aether to Einstein's space-time ([54], p. 57;[55]) but the reality of the displacement current $\varepsilon_0 \, \partial \mathbf{E}/\partial t$ did survive in the key equations (1) & (2). Without these equations, the propagation of light could not be understood. The equations and the phenomena they describe have survived the paradigm shift.

The physics of the Maxwell Current Law should not be hidden by the mathematics of the div and curl operators of vector calculus. The Maxwell Current Law (2) arises because the electric and magnetic fields created by electrodynamics move charges and atoms. Combined with the displacement current $\varepsilon_0 \, \partial \mathbf{E}/\partial t$, the charge movements guarantee that the total current does not accumulate.

The total current does not accumulate. Ever. Anywhere, with surprising consequences [56] particularly for single file transport in one-dimensional systems.[53] The conduction current—the movement of charges, e.g., charged atoms and electrons—and the displacement currents determined by the equations of electrodynamics create the Maxwell Current Law eq. (2). They are the physical reason for that law.

Conduction Current Accumulates. The conduction current $\mathbf{J}$ does accumulate even though $\mathbf{J}_{true}$ does not.

$$\mathbf{div}\, \mathbf{J} \; = -\mathbf{div}\, (\varepsilon_0 \, \partial \mathbf{E}/\partial t) \tag{3}$$

The divergence of $\mathbf{J}$ is not zero except when $\varepsilon_0 \, \partial \mathbf{E}/\partial t = 0$.

Indeed, the continuity equation (4) shows that conduction current $\mathbf{J}$ accumulates as charge density ρ changes.

$$\mathbf{div}\, \mathbf{J} \; = \; - \, \partial \rho/\partial t \tag{4}$$

The continuity equation (4) can be derived from the Ampere Maxwell Equation (1), and a form of Gauss' law [4]; eq. G of [25], p. 465 and 485). We reiterate for clarity that $\mathbf{J}$ is the conduction current of charge with mass, however brief, small, or transient. $\mathbf{J}$ includes the polarization current of an idealized dielectric $(\varepsilon_r - 1)\varepsilon_0 \, \partial \mathbf{E}/\partial t$. $\mathbf{J}$ excludes only the displacement current $\varepsilon_0 \, \partial \mathbf{E}/\partial t$.

Conduction Current Accumulates as Charge Density. Circuits found in our computers could hardly be analyzed if charges had to be considered explicitly. The complexity of the circuit structures produces an even larger complexity in the charges, as they carry signals and vary with time.

Integrated circuits contain too many charges to analyze with the continuity equation (4). Rather, integrated circuits are analyzed by the Kirchhoff current law eq. (5), without explicit consideration of charges.[44-50] It is easier to deal with currents, when the number of currents that must be considered is much less than the number of charges.

Conduction current is also harder to analyze than total current because conduction current depends on the accumulation of charges that diffuse and flow by convection. Those processes involve many parameters including the details of the structures in which diffusion and convection occur. Such complexity is particularly hard to deal with in biological systems like the mitochondrion where many types of conduction currents flow: electron, proton, and ionic, each driven by diffusion and migration, and sometimes convection.

Most scientists—including me for most of my life—have thought that knowledge of the locations and properties (and accumulation) of charges is needed to deal quantitatively with circuits or electromagnetic phenomena including circuits. Feynman says as much, for example, in [4], Vol 2, Section 13-4. However, engineers have built and used circuits without explicitly studying charges for a long time, for some 160 years since the introduction of the telegraph, using just the Kirchhoff current law eq. (5).They have shown how to design successful circuits—that bring light, information, (and power, voices, and images) to our homes and businesses—without detailed knowledge of the distribution of charges. [44-50, 57-67]

The properties of currents are important in our daily life because they determine the properties of circuits. Circuit laws like eq. (2) and (5) are needed to define circuits precisely.

Circuits are Important. We now look at the successful use of circuits to see how circuits can contribute to knowledge in general, and to understanding mitochondria in particular.

Circuits are the crucial component responsible for the use of electricity in technology and industry. Circuits are also used to understand signals in the nervous system of animals, the initiation of contraction in our muscles, and the coordination of contraction that allows the heart to function as a pump.[5-7, 68]

Circuits remade our world in the 1880's when they brought light and power to homes and businesses. Before circuits delivered electricity to homes and offices, homes were unpowered as they had always been, and poorly lit by flickering gas lamps.

Circuits remade our world in the 1840's, when they speeded long distance communication (e.g., across the Atlantic Ocean [69]) by factors of millions. Circuits remade our world in the 1870's when telephones allowed people to speak together without being together face to face. Before circuits delivered electricity to homes and offices, information was transmitted much as it had been by the Romans thousands of years ago.

The importance of circuits has hardly diminished in the last 170 years.

The community of engineers has always recognized the importance of circuits and current laws, but the importance of circuits is not generally addressed outside the community of engineers. Most textbooks of electrodynamics hardly mention the role of circuits in the delivery of electrical power. Most textbooks of electrodynamics just barely mention the role of circuits in the delivery of information. Nevertheless, current laws like eq. (2) & (5) are important in social

and economic history, as well as in science itself, because they allow design of the circuits that provide power and information to our civilization.

The community of biologists has not always recognized the importance of circuits because circuits appear only implicitly even where they are biologically important [5-7, 68], in nerve and muscle cells, for example.

Current is not confined to circuits. It is important for biology (in particular, and science in general) that the Maxwell Current Law eq. (2) does not require current to be confined to circuits. The Maxwell Current Law is true whenever classical electrodynamics are true. Maxwell's derivation ([1], Vol.1, Sect.328, p. 377) does not include circuits. Maxwell solves electric field problems without circuits—in explicit detail including boundary properties and conditions—showing how the time dependent solutions of those boundary value problems depend on the displacement current $\varepsilon_r \varepsilon_0 \, \partial \mathbf{E}/\partial t$. If the displacement current is not included, the solutions to the problems are incorrect. Maxwell's discussion is clear and detailed and does not require further elaboration, in my opinion. despite its age.

Kirchhoff Current Law is used throughout engineering and physics to define the properties of circuits. Kirchhoff Current Law eq. (5) is a special case of the Maxwell Current Law eq.(2). Conduction current $\mathbf{J}$ includes the current of an idealized dielectric, as explained earlier.

Kirchhoff Current Law for Fields $\quad \mathbf{div}\, \mathbf{J} = \mathbf{0} \quad$ $\mathbf{J}$ is conduction current (5)

This form of Kirchhoff's law is unfamiliar because it does not depend on $\mathbf{J}$ being inside a circuit.

