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Interdisciplinarity in modelling of biophysical processes

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ABSTRACT

In this article, the importance of interdisciplinary ideas for modelling and understanding signal propagation in nerve fibres is described as a fascinating problem of biophysics. A mathematical model involves the physical laws, assumptions, hypotheses, and finally, the governing equations. The analysis of this complex process is at the interface of physics, chemistry, and mathematics, together with experimental studies in electrophysiology. It is stressed that the mindsets of different communities may hinder cooperation.

1. Introduction

This article reflects the thoughts during the publication process of a research paper on mathematical modelling of signals in nerves, which is a fascinating biophysical process. A manuscript submitted to a journal with an excellent reputation had a usual length, but one of the reviews was twice the length of the submitted paper. This review resembled a research paper itself, criticising many aspects of the approach described in the manuscript, including the idea of mathematical modelling as a method. The reviewer's questions about the possible influence of many structural details of nerves were certainly justified and welcome. However, the reviewer stated: 'This reviewer is not a mathematician. Therefore, reference to classes of mathematical formulae, and many aspects of the derivation of the formulae presented are often obscure to me'. As far as the submitted manuscript has analysed the process of trying to use knowledge not only from experimental electrophysiology but also from basic physics and mathematics, the review raises questions about the usage of mathematical models in biology and the importance of underlying physics. Although much has been written about the benefits of interdisciplinarity, it seems that there are still barriers between the research communities that accept only the ideas known in their close field of interest. The Nobelist John Hopfield describes the different communities of physicists and biologists and the differences in biology and physics paradigms [25]. He recommends: 'Stick to the physics paradigm, for it brings refreshing attitudes and a different choice of problems to the interface'. In what follows, general thoughts are presented describing the ideas of the interdisciplinary approach in biological modelling.

2. Mathematical modelling

We know the saying of Galileo Galilei that the book of nature is written in the language of mathematics. Contemporary understanding keeps this idea but says that mathematical modelling means casting a real-world problem (a phenomenon) into a mathematical representation. A mathematical model is an abstraction of a real process/phenomenon presented in the language of mathematics. It means that the variables are quantified, and they are described by equations or functions. In general, a model includes the governing equations, initial and boundary conditions, and usually also certain constraints, all based on a specific set of assumptions. An input generates a certain output, and implicitly it means causality. It is clear that mathematical modelling must be based on definite rules but, on the other hand, be flexible enough to grasp possible modifications if required.

In the mathematical modelling of biological processes, attention must be paid to descriptive, integrative, and explanatory levels [37], summed up in integrative biological modelling [32]. Such an approach is actually based on the interface of

biology on one side and physics, chemistry, and mathematics on the other side. Examples described by Gavaghan et al. [21], Bialek [4], and others demonstrate vividly how fruitful such an approach is. However, this is not always a straightforward way. Cartwright [8] mentions that ‘To explain a phenomenon is to find a model that fits it into the basic framework of the theory and that thus allows us to derive analogues for the messy and complicated phenomenological laws which are true of it. The models serve a variety of purposes, and individual models are to be judged according to how well they serve the purpose at hand.’

However, mathematical modelling cannot solve the problem on its own. Kohl et al. [28] have said: ‘Mathematical models, however, need to be used with care. They are aids to thought, not a replacement for it. The only serious difference between a biologist who uses mathematical modelling and one who does not is that the former explores the consequences of his ideas quantitatively, including the implementation of computational experiments to assess the plausibility of those ideas. The potential benefits of doing so are obvious because quantitatively plausible predictions improve subsequent hypothesis-driven experimental research.’

Indeed, there are many fruitful aspects of modelling. A report from the US National Research Council [35] includes a special chapter ‘Computational modeling and simulation as enablers for biological discovery’ where the features of modelling were discussed. The list of properties and possibilities of models is worth repeating here:

‘models provide a coherent framework for interpreting data; models highlight basic concepts of wide applicability; models uncover new phenomena or concepts to explore; models identify key factors or components of a system; models can link levels of detail; models enable the formalization of intuitive understandings; models can be used as a tool for helping to screen unpromising hypotheses; models inform experimental design; models can predict variables inaccessible to measurement; models can link what is known to what is yet unknown; models can be used to generate accurate quantitative predictions; models expand the range of questions that can be meaningfully asked’.

