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Posted Date: 3 March 2025

doi: 10.20944/preprints202503.0073.v1

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Preprints.org (www.preprints.org) | NOT PEER-REVIEWED | Posted: 3 March 2025 doi:10.20944/preprints202503.0073.v1

Article

The Goldman Hodgkin and Katz Errors

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Abstract: The Goldman Hodgkin and Katz equation (GHK) is regarded as a cornerstone in the field of biology. The GHK equation expands upon Bernstein's hypothesis. Bernstein had originally employed the Nernst equation to validate his theory. Consequently, the GHK equation is also logically derived from the Nernst equation. Contemporary understanding in chemistry and electrochemistry conclusively indicates that the GHK equation contains fundamental flaws, as it deviates from the primary intent of the Nernst equation and incorporates parameters that are entirely inappropriate.

Keywords: membrane theory; membrane potential; Nernst; Bernstein; GHK equation; Biophysics; Biology

1. Introduction

During the early 20th century, Julius Bernstein concentrated on investigating the membrane potential and action potential [1]. He introduced a hypothesis (BH) suggesting that the membrane potential arises from the disparity in potassium ion concentration between the cell's interior and exterior. This concentration gradient was identified as the basis of the membrane potential. Concurrently, Walther Nernst developed a significant electrochemical equation [2], which too depended on a concentration difference.

In the latter part of the 20th century, Goldman, Hodgkin, and Katz sought to develop a more accurate and comprehensive explanation, based on Bernstein's potassium hypothesis [3]. Goldman specifically examined non-living experimental models comparable to a living cell and formulated an equation akin to the Goldman-Hodgkin-Katz equation. However, the physiological interpretation of this equation that is widely recognized today was introduced by Hodgkin and Katz [4].

Their ionic theory incorporated new variables into the Nernst equation, specifically the permeability coefficients. When a permeability is presumed to adjust to a stimulus, or if there is a shift in concentration, the ionic flux can consequently change, leading to a modification in the membrane potential as determined by the equation. The foundational theoretical framework established by Hodgkin and Huxley has been tremendously influential in current electrophysiology and even allows computation of the permeability of potassium and sodium during an action potential by applying the GHK equation. This led to the establishment of the famous HH model. In addition, the set of studies conducted by Hodgkin and Katz in 1952 is believed to anticipate the discovery of the ion transporter, currently referred to as the ion channel, which is fully understood at present [5–9].

2. Material

2.1. Definitions Used in the Text

Table 1 below presents all the variable and constant names referenced in this article that are shared between the Nernst equation and the GHK equation.

doi:10.20944/preprints202503.0073.v1

Table 1. Shared variables and constants.

Variable	Definition
R	universal ideal gas constant: $R = 8.31\ J\ K^{-1}\ mol^{-1}$
T	temperature in Kelvins
n	number of electrons transferred in the cell reaction or half-reaction
F	Faraday's constant: $F = 96485\ C\ mol^{-1}$

Table 2 provides explanations for the variables unique to the Nernst equation.

Table 2. Variables and constants used in the Nernst equation. When the electrodes are constructed from identical metals, then E^0_{red} equals 0.

Variable	Definition
E^0_{red}	standard half-cell reduction potential.
E_{cell}	cell potential (electromotive force) at the temperature of interest.
$[A]_{red}$	reducing component concentration
$[A]_{ox}$	concentration of the oxidizing component

Table 3 provides explanations for the variables unique to the GHK equation.

Table 3. Variables and constants used in the GHK equation.

Variable	Definition
E_{GHK}	membrane potential
P_K	potassium permeability
$[K^+]_{in}$	internal potassium concentration
$[K^+]_{out}$	external potassium concentration
P_{Na}	sodium permeability
$[Na^+]_{in}$	internal sodium concentration
$[Na^+]_{out}$	external sodium concentration
P_{Cl}	chlorine permeability
$[Cl^-]_{in}$	internal chlorine concentration
$[Cl^-]_{out}$	external chlorine concentration

2.2. The Nernst Equation

One of the most common forms of the Nernst Equation (2) is shown below.