Kirchhoff's law in texts of circuit design and analysis [44-50, 57-67] is often said more clearly in words than in equations: 'all the currents that flow into a node—positive quantities—flow out as negative quantities". Or 'the sum of all currents at a node is zero', 'Currents' in the texts of circuit design and analysis means conduction currents with direction and does not include a displacement term that depends on $\partial \mathbf{E}/\partial t$. For each node i, one sums the conduction currents from the k branches attached to that i^{th} node.

Classical Kirchhoff Current Law for Circuits $\quad \sum \mathrm{J}_{i(k)} = 0 \quad$ J_i conduction current (6)

The circuit representation (6) of the classical Kirchhoff Current Law eq. (5) is in wide use. It is, however, inconsistent with the Maxwell Current Law eq. (2), and thus the Ampere-Maxwell eq. (1). Eq. (2) and (5) contain displacement current $\varepsilon_0 \, \partial \mathbf{E}/\partial t$. Eq. (5) and (6) do not contain a displacement current or a time derivative at all, The classical Kirchhoff Current Law (5) is also inconsistent with Maxwell's statement "*that the time-variation of the electric displacement, must be considered".* [1] Vol. 2, Section 610, p. 232. Eq. (6) can be modified to contain the displacement current, as we shall see, eq.(9), thereby becoming consistent with eq. (2).

When treatments are inconsistent, their alternative ways of handling the equations produce alternative results, making it impossible to tell which result is correct, using theory alone. Experiments are needed to choose the correct result. Once the correct result is known, the theory can be changed appropriately.

Paradigm Change. We now consider ways to reconcile the Maxwell and Kirchoff Current laws, eq. (2) and (5). One way to reconcile is by approximation, as a low frequency law, with its limitations. Another way is to split off components from the field equation eq. (5) as 'stray capacitances' and add them as separate fictitious components to eq. (6). These components are generally small additions to the larger real (not fictitious) components of stray capacitance produced by coupling to nearby structures. See 'Layout' term in eq. (9).

The other way is to redefine current in eq. (5), but that redefinition itself upsets long standing paradigms.

Reconciliation by Approximation. The Kirchhoff Current Law eq. (6) is viewed as an approximation to the Maxwell Current Law (2) in most textbooks. When conduction current is much larger than displacement current $\mathbf{J} \gg \varepsilon_0 \, \partial\mathbf{E}/\partial t$, true current is mostly conduction current. In that case, at low frequencies, the usual Kirchhoff Current Law (6) may be good enough, helpful even when dealing with microwave circuits [70-73], if used with caution and care.

Care is important, however, even when the displacement term is small, because the initial condition associated with the time derivative $\partial\mathbf{E}/\partial t$ is lost in the approximation that $\partial\mathbf{E}/\partial t = 0$. Losing initial conditions causes difficulties in almost any system, as studied at length in singular perturbation theory [74].

Losing the initial condition in electrical systems can lead to paradoxes that make the role of charge hard to understand. If $\mathbf{J} \gg \varepsilon_0 \, \partial\mathbf{E}/\partial t$, all the conduction current that flows into a resistor flows out, so one must wonder how the charge that drives the conduction current accumulates in the first place. The charge arises, of course, in an initial condition that is not included in a treatment like eq. (5) where $\partial\mathbf{E}/\partial t = 0$.

The initial charge can be included as extra information added to supplement Kirchhoff's law, see eq.(7).

Reconciliation with Stray Capacitance. Another way to reconcile the Maxwell and Kirchhoff current laws eq. (2) & (6) is to change the system the laws describe. Idealized circuits of textbooks [48] are revised by adding virtual components, 'stray capacitances' that do not exist as isolated elements in the actual circuit [44-50, 57-67, 75]. These extra components allow circuits to describe coupling to nearby structures in the circuit layout, as well as the smaller but unavoidable displacement current $\varepsilon_0 \, \partial\mathbf{E}/\partial t$, see eq.(9). . The extra components allow circuits do deal with reality quite well at high frequencies, reaching to microwave frequencies in favorable cases.[70-73] They appear as extra terms (see eq. (9)) in addition to those included in the usual textbook formulation of the Kirchhoff Current Law eq. (6).

Successful circuit designs place 'stray capacitances' between all nodes in a circuit, and between the nodes and a far distant zero potential ground. The far distant ground is the typical far field boundary condition in circuit theory. Their existence is required to reconcile the Maxwell and Kirchhoff Current laws (2) & (6). Their existence is also required to deal with coupling between nearby structures, see 'Layout' term in eq. (9). Without both types of stray capacitances, idealized circuits [48] do not behave the way real circuits behave when they are actually wired up in a practical layout [49] and measured, as is shown explicitly below in eq. (9).

Stray capacitances are not included in idealized circuits because they depend on the layout of the circuit—the way it is wired up—not shown in idealized circuit diagrams. The conversion of idealized circuits into functional designs is a discipline of its own, of great importance in modern design of integrated circuits because stray capacitances and other non-ideal effects increase in importance as the density of devices increases, and the size of devices approach atomic dimensions.[44, 45, 47, 49, 75, 76] The values of stray capacitances are determined empirically in that design process.[75, 77]

The addition of both kinds of stray capacitances to circuits explains why circuits designed with Kirchhoff's Law (6) can describe bits that are 10^{-9} sec duration, even though the law eq. (5) is usually derived for low frequencies and long times.

Reconciliation by Redefinition. The Kirchhoff Current Law eq. (6) and the Maxwell Current Law (2) can be reconciled without approximation by defining a true current, as Maxwell advocates in the quotation that begins this paper.

The exact reconciliation by redefintion simply changes the definition of current (in the traditional Kirchhoff's law) from conduction current to true current. That redefined current is Maxwell's true current eq. (1), of the Ampere-Maxwell differential equation for the magnetic field. The true current includes the displacement current that Maxwell viewed as essential because it is needed so light can propagate as an electrodynamic wave in a vacuum.

Another exact reconciliation is possible by adding virtual components of 'stray capacitances' to the original circuit, along with the layout stray capacitances needed to describe coupling to nearby systems, without changing the definition of current as we demonstrate below eq. (9) following [78]. For circuits, the results are equivalent. For mitochondria, nerve, and cardiac cells, and other three-dimensional structures, the results are not equivalent because it is not always clear how to approximate the three-dimensional layout of (for example) biological systems with a circuit model. Indeed, the circuit representation of such complex structures is not unique.