In addition, as a summary, it is concluded: ‘Models are useful for formalizing intuitive understandings, even if those understandings are partial and incomplete. What appears to be a solid verbal argument about cause and effect can be clarified and put to a rigorous test as soon as an attempt is made to formulate the verbal arguments into a mathematical model. This process forces a clarity of expression and consistency (of units, dimensions, force balance, or other guiding principles) that is not available in natural language. As importantly, it can generate predictions against which intuition can be tested.’ A process can be described at various levels of abstraction. In this context, Carillo and Martinez [7] argued that ‘... different paths of abstraction can lead to a worthwhile diversity of models – even though at some point these models

may be interpreted as excluding alternatives, at a later time they can be appreciated as advancing our understanding.’ Besides practical applications, the idea that one could understand the unknown from the analysis of models (see the list above) follows Albert Einstein’s thoughts that ‘... mathematical construction enables us to discover the concepts and the laws connecting them...’ [13].

3. Nerve signals: a way to model

The propagation of signals in nerves is an extremely important chapter of biology. This complex problem is intensively studied not only because of its possible pathological effects but also because of its role in cognitive processes and the processing of information. In what follows, attention is paid to the fundamental behaviour of signal propagation in healthy nerves under normal conditions, focusing on physical phenomena. Numerous theoretical and experimental studies over the last two centuries have cast light on many details of this process. The Hodgkin–Huxley (HH) model, based on the ingenious description of ion currents and numerous experiments, is nowadays considered a cornerstone for describing the propagation of an action potential (AP) in axons [23]. However, Hodgkin [24] mentioned: ‘In thinking about physical basis of action potential perhaps the most important thing to do at the present moment is to consider whether there are any unexplained observations which have been neglected in an attempt to make experiments fit into a tidy pattern.’ Indeed, as demonstrated in experiments, the propagation of an AP as the main carrier of information is accompanied by mechanical and thermal effects. In addition to earlier experiments (see, for example, [44,45]), recent studies have also reported the mechanical response of mammalian neurons recorded by a label-free optical imaging method [6] and high-speed interferometric imaging [30]. In general, in addition to the AP, the accompanying effects include the longitudinal wave (LW) in the biomembrane and the corresponding transverse wave (TW), the pressure wave (PW) in the axoplasm, and temperature change (Θ) accompanied by some biochemical changes. This means that there is an ensemble of waves, and besides electrophysiology, attention must be paid to the complexity of the process involving physics, chemistry, and thermodynamics. In this context, mathematical modelling plays an important role because, besides the experiments, describing the physical mechanisms in nerves in mathematical terms helps to understand the causality and the coupling of effects. That is why studies of nerve propagation are at the interface of physics and mathematics. Extensive experimental studies have revealed many details of this process, but not all the mechanisms of interaction between the various effects are described with the required accuracy. That is why all the attempts to reach a better understanding should be welcomed. Mathematical modelling is one of the possibilities to improve our understanding [16].

Hereafter, we present our ideas about the steps of the modelling (and understanding) of the signals in nerves. The full process of modelling starts from philosophical principles,

although usually these are not formulated but taken as unwritten rules. For the full picture, we present these principles following DeLanda [12]:

1. General principles:

- complex processes are characterised by multiplicity, which is the activator of changes in the system;
- multiplicity is characterised by differences that are productive and cause interactions;
- the changes (gradients) are characterised by velocities;
- the causality for processes is related to multiplicities;
- emergence means a process where novel properties or capacities emerge from causal interactions.

