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# Solitons in the Heimburg–Jackson model of sound propagation in lipid bilayers are enabled by dispersion of a stiff membrane

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**Abstract** Experiments show that elastic constants of lipid bilayers vary greatly during the liquid-to-gel phase transition. This fact forms the cornerstone of the Heimburg–Jackson model of soliton propagation along membranes of axons, in which the action potential is accompanied by a traveling phase transition. However, the dispersion term, which is crucial for the existence of solitons, is added to the Heimburg–Jackson model ad hoc and set to fit experimental observations. In the present paper, we aim to consolidate this view with continuous membrane mechanics. Using literature data, we show that the compression modulus of a DPPC membrane is smaller by approximately an order of magnitude during phase transition. With a series expansion of the compression modulus, we write the action of a membrane and solve the corresponding wave equation analytically using an Exp-function method. We confirm that membrane solitons with speeds around 200 m/s are possible with amplitudes inversely proportional to their speed. We conclude that dispersion necessary for existence of solitons is directly related to a membrane's bending properties, offering a possible explanation for $h$. Our findings are in general agreement with existing literature and give insight into a general mechanism of wave propagation in membranes close to transition.

## Introduction

In 2005, Heimburg and Jackson proposed a thermodynamic theory of nerve pulse propagation in which the action potential (AP) is accompanied by a longitudinal pressure wave inside the cell membrane [1,2]. This pressure wave (soliton) is a local traveling liquid-to-gel phase transition of the lipid membrane that can propagate long distances without significant energy dissipation.

Various authors have considered the possibility of a mechanical wave propagating along axons [3,4]. The Heimburg–Jackson model correctly accounts for the observed heat reabsorption in axons not accounted for in the classic electrical theory of Hodgkin and Huxley [5,6], further enforcing that the AP is accompanied by an adiabatic soliton. Since lipid transitions happen close to physiological temperatures, the Heimburg–Jackson model presents a compelling case for adiabatic sound solitons whose existence and stability is predicted by simple physical arguments.

The existence of these solitons is wholly dependent on the fourth-order dispersive term $h$, added ad hoc to the classical one-dimensional sound equation [1]. This term exists as a free parameter setting the linear scale of the soliton and has not been measured experimentally [7], but has been determined theoretically from the expansion for the lateral speed of sound in lipid bilayers [8]. In the Heimburg–Jackson model, it was often adjusted to $h = 2\,\mathrm{m^4/s^2}$ in order to match the observed width of the nerve pulse, which is about 10 cm [1].

In the present paper, we propose an alternative approach to thinking about membrane solitons from the viewpoint of membrane mechanics in the vicinity of phase transition. Such continuous approach is feasible since the experimentally observed width of the nerve pulse is many orders of magnitude larger than phospholipid molecules size. We construct an energy density functional and show that the dispersive term of the fourth order follows naturally from the bending energy of the slightly curved membrane. We derive the action of a long unperturbed membrane close to transition and then use DPPC data from Heimburg and Jackson to show that the compression modulus of the membrane

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is temperature dependent. With a series expansion of the compression modulus close to phase transition, we obtain the nonlinear wave equation and solve it analytically using an Exp-function method, confirming he possibility of propagating mechanical solitons. We find that the soliton speed is around 200 m/s, which is within 10% of the predictions of the Heimburg–Jackson model, and that the amplitude of the solitons is inversely proportional to their speed. We conclude that dispersion necessary for existence of solitons is directly related to membranes' elastic properties, offering a possible explanation for $h$.

## Action of an excited membrane

The contour of a long cylindrical axon membrane can be represented as a curve in one dimension, where the transversal displacement from its non-excited state is both a function of dimension and time $u = u(x, t)$. A perturbed piece of the membrane carries both kinetic and potential energy. The latter comes from stretching with compression modulus $k_a$ and bending with bending modulus $k_b$. Let us assume for now that $k_a$ and $k_b$ are constant. The action of membrane of length $L$ in time $T$ is

$$\mathcal{S} = \frac{1}{2} \int_0^T \int_0^L \mu u_t^2 - k_a u_x^2 - k_b u_{xx}^2 \, dx dt. \qquad (1)$$

Here, $\mu$ is the one-dimensional density of the membrane. Near the phase transition temperature, $\mu$ changes as the lipids change from liquid to gel, but for simplicity let us assume that $\mu$ is kept constant. Note that curvature used for Helfrich's bending energy in one dimension is approximately given by the second spatial derivative. Following standard minimization procedure, this Lagrangian yields the equation of motion

$$k_a u_{xx} = \mu u_{tt} + k_b u_{xxxx}. \qquad (2)$$

This equation bears a resemblance to the sound propagation equation of the Heimburg–Jackson model [1]. The principal difference with the latter is that the lateral membrane density $\rho(x, t)$ is replaced by transversal displacement $u(x, t)$ and the dispersion term follows from membrane bending.