Using Maxwell's definition of current makes the current laws general. The Maxwell Current Law (2) does not require discussion of circuits, as Maxwell himself demonstrated. [1], Vol.1, Sect.328, p. 377The true current can be used to describe (1) electron flows in circuits, (2) current flows in mitochondria, including (3) proton flows and (4) trans-membrane electron flows and (5) horizontal electron flows, and (6) ionic flows in nerve whether in (7) membranes or (8) cytoplasm, carried by whatever ions are present.[78, 79]

Maxwell's definition of current is easy to use and does not involve approximation. It requires slight change in the treatment of existing idealized circuits or analyses of field problems in applied mathematics that use the dielectric constant approximation, as they usually do.

Analysis of circuits usually uses Laplace transforms because most circuits of technological interest are linear systems. Nonlinear technological devices are usually analyzed by linearization around the operating points where they function. Maxwell's definition of current in eq. (1)&(2) is easily formulated using Laplace transforms.

The Laplace transform $\widehat{\mathbf{J}}_{\boldsymbol{true}}(\boldsymbol{s})$ of the true current $\mathbf{J}_{\boldsymbol{true}}(t)$ of eq. (1) is

Laplace transform of true current $\widehat{\mathbf{J}}_{\boldsymbol{true}}(\boldsymbol{s}) = \hat{\boldsymbol{J}}(\boldsymbol{s}) + \varepsilon_0 \boldsymbol{s}\widehat{\boldsymbol{E}}(\boldsymbol{s}) - \varepsilon_0 \boldsymbol{E}(t=0)$ (7)

Here the symbol $\boldsymbol{s}$ is the Laplace transform frequency variable, Laplace transforms are indicated by a 'hat' as in the Laplace transform of the electric field $\widehat{\boldsymbol{E}}(\boldsymbol{s})$. If we set initial conditions $\mathbf{E}(t)$ to zero $\mathbf{E}(\mathrm{t}=0)$, as is customary in circuit analysis and synthesis, every modified current in a circuit contains an extra term like $\mathbb{C}\boldsymbol{s}\widehat{\boldsymbol{E}}(\boldsymbol{s})$, where the universal effective capacitance $\mathbb{C} = \varepsilon_0$ is simply the electrical constant, obviously independent of the properties of matter. $\mathbb{C}\boldsymbol{s}\widehat{\boldsymbol{E}}(\boldsymbol{s})$ is Maxwell's displacement current, the term essential for the understanding how electromagnetism in a vacuum supports a propagating wave like light.

Circuits analyzed with the Maxwell Current Law (2) will thus contain many effective capacitances $\mathbb{C}\boldsymbol{s}\widehat{\boldsymbol{E}}(\boldsymbol{s})$ that include the universal displacement current $\varepsilon_0\, \partial\mathbf{E}/\partial t$, one for each circuit element and wire. Combined, the effective capacitances will form an inescapable part of the stray capacitances discussed previously.

Saying the same thing in equations, we rewrite eq. (2) for the i^{th} node—with k branches attached—in a circuit using the Laplace transform variables of eq. (7) with zero initial conditions everywhere, as is customary in circuit analysis.

$$\sum \hat{\boldsymbol{J}}_{true;i(k)}(\boldsymbol{s}) = \sum \left(\hat{\boldsymbol{J}}_{i(k)}(\boldsymbol{s}) + \varepsilon_0 \boldsymbol{s}\widehat{\boldsymbol{E}}_{i(k)}(\boldsymbol{s}) \right) = 0 \tag{8}$$

This equation (8) can be rewritten so we recognize the *stray* capacitance currents $\varepsilon_0 \boldsymbol{s}\widehat{\boldsymbol{E}}_{i(k)}(\boldsymbol{s})$ added to the branch currents $\hat{\boldsymbol{J}}_{i(k)}(\boldsymbol{s})$ of the classical Kirchhoff Law eq. (6).

$$\overbrace{\sum \hat{\boldsymbol{J}}_{true;i(k)}(\boldsymbol{s})}^{\textbf{Maxwell Law}} = \overbrace{\sum \hat{\boldsymbol{J}}_{i(k)}(\boldsymbol{s})}^{\textbf{Kirchhoff Law}} + \overbrace{\sum (\varepsilon_0 + \boldsymbol{Layout}) \cdot \boldsymbol{s}\widehat{\boldsymbol{E}}_{i(k)}(\boldsymbol{s})}^{\textbf{Stray Capacitances}} = 0 \tag{9}$$

The last few equations show how Kirchhoff's law eq. (6) can create an exact description [78] of what flows through a resistor [79].

Eq. (9) includes the 'Layout' capacitance term $(\boldsymbol{Layout}) \cdot \boldsymbol{s}\widehat{\boldsymbol{E}}_{i(k)}(\boldsymbol{s})$ that arises from geometric coupling to nearby structures. These stray capacitances are often much larger than the unavoidable term $\varepsilon_0 \cdot \boldsymbol{s}\widehat{\boldsymbol{E}}_{i(k)}(\boldsymbol{s})$.

Current in Biological Systems. Kirchhoff's Current Law as usually formulated eq.(6) cannot be used with confidence in biological systems like mitochondria because they are not circuits. Their circuit representation has not been established and is unlikely to be unique. The Kirchhoff circuit formulation can be used successfully in nerve fibers because they have been shown experimentally to behave like circuits [5], and the circuit representation has actually been derived from one of the field equations of electrodynamics, the Poisson equation.[74] pp 218-238; [80]

The Maxwell redefinition of current is necessary when describing biological systems that have not been shown to be circuits, for example, mitochondria. The total current across all the membranes of a short system like a mitochondrion must sum to zero. The total current includes the membrane capacity current—a displacement current $\varepsilon_m \varepsilon_0\, \partial\mathbf{E}/\partial t$—and the conduction

currents carried by ions, electrons, and protons. A short organelle like a mitochondrion has a single internal potential in the matrix within the mitochondrion, almost independent of spatial location [80], and the membrane currents, arising in the lipid membrane, and the channels, and protein complexes in the mitochondrial membrane, has nowhere else to go. There is no long axon to conduct the current away, as in a nerve fiber [74] pp 218-238. The Maxwell and Kirchhoff Current Laws (2) & (6) combine with the shape and size of the mitochondria to force the total current of all types across all membranes to sum to zero.

Physical Basis of the Maxwell Current Law. The total currents across the mitochondrial membrane, and the total currents linking proteins complexes, are the true currents of Maxwell and follow the Maxwell Current Law (2), entirely independent of the nature of the charges that carry the currents, whether electrons or protons or ions.

