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NONLINEAR WAVES

On mechanical aspects of nerve pulse propagation and the Boussinesq paradigm

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Abstract. The dynamic behaviour of the Boussinesq-type equation governing longitudinal wave propagation in cylindrical biomembranes is analysed by making use of the pseudospectral method. It is shown how the dispersion type has a significant effect on the solution. The effects of other parameters are also considered.

Key words: biomembranes, Boussinesq paradigm, pseudospectral method, dispersion.

1. INTRODUCTION

Although initially derived for water waves, the Boussinesq-type equation appears in a number of problems where dynamic behaviour of the medium is considered. Examples include waves in rods, in microstructured materials, in crystals, and in biomembranes [1–6]. The main properties of Boussinesq-type equations are grasped in the Boussinesq paradigm that was described by Maugin and Christov [7]. These properties are (i) bi-directionality of waves, (ii) nonlinearity (of any order), and (iii) dispersion (of any order, modelled by space and time derivatives of the fourth order at least). An excellent overview of the properties of the Boussinesq equation and its generalization for nonlinear waves was presented by Christov et al. [8]. The Boussinesq paradigm in the case of nonlinear waves in microstructured materials was studied by Engelbrecht et al. [2].

Here we generalize these ideas for a living tissue. The cell membranes of almost all living organisms and viruses are made of a lipid bilayer made of phospholipids that have outward facing hydrophilic heads and inward facing hydrophobic tails. Although it is only a few nanometres thick, the lipid bilayer is impermeable for most water soluble molecules, hence making a perfect barrier between the exterior and interior of the cell. The transport of various molecules that need to enter and exit a cell is realized through specialized ion channels.

The lipid biomembranes are not only interesting from the physiological point of view but are also fascinating from the mechanical aspect. Recently much attention has been paid to the biophysical forces acting on neurons and their possible implication on neural activity [9]. Particular attention has been devoted to mechanical wave propagation along the nerve fibre [4,5,10,11].

Traditionally the nerve function has only been attributed to the electrical pulse propagation along the nerve fibre. It is described by the widely accepted Hodgkin–Huxley model [12], which is based on the

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electrical circuit analogy. Simpler models have been derived by Nagumo et al. [13] and Engelbrecht [14]. The former uses only one ionic current instead of three and is now known as the FitzHugh–Nagumo model, and the latter is an evolution equation (one-wave equation).

There are however phenomena that are not described by the aforementioned models. Most notably it has been shown in experiments by Iwasa et al. [10] and Tasaki et al. [11,15] that also a mechanical wave is accompanying the nerve pulse.

Heimburg and Jackson (HJ) [4] proposed a Boussinesq-type equation describing the nonlinear wave propagation along the cylindrical biomembrane. Their model is based on regular wave equation where velocity c is determined by $c^2 = c_0^2 + pu + qu^2$. Here c_0 is the velocity of low amplitude sound, p and q are determined from the experiments, and $u = \Delta\rho^A$ is the density change. Also a fourth-order ad hoc dispersive term $-hu_{xxxx}$ was added to account for the dispersion. Their governing equation then reads

$$u_{tt} = \left[\left(c_0^2 + pu + qu^2\right) u_x\right]_x - hu_{xxxx}. \tag{1}$$

An analytical solution to Eq. (1) was derived in [16] in a form of a solitary wave solution with a width of 10 cm. A more realistic soliton width of 0.2 cm was derived by Vargas et al. [17] for the locust nerve.

Recently the HJ model was revised by Engelbrecht et al. [5] from the viewpoint of solid mechanics. Taking inspiration from the well-known rod models, it was shown that the propagation of certain disturbances at infinite velocities can be avoided if a fourth-order mixed derivative dispersive term is added. In addition, it is well known that the presence of only fourth-order spatial derivatives can lead to instabilities (see Maugin [3] for example). The importance of higher-order mixed derivatives has also been demonstrated in many studies (see [8] and references therein). The improved HJ model then reads [5]

$$u_{tt} = \left[\left(c_0^2 + pu + qu^2\right) u_x\right]_x - h_1 u_{xxxx} + h_2 u_{xxtt}, \tag{2}$$

where $h_1 = h$ and h_2 is a new ad hoc dispersion constant.