2. For dynamical systems:

- one should distinguish between intensive and extensive properties of systems: intensive properties such as pressure, temperature, density, etc. cannot be divided; extensive properties such as length, area, volume, and amount of energy can be divided into parts; intensive properties have critical thresholds, and differences (gradients) in intensity store potential energy;
- one should distinguish between intrinsic (belonging to the system) and extrinsic (originating from outside) conditions for a system;
- one should understand the inertiality of a system and the role of thresholds and triggers in dynamical processes;
- every physical process also means the transfer of information.

3. Finally:

- for understanding complex processes, interdisciplinarity is required.

Next, modelling starts with setting up the set of assumptions:

- electrical signals are the carriers of information and trigger all the other processes [23];
- the axoplasm can be modelled as a fluid where a pressure wave is generated due to the electrical signal [45];
- the biomembrane can deform (stretch, bend) under the mechanical impact [17,22];
- the ion channels in biomembranes can be opened and closed under the influence of electrical signals as well as mechanical input [33].

This means that we follow the HH paradigm. To explain the accompanying effects, the existence of interaction forces between the components of the signal coupled into a whole is required. The physical mechanisms responsible for coupling and generating an ensemble of waves are:

- electric-biomembrane interaction resulting in mechanical waves (LW and TW) in the biomembrane;
- electric-fluid (axoplasm) interaction resulting in a mechanical wave in the axoplasm (PW);
- electric-fluid (axoplasm), electric-biomembrane, and mechanical-biomembrane interaction resulting in a thermal response (Θ) in the fibre.

The following hypotheses are made [15,16]:

- every field variable (a component of a signal) is influenced by changes in other field variables;
- the interactions are modelled by the coupling forces between the components of a signal;

- all mechanical waves in the axoplasm and the surrounding biomembrane, together with the heat production, are generated due to changes in electrical signals (AP or ion currents) that dictate the functional shape of coupling forces; in mathematical terms, changes are described by derivatives of field variables;
- the formalism of internal variables can be used for describing the exo- and endothermic processes of heat production;
- not only the influence of an AP on other effects but also possible feedback is considered.

Based on these assumptions and hypotheses, the governing equations are derived following the physical laws:

1. The AP is modelled either by the simplified FitzHugh–Nagumo (FHN) model [34], the HH model [23], or the Lieberstein [29] model. The FHN model includes only one ion current and is capable of modelling the main properties of the AP.
2. The PW in the axoplasm is modelled by a wave equation with viscous and coupling terms. The coupling terms model the electric-fluid interaction. Depending on the parameters of the coupling force, the PW might also have a bipolar shape as demonstrated by Terakawa [45].
3. The LW in the biomembrane is modelled by the improved Heimburg–Jackson (HJ) model [17,22] with coupling terms. The improved HJ model accounts for the elasticity and inertia of the embedded lipid structure of the biomembrane. The coupling terms model the electric biomembrane interaction and a possible interaction with the PW.
4. The TW is calculated from the LW, taking it proportional to the gradient of U , as in the theory of rods [39]. The TW typically has a bipolar shape.
5. The thermal response Θ is governed by the classical heat equation with coupling terms. Coupling terms arise from the Joule heating, dissipation from the mechanical waves, and possible exo- and endothermic effects. The formalism of internal variables [14,31] is used for modelling the exo- and endothermic effects.

To sum up, the model describing a wave ensemble in axons includes principles, assumptions, hypotheses, and last but not least, governing equations with their initial and boundary conditions. The verification of a model is achieved through experiments. The physical and geometrical structure of nerve fibres must be taken into account as accurately as possible. However, there is still much to be understood in neuroscience about what can be described by a mathematical model and what cannot. Every model is an abstraction of reality and can describe the process within the framework of assumptions and hypotheses made [27]. The modelling described above is similar to the ideas of Bialek [4]: the modelling starts with identifying principles, followed by the expression of principles in mathematical terms.

4. Interdisciplinarity and complexity

Even a brief summary of modelling the propagation of signals in nerves demonstrates that functional integration of many

disciplines is required for a proper understanding of the complex processes in nerves. Modelling involves not only biology or more definitely electrophysiology, but it also involves physics, including thermodynamics and the theory of continua, chemistry, mathematics, and even philosophy for proper theoretical considerations.