The physical basis of the Maxwell Current Law (2) lies in the electrical and magnetic fields produced by the Ampere-Maxwell equation (1) and the other Maxwell partial differential equations.

The divergence of the magnetic field is zero because no magnetic monopoles exist (comparable to the electrical monopoles the electron or proton). The Ampere-Maxwell equation (1) is the only source of the magnetic field, when the boundary conditions of the equation are included.

The Ampere-Maxwell equation (1) guarantees that the electric and magnetic fields take on values that prevent the accumulation of true current. The total current across the mitochondrial membrane does not accumulate. The total current flowing from one protein complex to another, linking them into a functional unit, does not accumulate, even if the conduction components of that linking currents do accumulate. That is the physical counterpart to the mathematical derivation of the Maxwell Current Law given previously.

Maxwell Coupling. The fluxes of ions and electrons across membranes are coupled by their summation in systems like short organelles, like mitochondria. The fluxes of ions and electrons across membranes cannot be independent in such systems. They are coupled because they have a definite sum, zero, under all conditions. If one membrane conduction current increases, the other must decrease, or be balanced by a membrane capacity current $\varepsilon_m \varepsilon_0 \, \partial \mathbf{E}/\partial t$, to keep the sum zero, as required by eq. (2).

The Maxwell coupling produced by summation is enforced whether the currents are carried by ions, or electrons, or displacement, no matter how the currents vary with time or the driving forces that create them [28-30]. The Maxwell Current Law (2) applies to currents driven by chemical reactions, protonmotive forces, electrochemical potentials, convection, heat flow, and so on. It is a corollary of the Maxwell equations of electrodynamics, including eq.(1). The coupling is produced by the equations of electrodynamics that produce the changes in electrical and magnetic forces necessary to generate the coupling.

Total currents cannot accumulate in any conditions in which electricity follows the laws of electrodynamics as we know them in the physical world. Those laws do not depend on the physical systems that generate the currents and so those laws also apply to biological systems, including the electron transport chain of mitochondria.

Local Coupling. The membrane and linking currents in mitochondria are coupled globally as we have discussed. The conduction currents are also coupled locally by chemical reactions within the protein complexes in and near the membrane. They are coupled by local chemical reactions linking proton and electron flows, sometimes to ATP production. The complexes of the electron transport chain function together as one system. These local chemical reactions also involve intra-molecular, atomic scale electrical potentials as they appear in the Schrödinger equations that govern them, but that potential is beyond the resolution of the analysis in this paper. It is possible that biologically significant couplings involving the potential in the Schrödinger equation will emerge in a higher resolution treatment. A glimpse of such effects is seen in the multiple guises of 'protons', as positively charged water of various types.[8-11]

Actual calculations of coupled currents have been done, without particular difficulties, for one of the complexes (Respiratory Complex 4, the cytochrome c oxidase system) using standard numerical methods of partial differential equations applied to 'multiphysics' systems, where migration and diffusion occur in specialized structures.[30] This work is a practical application of the general ideas of this paper and shows that a respiratory complex can be analyzed by analysis of currents and chemical reactions without explicit discussion of charges or use of the continuity equation (4).

Chemiosmotic Hypothesis, Revisited. Maxwell's Current Law (2) provides another interpretation of the Chemiosmotic Hypothesis of Peter Mitchell [12-18].

Using Maxwell's Current Law (2), the chemiosmotic electrical process can now be viewed as the total current across the electron transport complexes and lipid membrane. Perplexing issues of complexity in electron and proton flow [12-15] do not have to be explained by words alone. They can be estimated by the Maxwell Current Law (2), with the methods used to analyze cytochrome c oxidase, Respiratory Complex 4.[30] The total current produced by Complex 4 generates ATP in the synthase enzyme of Complex 5. It is the total current that generates the ATP, not just the proton flux. An explicit treatment of the coupling of Complex 4 and 5 is a goal as we extend the work of ref.[30]. Extension does not seem to require new mathematical or numerical methods.

Viewed this way, the chemiosmotic hypothesis [12-20] fits into the general treatment of electricity in the physical sciences [26].

In the chemiosmotic hypothesis, conduction currents did not fit so naturally. Flows of electrons and protons (and currents) were not identified as the currents of physics, as defined in the Maxwell equations of electrodynamics, e.g. eq. (1). Currents were hard to specify [12-20] because they vary so much in composition, and in space. A current law was not used to explicitly describe their flow because a precise definition of current was not given, nor was the word current identified with the currents of classical electrodynamics.

In my view, a current law is needed that applies to the complexity of three-dimensional mitochondria where current carriers switch from electrons, to ions, to protons (or hydronium ions [14]). Analysis based on charges and the continuity equation (4) is not practical because all the charges in a mitochondrion are involved and that is a very large number, more or less impossible to compute directly when interactions are included, that are required by Coulomb's law.

In the chemiosmotic hypothesis, the flows of protons are multifaceted, particularly hard to discern and difficult to deal with because protons might protonate weak acids and bases throughout the mitochondria. The protons would then vary in concentration, changing the conduction current of Kirchhoff's current law. Treatments of total current sidestep the issue of protonation because they deal with entire true current at once without worrying about its components. The flows of electrons are also multifaceted, hard to deal with as they move through so many systems. The multifaceted flows of electrons are also a characteristic of current flow in the integrated circuits of our technology, where the properties of electron flow in wires, resistors, transistors, and capacitors are quite different. Current laws successfully bypass such complexities in integrated circuits and are likely to help bypass complexities in mitochondria as well.

Chemiosmotic Hypothesis, Revised. In this revised version of the chemiosmotic theory, the rules are simple. Current is now the current of the Maxwell equations, e.g. eq. (1). Total current does not accumulate. The Maxwell Current Law (2) is quantitative, indeed exact. It replaces the rather vague discussion of how complexes in mitochondria interact (found in the chemisosmotic hypothesis [12-20]) with the precision of physics and electrodynamics.[4]

To the extent that total current describes the flow of energy in the mitochondria, details of the charge movements in conduction currents are unimportant, just as details of the charge movements in the conduction currents are unimportant in the circuits of our computers or in the propagation of the actional potential of nerve and muscle, as described below. The total current provides the input to the enzymes, transporters, and channels of the complexes of the electron transport chain. The proteins of the complexes can provide the selectivity to choose the form of charge needed as a substrate for the chemical reaction or transport properties of the protein. The current itself need not be carried by a particular charged species in this case.