It was shown in [5] that if the biomembrane is regarded as a microstructured solid, then the parameter h_2 can be related to the microinertia and the parameter h_1, which is related to elasticity of the biomembrane, can be expressed as $h_1 = c_1^2 h_2$, where $c_1^2 = h_1/h_2$ is a certain bounding velocity for the higher frequencies.

Equations (1) and (2) are of Boussinesq type with unusual terms of nonlinearity. The nonlinearity in terms of plain u is uncommon in Boussinesq-type equations although mathematically nothing prevents it. It can be shown that such a nonlinearity can be achieved with Lagrangian formalism by using nonlinear terms containing $u \cdot u_x^2$ and $u^2 \cdot u_x^2$ with coefficients p and q, respectively, in the expression for potential energy. A similar equation can also be derived for the strain waves in elastic rods using the so-called nine-points Murnaghan model as a starting point [18]. It should be emphasized that the unusual nonlinear terms in Eq. (1) were introduced on the basis of experimental results by Heimburg and Jackson [4]. Finally we note that the amplitude-dependent nonlinearities are also encountered in the case of evolution equations like the Gardner equation [19], but these cannot be directly compared to Boussinesq-type equations like Eq. (2).

2. MATHEMATICAL MODEL AND DISPERSION

The dimensionless form of Eq. (2) is

$$U_{TT} = (1 + PU + QU^2)U_{XX} + (P + 2QU)U_X^2 - H_1 U_{XXXX} + H_2 U_{XXTT}, \tag{3}$$

where $X = x/l$, $T = c_0 t/l$, $U = u/\rho_0$, $P = p\rho_0/c_0^2$, $Q = q\rho_0^2/c_0^2$, $H_1 = h_1/(c_0^2 l^2)$, and $H_2 = h_2/l^2$. Here l is a certain length and ρ_0 is the lateral equilibrium density.

Making use of the idea that $h_1 = c_1^2 h_2$ [5], we can rewrite the equation as

$$U_{TT} = (1 + PU + QU^2)U_{XX} + (P + 2QU)U_X^2 + H_2(U_{TT} - \gamma^2 U_{XX})_{XX} \tag{4}$$