In acoustic theory and rod mechanics, Eq. (2) is sometimes referred to as the *stiff string* or the *bad Boussinesq* equation with the dispersion relation $\omega^2 = k^2 - k^4$, known for its short wavelength instabilities. When such a stiff string is bent, a new restoring force apart from tension arises from some of the parts being compressed and others stretched by bending. The solutions of Eq. (2) are seldom addressed in the literature and are usually given in context of fixed or clamped boundary conditions [9]. To the best of our knowledge, there has been no attempt at a soliton solution. In Appendix A, we show that solutions of Eq. (2) are analytical and called peakons.

## Membrane's elastic constants close to transition

A lipid membrane's elastic constants change when the lipids undergo a phase transition. Depending on the type of bilayer, the compression modulus $(k_a)$ of the liquid phase can be 2–7 times greater than the gel phase [1,2,10,11]. We can approximate the experimental dependencies found in experiments with DPPC lipids [2] by analytic functions (Fig. 1).

For a membrane close to transition, however, $k_a$ is characterized by a momentary decrease; the elastic modulus decreases with increasing lateral pressure and the membrane resembles a spring that becomes softer when compressed (Fig. 1(c)).

We intend to write the dependence $k_a(T)$ as the dependence on $k_a(u(x, t))$. Using data of lateral density of DPPC vesicles given in [2], we find that the length of the molecules in both phases is given by taking a quotient of their specific area and specific volume. We therefore calculate that $d_f = \sigma_f/\rho_f = 3.96$ nm and $d_g = \sigma_g/\rho_g = 4.98$ nm for fluid and gel states, respectively.

The unperturbed membrane in the Heimburg–Jackson model corresponds to the fluid state $\rho_{\text{fluid}}^A = 4.035 \cdot 10^{-6} \text{kg/m}^2$ and $u = 0$ in our one-dimensional model (Fig. 2b). When molecules start to transition to the gel state, the displacement of the membrane increases and $u > 0$. We can relate transversal displacement $u$ and lateral membrane density $\rho$ through a linear dependence:

$$u(\rho) = k\rho + N, \qquad (3)$$

where $k = 8.5 \cdot 10^{-4} \, \text{m}^3/\text{kg}$ and $N = -3.4 \cdot 10^{-9}$ m.

## Series expansion of the spatially dependent compression modulus

Since we have appoximated the experimental data with analytic functions $k_a(T)$, $\rho(T)$ and $u(\rho)$, it is easy to relate $k_a$ and $u$; we simply express $\rho$ as a function of $u$ from the linear dependency and insert into $k_a(T)$. This procedure is analogous to finding the $y(x)$ dependency when both $x(t)$ and $y(t)$ are given with a parametric dependence on $t$. Figure 2 shows the $k_a(u)$ dependency calculated this way from data shown in Fig. 1c.

The compression modulus displays a pronounced minimum before increasing further as the membrane transitions from a liquid to gel state. The dependence of $k_a$ near the transition can be approximated with a series expansion around the minimal value of $k_a$:

$$k_a(u) = a(u - P)^2 + Q. \qquad (4)$$

Here, $a$, $P$ and $Q$ are expansion constants. For DPPC data shown in Fig. 2, $a = 0.547 \, \text{N}/\mu\text{m}^3$, $P = 0.532 \, \text{nm}$ and $Q = 0.032 \, \text{N/m}$. For other lipids, these constants
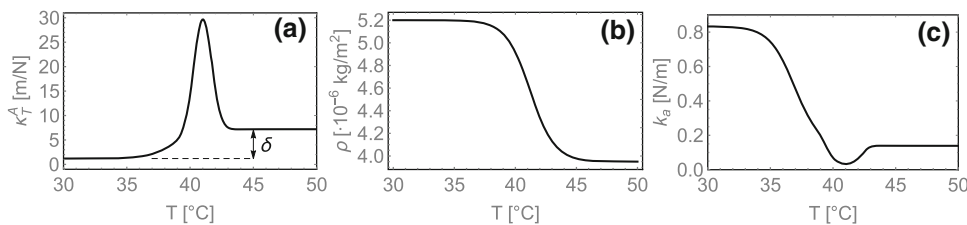
**Fig. 1** Lateral compressibility $\kappa_T^A$ (**a**) and lateral density (**b**) of DPPC extruded vesicles near the phase transition around 41°C (Adapted from Chapter 14, Heimburg, 2008). Compression modulus $k_a = 1/\kappa_T^A$ (c) can be calculated from panel (**a**). The lateral compressibility $\delta$ of the fluid phase is taken to be several times larger than the gel phase in accordance with data given in [2]
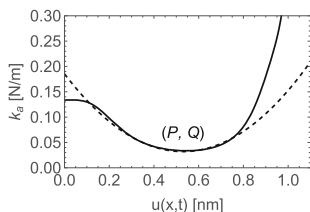