Consequently, one must deal with interdisciplinary studies. Briefly, interdisciplinarity analyses, synthesises and harmonises links between disciplines into a coordinated and coherent whole [2]. More specifically: 'Interdisciplinary research is a mode of research by teams and individuals that integrates information, data, techniques, tools, perspectives, concepts, and/or theories from two or more disciplines or bodies of specialized knowledge to advance fundamental understanding or to solve problems whose solutions are beyond the scope of a single discipline or area of research practice' [20].

Undoubtedly, experimental studies in electrophysiology, starting from Luigi Galvani in the 18th century, have paved the way for contemporary understanding of processes in nerves. However, there is a need '... to frame a theory that incorporates all observed phenomena in one coherent and predictive theory of nerve signal propagation' [3]. Indeed, modelling of biological complexity is a challenge not only for predictions but also for understanding the processes [11].

All dynamic processes in nature are governed by the laws of physics. This concerns all the electrical, mechanical, and thermal components of the wave ensemble in nerves. Electrical processes are governed by Maxwell equations, involving also the conservation laws for charges and fluxes and constitutive laws (Ohm's law, etc.). The HH model [23] and the Lieberstein model [29] are derived from Maxwell equations using assumptions based on experiments. The governing equations for mechanical waves (LW, PW, TW) are derived within the framework of continuum mechanics, where all the processes are described by conservation laws. Understanding thermal effects relies on the fact that heat is related to the electric current by Joule's law and heat flux is related to the temperature gradient by Fourier's law. The single effects are coupled to each other, and again, according to continuum physics, the concept of forces helps to understand the coupling mechanisms of fields. In physical terms, one should use Euler's first law: 'The time rate of change of momentum of a body is equal to the sum of the forces acting on the body' [43]. The importance of biophysical forces in neuronal signalling is demonstrated in an overview by Mueller and Tyler [33]. The coupling forces reflect the physical mechanisms of interactions between the components of the wave ensemble.

Mathematical modelling means that the physical processes are described using the language (equations, functions) of mathematics. Concerning the propagation of signals in nerves, mathematical analysis is presented in many studies (see, for example, [16,19,36]). First, the governing equations are derived from physical laws, taking into account experiments in electrophysiology. Second, in modelling the interactions between the various effects, one should consider that the changes in one field will affect the other fields. In mathematical terms, it means that the changes are reflected by

derivatives of variables with respect to time or space coordinates. Consequently, the coupling forces must include derivatives of variables that help to clarify the possible physical mechanisms of coupling. Third, it is well known in continuum mechanics [39] that transverse displacement of a slender tube is proportional to longitudinal deformation. This means that if longitudinal displacement is unipolar, then transverse displacement, as the derivative of it, must be bipolar. The experiments have demonstrated the correctness of this rule [44,45]. Finally, the full system of coupled equations involving the AP and accompanying effects is a system of nonlinear and linear partial differential equations (PDEs). It involves hyperbolic (for wave-type) phenomena and parabolic (for heat-type) phenomena, and solving this system needs numerical methods of high accuracy. McCulloch and Huber [32] call such an analysis 'integrative biological modelling *in silico*'. Numerical calculations may also clarify the accuracy of the hypothesis. For example, the formation of a possible soliton from an arbitrary input according to the HJ model of a bi-layer will take much more time than the propagation time of a signal along an average axon. This is a good example that demonstrates the effectiveness of the *in silico* analysis. We can recall here Cohen [9] who says: '... mathematics is biology's next microscope.'

Neurochemistry is related to the biochemistry of the brain and nerves, studying the structure and functions of the nervous system at a molecular level. Very generally speaking, the physical parameters of intra- and extracellular fluids and biomembranes depend on their chemical compounds. Concerning the propagation of signals, the processes in synapses that generate the signals in nerves are characterised by chemical reactions. In addition, during the propagation, exothermic and endothermic chemical reactions may influence the heat production in nerves [1].