In this revised approach, the Maxwell Current Law (2) shows precisely how the total current couples the output of Respiratory Complex 4 to the synthesis of ATP in Respiratory Complex 5 although a full model requires an extension of our previous work [30]. The input to the ATPase of Complex 5 is a true current. It cannot accumulate because it is true current as Maxwell defined it. Driven by the protonmotive forces, including the electrical potential of the Maxwell equations, the true current carries protons that help generate ATP while obeying the laws of electrodynamics as it does so, eq. (1)–(5). Those laws guarantee that the electrical potential of the protonmotive forces is coupled to the movement of all charges and displacement currents. Most of the details of the charge movements do not matter. It is the true total current that provides the energy that generates the ATP, not just the protonmotive force.

Ionic Signals in Biology. The idea of total current is useful in another biological system, the signaling system of nerve and muscle. The total current of the Maxwell Current Law (2) helps define the circuit models familiar in the treatment of the nerve action potential [5, 6], and the action potential of cardiac and skeletal muscle [7]. The circuits have been derived from the Green's functions of a structural description of complex tissues [80-82] thereby linking the biological treatment of electricity and the physical treatment of electrodynamics. Singular perturbation techniques [74], p. 218-238, are helpful in applying the Maxwell Current Law (2) to biological systems of some complexity [80, 82, 83]. The general approach is reviewed in [82].

The approximations inherent in the circuit representation of nerve and muscle have been extensively examined by many methods. The first approximation involves the cell interior. Experiments [84-87] show that the interior of cells can be approximated as resistors. Only the resistance is important. The specific ionic contents of the interior do not matter very much [78, 79, 86, 88, 89].

The second approximation in the circuit representation represents the membrane as a capacitance. Experiments show that membranes have well defined capacitances.[90-95] The capacitances arise in lipids that provide pathways for displacement currents $\varepsilon_m \varepsilon_0 \, \partial \mathbf{E} / \partial t$ where ε_m is the effective dielectric constant of the lipid membrane.

The third approximation in the circuit shows that the ion channels and transporters do not change the membrane capacitance under most conditions. They add current to the lipid membrane current [96] without changing it very much [97-99] except when gating currents [97] are created by specialized structures within membrane proteins that sense voltage.[100, 101]

It is historically interesting that the analysis of the action potential depends on the Maxwell Current Law (2) in the form of the cable equation used in 1850 [102, 103] to describe the telegraph under the ocean [69], the trans-Atlantic cable. Hodgkin and Huxley used the cable equation [5, 6] and Cole's voltage clamp [7] to show that action potentials arose from conduction currents through channels (then called conductances) in the membrane of nerve fibers. The conduction currents cross the membrane inside distinct proteins, called ion channels, which are selective and carry either Na^+ or K^+ currents flow. The currents are then converted into longitudinal currents in the cytoplasm that spread the action potential down a nerve axon. The axonal currents are carried by whatever ions happen to be in the axoplasm. The chemical identity of the ions that carry the longitudinal current is not important for conduction.[86, 88, 89]

Early leaders in biophysics [104] thought these conduction currents would be propagated by coupled chemical reactions, but we now know that the channels that conduct those currents are not chemically coupled. They are electrically coupled.[105, 106] They are too far apart to interact even through their ionic atmospheres.[107]

In fact, only electricity couples the conduction currents of the action potential. The conduction currents are coupled by the global electrical potential [68] of the cable equation. The electrical coupling creates the propagating action potentials from the otherwise independent conduction currents ([7]; Fig. 10 and eq. 11 of [108]). The potential change accompanying inward sodium Na^+ currents at one location is spread by total longitudinal current—described by the cable equation—to other locations, where the potential change opens sodium channel proteins and produce inward Na^+ currents of their own, that in turn propagate further. The type of ions that carry the total longitudinal current are not important.[86, 88, 89]

The energy for the action potential comes from gradients of concentration maintained by other systems of membrane proteins called pumps or transporters that use the hydrolysis of ATP as their ultimate source of energy. The gradients of concentration of Na^+ power the flows of ions modulated by the channel proteins that are the conduction currents that propagate the action potential, as described above. The ATP hydrolyzed by pumps and transporters is created by the electron transport systems of mitochondria and chloroplasts. Analyzing electron transport, along with ion and proton transport, using Maxwell's Current Law (2) is likely to help understand these

systems as it has helped understand the propagation of the action potential, and so much of our electrical technology.

Conclusion. Maxwell defined current differently from most scientists today. He said that total current must include the displacement current to be the true current that creates the electric and magnetic field. Without the displacement current, there could be no current in a vacuum, and the current in the vacuum was truly needed to create light. Maxwell said that the true current must be considered to understand the total movement of electricity because that included the propagation of light in a vacuum.

Modern vector calculus provides a neat restatement of his definition and shows what Maxwell knew: true current does not accumulate. The resulting Maxwell Current Law (2) is a generalization of the Kirchhoff Current Law (5). The usual Kirchhoff Current Law, however, ignores Maxwell's statement "*that the time-variation of the electric displacement, must be considered".*

It comes as a surprise then that Kirchhoff's Current Law (5) is used successfully, in modern circuits operating at frequencies that are not low. Modern circuits, designed with Kirchhoff's Law (5) operate successfully with bits of information that last 10^{-9} seconds [44-50, 57-67], reaching to microwave frequencies in favorable cases [70-73]. The surprise is removed by both types of 'stray capacitances' introduced by engineers as supplements to idealized circuits as discussed near eq.(9).

Generalization of Kirchhoff's law (5) creates the Maxwell Current Law (2) that is not confined to circuits. It is not confined to low speeds. It is true in three dimensions, in complex biological systems with many energy sources, including chemical reactions.

The Maxwell Current Law (2) can be immediately applied to biological systems like nerve fibers, muscle cells, mitochondria, and chloroplasts. In ion channels, the only coupling is by the Maxwell Current Law (2) because the channels are distinct, disjoint proteins far apart. In channels, the electric field is created by the flow of all currents. The currents are globally coupled by their joint origin as solutions of the Maxwell set of partial differential equations. That is the only way currents are coupled during a propagating action potential in nerve and muscle, whether the currents are carried by ions through selective membrane channels, or through cytoplasm by whatever ions happen to be present.[78, 79]

In mitochondria currents are coupled. The coupling is the basis of active transport in biology in general [109, 110] and the coupling of electron and proton flow with ATP synthesis [12-24]. The coupling is usually considered to be a property of the chemical reactions involved. In mitochondria, those chemical reactions exist locally in the protein complex of the mitochondrial membrane. Here we point out that currents in mitochondria are also coupled globally, as they are in propagating action potentials. The currents are coupled globally by electrodynamics because the Ampere Maxwell equation (1) is true everywhere, at all times, in biological and physical systems. Both local and global coupling occur in mitochondria.