**Fig. 2** Dependence of the compression modulus on the transversal displacement of the membrane can be calculated directly from Figure 1 (full line). An approximation of this dependence is obtained by a series expansion around the minimal point with the fitted parabola $k_a(u) = a(u-P)^2 + Q$ having the values $a = 0.547\,\mathrm{N}/\mu\mathrm{m}^3$, $P = 0.532\,\mathrm{nm}$ and $Q = 0.032\,\mathrm{N/m}$ (dashed line) (Eq. (4)). Note that $u = 0$ corresponds to the unperturbed membrane just above the melting transition

will be different and ultimately depend on the experimental measurements of heat capacity $c_p$ [1]. With this displacement dependence of the compression modulus, we may rewrite Eq. (1):

$$ S = \frac{1}{2}\int_0^T \int_0^L \mu u_t^2 - k_a(u)u_x^2 - k_b u_{xx}^2 \, dx dt. \quad (5) $$

Minimization of this action results in a nonlinear equation of motion

$$ a(u-P)u_x^2 + (a(u-P)^2 + Q)u_{xx} = \mu u_{tt} + k_b u_{xxxx}, \quad (6) $$

which is investigated for the possibility of propagating solitons. We notice that $a = 0$ immediately simplifies to Eq. (2). We are therefore interested in cases where $a \neq 0$, implying that nonlinearity of elastic constants, granted by the phase transition, is crucial for finding new solutions.

**Nondimensionalization**

We nondimenzionalize Eq. (6) by setting $u = x_0\tilde{u}$, $x = x_0\tilde{x}$ and $t = t_0\tilde{u}$, where the tilde variables are unitless. For DPPC lipids near transition, we use values from Heimburg and Jackson, $k_b = 2 \cdot 10^{-20}$ J and $\mu = 4.035 \cdot 10^{-6} - 5.2 \cdot 10^{-6}$ kg/m [1]. A more precise treatment would also include a spatial dependence of $k_b$.

However, since $k_b$ is related to the fourth derivative of position, we assume it to be constant. Setting a length scale $x_0 = u_0 = \sqrt{k_b}/P\sqrt{a}$, a time scale $t_0 = \sqrt{k_b\mu}/P^2 a$ and two dimensionless constants $\gamma = \sqrt{k_b}/P^2\sqrt{a}$ and $\beta = Q/P^2 a$, Eq. (6) is simplified:

$$ \gamma(\gamma u - 1)u_x^2 + ((\gamma u - 1)^2 + \beta)u_{xx} = u_{tt} + u_{xxxx}. \quad (7) $$

Here, tilde is omitted for clarity and all variables and their derivatives are dimensionless. We attempt to solve this equation using a standard Exp-function method for nonlinear wave equations [12].

## Nonlinear wave solutions with the Exp-function method

Seeking localized soliton solutions, we use the standard transformation $u(\eta)$ with $\eta = x - vt$, where $v$ is the speed of the wave. Equation (7) can be rewritten as

$$ \gamma(\gamma u - 1)u'^2 + ((\gamma u - 1)^2 + \beta - v^2)u'' = u''''. \quad (8) $$

Here, the prime denotes the differential with respect to $\eta$. Following the Exp-function method, we assume that the solutions to Eq. (8) can be expressed in the following form [12]:

$$ u(\eta) = \frac{\sum_{n=-d}^c a_n \exp(n\eta)}{\sum_{m=-s}^r b_m \exp(m\eta)}, \quad (9) $$

where $c$, $d$, $r$ and $s$ are positive integers which are unknown and need to be determined and $a_n$ and $b_m$ are unknown constants. Equation (9) can be rewritten:

$$ u(\eta) = \frac{a_c \exp(c\eta) + \cdots + a_{-d}\exp(-d\eta)}{a_r \exp(r\eta) + \cdots + a_{-s}\exp(-s\eta)}. \quad (10) $$

To determine the value of $c$ and $r$, we have to balance the linear term of the highest order of Eq. (8) with the highest nonlinear term, which are $u''''$ and $u^2 u''$, respectively. With a simple calculation and the help of Wolfram Mathematica, we get

$$ 3c + 2r = c + 4r \rightarrow c = r. \quad (11) $$

Similarly we need to balance the lowest order of the linear term in Eq. (8) with the lowest order of the nonlinear term. This results in the equation

$$-(3d + 2s) = -(d + 4s) \rightarrow d = s. \quad (12)$$

The values of $c$ and $d$ can be freely chosen, but for simplicity we set $c = r = 1$ and $d = s = 1$. Our trial solution then reduces to

$$u(\eta) = \frac{a_1 \exp(\eta) + a_0 + a_{-1} \exp(-\eta)}{b_1 \exp(\eta) + b_0 + b_{-1} \exp(-\eta)}. \quad (13)$$

Substituting Eq. (13) into Eq. (8), we have

$$\frac{1}{A}(c_9 \exp(9\eta) + c_8 \exp(8\eta) + \cdots + c_2 \exp(2\eta) + c_1 \exp(\eta)) = 0, \quad (14)$$

where $A = (b_{-1} + b_0 \exp(\eta) + b_1 \exp(2\eta))^5$ and the constants $c_i (i = 1, \ldots, 9)$ are obtained and given in Appendix B. Equating the coefficients of of $\exp(n\eta)$ to be zero, we obtain a system of equations

$$\{c_i = 0, (i = 1, \ldots, 9)\}. \quad (15)$$

Solving this system simultaneously results in many non-trivial solutions.