Interdisciplinary studies based on physics, mathematics, and chemistry make the modelling of nerve signals a fascinating chapter of electrophysiology. The main carrier of information is the AP, but there are several accompanying effects, and a signal must be treated as a wave ensemble. In other words, the pieces are collected into a whole, and interactions between the pieces are important. This is a clear sign of complexity. An intriguing question is whether the interactions are fully understood and modelled with the required accuracy. Already Hodgkin and Huxley faced this problem when they proposed the ion mechanism by introducing three phenomenological variables that characterised the sodium and potassium ion currents [23]. They also constructed evolution equations with definite rate constants based on the careful analysis of experimental results. The idea of using phenomenology means that the mechanism of a process is not fully understood and described with the required accuracy, but the initial and final stages are known (measured). Such an idea was proposed by Heisenberg about 100 years ago for describing the behaviour of electrons. His idea of matrix mechanics was seminal for quantum mechanics (see a beautiful description of his ideas in a book by Rovelli [40]). In continuum mechanics, the concept of internal variables is

used [31]. According to this concept, similarly to what Hodgkin and Huxley [23] did, the initial and final stages together with a time scale (fast or slow) permit the construction of an evolution equation that governs the process. The general ideas of phenomenological modelling are analysed by Engelbrecht et al. [18] in more detail.

A central point in the analysis of complex systems is the modelling of interactions between its components. The mathematical model described in Section 3 describes the interactions between the components of the wave ensemble by coupling forces, as is done in continuum physics.

5. Some remarks on misunderstandings

As mentioned in Introduction (Section 1), this overview of the interdisciplinarity of biophysics was initially written as a reaction to a review that overlooked the variety of notions used in different fields of research. Hereafter, some misunderstandings are described that should be avoided when dealing with the analysis of such a complicated process.

For example, one might ask whether to use in the mathematical description of the process the notion of ‘models’ or just ‘equations’. In the context of mathematical modelling, the concept of models is widely used because it is more general (see Section 2) than just an equation, as a model includes more than just a mathematical representation (i.e. equations) of a process. That is why we have used in describing the nerve pulse propagation the notion of ‘HH model’ and not just ‘HH equation’ [5,10,19,26,38,46].

Furthermore, undoubtedly, the principles of physics in describing the mathematical models of dynamical processes must be followed. In continuum mechanics, for example, the conservation laws are always stressed as cornerstones in the analysis. Stressing the principles of physics is not inherently offensive but required to understand possible additional assumptions or hypotheses. Shrivastava and Schneider [42] point out, for example, that many ‘textbook models of biological communication ... violate momentum conservation...’.

One could ask whether to prefer conceptual modelling (words, diagrams) or mathematical modelling (resulting in equations derived using certain assumptions and simulations), as detailed by Torres et al. [46]. Both approaches must be developed in order to find the best explanation for complex processes. Unfortunately, this requirement is sometimes overlooked, whatever the reasons are. Interdisciplinarity, as it is understood, is used for analysing and synthesising lines between scientific disciplines into a coordinated and coherent whole [2]. One should value the knowledge obtained in different fields and learn to understand various ways of analysis for enhancing general knowledge. After all, whatever the particular methods, science, in principle, aims to describe and, most importantly, understand the causality of reality.

6. Conclusion

Biology is a very complicated field, and many studies try to reveal the secrets of life. This is a challenge, and all the attempts, experimental and theoretical, should be welcome.

The idea that living systems should be approached from physical principles is not original but supported by many studies [13,16,25,42].

Mathematical modelling [37] helps not only to predict the processes in biological systems but serves also to understand them [35]. We have recently formulated a set of guidelines for building a solid basis for mathematical models [18]. Bearing in mind the processes in nerves, these are:

Guideline 1: Physics rules electrical, mechanical, and thermal biological processes.

Guideline 2: Changes in one variable (field) will cause changes in other variables (fields).