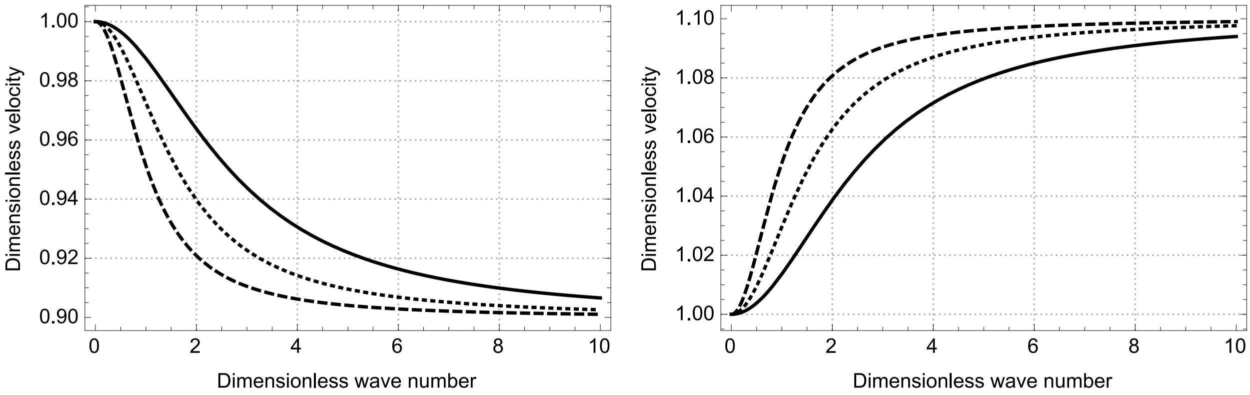

Fig. 1. Dispersion curves for Eq. (5) in case $\gamma = 0.9$ (left figure) and $\gamma = 1.1$ (right figure). $H_2 = 1$ (dashed), $H_2 = 0.4$ (dotted line), and $H_2 = 0.15$ (solid line) in both figures.

with the following dispersion relation

$$\Omega = K\sqrt{1+\gamma^2 H_2 K^2}/\sqrt{1+H_2 K^2}, \tag{5}$$

where $\gamma = c_1/c_0$ is the dimensionless bounding velocity and Ω and K are dimensionless frequency and wave number, respectively.

Rewriting the governing equation as in the case of Eq. (4) gives more explicit explanation for the dispersive terms. The parameter γ defines the velocity difference between the low and high frequency harmonics. Also, in case $\gamma < 0$ we have normal dispersion and in case $\gamma > 0$ anomalous dispersion. The parameter H_2 is related to the velocity change gradient; the higher the value of H_2, the more rapid is the transition from the low frequency velocity to the bounding velocity. Since the parameter H_2 is related to the microinertia of the lipid bilayer structure, the slope of the dispersion curve is related to that effect (see Fig. 1 for details). We also note that in [4] the dispersion is chosen to be anomalous.

3. NUMERICAL SCHEME AND INITIAL CONDITIONS

Equation (4) is solved by using the Discrete Fourier Transform (DFT) based pseudospectral method (PSM). To that end the governing equation needs to be in a specific form with only time derivatives in the right-hand side and only spatial derivatives in the left-hand side of the equation. This is not the case with Eq. (4) where a mixed partial derivative is present. For circumventing that, a new variable is introduced and the variable U and its spatial derivatives can be expressed in terms of the variable Φ as

$$\Phi = U - H_2 U_{XX}, \quad U = \mathrm{F}^{-1}\left[\frac{\mathrm{F}(\Phi)}{1+H_2 k^2}\right], \quad \frac{\partial^m U}{\partial X^m} = \mathrm{F}^{-1}\left[\frac{(\mathrm{i}k)^m \mathrm{F}(\Phi)}{1+H_2 k^2}\right]. \tag{6}$$

In (6) F^{-1} denotes inverse Fourier transform and F is the Fourier transform. Equation (4) is now rewritten in terms of the variable Φ as

$$\Phi_{TT} = (1+PU+QU^2)U_{XX} + (P+2QU)(U_X)^2 - \gamma^2 H_2 U_{XXXX}. \tag{7}$$

Equation (7) can be easily solved by making use of the PSM after reducing it to a system of two first-order differential equations (see [20] for details).

A bell-shaped pulse $U(X,0) = A_0 \cdot \mathrm{sech}^2(B_0 \cdot X)$ is used as an initial condition. Initial velocity of the pulse is taken to be zero; in that case the pulse splits into two bell-shaped pulses with half of the initial amplitude and propagating in opposite directions. Further on we take $B_0 = 1/512$ (the width parameter of the sech^2-type initial pulse), $A_0 = 2$ (the amplitude of the initial pulse), and the spatial length is 128π. The number of grid points in space is $n = 2^{12}$. The governing equations are solved and results presented in the dimensionless form. Periodical boundary conditions are used.