The Maxwell Current Law (2) can help scientists understand how local and global coupling combine to determine proton conduction current. Proton currents generate ATP. The proton currents are driven by the protonmotive force of the chemiosmotic theory that includes the electric field of Maxwell's electrodynamics. The electric field can be calculated by the Maxwell's

Current Law eq. (2) that implements electrodynamics in the form of the Ampere-Maxwell equation (1). Current laws eq. (2) & (5) couple the protonmotive force to the electric field, and thus to the movement of all charges and membrane currents.

The treatment here allows the chemiosmotic hypothesis to take advantage of the knowledge of current flow in the physical and engineering sciences, particularly its Kirchhoff and Maxwell Current Laws. That knowledge has been helpful in understanding action potentials in biology, and in technology in general. Knowing the current means knowing an important part of the mechanism of ATP synthesis.

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References

1. Maxwell, J.C., *A Treatise on Electricity and Magnetism (reprinted 1954)*. Third ed. Vol. One and Two. 1865, New York: Dover Publications.
2. Qiao, Z., et al., *Structure-preserving numerical method for Maxwell-Ampère Nernst-Planck model.* Journal of Computational Physics, 2023. **475**: p. 111845.
3. Qiao, Z., et al., *A Maxwell–Ampère Nernst–Planck Framework for Modeling Charge Dynamics.* SIAM Journal on Applied Mathematics, 2023. **83**(2): p. 374-393.
4. Feynman, R.P., R.B. Leighton, and M. Sands, *The Feynman: Lectures on Physics, Vol, 1, 2, 3*. 1963, New York: Addison-Wesley Publishing Co., also at http://www.feynmanlectures.caltech.edu/II_toc.html. 592.
5. Hodgkin, A.L. and W.A.H. Rushton, *The electrical constants of a crustacean nerve fiber.* Proc. Roy. Soc. (London) Ser. B, 1946. **133**: p. 444-479.
6. Davis, L.D., Jr., and R.L. de No, *Contribution to the Mathematical Theory of the electrotonus.* Studies from the Rockefeller Institute for Medical Research, 1947. **131**: p. 442-496.
7. Huxley, A., *The Quantitative Analysis of Excitation and Conduction in Nerve. From Nobel Lectures, Physiology or Medicine 1963–1970*. 1972, Elsevier, Amsterdam.
8. Yamashita, T. and G.A. Voth, *Insights into the Mechanism of Proton Transport in Cytochrome c Oxidase.* Journal of the American Chemical Society, 2012. **134**(2): p. 1147-1152.
9. Knight, C. and G.A. Voth, *The Curious Case of the Hydrated Proton.* Acc Chem Res, 2011. **45**(1): p. 101-109.
10. Knight, C., et al., *Defining Condensed Phase Reactive Force Fields from ab Initio Molecular Dynamics Simulations: The Case of the Hydrated Excess Proton.* Journal of Chemical Theory and Computation, 2010. **6**(10): p. 3223-3232.
11. Chen, H., et al., *Charge delocalization in proton channels, I: the aquaporin channels and proton blockage.* Biophys J, 2007. **92**(1): p. 46-60.
12. Morelli, A.M., et al., *An update of the chemiosmotic theory as suggested by possible proton currents inside the coupling membrane.* Open biology, 2019. **9**(4): p. 180221.
13. Juhaszova, M., et al., *Setting the Record Straight: A New Twist on the Chemiosmotic Mechanism of Oxidative Phosphorylation.* Function, 2022. **3**(3).
14. Boyer, P.D., *Bioenergetic coupling to protonmotive force: should we be considering hydronium ion coordination and not group protonation?* Trends in Biochemical Sciences, 1988. **13**(1): p. 5-7.
15. Wikstrom, M., et al., *New perspectives on proton pumping in cellular respiration.* Chem Rev, 2015. **115**(5): p. 2196-221.
16. Mitchell, P. and J. Moyle, *Chemiosmotic hypothesis of oxidative phosphorylation.* Nature, 1967. **213**(5072): p. 137-139.
17. Mitchell, P., *The protonmotive Q cycle: A general formulation.* FEBS Letters, 1975. **59**(2): p. 137-139.
18. Mitchell, P., *Vectorial chemiosmotic processes.* Annual review of biochemistry, 1977. **46**(1): p. 996-1005.
19. Stryer, L., *Biochemistry*. Fourth ed. 1995, New York: W.H. Freeman. 1064.
20. Mitchell, P., *Coupling of phosphorylation to electron and hydrogen transfer by a chemi-osmotic type of mechanism.* Nature, 1961. **191**(4784): p. 144-148.
21. Berg, J.M., J.L. Tymoczko, and L. Stryer, *Biochemistry*. Seventh ed. 2010, New York: W. H. Freeman. 1120.
22. Nicholls, D.G., *Bioenergetics*. 2013: Academic press.