Guideline 3: Modelling of electrophysiological processes requires interdisciplinary studies.

Guideline 4: Phenomenology considerably helps to understand measurements.

Guideline 5: The experiments in electrophysiology serve as a basis for theoretical models. Citations in the above text demonstrate that we have tried to generalise the ideas of many researchers who are interested in interdisciplinary studies.

The interdisciplinary approach will certainly be helpful in modifying mathematical models that describe the processes in nerves. Although much is understood (see, for example, monographs [5,16,24,33,41]), further studies are required to understand the influence of structural elements of nerve fibres in the generation and propagation of signals in nerves. The existence of myelin sheaths, proteins in the axoplasm, the structure of the axon hillock, and the possible effects of inductivity or other physical phenomena, usually assumed negligible, may play a certain role in understanding neural function.

Data availability statement

All data are available in the article.

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References

1. Abbott, B. C., Hill, A. V. and Howarth, J. V. The positive and negative heat production associated with a nerve impulse. *Proc. R. Soc. Lond. B*, 1958, **148**(931), 149–187. <https://doi.org/10.1098/rspb.1958.0012>
2. Alvargonzález, D. Multidisciplinarity, interdisciplinarity, transdisciplinarity, and the sciences. *Int. Stud. Philos. Sci.*, 2011, **25**(4), 387–403. <https://doi.org/10.1080/02698595.2011.623366>
3. Andersen, S. S. L., Jackson, A. D. and Heimburg, T. Towards a thermodynamic theory of nerve pulse propagation. *Prog. Neurobiol.*, 2009, **88**(2), 104–113. <https://doi.org/10.1016/j.pneurobio.2009.03.002>
4. Bialek, W. Perspectives on theory at the interface of physics and biology. *Rep. Prog. Phys.*, 2018, **81**(1), 012601. <https://doi.org/10.1088/1361-6633/aa995b>
5. Bressloff, P. C. *Waves in Neural Media. From Single Neurons to Neural Fields*. In *Lecture Notes on Mathematical Modelling*