4. NUMERICAL RESULTS

Equation (4) is of Boussinesq type and therefore a certain behaviour such as the emergence of solitary trains is expected. The parameters in Eq. (4) can roughly be divided into two groups: the dispersive parameters (γ and H_2) and the nonlinear parameters (P and Q). Both effects are equally important in the analysis of the dynamic behaviour of Boussinesq-type equations, and complete understanding of these effects is desirable. It must emphasized that although the nonlinear parameters in [4] are determined from experiments, here we use another set of parameters in order to study the behaviour of Eq. (4). Such a choice provides an important insight into the dynamics of the governing equation and the meaning of the parameters. It is especially true for the dispersive parameters as these are not determined from experiments like the nonlinear parameters. Here we present only a certain basic analysis of the complex behaviour of solutions of Eq. (4). In all figures the waves propagate from left to right.

4.1. Influence of the dispersive parameters

In order to study the influence of the dispersive parameters the nonlinear parameters are fixed at $P = 0.05$ and $Q = 0.075$; the dispersive parameters γ and H_2 are different in Fig. 2 and in Fig. 3. The corresponding dispersion curves can be seen in Fig. 1.

It can be seen in Fig. 2 that under the used parameter combination a train of solitary waves emerges. The dispersive parameter H_2 clearly has an effect on the amplitude of the leading solitary wave and its velocity. A lower value of H_2 is also related to the larger number of emerging solitary waves. In case of anomalous dispersion (Fig. 3) an Airy-like pulse can emerge and the dispersive parameter H_2 is directly related to the frequency and the velocity of the front of the pulse.

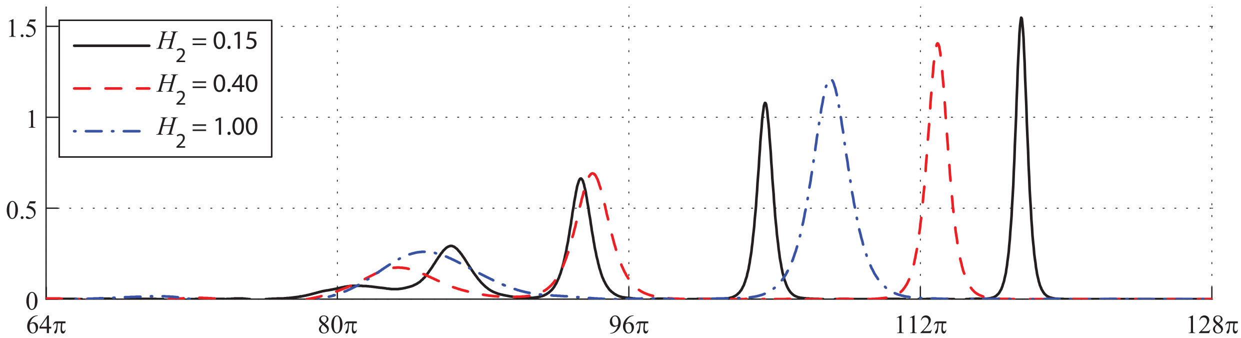

Fig. 2. Wave profiles at $T = 3682$, $\gamma = 0.9$, $P = 0.05$, and $Q = 0.075$.

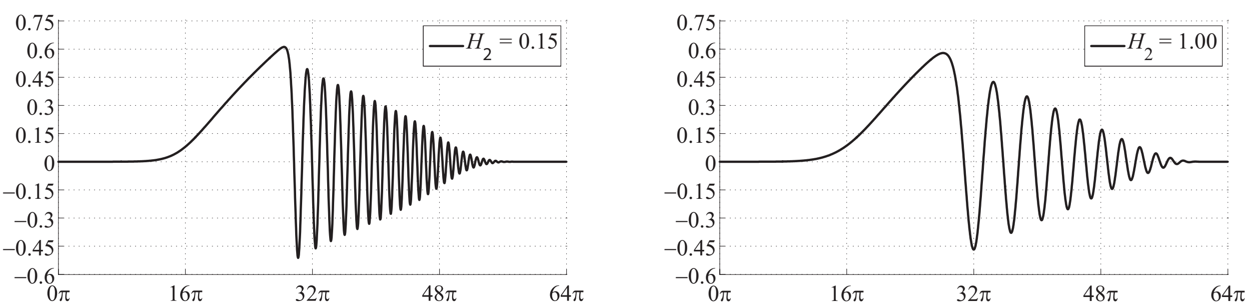

Fig. 3. Wave profiles at $T = 1069$, $\gamma = 1.1$, $P = 0.05$, and $Q = 0.075$.