The Nernst equation connects the actual concentrations, or activities, of substances involved in a cellular reaction with the standard cell potential. This is applicable for a straightforward reduction of the type;

$$\mathrm{M}^{n+} + \mathrm{ne}^- \rightarrow \mathrm{M} \tag{1}$$

The principle indicates that a half-cell potential will vary by $59/n\ mV$ for every ten-fold modification in ion activity. When the total ion concentration remains below approximately $0.001M$, ionic concentrations can usually replace activities.

Equation (2) can be modified to Equation (3) under the conditions described above, specifically when the electrode pair is composed of identical materials.

Here, the value of E^0_{Red} is $0\ V$.

$$E_{cell} = E^0_{Red} - \frac{RT}{nF} \ln \frac{[A]_{red}}{[A]_{ox}} \tag{2}$$

$$E_{cell} = -\frac{RT}{nF} \ln \frac{[A]_{red}}{[A]_{ox}} \tag{3}$$

The Nernst equation possesses a number of significant limitations.The potential is determined entirely by the concentration gradient, relying solely on this difference in concentration.

Calculating the electron flow in redox reactions is not feasible. The flow rate or current is inherently dependent on the specific setup. Although augmenting the electrode surface area or altering the involved volumes could be considered, the potential remains constant, being solely determined by the concentration gradient.

As a result, the current values have to be obtained through experimental measurement because they cannot be computed.

In an experiment utilizing the Nernst equation, tracking the potential value changes over time is not feasible, as there is no time variable involved.

The Nernst equation cannot be used when an oxidation-reduction reaction is absent.

2.3. The GHK Equation

The Goldman Hodgkin and Katz equation (4) takes the following form:

$$E_{GHK} = \frac{RT}{F} \ln\left(\frac{P_K[K^+]_{in} + P_{Na}[Na^+]_{in} + P_{Cl}[Cl^-]_{out}}{P_K[K^+]_{out} + P_{Na}[Na^+]_{out} + P_{Cl}[Cl^-]_{in}}\right) \tag{4}$$

The Nernst equation is adjusted by incorporating permeability coefficients for each pair of internal and external concentrations.

The incorporation of these coefficients provides an elegant explanation for the changes in membrane potential throughout an action potential. These permeability factors might account for the preference of potassium over sodium in swaps that occur during the resting potential, which is also known as the membrane potential. The permeabilities are perfectly aligned with the conductance (g) described in the HH model. A variation in permeability results in a corresponding adjustment in conductance, which consequently affects the resistance to passage of ions. Applying the well-known equation:

$$U = E_{mem} = \frac{1}{g} I = RI \tag{5}$$

completes the explanation. With a reduction in resistance paired with an increase in current, there is an inevitable alteration in potential.

The authors emphasize that a negligible number of ions is required to determine a potential equivalent to the membrane potential. They point out that this minuscule amount is inadequate to alter the existing concentrations.

It is important to observe that frequently the membrane potential or the different values observed in the action potential are computed based on a charge q and a capacitance C, as demonstrated below:

$$q = CU \implies U = \frac{q}{C} \tag{6}$$

The authors noted that, while ionic theory partially clarifies the electrical aspects of membrane potentials and the generation of action potentials, it does not fully account for all observed phenomena. Despite this limitation, the theory remains widely accepted and is still a topic of debate and discussion. Its enduring appeal can be attributed to its simplicity.

3. Discussion

Although it is conceivable to assume that Bernstein might have employed the Nernst equation due to a lack of knowledge, as it was the sole equation he had access to that appeared to support his hypothesis, it is improbable to think he was unaware of the redox reactions identified since Lavoisier's era over a century ago.

3.1. Potassium Flows in the Wrong Direction

Conversely, Bernstein overlooks a critical question: Given that the membrane potential results from the leakage of potassium out of the cell, which was almost 30 times higher inside compared to the external environment, how can it accumulate within the cell if its source is the same external environment?

