# Waves in Biomembranes with Amplitude-Dependent Nonlinearities

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*Summary*. Recent studies have shown that mechanical waves accompanying the action potentials can propagate in biomembranes. A mathematical model describing such waves was proposed by Heimburg and Jackson (2005) and later improved by Engelbrecht et al (2015). The governing equation is of the Boussinesq-type with amplitude-dependent nonlinearities and the fourth-order dispersive terms. The improved model takes into account the microinertia of the lipids in biomembranes. The full analysis of such a model is presented.

## Modelling and the governing equation

During the last decade the interest to mechanical waves in biomembranes has been growing fast [1, 2] because of their importance in physiology. They have a special structure made of phospholipids with hydrophobic tails directed to inside of a membrane [1, 3]. Such a membrane represents a special biological microstructure which exhibit strong nonlinear effects when deformed. Based on experimental results, the nonlinearity in biomembranes can be accounted in the effective velocity $c_e$ like [1]:

$$c_e^2 = c_0^2 + pu + qu^2, \tag{1}$$

where $c_0$ is the unperturbed velocity, $p$ and $q$ are coefficients and $u$ is the density change along the axis of a biomembrane. In order to model mechanical waves in biomembranes, a mathematical model proposed in [1] involved also the dispersive effects. The improved model [4] has taken into account the inertia of constituent lipids and removed a possibility of instabilities [5]. In this case the governing equation takes the form

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

where $h_1$ and $h_2$ are dispersion coefficients. This equation is of the Boussinesq-type with amplitude- dependent nonlinearities and the fourth-order dispersion terms.
The focal point of this talk is the full analysis of Eq. (2). Further it is convenient to use its dimensionless form

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

where $X = x/l, T = c_0 t/l, U = u/\rho_A$ and $P = p\rho_A/c_0^2$, $Q = q\rho_A^2/c_0^2$. Here $l$ is a certain length, for example, the fibre diameter and $\rho_A$ is the density.

## Analysis

### Steady solutions

Due to the existence of nonlinearity and dispersion, Eq. (3) has a soliton-type (solitary) solution

$$u(\xi) = \frac{6(c^2-1)}{P(1+\sqrt{1+6Q(c^2-1)/P^2}\cosh(\xi\sqrt{(1-c^2)/(H_1-H_2c^2)})}, \tag{4}$$

where $\xi = X - cT$ and $c$ is the velocity of the soliton. The term with $H_2$ regulates the width of the soliton like shown in Fig. 1. The phase analysis demonstrates the various classes of solutions including oscillatory solutions depending on signs of the coefficients in Eq. (3).

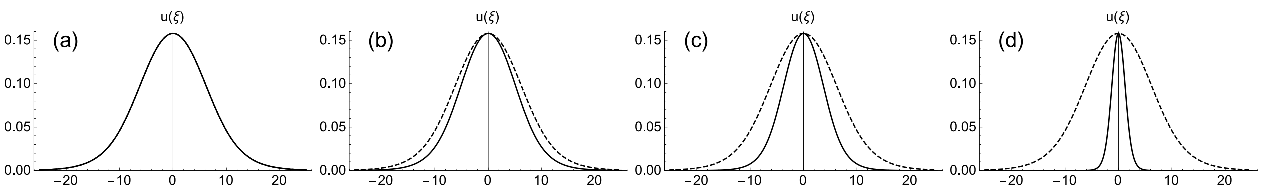


Figure 1: The effect of the second dispersive term $H_2U_{XXTT}$ on the width of a solitary wave. Here $P = -10$, $Q = 40$, $H_1 = 2$; (a)$H_2 = 0$, (b)$H_2 = 2$, (c)$H_2 = 4$ and (d)$H_2 = 6$. Dashed line with $H_2 = 0$ is plotted for reference.

### Solutions emerging from arbitrary initial conditions

From an arbitrary initial condition the trains of solitary waves emerge. Depending on the signs of coefficients in the governing equation (3), either the smaller or larger solitons travel faster. A typical train of solitons is shown in Fig. 2.a

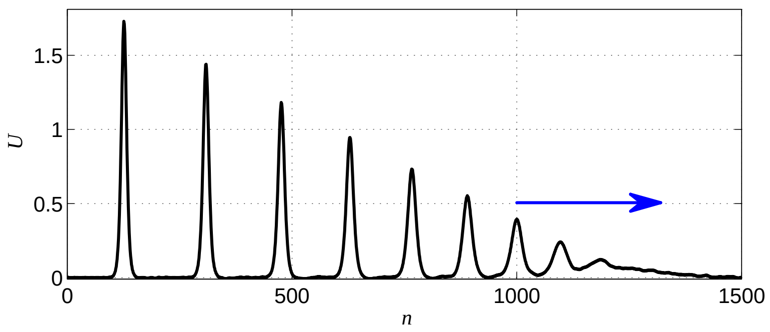


Figure 2: Formation of soliton train propagating from left to right with smaller amplitude solitons traveling faster than the larger amplitude ones. Here $P = -0.2186$, $Q = 0.004230$, $H_1 = 72.14$, $H_2 = 1.000$, dimensionless time $t \approx 9800$.

**Interaction of solitons**

It is of interest to study the interaction of solitary waves in order to establish whether these waves are solitons or not. In the classical sense, solitons interact with each other elastically restoring their speed and structure after interaction. The numerical analysis shows that in the case of Eq. (3) after several interactions the radiation effects are visible which shows that in the present case the term 'soliton' can be used only conditionally.

## Conclusions

The analysis can be summarised with following conclusions:

- The improved model (Eqs (2), (3)) removes the discrepancy that at higher frequencies the velocities are unbounded (see [4]);
- The additional dispersive term $u_{xxtt}$ with the coefficient $h_2$ (or $H_2$ in the dimensionless form) in addition to the *ad hoc* dispersive term $u_{xxxx}$ [1] describes actually the influence of the inertiality of the microconstituents (lipids) of the biomembrane. This term regulates the width of the solitary pulse (see Fig. 1) and such an effect can be used for determining the value of $h_2$ from experiments.
- The governing equation (3) involves several solution types of solitary waves and under certain conditions ($Q > 0$, $H_2 >> H_1$) an oscillatory solution exists (see [6]);
- Soliton trains can be emerged from an arbitrary initial condition. These results were obtained by numerical simulation by using the pseudospectral method. Depending on the signs of coefficients $Q$ and $P$, the nonlinear effects start to influence the emergence either from the front or from the back of the propagating pulse (see [6]). For the case of a biomembrane one has $Q < 0$, $P > 0$ and the train emerging from a positive input starts with smaller solitons which travel faster than the bigger ones. This is different from the conventional case of nonlinear evolution equations (the KdV equation, for example). In the case of a negative input, the train is headed by bigger solitons which travel faster. It has been shown that there are several wave types possible: solitary waves, oscillatory (Airy-type) waves, and hybrid solutions (see [6]).
- The interaction of solitary waves is not fully elastic, which shows that these solitary waves are not solitons in the strict sense. However, like in other Boussinesq-type equations [5], the radiation effects accompanying every interaction start cumulating rather slowly and the interacting solitons keep their shape for a rather long time. It gives the ground to call emerging solitary waves modelled by Eq. (2) (or Eq. (3)) solitons like it is done in other physical cases.

## References


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