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Signals in nerves from the philosophical viewpoint

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Abstract. Signals in nerves include electrical, mechanical and thermal components and are characterised by the complexity of processes. The modelling of these signals is analysed from the viewpoint of DeLanda, who has demonstrated the possibility of revealing Deleuze's philosophical theories by using the notions from nonlinear dynamics. It is shown that the mathematical modelling of processes in nerves by the authors of this paper follows the general ideas of multiplicity and causal interactions described by DeLanda.

Keywords: nerve signals, interdisciplinarity, modelling, complexity, epistemological analysis.

1. INTRODUCTION

The propagation of signals in nerves is a fascinating problem which is related to cognitive processes and processing of neural information. Much is known about signal propagation in nerves from the physical and physiological viewpoints. Experimental studies and theoretical predictions over the last two centuries have cast light on the main mechanisms responsible for signal formation and propagation. Besides the physical description, this complex process or the physics of thought should be analysed also from the philosophical viewpoint. Noble [43] has stressed the need "to unravel the complexity of biological processes" and suggested modelling in an integrative way. This is important for understanding the emergent properties in biological systems and the interaction processes responsible for them [38]. The nervous system is a complex structure, and as Koch and Laurent [35] stress, one should take into account "the highly nonlinear, nonstationary, and adaptive nature of the neuronal elements", which requires the understanding of the context in which the system operates. Much attention has been paid to physical complex systems, which require the use of mathematical descriptions developed in nonlinear dynamics [25,37,42]. Overviews of modelling the signal propagation in nerves [14,17,29,45,47] demonstrate the complexity of the process. Keywords of this process such as nonlinearity, coupling, emergent structures, etc. are characteristic of many phenomena which have motivated the analysis from a wider perspective than only nonlinear dynamics or system biology. Many philosophers have paid attention to complex systems, among them Morin [39] and Deleuze and Guattari [12], to mention a few. From the viewpoint of physical systems, DeLanda's studies [8] are important because he has explained the philosophical ideas of Deleuze in terms of nonlinear dynamics.

It should be noted that philosophers have often used the modelling of neurophysiology or cognitive processes as an example for explaining abstraction [3,4,13,32,36]. In this context, the celebrated Hodgkin–Huxley model is used for demonstrating the role of physical laws and simplifications or modifications for deriving the governing equations [1,3,4,6,36].

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It should also be noted that the development of complexity sciences, which includes ideas from physics, mathematics and social sciences, has been influenced by philosophers [5]. Paul Cilliers and Edgar Morin, Manuel DeLanda et al. are all mentioned in the Castellani map [5]. Concerning the biophysical phenomena, the ideas of synergetics developed by Haken [27] are also relevant. Although the focus of synergetics is the self-organisation of patterns and structures, it has opened a gateway for studying coupled systems. The ensemble of waves described above is also a macroscopic system in the sense of synergetics.

In what follows, the ideas of DeLanda and Deleuze are used to characterise the modelling of signals in nerves proposed by Engelbrecht, Tamm and Peets [17,24]. It is demonstrated that such modelling corresponds to general philosophical ideas. In Section 2, the ideas of modelling [17] are briefly explained. Section 3 presents the ideas of DeLanda [8] based on Deleuze's philosophical notions, but reconstructs them within the framework of mathematical terminology. Section 4 deals with the modelling of signals in nerves by comparing the ideas with the philosophical framework. Section 5 presents some conclusions.

2. MATHEMATICAL MODELLING OF SIGNAL COMPONENTS IN NERVES

Herein we follow the ideas of modelling proposed by Engelbrecht, Tamm and Peets in their recent publications [16,18–24], see also [44]. The modelling is based on the careful analysis of the mechanisms of electro-mechano-physiological interactions (see summary in [23,24]). An overview of the principles of modelling is presented by Engelbrecht et al. [17]. This model follows the **scheme**:

1. derive time-dependent models (equations) for all the effects that seem to be significant for the whole process, based on physical laws;
2. propose coupling mechanisms between the effects;
3. solve the coupled system of equations;
4. validate the results by comparing them with experiments.