4.2. Influence of the nonlinear parameters

The influence of the nonlinear parameter P is studied in case of the normal ($\gamma = 0.9$) and anomalous ($\gamma = 1.1$) dispersion, which can be seen in Figs 4 and 5, respectively. In both figures this nonlinear parameter is chosen $P = -0.15$ in the left figure and $P = 0, 0.15$ in the right figure.

It is clear that the sign and value of the nonlinear parameter P has a significant effect on the solution. The negative value of the parameter P creates a reversed Airy-like pulse (oscillatory tail in front of the pulse) in case of normal dispersion. In case of the positive value of P a soliton train emerges and the velocity and the amplitude of the leading soliton and the number of solitons are directly related to the value of the nonlinear parameter P.

In case of the anomalous dispersion (Fig. 5) the effect of the sign of the parameter P is reversed: the Airy-like pulse emerges when $P \geq 0$ and a soliton train appears when $P < 0$. There is one significant difference: in case of anomalous dispersion and negative values of P smaller amplitude solitons travel faster. This is a relatively uncommon phenomenon although it exists in the case of some KdV like equations and the classical Boussinesq equation under some parameter combinations [21,22]. The velocity of the front of the emerged Airy-like pulse increases with the nonlinear parameter P.

The effect of the nonlinear parameter Q is seen in Fig. 6 in the case of normal dispersion ($\gamma = 0.9$). With negative values of Q an Airy-like pulse emerges, and when $Q \geq 0$ a soliton train can be seen. The number of solitons and the velocity and the amplitude of the leading soliton increase with the nonlinear parameter Q. The examples of the anomalous dispersion case are omitted as the differences are minor.

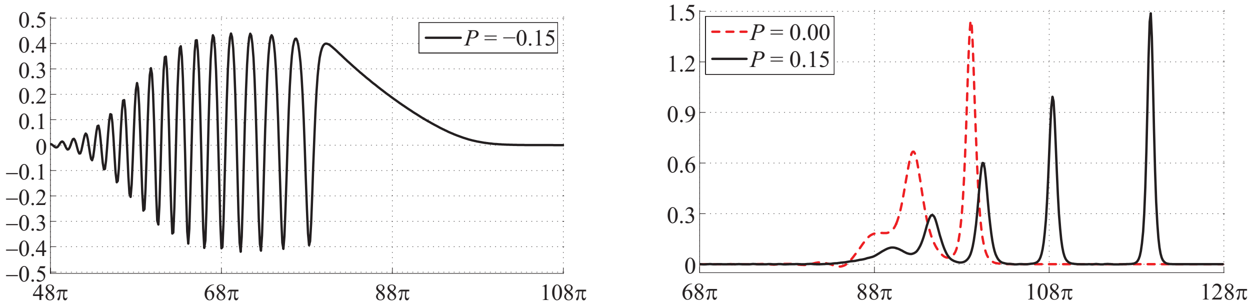

Fig. 4. Wave profiles at $T = 1694$, $\gamma = 0.9$, $H_2 = 0.25$, and $Q = 0.075$.