Indeed, implementing a hypothesis in which diffusion serves as the optimal solution is not feasible. Certain observations substantiate this exception: although hyperkalemia can result in critical disorders and cell death, such a fatal effect takes place well before the external concentration matches the cell's internal environment level. Why?

A singular logical deduction is clear: As the potassium level in the surrounding medium increases, it enters the cell through a method that deviates from simple diffusion. This has been repeatedly validated by Gilbert Ling [10,11]. The reluctance of biologists to acknowledge this is due to its potential to disrupt a significant sector of biological study.

Additional evidence is derived from the expansion of living organisms. As implied by the term itself, growth indicates an enlargement in size, volume, and consequently, surface area. Furthermore, considering that the various elements of the cell are sourced from the external environment, it is necessary to acknowledge that potassium should infiltrate the cell throughout its growth, even when faced with a plasma concentration that challenges the diffusion theories we have proposed for such transmembrane transport [12]. Our famous Na / K pump cannot perform miracles, as it only accounts for a small proportion of the generation of membrane potential, and we have known for a very long time that the amount of ATP available is not sufficient for such a task[4,13,14].

Bernstein should have sought an alternative hypothesis that more accurately described the observed facts, given the lack of an oxido-reduction chemical equation in his original proposal.

Indeed, the Nernst equation marked a significant breakthrough in chemistry and electrochemistry. It could even be argued that its impact was so substantial that it might have overshadowed the constraints inherent in its assumptions and the potential conditions under which it can be applied.

This finding sparked a significant debate that persisted for more than 50 years. Known as the great Nernstian hiatus [15,16], it was the starting point for numerous transformative changes in the fields of chemistry and electrochemistry.

3.2. Exceeding Limits for Concentrations

The Nernst equation is accurate primarily for total concentrations less than one millimole, that is, 0.001 M. This significant limitation has led to discrepancies between the experimental results and the theoretically predicted outcomes, which the chemists presumed to be flawless. There was an undetected factor, perhaps even multiple, that could explain the observed phenomena.

Our biological metrics clearly indicate total concentrations that exceed 150 times the norm. At the time, the concentration constraints of the Nernst equation were widely recognized. Like many other biologists of their era, Goldman Hodgkin and Katz did not attempt to stay abreast of contemporaneous chemical advancements, a decision made justifiably given Nernst's established reputation.

Therefore, it's understandable not to fault them, considering that the counterverse is still operating in the 2000s.

By 1977, Healy [17] was already writing:

"When the material is not an electrode but an isolated particle of an aqueous colloidal dispersion or when the material is an insulator such as SiO 2 or a clay particle, or when the solid part of the interface is a monolayer of ionic surfac- rants or a membrane with exposed ionizable groups, then the validity of the electrochemical approach to interface potentials is not certain."

Cheng wrote in 1998 [16]:

"The mechanism is most important for understanding the electrode process and potential origin. The thermodynamics shows only the DG, the energy change, not the mechanism. In the textbooks of quantitative analysis and electroanalytical chemistry, the thermodynamics has been overemphasized, neglecting the mechanism."

doi:10.20944/preprints202503.0073.v1

and further in this article:

...

"First of all, the Nernst equation is not related to the capacitance potential. Second, a common slope, 59 mV, may be calculated from other equations from different mechanisms."

and even further in this article,

...

"The potential origin of membrane electrodes comes from the adsorption of charged ions or particles on the electrode surface, following the Boltzmann distribution, capacitance law, E = q/C, and Fruendlich isotherm. Contrary to what's shown in the Nernst equation, that the slope is infinitely linear, E = q/C is linear only in a limited range depending on the nature of ions, the electrode surface and thickness, etc."

In 2002, Cheng continues with; [18]:

"The non-faradaic potentiometry may be classified as faradaic and non-faradaic. The former deals with the redox reactions using the Nernst equation to explain the potential mechanism. The latter deals with the non-redox reactions using the Boltzmann and modified Boltzmann equation to explain the potential origin. The non-faradaic potentiometry has been neglected in the literature."