23. Ogawa, S. and T.M. Lee, *The relation between the internal phosphorylation potential and the proton motive force in mitochondria during ATP synthesis and hydrolysis.* J Biol Chem, 1984. **259**(16): p. 10004-11.
24. Walker, J.E., *ATP Synthesis by Rotary Catalysis (Nobel lecture).* Angew Chem Int Ed Engl, 1998. **37**(17): p. 2308-2319.
25. Maxwell, J.C., *A Dynamical Theory of the Electromagnetic Field.* Philosophical Transactions of the Royal Society of London, 1865. **155**: p. 459-512.
26. Feynman, R.P., R.B. Leighton, and M. Sands, *The Feynman: Lectures on Physics, Vol. 2. Mainly Electromagnetism and Matter*. Vol. 2. 1963, New York: Addison-Wesley Publishing Co., also at http://www.feynmanlectures.caltech.edu/II_toc.html. 592.
27. Purcell, E.M. and D.J. Morin, *Electricity and magnetism*. 2013: Cambridge University Press.
28. Eisenberg, B., C. Liu, and Y. Wang, *On Variational Principles for Polarization Responses in Electromechanical Systems.* Communications in Mathematical Sciences, 2022. **20**(6): p. 1541-1550.
29. Xu, S., et al., *Mathematical models for electrochemistry: Law of mass action revisited* arXiv 2305.12165, 2023. .
30. Xu, S., et al., *Mathematical Model for Chemical Reactions in Electrolyte Applied to Cytochrome c Oxidase: an Electro-osmotic Approach.* 0.48550/arxiv.2207.02215, 2022.
31. Eisenberg, B., *Interacting ions in Biophysics: Real is not ideal.* Biophysical Journal, 2013. **104**: p. 1849-1866.
32. Barthel, J., R. Buchner, and M. Münsterer, *Electrolyte Data Collection Vol. 12, Part 2: Dielectric Properties of Water and Aqueous Electrolyte Solutions*. 1995, Frankfurt am Main: DECHEMA.
33. Barthel, J., H. Krienke, and W. Kunz, *Physical Chemistry of Electrolyte Solutions: Modern Aspects*. 1998, New York: Springer.
34. Kremer, F. and A. Schönhals, *Broadband Dielectric Spectroscopy*. 2003: Springer. 729.
35. Barsoukov, E. and J.R. Macdonald, *Impedance spectroscopy: theory, experiment, and applications*. 2018: John Wiley & Sons.
36. Eisenberg, R.S., *Dielectric Dilemma.* preprint available at https://arxiv.org/abs/1901.10805, 2019.
37. Jimenez-Morales, D., J. Liang, and B. Eisenberg, *Ionizable side chains at catalytic active sites of enzymes.* European Biophysics Journal, 2012. **41**(5): p. 449-460.
38. Banwell, C.N. and E.M. McCash, *Fundamentals of molecular spectroscopy*. Vol. 851. 1994: McGraw-Hill New York.
39. Stuart, B., *Infrared spectroscopy*. 2005: Wiley Online Library.
40. Jaffé, H.H. and M. Orchin, *Theory and applications of ultraviolet spectroscopy.* 1962: p. 624.
41. Parsegian, V.A., *Van der Waals Forces: A Handbook for Biologists, Chemists, Engineers, and Physicists*. 2006, New York: Cambridge University Press. 396.
42. Oriols, X. and D. Ferry, *Quantum transport beyond DC.* Journal of Computational Electronics, 2013. **12**(3): p. 317-330.
43. Eisenberg, R., X. Oriols, and D.K. Ferry, *Kirchhoff's Current Law with Displacement Current.* arXiv: 2207.08277, 2022.
44. Ayers, J.E., *Digital Integrated Circuits: Analysis and Design, Second Edition*. 2018: CRC Press.
45. Gielen, G. and W.M. Sansen, *Symbolic analysis for automated design of analog integrated circuits*. Vol. 137. 2012: Springer Science & Business Media.
46. Gray, P.R., et al., *Analysis and Design of Analog Integrated Circuits*. 2009: Wiley.
47. Hall, S.H. and H.L. Heck, *Advanced signal integrity for high-speed digital designs*. 2011: John Wiley & Sons.
48. Horowitz, P. and W. Hill, *The Art of Electronics*. Third Edition ed. 2015: Cambridge University Press. 1224.

49. Scherz, P. and S. Monk, *Practical electronics for inventors*. 2006: McGraw-Hill, Inc. 1056.
50. Sedra, A.S., et al., *Microelectronic Circuits*. 2020: Oxford University Press, Incorporated.
51. Zank, G. and W. Matthaeus, *The equations of nearly incompressible fluids. I. Hydrodynamics, turbulence, and waves.* Physics of Fluids A: Fluid Dynamics, 1991. **3**(1): p. 69-82.
52. Christodoulou, D. and S. Miao, *Compressible flow and Euler's equations*. Vol. 9. 2014: International Press Somerville, MA.
53. Landauer, R., *Conductance from transmission: common sense points.* Physica Scripta, 1992. **1992**(T42): p. 110.
54. Einstein, A., *Essays in science, originally published as Mein Weltbild 1933, translated from the German by Alan Harris*. 1934: Open Road Media.
55. Whittaker, E., *A History of the Theories of Aether & Electricity*. 1951, New York: Harper.
56. Eisenberg, R.S., *Electrodynamics Correlates Knock-on and Knock-off: Current is Spatially Uniform in Ion Channels.* Preprint on arXiv at https://arxiv.org/abs/2002.09012, 2020.
57. Bush, V. and N. Wiener, *Operational Circuit Analysis: With an Appendix by Norbert Wiener*. 1929: Chapman & Hall.
58. Tuttle, D.F., *Network synthesis*. Vol. 1. 1958: Wiley.
59. Ghausi, M.S. and J.J. Kelly, *Introduction to distributed-parameter networks: with application to integrated circuits*. 1968: Holt, Rinehart and Winston.
60. Guillemin, E.A., *Communications Networks Vol. 1 The Classical Theory of Lumped Constant Networks*. 1931: John Wiley.
61. Guillemin, E.A., *Theory of Linear Physical Systems: Theory of physical systems from the viewpoint of classical dynamics, including Fourier methods*. 2013: Dover Publications.
62. Balabanian, N. and T.A. Bickart, *Electrical network theory*. 1969: Wiley.
63. Weinberg, L., *Network analysis and synthesis*. 1975: Krieger Pub. Co.
64. Valentinuzzi, M.E. and A.J. Kohen, *James Clerk Maxwell, Kirchhoff's Laws, and their implications on modeling physiology [Retrospectroscope].* IEEE pulse, 2013. **4**(2): p. 40-46.
65. Bhat, H.S. and B. Osting, *Kirchhoff's Laws as a Finite Volume Method for the Planar Maxwell Equations.* Antennas and Propagation, IEEE Transactions on, 2011. **59**(10): p. 3772-3779.
66. Eisenberg, R., *A Necessary Addition to Kirchhoff's Current Law of Circuits, Version 2.* Engineering Archive EngArXiv, 2022. **https://doi.org/10.31224/2234**.
67. Eisenberg, R., *Circuits, Currents, Kirchhoff, and Maxwell.* Qeios, 2023. **Qeios ID: L9QQSH.2**.
68. Hodgkin, A.L. and A.F. Huxley, *A quantitative description of membrane current and its application to conduction and excitation in nerve.* J. Physiol., 1952. **117**: p. 500-544.
69. Gordon, J.S., *A Thread Across the Ocean: The Heroic Story of the Transatlantic Cable*. 2008: Paw Prints.
70. Okoshi, T., *Planar circuits for microwaves and lightwaves*. Vol. 18. 2012: Springer Science & Business Media.
71. Schwierz, F. and J.J. Liou, *Modern microwave transistors: theory, design, and performance*. 2003: Wiley-Interscience.
72. Fukunaga, K. and S. Kurahashi. *Dielectric properties of printed circuit board insulations at microwaves and millimetre waves*. in *Electromagnetics in Advanced Applications, 2007. ICEAA 2007. International Conference on*. 2007. IEEE.
73. Mei, K.K. *From Kirchoff to Lorentz modifying-circuit theory for microwave and mm-wave structures*. in *Infrared and Millimeter Waves, 2000. Conference Digest. 2000 25th International Conference on*. 2000. IEEE.
74. Kevorkian, J. and J.D. Cole, *Multiple Scale and Singular Perturbation Methods*. 1996, New York: Springer-Verlag. pp. 1-632.