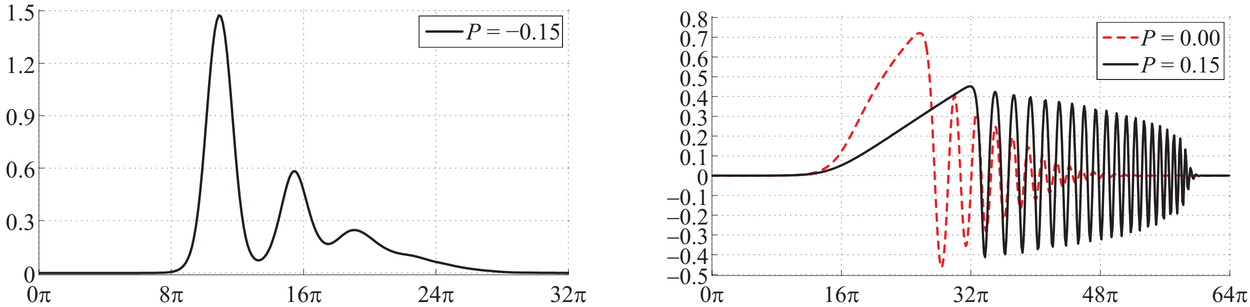

Fig. 5. Wave profiles at $T = 1069$, $\gamma = 1.1$, $H_2 = 0.25$, and $Q = 0.075$.

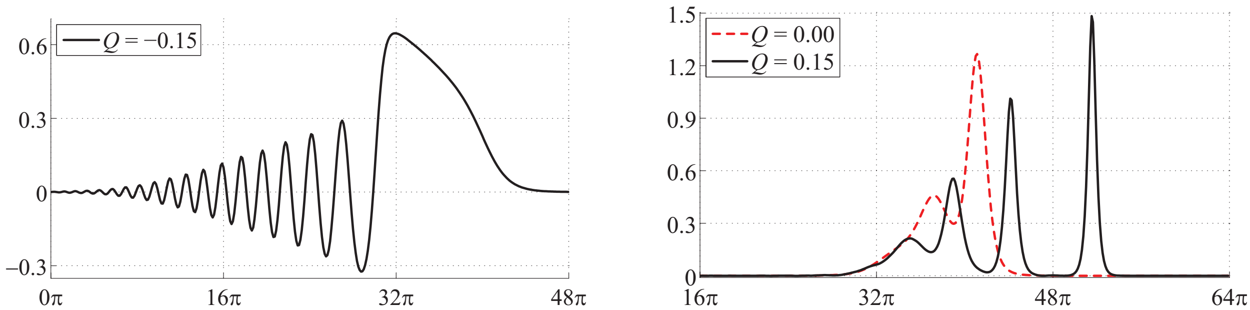

Fig. 6. Wave profiles at $T = 1119$, $\gamma = 0.9$, $H_2 = 0.25$, and $P = 0.05$.

5. CONCLUSIONS

The numerical analysis of Eq. (2) shows that either trains of solitary waves or dispersive Airy-type solutions can exist. Moreover, it has been shown that the behaviour of the solution is strongly influenced by the sign of the nonlinear parameters P and Q and by the dispersion type, which depends on the dispersive parameter γ. The effect of the dispersive parameter H_2 is more subtle as it only changes the velocity of individual harmonics but not the solution type. The exact physical meaning of these parameters in the context of mechanical waves in biomembranes is an open question.