As usual, one should start from the **assumptions**:

1. electrical signals are the carriers of information [7] and trigger all the other processes (called the Hodgkin–Huxley paradigm for short);
2. axoplasm in a nerve fibre can be modelled as fluid where a pressure wave is generated due to an electrical signal;
3. biomembrane can deform (stretch, bend) under mechanical impact [28];
4. channels in biomembranes can be opened and closed under the influence of electrical signals as well as mechanical input [40];
5. there is strong experimental evidence of electrical or chemical transmittance of signals from one neuron to another [31].

Next, the hypotheses are introduced [19,21,24]:

1. all mechanical waves in the axoplasm and the surrounding biomembrane together with the heat production are generated due to changes in electrical signals (action potential or ion currents) that dictate the functional shape of coupling forces;
2. formalism of internal variables can be used for describing the exo- and endothermic processes of heat production;
3. changes in the pressure wave may also influence the waves in a biomembrane.

Based on these assumptions and hypotheses, the following are essential **remarks**:

1. changes in variables mean mathematically either their space or time derivatives;
2. pulse-type profiles of electrical signals mean that the derivatives have a bi-polar shape which is energetically balanced;
3. coupling is assumed due to forces in corresponding governing equations;
4. functional shapes of coupling forces are proposed in the form of first-order polynomials of gradients or time derivatives of variables [16,18].

As a result of modelling, it is possible to simulate an **ensemble** of waves in the axon. This ensemble has the following components (notations correspond to the dimensionless case):

1. action potential AP which has an amplitude Z, and the ion currents. In the case of the Hodgkin–Huxley (HH) model, these ion currents are J_K, J_{Na} and J_L, in the case of the FitzHugh–Nagumo (FHN) model, there is only one ion current J (here the ion currents for the HH model denote potassium, sodium and leakage currents, respectively);
2. longitudinal wave LW in the biomembrane with an amplitude U;
3. transverse displacement TW in the biomembrane with an amplitude W;
4. pressure wave PW in the axoplasm with an amplitude P;
5. temperature change Θ.

The ensemble is composed of primary and secondary components: the primary components (AP, LW, PW) are characterised by finite velocities while the secondary components (TW, Θ) have no characteristic velocities.

This is the backbone of modelling, the details of which are explained in the references above. The final mathematical model is a system of coupled differential equations [20,21,24]. The system in the equilibrium state is excited by an electrical signal above a certain threshold, which generates the AP, and then all the other components of the ensemble are generated, which is qualitatively similar to the experimental data (cf. the analysis by Engelbrecht et al. [16,21]). The backbone of modelling is based on consistent physical laws but is open to further modifications. The structure of the mathematical model and the interactions between its components are depicted in Fig. 1. It demonstrates the coupling between the components of the ensemble, reflecting the structure of a model used for numerical verification. In principle, the feedback may also be taken into account.

For numerical simulations, the system of governing equations is solved by using the pseudospectral method [24,44]. Leaving aside the structure of this system with its coefficients, a typical ensemble in dimensionless variables is shown in Fig. 2. The input (Fig. 2a) is above the threshold and it takes some time before a typical AP is formed. The ensemble (Fig. 2b) corresponds qualitatively to the experimental results as well as the shape of the TW (Fig. 2c).

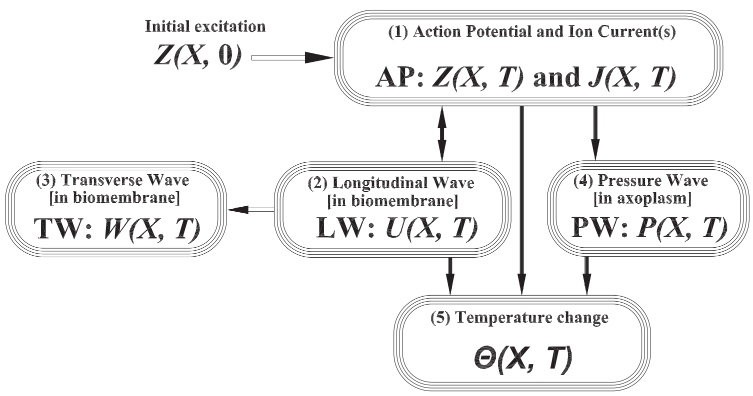

Fig. 1. Components and interactions of the mathematical model. The ensemble starts with an initial excitation $Z(X,T)$ at $T = 0$ above a threshold value leading to the emergence of an electrical signal AP. Then the other members of the ensemble emerge over a certain period of time, caused by coupling forces (indicated by bold vertical arrows). Here X,T denote dimensionless space and time, respectively.