Similarly, it is unfair to hold the authors of the GHK equation entirely responsible for not being completely informed of the complex debates, contradictions, and discussions associated with the Nernst equation, as these issues arose practically at the same time as their research.

The problems discussed earlier are likely the result of several factors. In particular, one factor is the limited scientific understanding available during that period, and another is probably the underdeveloped state of experimental technology.

In contrast, researchers have possessed advanced scientific instruments early in this field, including thermodynamics that is applicable to real systems. Certain solution systems, such as colloidal solutions, exhibit non-ideal behavior [19], a characteristic shared by living cells [4,20]. From a thermodynamic standpoint, living cells function as real solution systems rather than ideal ones. Consequently, the thermodynamic principles for ideal systems are inadequate for analyzing these systems. Instead, an understanding of thermodynamics for real systems is essential to conceptualize the properties of living cells.

In fact, Gilbert Lewis laid down this theoretical groundwork for physical chemistry in the early 20th century [21]. However, it remains unintegrated into physiological studies even now. Physiological researchers still conceptually model living cells as if they were simple plasma membrane sacs containing a thermodynamically ideal aqueous electrolyte. Such an approach has resulted in physiological paradoxes comparable to the use of epicycles in ancient geocentric models [4,13,20,22].

3.3. Possible Mathematical Error

While it may be considered a minor mistake to apply the Nernst equation with concentrations beyond the limits set by its initial conditions, the same cannot be claimed regarding the inclusion of permeability coefficients and, especially, their application within the equation.

Equation (3) can be written as follows:

$$E_{cell} = -\frac{RT}{nF}\ln\left(\frac{a}{b}\right) \tag{7}$$

with

$$a = (a_1 + a_2 + a_3) \text{ and } b = (b_1 + b_2 + b_3) \tag{8}$$

Within mathematics, every element of a fraction can be scaled by p, as demonstrated by the subsequent equation:

$$E_{cell} = -\frac{RT}{nF}\ln\left(\frac{pa}{pb}\right) \tag{9}$$

And by replacing the values of a and b by the values defined in (8), we finally obtain:

$$E_{cell} = -\frac{RT}{nF}\ln\left(\frac{pa_1 + pa_2 + pa_3}{pb_1 + pb_2 + pb_3}\right) \tag{10}$$

However, deriving the structure of the subsequent equation appears to be unattainable;

$$E_{cell} = -\frac{RT}{nF}\ln\left(\frac{p_1a_1 + p_2a_2 + p_3a_3}{p_1b_1 + p_1b_2 + p_3b_3}\right) \tag{11}$$

This is clearly the definitive version of the GHK equation!

From a mathematical perspective, differentiating the permeability coefficients appears impractical.

Furthermore, the GHK equation lacks a rigorous demonstration.

3.4. No Current in a Capacitor

It makes sense that scientific research should be based on the achievements of its predecessors. Maintaining an open mindset and a keen critical eye is essential to the essence of scientific inquiry. However, challenging the foundational elements of science is not a simple task, but it is crucial to advance and expand our understanding. It is unavoidable.

However, one aspect that remains puzzling about this group of exceptional biologists is their model. In their theoretical framework, Goldman, Hodgkin, and Katz introduced a membrane with capacitance; they computed it and somewhat incorporated it into the equations governing action potential propagation.

An novice learning about electricity may incorrectly perceive the functioning of a capacitor. Numerous textbooks describe the process of a capacitor's charging and discharging. However, it is essential to remember that the current does not pass through an electric capacitor.

It is undeniable that the potential increases across the terminals as a result of variations in the electric field between the armatures. For an ionic capacitor, as considered in our model, chemistry[15,16,23] and biology [4,14,20,24–28] have long established—and repeatedly confirmed—that voltage can change by ion adsorption even without current flow. A complete electrical circuit is needed for the current to exist, and at the cellular level such a circuit has not been verified.

Chemistry has acknowledged its mistakes and now encourages chemists, along with individuals planning to utilize chemical knowledge, to adopt this concept as it provides a clearer explanation of the facts observed and measured. Consequently, the Nernst equation can no longer be misused to account for fluctuations in the membrane potential in biology.