## Results

### Kinks

A possible solution to the system Eq. (15) is

$$a_0 = \frac{b_0(1 + \sqrt{2})}{\gamma}, \qquad a_{-1} = \frac{b_{-1}(1 - \sqrt{2})}{\gamma},$$
$$a_1 = 0, \qquad b_1 = 0, \qquad v = \pm v_0 \sqrt{1 + \beta}. \quad (16)$$

Here, $b_0$ and $b_{-1}$ are free parameters and $v$ is the speed of the wave. The parameter $v_0 = x_0/t_0 = P\sqrt{a}/\sqrt{\mu} = 185.5$ m/s, taking the average value of $\mu$. Inserting these coefficients into Eq. (13) gives

$$u(\eta) = \frac{1}{\gamma}(1 + \sqrt{2} - \frac{2\sqrt{2}b_{-1}}{b_{-1} + b_0 e^\eta}). \quad (17)$$

For the case $b_0 = b_{-1} = 1$ and substituting back from $\eta = x - vt$, this simplifies to

$$u(x, t) = \frac{1}{\gamma}(1 + \sqrt{2}\tanh(\frac{x - vt}{2})). \quad (18)$$

Such a solution is called a *kink* [13] and is shown in Fig. 3. This is a step-like disturbance propagating across the membrane with speed $v = v_0\sqrt{1 + \beta}$. For DPPC values given prior, $\beta = 0.21$, $\gamma = 0.68$ and $v = 203.9$ m/s. Changing the free parameters $b_0$ and $b_{-1}$ corresponds
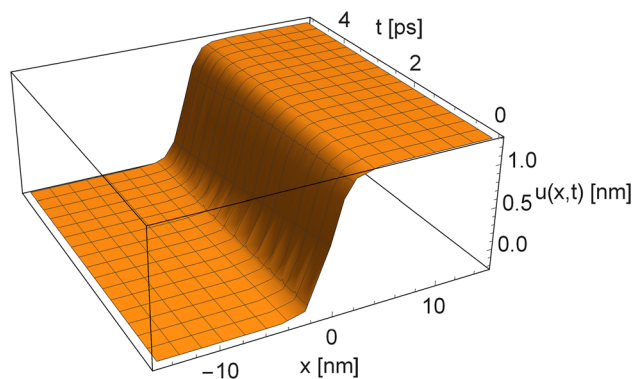


**Fig. 3** A kink given by Eq. (18) for $v = 203.9$ m/s. This is an example of a nonlinear wave that solves the propagating PDE (Eq. (7))

to translation of the kink, while $\gamma$ serves as a scaling factor.

The kink is physically a shock wave of a freezing transition, a traveling disruption that changes the displacement of the membrane in a step-like manner from fluid to gel state, respectively. The height of the step is the change $d_g - d_f = 1$ nm, resulting in a 20% thickening for DPPC data, which is in accordance with experiments [2]. However, this change is permanent and the membrane does not return to its unperturbed, fluid state. Kinks traveling in the opposite direction is also possible.

### Solitons

A soliton solution to the system Eq. (15) is the sum of two particular solutions with coefficient values

$$a_0 = \frac{b_0 + \sqrt{2(b_0^2 - 4b_{-1}b_1)}}{\gamma}, \qquad a_{-1} = \frac{b_{-1}(1 + \sqrt{2})}{\gamma},$$
$$a_1 = \frac{b_1(1 \pm \sqrt{2})}{\gamma}, \qquad v = v_0\sqrt{1 + \beta}. \quad (19)$$

The free parameters are now $b_0$, $b_{-1}$ and $b_1$ and give the localized bell-like solution

$$u(\eta) = \frac{2}{\gamma}\left(1 + \frac{e^\eta\sqrt{2(b_0^2 - 4b_{-1}b_1)}}{b_{-1} + e^\eta(b_0 + b_1 e^\eta)}\right). \quad (20)$$

Real solutions demand that $b_0^2 \geq 4b_{-1}b_1$. When the equality holds, the trivial solution gives a constant $2/\gamma$, while $b_0^2 > 4b_{-1}b_1$ results in localized hyperbolic secant-like solutions shown in Fig. 4. When $b_{-1} = b_1$, the solitons are symmetric around the $y$-axis (Fig. 4a) and shifted left or right when $b_{-1} > b_1$ and $b_{-1} < b_1$, respectively (Fig. 4b). Parameter $\gamma$ again only scales the soliton amplitude and is entirely determined by membrane stiffness $k_b$ and $aP^2$. Using DPPC data, a typical soliton profile is shown in Fig. 5a.