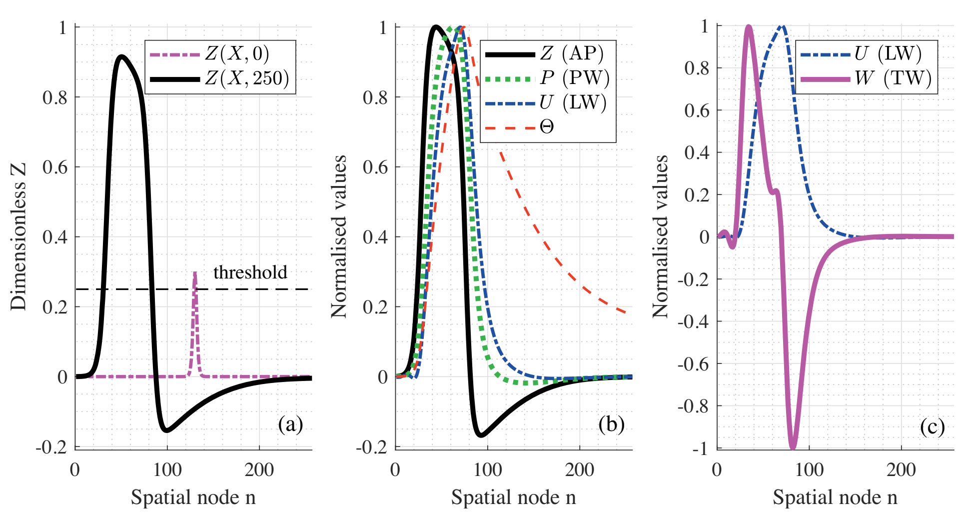

Fig. 2. Typical nerve pulse ensemble formation and propagation: (a) generation of the AP (solid line, at $T = 250$) from an initial input (dash-dot line, at $T = 0$). At $T = 250$, a typical shape of the AP has been formed from the narrow 'spark' type initial condition; (b) the components of AP, PW, LW and Θ; (c) the components of LW and TW. The initial condition in the middle of the spatial period ($n = 2048$) forms left and right propagating AP, which, in turn, generates all the other signals through coupling forces. Left propagating waveprofiles are shown in a moving frame of reference ($n = 256$) at $T = 250$ for (a) and at $T = 800$ for (b) and (c). Here n is a computational node in a dimensionless space X and T denotes dimensionless time. For mathematical details and values of model parameters, see [23].

The model described in this section is focused on the ensemble and does not elaborate on the details of the generation of the AP.

3. MODELLING VIEWED FROM THE PHILOSOPHICAL VIEWPOINT

The following analysis is based, first, on DeLanda's [8] analysis of the ideas of Deleuze and Guattari [12] by the conceptual explanation of mathematics involved and, second, on the analysis of DeLanda's assemblages [10]. Deleuze and Guattari [12] conceptualise multiplicities by using the concept of manifolds. The notion of manifolds in mathematical physics permits to describe complicated structures in terms of the topological properties of simpler spaces. They also demonstrate that morphogenesis (things taking forms) can be characterised in terms of singularities. DeLanda [8] explains how the ideas of multiplicity developed by Deleuze can be described within the theory of differentiable manifolds that are widely used in nonlinear dynamics. This permits an explanation of the basic ontological concepts such as (1) extensive and intensive spaces and (2) actual and virtual spaces in terms that are understandable to physicists and mathematicians. Actually, DeLanda's explanations build an excellent basis for understanding complexity in many fields [5]. As emphasised by Holdsworth [30], DeLanda "recovers for mathematical practice a capacity to clarify the meaning of events as they arise within a synthetic process of becoming interdisciplinary". The focus of Deleuze's studies is on dynamical processes, and in this context one has to analyse the system being modelled, taking into consideration: (1) a range of behaviours, fluctuations, patterns and thresholds; (2) in the dynamical model: phase space, trajectory, attractors and bifurcations; (3) in the mathematics used to construct the model: manifold, function and singularity [46]. This has been done in detail by DeLanda [8]. However, it should be added to the modelling of physical processes that the basic physical laws must always be checked [17,20]. This is emphasised by DeLanda [8] by stressing the need to understand the basics. He assumes a minimum of objective knowledge to initiate the process and the rest emerges from there. This corresponds to the well-known principle of Occam's razor – entities are not to be multiplied without necessity. Such an attitude is also supported by Einstein [15]: "... the supreme goal of all theory is to make irreducible basic elements as simple and as few as possible ...". Without going into details, let us list the essential ideas of DeLanda [8] which will be useful in the analysis of signals in nerves:

- Interdisciplinarity is needed for understanding complex processes.
- Complex processes are characterised by multiplicity, which is the activator for changes in the system.
- Multiplicity is characterised by differences that are productive and cause interactions.
- 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, differences (gradients) in intensity store potential energy.
- A whole emerges from parts by causal interactions.
- Changes (gradients) are characterised by velocities (or differential relations).
- Causality for processes is related to multiplicities.
- Non-equilibrium (according to DeLanda intensive) states demonstrate explicitly the potential for nonlinearities that do not cause essential differences in or close to equilibrium states.
- One should distinguish between intrinsic (belonging to the system) and extrinsic (originating from outside) conditions for a system.
- Emergence means a process where novel properties and capacities emerge from causal interaction.
- 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.

In addition, DeLanda [10] argues about the notion of 'assemblage', which is also introduced by Deleuze. Assemblage in English means gathering of things into unities, which is actually different from the French notion of 'agencement', as proposed by Deleuze. Unity in the assemblage is defined "by the intrinsic relations that various parts have to one another in a whole" [41] while Deleuze and Guattari [11] take into account the external relations by using 'agencement' and in this way also include the process of formation in the notion. From the physical viewpoint, the concept of nonlinearity (loss of proportionality) is also relevant in philosophy. For example, Knyazeva [34] has formulated the principles of nonlinear thinking. Those principles are related to multiplicity [12] and synergetics [27], and are needed for the management of nonlinear processes.

4. HOW THE MODELLING OF SIGNALS IN NERVES CORRESPONDS TO PHILOSOPHICAL IDEAS

First, it should be stressed that the modelling of signals in nerves briefly described in Section 2 is based on interdisciplinary considerations [22]. Indeed, the knowledge from physics and continuum mechanics is used for describing the physiological effects within the framework of mathematics. The laws of physics (balance of momentum, the Fourier's law) are basic, although they are modified to grasp the physiological effects. From the epistemological viewpoint, the basic laws constitute propositional knowledge (knowing that). An ensemble of waves emerges as a result of interactions between intensive properties of the system and the coupling forces that are related to changes in field variables (time or space derivatives), and it all has a corresponding mathematical description. To model temperature changes, the role of possible chemical reactions (exo- and endothermic processes) is described by the concept of internal variables widely used in continuum mechanics. The main role in signal formation is related to the intrinsic properties of the structural elements of axons, but is also dependent on the extrinsic properties such as the temperature of the environment or the ion concentration of the extracellular fluid. Signal formation is influenced by the multiplicity of processes – for example, temperature effects are caused by several mechanisms. The system is characterised by a trigger threshold – the initial condition for generating the AP should be above the threshold. The mechanical components of the ensemble depend on inertia, as it should be for wave processes. This dependence has a direct consequence on the width of the LW in the biomembrane.

In terms of DeLanda, an ensemble of waves can be called an 'assemblage'. However, as far as the notion of 'ensemble' does not describe the process of formation, in order to associate the two notions one could use 'dynamical ensemble', which emphasises possible changes, i.e., not only the propagation but also the process of formation. This way or another, an ensemble of waves in nerves is the result of a causal interaction resulting in a complex. This complex is a carrier of information and serves as a basic element for neural networks. Figure 1 also demonstrates the importance of using the diagrams noted by DeLanda [10] for explaining causal relations in his philosophical analysis.

As a matter of fact, this modelling follows the ideas of Weber [50] who states that "... all the crucial explanatory burden in experimental biology (including electrophysiology) is and must be borne by laws of physics and chemistry". However, Craver [6] also stresses the importance of biological facts, which brings us directly to interdisciplinarity in order to describe the mechanisms responsible for the generation of signals in nerves.