3.5. Non-Logical Transformation

The Nernst equation expresses the potential in terms of concentration differences, highlighting both its elegance and its necessity. It represents the conversion of chemical energy to electrical energy through redox reactions within the framework of thermodynamics.

Faced with a hypothesis where diffusion appeared to be the dominant factor, biologists reasoned that altering ion flow would similarly affect ion current (the rate of flow), since resistance—which is the reciprocal of conductance—changes correspondingly.

Our application of Ockham's razor often leads us to form hypotheses that appeal to our intellect, though they may occasionally deviate considerably from true accuracy.

This method is unaffected by flow, as it does not consider volumes, and dismisses the concept of time travel due to its lack of practical use. The key factor is that the potential stays constant, regardless of fluctuations in flow rate or alterations in resistance. This claim is validated in the production of our batteries. Although they may vary in capacity, resulting in differing flow rates (electric current) and internal resistances, the voltage at their terminals remains consistent as they adhere to the same principle.

When Goldman, Hodgkin, and Katz introduced arbitrary parameters to alter the result of an equation intended to remain nearly constant concerning its original parameters, they overlooked the theoretical principle at the foundation of the Nernst equation.

Moreover, the key aspect here is that a constant potential value can be achieved using two variables, R and I. The authors emphasized this crucial differentiation: conductance and current have variability. Since these two unknowns are not related to a constant E_{mem}, endless solutions can be derived.

Below are several numerical instances;

$$U = E_{mem} = \frac{1}{g} I = RI = 100 \cdot 2 = 2025 \cdot 0.0987 = 1M \cdot 0.0002\ etc \tag{12}$$

Consequently, one could assert that the theoretical rationale for the GHk equation lacks validity and empirical support. Additionally, the values have been derived from variations in concentrations within both external and occasionally internal media. Thus, it cannot be conclusively determined that diffusion occurs, as these concentration changes also result in altered adsorption at the membrane, which has numerous available binding sites. This hypothesis is universally acknowledged by chemists and is undeniable by biologists.

To summarize, the GHK equation does not align with the core principles of Nernst's original theory. It is now recognized that generating a potential does not rely on a current. Instead, this potential is directly achieved through the adsorption of ions onto the numerous sites found in proteins of various forms, including IDPs (intrinsic disordered proteins), globular proteins, and ion channels, whose structures and functions are still subjects of discussion. We are moving beyond the simplistic view of the cytosol, acknowledging that the cytoplasm houses numerous organelles and fluid environments, with the cell frequently transitioning through different phases to precisely release the ions contained within.

It is evident that potential variations can be achieved by altering the phases, shapes, and binding of ion-bearing structures. Proteins represent a significant area of investigation for understanding not only electrical behavior but also structural and thermal aspects [29–31]. Some early pioneers had already highlighted this area [20]; it is regrettable that such a forward-thinking theory was neglected, even as chemists and physicists persist in questioning and proposing more precise hypotheses that elucidate observed phenomena and address the deficiencies in past theories.

4. Conclusions

An in-depth analysis of the GHK equation, considering recent developments in chemistry, physics, and mathematics, reveals its fundamental flaws in both its assumptions and its incorporation of parameters that deviate significantly from the original context of the Nernst equation. It is evident that this equation was developed at a time when our understanding was limited. Surprisingly, biology continues to cling to outdated perspectives and appears to remain entrenched in past simplifications and theories designed primarily to preserve dogmatic, unchangeable understanding. It is unnecessary to start from scratch, as existing evidence is already available, and previously debated theories that rely on stronger scientific foundations are now emerging to lead a scientific resurgence in biology.

Author Contributions: Conceptualization, B.D., H.T. and V.M.; investigation, B.D.; writing—original draft preparation, B.D., H.T. and V.M; writing—review and editing, B.D., H.T. and V.M; visualization, B.D.; All authors have read and agreed to the published version of the manuscript.

Funding: This work was not subsidized.

Conflicts of Interest: The authors declare no conflict of interest.

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