An interesting case occurs when $b_0^2 \gg 4b_{-1}b_1$. While retaining their bell-shaped, localized nature, these soli-
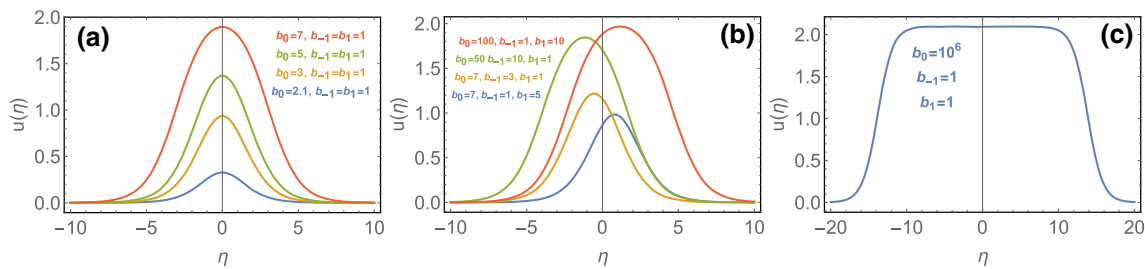
**Fig. 4** With changing parameters $b_0$, $b_{-1}$ and $b_1$, Eq. (20) gives different solutions; when $b_{-1} = b_1$, the solitons are symmetric about the y-axis (**a**). When either $b_{-1}$ or $b_1$ is greater, while still obeying $b_0^2 > 4b_{-1}b_1$, solitons are shifted left or right, respectively (**b**). When $b_0^2 \gg 4b_{-1}b_1$, the soli- ton's width is many of orders of magnitude greater than its amplitude (**c**), similar to a soliton in the Heimburg–Jackson model. All solutions displayed here are calculated for DPPC data, where $v = 203.9\,\mathrm{m/s}$
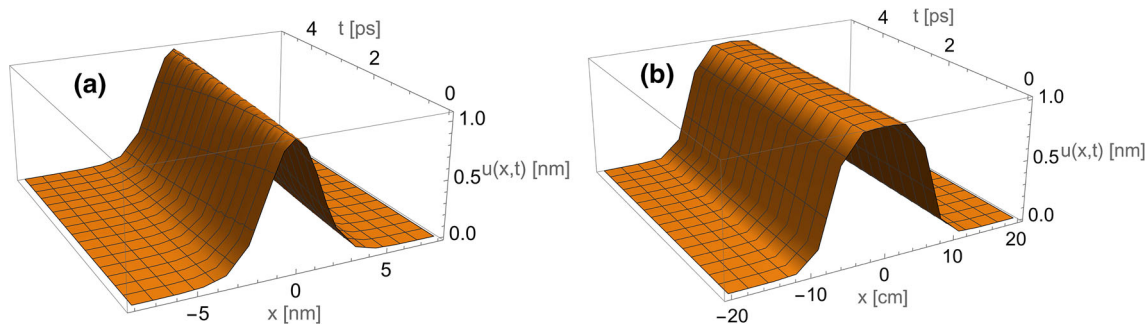


**Fig. 5** 3D plots of the solution $u(x,t)$ of Eq. (20) for different values of $b_0$, $b_{-1}$ and $b_1$. For parameters $b_0 = 6$, $b_{-1} = b_1 = 1$, the soliton is 10 nm wide with an amplitude of 1 nm, marking the propagating fluid-to-gel transition (**a**). For $b_0 = 10^8$, $b_{-1} = b_1 = 1$, the width of the soliton is orders of magnitude greater than its amplitude (**b**). For both cases, DPPC data are used and $v = 203.9\,\mathrm{m/s}$

tons are many of orders of magnitude wider than their amplitude (Figs. 4c and 5b). This is in accordance with the Heimburg–Jackson model, where pulses of solid gel states are of the order of centimeters, while the thickness change of the membrane is around 1 nm [1].

## Discussion

Solitary waves in our model are possible only due to the dispersion term $u_{xxxx}$ which is provided by the slight bending of the membrane and proportional to $\gamma$. Interestingly, $\gamma$ serves only as an amplitude scaling factor and has no effect on propagation speed, which is in total agreement with the role of the dispersion parameter $h$ in the Heimburg–Jackson model [1]. Our model thus provides a possible explanation of the emergence of dispersion in lipid membranes postulated by Heimburg and Jackson.

The amplitudes of solitons in our model are proportional to $1/\gamma$. Since propagating speed increases with $\beta$ and $\gamma$, faster solitons have smaller amplitudes, which is also true in the Heimburg–Jackson model. We found that the governing PDE allows for analytic solutions not only on the length scales of centimeters, but also on smaller length and time scales. However, it is not clear how these waves relate to the axonal structure, which is not homogenous: recent imaging experiments have shown that a system of actin rings may be crucial to propagation, but their function is still disputed [14]. It would be possible to further expand the present model to include mechanosensitive ion channels [15] that are crucial in signal transmission, so a swelling of the membrane could have a direct influence on the propagating action potential.