- in the Life Sciences. Springer, New York, 2014. <https://doi.org/10.1007/978-1-4614-8866-8>
6. Brohawn, S. G., Wang, W., Handler, A., Campbell, E. B., Schwarz, J. R. and MacKinnon, R. The mechanosensitive ion channel TRAAK is localized to the mammalian node of Ranvier. *eLife*, 2019, **8**, e50403. <https://doi.org/10.7554/eLife.50403>
 7. Carrillo, N. and Martínez, S. Scientific inquiry: from metaphors to abstraction. *Perspect. Sci.*, 2023, **31**(2), 233–261. https://doi.org/10.1162/posc_a_00571
 8. Cartwright, N. *How the Laws of Physics Lie*. Oxford University Press, Oxford, 1983. <https://doi.org/10.1093/0198247044.001.0001>
 9. Cohen, J. E. Mathematics is biology's next microscope, only better; biology is mathematics' next physics, only better. *PLOS Biol.*, 2004, **2**(12), e439. <https://doi.org/10.1371/journal.pbio.020439>
 10. Coombes, S. and Wedgwood, K. C. A. *Neurodynamics. An Applied Mathematics Perspective*. In *Texts in Applied Mathematics*, **75**. Springer, Cham, 2023. <https://doi.org/10.1007/978-3-031-21916-0>
 11. Coveney, P. V. and Fowler, P. W. Modelling biological complexity: a physical scientist's perspective. *J. R. Soc. Interface*, 2005, **2**(4), 267–280. <https://doi.org/10.1098/rsif.2005.0045>
 12. DeLanda, M. *Intensive Science and Virtual Philosophy*. Continuum, London, 2004.
 13. Einstein, A. On the method of theoretical physics. *Philos. Sci.*, 1934, **1**(2), 163–169.
 14. Engelbrecht, J., Tamm, K. and Peets, T. Internal variables used for describing the signal propagation in axons. *Continuum Mech. Thermodyn.*, 2020, **32**(6), 1619–1627. <https://doi.org/10.1007/s00161-020-00868-2>
 15. Engelbrecht, J., Tamm, K. and Peets, T. Modeling of complex signals in nerve fibers. *Med. Hypotheses*, 2018, **120**, 90–95. <https://doi.org/10.1016/j.mehy.2018.08.021>
 16. Engelbrecht, J., Tamm, K. and Peets, T. *Modelling of Complex Signals in Nerves*. Springer, Cham, 2021. <https://doi.org/10.1007/978-3-030-75039-8>
 17. Engelbrecht, J., Tamm, K. and Peets, T. On mathematical modelling of solitary pulses in cylindrical biomembranes. *Biomech. Model. Mechanobiol.*, 2015, **14**(1), 159–167. <https://doi.org/10.1007/s10237-014-0596-2>
 18. Engelbrecht, J., Tamm, K. and Peets, T. On the phenomenological modelling of physical phenomena. *Proc. Estonian Acad. Sci.*, 2024, **73**(3), 264–278. <https://doi.org/10.3176/proc.2024.3.10>
 19. Ermentrout, G. B. and Terman, D. H. *Mathematical Foundations of Neuroscience*. In *Interdisciplinary Applied Mathematics*, **35**. Springer, New York, 2010. <https://doi.org/10.1007/978-0-387-87708-2>
 20. National Academies. *Facilitating Interdisciplinary Research*. National Academies Press, Washington, D. C., 2004. <https://doi.org/10.17226/11153>
 21. Gavaghan, D., Garny, A., Maini, P. K. and Kohl, P. Mathematical models in physiology. *Phil. Trans. R. Soc. A*, 2006, **364**(1842), 1099–1106. <https://doi.org/10.1098/rsta.2006.1757>
 22. Heimburg, T. and Jackson, A. D. On soliton propagation in biomembranes and nerves. *Proc. Natl. Acad. Sci. U. S. A.*, 2005, **102**(28), 9790–9795. <https://doi.org/10.1073/pnas.0503823102>
 23. Hodgkin, A. L. and Huxley, A. F. A quantitative description of membrane current and its application to conduction and excitation in nerve. *J. Physiol.*, 1952, **117**(4), 500–544. <https://doi.org/10.1113/jphysiol.1952.sp004764>
 24. Hodgkin, A. L. *The Conduction of the Nervous Impulse*. Liverpool University Press, 1964.
 25. Hopfield, J. J. Two cultures? Experiences at the physics-biology interface. *Phys. Biol.*, 2014, **11**(5), 053002. <https://doi.org/10.1088/1478-3975/11/5/053002>
 26. Izhikevich, E. M. *Dynamical Systems in Neuroscience. The Geometry of Excitability and Bursting*. The MIT Press, London, 2006. <https://doi.org/10.7551/mitpress/2526.001.0001>
 27. Kaplan, D. M. and Craver, C. F. The explanatory force of dynamical and mathematical models in neuroscience: a mechanistic perspective. *Philos. Sci.*, 2011, **78**(4), 601–627. <https://doi.org/10.1086/661755>