75. Lienig, J. and J. Scheible, *Fundamentals of layout design for electronic circuits*. 2020: Springer Nature.
76. Howe, R.T. and C.G. Sodini, *Microelectronics: an integrated approach*. 1997, Upper Saddle River, NJ USA: Prentice Hall. 908.
77. Hastings, A., *The art of analog layout*. 2001: by prentice-Hall. inc.
78. Eisenberg, R.S., *Kirchhoff's Law can be Exact.* arXiv preprint available at https://arxiv.org/abs/1905.13574, 2019.
79. Eisenberg, B., et al., *What Current Flows Through a Resistor?* arXiv preprint arXiv:1805.04814, 2018.
80. Barcilon, V., J. Cole, and R.S. Eisenberg, *A singular perturbation analysis of induced electric fields in nerve cells.* SIAM J. Appl. Math., 1971. **21**(2): p. 339-354.
81. Eisenberg, R.S. and E.A. Johnson, *Three dimensional electrical field problem in physiology.* Prog. Biophys. Mol. Biol., 1970. **20**: p. 1-65.
82. Eisenberg, R., *Structural Analysis of Fluid Flow in Complex Biological Systems.* Modeling and Artificial Intelligence in Ophthalmology. , 2022. **doi: 10.20944/preprints202205.0365.v1**.
83. Eisenberg, R.S., V. Barcilon, and R.T. Mathias, *Electrical properties of spherical syncytia.* Biophys J, 1979. **25**(1): p. 151-80.
84. Mobley, B.A., J. Leung, and R.S. Eisenberg, *Longitudinal impedance of skinned frog muscle fibers.* J Gen Physiol, 1974. **63**(5): p. 625-37.
85. Mobley, B.A., J. Leung, and R.S. Eisenberg, *Longitudinal impedance of single frog muscle fibers.* J Gen Physiol, 1975. **65**(1): p. 97-113.
86. Chandler, W.K., A.L. Hodgkin, and H. Meves, *The effect of changing the internal solution on sodium inactivation and related phenomena in giant axons.* J Physiol, 1965. **180**(4): p. 821-36.
87. Baker, P.F., A.L. Hodgkin, and H. Meves, *The Effect of Diluting the Internal Solution on the Electrical Properties of a Perfused Giant Axon.* J Physiol, 1964. **170**: p. 541-60.
88. Baker, P.F., A.L. Hodgkin, and T.I. Shaw, *Replacement of the axoplasm of giant nerve fibres with artificial solutions.* J Physiol, 1962. **164**: p. 330-54.
89. Baker, P.F., A.L. Hodgkin, and T.I. Shaw, *The effects of changes in internal ionic concentrations on the electrical properties of perfused giant axons.* J Physiol, 1962. **164**: p. 355-74.
90. Hanai, T., D.A. Haydon, and J. Taylor, *The variation of capacitance and conductance of bimolecular lipid membranes with area.* J Theor Biol, 1965. **9**(3): p. 433-43.
91. Hanai, T., D.A. Haydon, and J. Taylor, *The influence of lipid composition and of some adsorbed proteins on the capacitance of black hydrocarbon membranes.* J Theor Biol, 1965. **9**(3): p. 422-32.
92. Everitt, C.T. and D.A. Haydon, *Electrical capacitance of a lipid membrane separating two aqueous phases.* J Theor Biol, 1968. **18**(3): p. 371-9.
93. Fricke, H., *The electric capacity of suspensions with special reference to blood.* The Journal of general physiology, 1925. **9**(2): p. 137-152.
94. Fricke, H., *The electric capacity of suspensions of red corpuscles of a dog.* Physical Review, 1925. **26**(5): p. 682.
95. Fricke, H. and S. Morse, *The electric resistance and capacity of blood for frequencies between 800 and 4½ million cycles.* The Journal of general physiology, 1925. **9**(2): p. 153.
96. Cole, K.S. and H.J. Curtis, *Electric impedance of the squid giant axon during activity.* The Journal of general physiology, 1939. **22**(5): p. 649-670.
97. Bezanilla, F., *Gating currents.* The Journal of General Physiology, 2018. **150**(7): p. 911-932.
98. Catacuzzeno, L., et al., *Gating current noise produced by Brownian models of a voltage sensor.* Biophysical Journal, 2021. **120**(September 21, 2021): p. 1–19.

99. Catacuzzeno, L., et al., *Multiscale modeling shows that dielectric differences make NaV channels faster than KV channels.* Journal of General Physiology, 2021. **153** (2): p. DOI: 10.1085/jgp.202012706.
100. Catacuzzeno, L. and F. Franciolini, *The 70-year search for the voltage sensing mechanism of ion channels.* The Journal of Physiology, 2022.
101. Bezanilla, F., *Voltage Sensor Movements.* J. Gen. Physiol., 2002. **120**(4): p. 465-473.
102. Kelvin, L., *On the theory of the electric telegraph.* Proceedings of the Royal Society (London), 1855. **7**: p. 382-399.
103. Kelvin, L., *On the theory of the electric telegraph.* Philosophical Magazine, 1856. **11**: p. 146-160.
104. Hill, A.V., *Chemical Wave Transmission in Nerve*. 1932: Cambridge University Press. 74.
105. Hodgkin, A.L., *Evidence for electrical transmission in nerve: Part II.* J Physiol, 1937. **90**(2): p. 211-32.
106. Hodgkin, A.L., *Evidence for electrical transmission in nerve: Part I.* J Physiol, 1937. **90**(2): p. 183-210.
107. Chazalviel, J.-N., *Coulomb Screening by Mobile Charges*. 1999, New York: Birkhäuser. 355.
108. Hodgkin, A.L., A.F. Huxley, and B. Katz, *Measurement of current- voltage relations in the membrane of the giant axon of Loligo.* J. Physiol. (London), 1952. **116**: p. 424-448.
109. Sperelakis, N. and N. Sperelakis, *Cell Physiology Source Book: Essentials of Membrane Biophysics*. 2012: Elsevier Science.
110. Tosteson, D., *Membrane Transport: People and Ideas*. 1989, Bethesda MD: American Physiological Society. 414.