We compare the values of mechanical wave speed in lipid membranes with existing literature by inserting units in the equation

$$v = \pm\sqrt{\frac{aP^2 + Q}{\mu}}. \tag{21}$$

For DPPC data in Fig. 2, this results in speeds of 203.9 m/s, which is an overestimate in comparison to the values of 115-176 m/s in the Heimburg–Jackson model [1,16], but still in accord with the conduction velocity of myelinated fibers (120 m/s) and the theoretical limit for maximally stiff myelin sheaths (1535 m/s) [17]. Measurements of propagating sound waves in a DPPC monolayers at the air-water interface were shown to range from 1-100 m/s, depending on the type of monolayer stimulation and frequency [18,19]. A possible reason for an overestimation of speed in comparison with experiments is in neglecting the viscous environment in which these waves take place. In future work, a viscous force could be included. To our knowledge there was

no direct reliable measurement of propagating waves in bilayers at the water-water interface, although promising experiments are being made in recent years [20].

Different types of lipids have different $c_p(T)$ dependencies resulting in unique functions $k_a(T)$. Using the methods presented in this paper, constants $a$, $P$ and $Q$ can be numerically determined to find propagation speeds of mechanical waves in different lipid bilayers from thermodynamic properties. Future work could also examine how a shift in position or amplitude of the $c_p$ curve, for example by addition of solvents, could explicitly impact $v$.

## Conclusion

In the present paper, we considered mechanical wave propagation along lipid membranes close to phase transition. Inspired by the thermodynamic Heimburg–Jackson model for propagation along axons, we derived an action of a continuous elastic membrane with a bending and stretching modulus. We found that the fourth-order dispersion term added ad hoc to the Heimburg–Jackson model, crucial for sustaining solitons, follows naturally from bending moduli of the axonal membrane under tension.

Acknowledging experimental evidence for temperature-dependent elastic moduli of DPPC lipids, we constructed an action of the membrane close to transition. In this regime, we found that stiffness is dependent on transversal displacement and derived a nonlinear fourth-order wave equation. Using the Exp-function method, we found that membranes close to transition allow for propagating nonlinear waves with analytic solutions—kinks and bell-shaped localized solitons. Using experimental data for DPPC lipids from literature, we found our model predicts propagation speeds of around 200 m/s, which is in good agreement with existing data (177 m/s).

Our model sheds light on the emergence of the fourth-order dispersion term that is necessary for membrane solitons. Our findings support the thermodynamic Heimburg–Jackson model and indicate that the dispersion term can regulate the length scale of the mechanical pulse. Furthermore, our model predicts propagating speeds in lipid membranes based solely on the thermodynamic properties of their constituents.

## Author contribution statement

MD: Conceptualization, Investigation, Methodology, Visualization, Writing—original draft, Writing—review & editing. Matej Daniel: Supervision, editing, reviewing, funding. Veronika Kralj-Iglič: Conceptualization, supervision, editing, reviewing, funding. Aleš Iglič: Conceptualization, supervision, editing, reviewing, funding.

**Data Availability Statement** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

### Declarations

**Conflict of interest** The authors declare no conflict of interest.

## Appendix A - Peakons

The solitary wave solutions are assumed to be of the form $u(z)$, $z = x - vt$ where $v$ is the speed of propagation. Since we are looking for localized wave packets, our solutions have to obey $u(z)$, $u'(z)$, $u''(z) \to 0$ as $z \to \pm\infty$. The primes denote derivatives with respect to $z$. After substitution and chain rule, Eq. (2) becomes

$$v^2 \left( \frac{\partial^2 u}{\partial z^2} \right) = c^2 \left( \frac{\partial^2 u}{\partial z^2} \right) - h \left( \frac{\partial^4 u}{\partial z^4} \right). \quad (22)$$

Here, $c^2 = k_a/\mu$ and $h = k_b/\mu$. Rearranging, we get

$$0 = \frac{\partial^2}{\partial z^2} \left[ u(c^2 - v^2) - h \frac{\partial^2 u}{\partial z^2} \right]. \quad (23)$$

Following the assumption that solitons are localized and vanish for $z \to \pm\infty$, we can perform double integration immediately. After multiplying both sides by $2(\partial u/\partial z)$ and considering the identity $2(\partial u/\partial z)(\partial^2 u/\partial z^2) = \partial/\partial z(\partial u/\partial z)^2$, we get

$$\left( \frac{\partial u}{\partial z} \right)^2 = \frac{(c^2 - v^2)}{h} u^2. \quad (24)$$

We see that solitons are possible only for the cases where $|v| < c$, otherwise the solutions do not decay to zero at infinity. The solution is

$$u(x, t) = c_1 e^{-|x-vt|\sqrt{(c^2 - v^2)/h}}, \quad (25)$$

where $c_1$ is given by the initial conditions. The solution is smooth apart from the peak at its crest leading to a finite jump in the first derivative of the solution. Such solutions are sometimes called peaked solitary wave solutions or peakons in short [13].