The multiplicity of effects characteristic of signals in nerves analysed above is limited to propagation effects. The modification of intrinsic and extrinsic properties could certainly improve the predictive power of the model. For example, the coupling (activation) forces may need to be specified by a more refined description of lipids in the biomembrane or filaments in the axoplasm. The molecular effects related to ion movement and the influence of membrane proteins might influence the emergence of an ensemble. The influence of environmental temperature as an extrinsic property can be accounted for by the coefficients of the governing system.

The present model [24] pays attention to coupling effects and keeps the models rather simple as far as the components of an ensemble are concerned. Recent experiments have demonstrated more details about the structure of the biomembrane, axoplasm and ion channels. For example, the influence of the myelin sheath is relevant to the propagation of the AP. It has been shown how this myelin sheath can be taken into account for the LW [49]. As mentioned above, the structure of the axoplasm is not homogenous but consists of filaments and proteins. Singh et al. [48] have shown experimentally how the structures inside a nerve influence the propagating signal. They even suggested that different waves coexist with an ionic spike. It is an interesting challenge to formulate these ideas by a mathematical model.

The propagation of signals in nerves is part of the phenomena in the brain which are much more complicated. Goriely et al. [26] have shown how interdisciplinarity can help to understand the multiplicity of processes needed for the analysis of the extremely complex function of the brain at many scales (at molecular, cellular, and tissue levels).

5. FINAL REMARKS

In Section 4, it is demonstrated that the descriptions presented in Sections 2 and 3 follow similar lines. Historically, the analyses and explanations have used different terminology, but in essence, the ideas are similar. The mathematical model described above is based on the analysis of physical mechanisms [23,24]. Kaplan and Craver [32] have formed a model-to-mechanism-mapping requirement that says: "In successful explanatory models in cognitive and systems neuroscience (a) the materials in the model correspond to components, activities, properties, and organisational features of the target mechanism that produces, maintains, or underlines the phenomenon, and (b) the (perhaps mathematical) dependencies posited among these variables in the model correspond to the (perhaps quantifiable) causal relations among the components of the target mechanism". This is exactly the ideology followed in our modelling. For nerve signals, models of single effects are brought together by coupling forces that depend on changes in intensive field variables. As a result, an ensemble is formed, which is a carrier of information. All the keywords of Section 3 on the philosophical ideas –

interdisciplinarity, basic laws, multiplicity, changes in intensive variables, nonlinearities, and causality – are used in the mathematical modelling of signals in nerves. Certainly, it is not only the collection of keywords that correspond to the philosophy of DeLanda but the whole construction of modelling that follows the idea of assemblage, which is the emergence of a whole from parts due to interactions. In a nutshell, as stressed by DeLanda [9], intensive differences are productive – this is actually the essence of the philosophy behind the modelling of signals in nerves.

Such philosophy is characteristic of the modelling of nervous systems from the viewpoint of complexity including nonlinear and nonstationary effects [35]. The role of interactions in systems biology is emphasised in many studies [33,43] and it also reflects the philosophical ideas briefly addressed above. Finally, it should be stressed that the discussion on explanatory and modelling strategies in systems biology also involves the question of whether these strategies are mechanistic [2]. Clearly, the studies of philosophical accounts in systems biology serve a better understanding. Attention should be paid to causality and possible idealisation [3] and to the basic laws of physics [50] together with biological facts [6]. In principle, we agree with Driessen [13] who says that "philosophy is a good school for developing the intuitive capacity of scientist".

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Signaalid närvirakkudes filosoofia mõistetes

Jüri Engelbrecht, Kert Tamm ja Tanel Peets

Närvikiududes leviv signaal koosneb elektrilise komponendi kõrval ka mehaanilistest ja termilistest komponentidest, mis kokku moodustavad ansambli. Sellise ansambli modelleerimine on kirjeldatud DeLanda filosoofilist analüüsi järgides, kasutades mittelineaarse dünaamika mõisteid. On näidatud, et autorite poolt konstrueeritud närvikius leviva ansambli matemaatiline mudel on kooskõlas DeLanda ideega kausaalsete seoste olulisusest ning ekstensiivsetest ja intensiivsetest muutujatest.