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REFERENCES

1. Abramson, H. N., Plass, H. J., and Ripperger, E. A. Stress wave propagation in rods and beams. In *Advances in Applied Mechanics*, Vol. 5 (Dryden, H. and von Karman, T., eds). Academic Press, New York, 1958, 111–194.
2. Engelbrecht, J., Salupere, A., and Tamm, K. Waves in microstructured solids and the Boussinesq paradigm. *Wave Motion*, 2011, **48**(8), 717–726.
3. Maugin, G. A. *Nonlinear Waves in Elastic Crystals*. Oxford University Press, Oxford, 1999.
4. Heimburg, T. and Jackson, A. D. On soliton propagation in biomembranes and nerves. *P. Natl. Acad. Sci. USA*, 2005, **102**(28), 9790–9795.
5. Engelbrecht, J., Tamm, K., and Peets, T. On mathematical modelling of solitary pulses in cylindrical biomembranes. *Biomech. Model. Mechanobiol.*, 2015, **14**(1), 159–167.
6. Tamm, K. and Peets, T. On solitary waves in case of amplitude-dependent nonlinearity. *Chaos Soliton. Fract.*, 2015, **73**, 108–114.
7. Maugin, G. A. and Christov, C. I. Nonlinear duality between elastic waves and quasi-particles. In *Selected Topics in Nonlinear Wave Mechanics* (Christov, C. I. and Guran, A., eds). Birkhäuser, Boston, MA, 2002, 101–145.
8. Christov, C. I., Maugin, G. A., and Porubov, A. V. On Boussinesq's paradigm in nonlinear wave propagation. *C. R. Mécanique*, 2007, **335**(9–10), 521–535.
9. Mueller, J. K. and Tyler, W. J. A quantitative overview of biophysical forces impinging on neural function. *Phys. Biol.*, 2014, **11**(5), 051001.
10. Iwasa, K., Tasaki, I., and Gibbons, R. Swelling of nerve fibers associated with action potentials. *Science*, 1980, **210**(4467), 338–339.
11. Tasaki, I. A macromolecular approach to excitation phenomena: mechanical and thermal changes in nerve during excitation. *Physiol. Chem. Phys. Med. NMR*, 1988, **20**, 251–268.

12. 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**, 500–544.
13. Nagumo, J., Arimoto, S., and Yoshizawa, S. An active pulse transmission line simulating nerve axon. *Proc. IRE*, 1962, **50**(10), 2061–2070.
14. Engelbrecht, J. On theory of pulse transmission in a nerve fibre. *P. Roy. Soc. Lond. A Mat.*, 1981, **375**(1761), 195–209.
15. Tasaki, I., Kusano, K., and Byrne, P. M. Rapid mechanical and thermal changes in the garfish olfactory nerve associated with a propagated impulse. *Biophys. J.*, 1989, **55**(6), 1033–1040.
16. Heimburg, T. and Jackson, A. D. On the action potential as a propagating density pulse and the role of anesthetics. *Biophys. Rev. Lett.*, 2007, **2**, 57–78.
17. Vargas, E. V., Ludu, A., Hustert, R., Gumrich, P., Jackson, A. D., and Heimburg, T. Periodic solutions and refractory periods in the soliton theory for nerves and the locust femoral nerve. *Biophys. Chem.*, 2011, **153**(2–3), 159–167.
18. Porubov, A. V. and Maugin, G. A. Longitudinal strain solitary waves in presence of cubic non-linearity. *Int. J. Nonlinear Mech.*, 2005, **40**, 1041–1048.
19. Slyunyaev, A. V. and Pelinovski, E. N. Dynamics of large-amplitude solitons. *J. Exp. Theor. Phys.*, 1999, **89**(1), 173–181.
20. Salupere, A. The pseudospectral method and discrete spectral analysis. In *Applied Wave Mathematics* (Quak, E. and Soomere, T., eds). Springer, Berlin, 2009, 301–334.
21. Salupere, A., Engelbrecht, J., and Maugin, G. A. Solitonic structures in KdV-based higher-order systems. *Wave Motion*, 2001, **34**(1), 51–61.
22. Bona, J. L. and Sachs, R. L. Global existence of smooth solutions and stability of solitary waves for a generalized Boussinesq equation. *Commun. Math. Phys.*, 1988, **118**, 15–29.

Närviimpulsi leviku mehaanilised aspektid ja Boussinesqi paradigma

Tanel Peets ja Kert Tamm

On uuritud solitonide formeerumist täiendatud Heimburgi-Jacksoni (HJ) mudeli korral, mis kirjeldab mehaanilise laine levikut silindrilistes biomembraanides. Lahendid on leitud numbriliselt, kasutades Fourier' teisendusel baseeruvat pseudospektraalmeetodit. On näidatud, et dispersiooniliigil (normaalne või anomaalne) on lahendi käitumisele oluline mõju.