## Appendix B - Coefficient list

Coefficients from Eq. (14) are

$$
\begin{aligned}
c_1 = {}& a_{-1}^2 a_0 b_{-1}^2 \gamma^2 - a_{-1}^3 b_0 b_{-1} \gamma^2 - 2a_{-1} a_0 b_{-1}^3 \gamma \\
& + 2a_{-1}^2 b_0 b_{-1}^2 \gamma - a_0 b_{-1}^4 + a_{-1} b_0 b_{-1}^3, \\
c_2 = {}& 3a_{-1} a_0^2 b_{-1}^2 \gamma^2 + 4a_{-1}^2 a_1 b_{-1}^2 \gamma^2 \\
& - 5a_{-1}^2 a_0 b_0 b_{-1} \gamma^2 - 4a_{-1}^3 b_1 b_{-1} \gamma^2 \\
& + 2a_{-1}^3 b_0^2 \gamma^2 - 3a_0^2 b_{-1}^3 \gamma - 8a_{-1} a_1 b_{-1}^3 \gamma \\
& + 4a_{-1} a_0 b_0 b_{-1}^2 \gamma
\end{aligned}
$$

$$+8a_{-1}^2 b_1 b_{-1}^2 \gamma - a_{-1}^2 b_0^2 b_{-1} \gamma - 16a_1 b_{-1}^4$$
$$+11a_0 b_0 b_{-1}^3 + 16a_{-1} b_1 b_{-1}^3 - 11a_{-1} b_0^2 b_{-1}^2,$$
$$c_3 = 7a_{-1}^3 b_0 b_1 \gamma^2 + 3a_0 a_{-1}^2 b_0^2 \gamma^2$$
$$-3a_1 a_{-1}^2 b_{-1} b_0 \gamma^2$$
$$-18a_0 a_{-1}^2 b_{-1} b_1 \gamma^2 + 14a_0 a_1 a_{-1} b_{-1}^2 \gamma^2$$
$$-5a_0^2 a_{-1} b_{-1} b_0 \gamma^2$$
$$+2a_0^3 b_{-1}^2 \gamma^2 - 3a_{-1}^2 b_1 b_0^3 \gamma + 4a_0 a_{-1} b_{-1} b_0^2 \gamma$$
$$-8a_1 a_{-1} b_{-1}^2 b_0 \gamma + 22a_0 a_{-1} b_{-1}^2 b_1 \gamma$$
$$-14a_0 a_1 b_{-1}^3 \gamma - a_0^2 b_{-1}^2 b_0 \gamma$$
$$+11a_{-1} b_{-1} b_0^3 - 77a_{-1} b_{-1}^2 b_0 b - 11a_0 b_{-1}^2 b_0^2$$
$$+a_1 b_{-1}^3 b_0 + 76a_0 b_{-1}^3 b_1,$$
$$c_4 = a_{-1} a_0^2 b_0^2 \gamma^2 + 2a_{-1}^2 a_1 b_0^2 \gamma^2$$
$$-a_0^3 b_{-1} b_0 \gamma^2 - 2a_{-1} a_0 a_1 b_{-1} b_0 \gamma^2 + 11a_{-1}^2 a_0 b_1 b_0 \gamma^2$$
$$+12a_{-1} a_1^2 b_{-1}^2 \gamma^2 + 11a_0^2 a_1 b_{-1}^2 \gamma^2$$
$$+8a_{-1}^3 b_1^2 \gamma^2 - 22a_{-1} a_0^2 b_{-1} b_1 \gamma^2 - 20a_{-1}^2 a_1 b_{-1} b_1 \gamma^2$$
$$-2a_{-1} a_0 b_0^3 \gamma$$
$$+2a_0^2 b_{-1} b_0^2 \gamma - 2a_{-1} a_1 b_{-1} b_0^2 \gamma$$
$$-13a_{-1}^2 b_1 b_0^2 \gamma - 20a_0 a_1 b_{-1}^2 b_0 \gamma$$
$$+24a_{-1} a_0 b_{-1} b_1 b_0 \gamma - 12a_1^2 b_{-1}^3 \gamma - 4a_{-1}^2 b_{-1} b_1^2 \gamma$$
$$+11a_0^2 b_{-1}^2 b_1 \gamma + 16a_{-1} a_1 b_{-1}^2 b_1 \gamma$$
$$-a_{-1} b_0^4 + a_0 b_{-1} b_0^3 - 11a_1 b_{-1}^2 b_0^2 + 58a_{-1} b_{-1} b_1 b_0^2$$
$$-47a_0 b_{-1}^2 b_1 b_0 - 176a_{-1} b_{-1}^2 b_1^2 + 176a_1 b_{-1}^3 b_1,$$
$$c_5 = -8a_0^3 b_{-1} b_1 \gamma^2 + 3a_1 a_0^2 b_{-1} b_0 \gamma^2 + 3a_{-1} a_0^2 b_0 b_1 \gamma^2$$
$$+17a_1^2 a_0 b_{-1}^2 \gamma^2 + 2a_{-1} a_1 a_0 b_0^2 \gamma^2$$
$$+17a_{-1}^2 a_0 b_1^2 \gamma^2 - 44a_{-1} a_1 a_0 b_{-1} b_1 \gamma^2 + 5a_{-1} a_1^2 b_{-1} b_0 \gamma^2$$
$$+5a_{-1}^2 a_1 b_0 b_1 \gamma^2$$
$$+18a_0^2 b_{-1} b_0 b_1 \gamma - 8a_1 a_0 b_{-1} b_0^2 \gamma$$
$$+10a_{-1} a_0 b_{-1} b_1^2 \gamma + 10a_1 a_0 b_{-1}^2 b_1 \gamma$$
$$-8a_{-1} a_0 b_0^2 b_1 \gamma - 2a_{-1} a_1 b_0^3 \gamma - 22a_{-1}^2 b_0 b_1^2 \gamma$$
$$-22a_1^2 b_{-1}^2 b_0 \gamma + 24a_{-1} a_1 b_{-1} b_0 b_1 \gamma - 230a_0 b_{-1}^2 b_1^2$$
$$+10a_0 b_{-1} b_0^2 b_1 - 5a_1 b_{-1} b_0^3$$
$$+115a_{-1} b_{-1} b_0 b_1^2 - 5a_{-1} b_0^3 b_1 + 115a_1 b_{-1}^2 b_0 b_1,$$
$$c_6 = 2a_{-1} a_1^2 b_0^2 \gamma^2 + a_0^2 a_1 b_0^2 \gamma^2 + 11a_0 a_1^2 b_{-1} b_0 \gamma^2$$
$$-a_0^3 b_1 b_0 \gamma^2 - 2a_{-1} a_0 a_1 b_1 b_0 \gamma^2$$
$$+8a_1^3 b_{-1}^2 \gamma^2 + 11a_{-1} a_0^2 b_1^2 \gamma^2 + 12a_{-1}^2 a_1 b_1^2 \gamma^2$$
$$-20a_{-1} a_1^2 b_{-1} b_1 \gamma^2$$
$$-22a_0^2 a_1 b_{-1} b_1 \gamma^2 - 2a_0 a_1 b_0^3 \gamma - 13a_1^2 b_{-1} b_0^2 \gamma$$
$$+2a_0^2 b_1 b_0^2 \gamma - 2a_{-1} a_1 b_1 b_0^2 \gamma - 20a_{-1} a_0 b_1^2 b_0 \gamma$$
$$+24a_0 a_1 b_{-1} b_1 b_0 \gamma - 12a_{-1}^2 b_1^3 \gamma + 11a_0^2 b_{-1} b_1^2 \gamma$$
$$+16a_{-1} a_1 b_{-1} b_1^2 \gamma - 4a_1^2 b_{-1}^2 b_1 \gamma - a_1 b_0^4 + a_0 b_1 b_0^3$$
$$-11a_{-1} b_1^2 b_0^2 + 58a_1 b_{-1} b_1 b_0^2 - 47a_0 b_{-1} b_1^2 b_0$$
$$+176a_{-1} b_{-1} b_1^3 - 176a_1 b_{-1}^2 b_1^2,$$
$$c_7 = 2a_0^3 b_1^2 \gamma^2 - 5a_1 a_0^2 b_0 b_1 \gamma^2 + 3a_1^2 a_0 b_0^2 \gamma^2$$
$$+14a_{-1} a_1 a_0 b_1^2 \gamma^2 - 18a_1^2 a_0 b_{-1} b_1 \gamma^2$$
$$+7a_1^3 b_{-1} b_0 \gamma^2 - 3a_{-1} a_1^2 b_0 b_1 \gamma^2 - a_0^2 b_0 b_1^2 \gamma$$
$$-14a_{-1} a_0 b_1^3 \gamma + 22a_1 a_0 b_{-1} b_1^2 \gamma$$
$$+4a_1 a_0 b_0^2 b_1 \gamma - 3a_1^2 b_0^3 \gamma - 8a_{-1} a_1 b_0 b_1^2 \gamma$$