 28. Kohl, P., Crampin, E. J., Quinn, T. A. and Noble, D. Systems biology: an approach. *Clin. Pharmacol. Ther.*, 2010, **88**(1), 25–33. <https://doi.org/10.1038/clpt.2010.92>
 29. Lieberstein, H. M. On the Hodgkin-Huxley partial differential equation. *Math. Biosci.*, 1967, **1**(1), 45–69. [https://doi.org/10.1016/0025-5564\(67\)90026-0](https://doi.org/10.1016/0025-5564(67)90026-0)
 30. Ling, T., Boyle, K. C., Zuckerman, V., Flores, T., Ramakrishnan, C., Deisseroth, K. et al. High-speed interferometric imaging reveals dynamics of neuronal deformation during the action potential. *Proc. Natl. Acad. Sci. U. S. A.*, 2020, **117**(19), 10278–10285. <https://doi.org/10.1073/pnas.1920039117>
 31. Maugin, G. A. Internal variables and dissipative structures. *J. Non-Equilib. Thermodyn.*, 1990, **15**(2), 173–192. <https://doi.org/10.1515/jnet.1990.15.2.173>
 32. McCulloch, A. D. and Huber, G. Integrative biological modelling in silico. In 'In Silico' *Simulation of Biological Processes: Novartis Foundation Symposium* (Bock, G. and Goode, J. A., eds), **247**, 4–25. John Wiley & Sons, Chichester, 2002. <https://doi.org/10.1002/0470857897.ch2>
 33. Mueller, J. K. and Tyler, W. J. A quantitative overview of biophysical forces impinging on neural function. *Phys. Biol.*, 2014, **11**(5), 051001. <https://doi.org/10.1088/1478-3975/11/5/051001>
 34. Nagumo, J., Arimoto, S. and Yoshizawa, S. An active pulse transmission line simulating nerve axon. *Proc. IRE*, 1962, **50**(10), 2061–2070. <https://doi.org/10.1109/JRPROC.1962.288235>
 35. National Research Council. *Catalyzing Inquiry at the Interface of Computing and Biology*. National Academies Press, Washington, D. C., 2005. <https://doi.org/10.17226/11480>
 36. Nelson, P. *Biological Physics: Energy, Information, Life*. W. H. Freeman, New York, 2003.
 37. Noble, D. The rise of computational biology. *Nat. Rev. Mol. Cell Biol.*, 2002, **3**(6), 459–463. <https://doi.org/10.1038/nrm810>
 38. Nolte, D. D. *Introduction to Modern Dynamics: Chaos, Networks, Space and Time*. Oxford University Press, Oxford, 2015.
 39. Porubov, A. V. *Amplification of Nonlinear Strain Waves in Solids*. World Scientific, Singapore, 2003.
 40. Rovelli, C. *Helgoland*. Penguin Random House, London, 2022.
 41. Scott, A. *Neuroscience: A Mathematical Primer*. Springer, New York, 2002.
 42. Shrivastava, S. and Schneider, M. F. Evidence for two-dimensional solitary sound waves in a lipid controlled interface and its implications for biological signalling. *J. R. Soc. Interface*, 2014, **11**(97), 20140098. <https://doi.org/10.1098/rsif.2014.0098>
 43. Slattery, J. C. *Momentum, Energy, and Mass Transfer in Continua*. McGraw-Hill, New York, 1971.
 44. Tasaki, I. A macromolecular approach to excitation phenomena: mechanical and thermal changes in nerve during excitation. *Physiol. Chem. Phys. Med. NMR*, 1988, **20**(4), 251–268.
 45. Terakawa, S. Potential-dependent variations of the intracellular pressure in the intracellularly perfused squid giant axon. *J. Physiol.*, 1985, **369**(1), 229–248. <https://doi.org/10.1113/jphysiol.1985.sp015898>
 46. Torres, N. V. and Santos, G. The (mathematical) modeling process in biosciences. *Front. Genet.*, 2015, **6**, 1–9. <https://doi.org/10.3389/fgene.2015.00354>

Interdistsiplinaarsus biofüüsikaliste protsesside modelleerimisel

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Signaalide levi närvikius (aksonis) on äärmiselt huvitav biofüüsikaline protsess, mille modelleerimisel tuleb tugineda interdistsiplinaarsele lähenemisele. Vastav matemaatiline mudel põhineb füüsikaseadustel, millest tuletatakse rea hüpoteeside ja oletuste põhjal protsessi kirjeldavad võrrandid. Sellise keeruka protsessi kirjeldus nõuab interdistsiplinaarseid teadmisi füüsikast, keemiast ja matemaatikast ning elektrofüsioloogia katseid, mis tuleb siduda terviklikuks mudeliks. Interdistsiplinaarsete põhimõtete rakendamist võivad aga raskendada erinevused teadusvaldkondade mõttelaadis.