$$+76a_0 b_{-1} b_1^3 - 11a_0 b_0^2 b_1^2$$
$$+a_{-1} b_0 b_1^3 - 77a_1 b_{-1} b_0 b_1^2 + 11a_1 b_0^3 b_1,$$
$$c_8 = 4a_{-1} a_1^2 b_1^2 \gamma^2 + 3a_0^2 a_1 b_1^2 \gamma^2 - 4a_1^3 b_{-1} b_1 \gamma^2$$
$$-5a_0 a_1^2 b_0 b_1 \gamma^2 + 2a_1^3 b_0^2 \gamma^2 - 3a_0^2 b_1^3 \gamma$$
$$-8a_{-1} a_1 b_1^3 \gamma + 8a_1^2 b_{-1} b_1^2 \gamma + 4a_0 a_1 b_0 b_1^2 \gamma$$
$$-a_1^2 b_0^2 b_1 \gamma - 16a_{-1} b_1^4$$
$$+16a_1 b_{-1} b_1^3 + 11a_0 b_0 b_1^3 - 11a_1 b_0^2 b_1^2,$$
$$c_9 = a_0 a_1^2 b_1^2 \gamma^2 - a_1^3 b_0 b_1 \gamma^2 - 2a_0 a_1 b_1^3 \gamma$$
$$+2a_1^2 b_0 b_1^2 \gamma - a_0 b_1^4 + a_1 b_0 b_1^3.$$

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