

Nonlinear Physics and Instabilities
Wednesday 4 November 2020
Duration : 3h

Answers can be written in French or English.

1 Nonlinear waves in an excitable media

We have seen that the coexistence of dispersion and nonlinearity could lead to solitons. We can also have soliton waves with a constant profile when the nonlinearity is compensated by the diffusion. This is the case of the impulse in a nerve fiber of which we will examine a very simplified model.

The axon of the neuron, as shown in figure 1, is made of a tube whose wall is a lipid membrane. Its outer surface is covered by a sheath of myelin which is regularly interrupted. The part of the membrane that is not covered by myelin is crossed by ion channels, through which Na^+ and K^+ ions can pass and are present at different concentrations in the electrolytes inside and outside the axon.

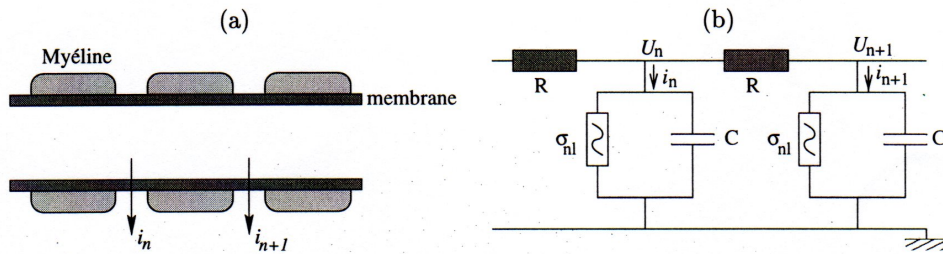


FIGURE 1 – (a) Schematic of the nerve fiber of an axon. (b) Electrical diagram equivalent to a portion of the axon. σ_{nl} is the nonlinear conductance of the membrane as defined by (1), and R is the resistance of the inner electrolyte over a length equal to that between two interruptions of the myelin sheath.

The nerve impulse, which propagates along the axon, corresponds to the passage of currents i_n , through these channels in the n th myelin-free zone, accompanied by a variation of the potential difference U_n so that the membrane of this myelin-free zone can be seen as a nonlinear conductance. The relationship between the current i flowing through this conductance and the voltage U at these terminals is of the form

$$i = f(u) = \sigma U(U - U_a)(U - U_b) \tag{1}$$

where U_a and U_b are characteristic voltages of the ion channels ($0 < U_a < U_b$).

In addition, the membrane of the myelin-free zone has a capacity C that must be taken into account to establish the circuit equivalent to the axon, which is shown in figure 1b. The resistance R shown here is that of the internal electrolyte over the length between two interruptions in the myelin sheath.

1(a) From the electrical diagram of figure 1b, establish the system of differential equations linking the potential differences U_n at the level of the different zones without myelin.

A solution to this system is sought by approximating the continuous media, replacing the finite difference appearing in the equations by a spatial derivative (approximation performed in the lowest order).

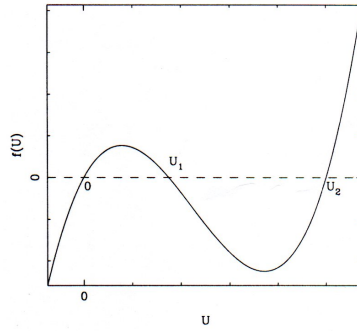


FIGURE 2 – Representation of $f(U)$.

1(b) Show that this approximation, associated with appropriate changes in timescales and lengthscales allows to obtain a partial differential equation for a dimensionless quantity u , which we will define, which is of the form

$$\frac{\partial u}{\partial \tau} - \frac{\partial^2 u}{\partial x^2} + u(u - \alpha)(u - 1) = 0 \quad (0 < \alpha < 1). \quad (2)$$

Give the expression of all the quantities in this equation, known as the Fischer equation.

1(c) Verify that this equation has three stationary solutions corresponding to spatially uniform states. How stable are they?

1(d) We are looking for a solution with a constant profile linking a region where $u = 0$ to a region where $u = 1$. Show that the search for this solution is equivalent to the study of the damped motion of a particle in a quadratic potential having two maxima, generally having two different values. Represent qualitatively this potential for $\alpha < 1/2$, $\alpha = 1/2$ and $\alpha > 1/2$.

1(e) Show by qualitative reasoning that, for given α , there is only one possible propagation speed for the solution, and that the direction of propagation changes depending on whether $\alpha < 1/2$ or $\alpha > 1/2$.

The expression of $f(U)$ that we have used for ion channels actually describes only the rising edge of the nerve impulse, in which U passes from its rest value $U = 0$ upstream of the nerve impulse to a value that corresponds to the maximum of the signal. What is the range of values of α that corresponds to a nerve fiber? In the axon, there is a second mechanism that returns U to its resting value after the nerve impulse has passed. It is not included in equation (2).

1(f) In the case $\alpha = 1/2$, there is a static solution. Give its expression (note that you can use a course result to avoid recalculating it).

Find out more : A. C. Scott, *The electrophysics of a nerve fiber*, Review of Modern Physics **47**, 487-533 (1975).

Correction de l'examen du 31 Octobre 2011

1 Ondes nonlinéaires dans un milieu excitable

1(a) The law of nodes applied between the two resistances of the figure 1b gives

$$I_{n-1} = I_n + i_n = I_n + \frac{dQ_n}{dt} + \sigma u_n (u_n - u_a)(u_n - u_b). \quad (3)$$

with $u_{n-1} - u_n = RI_{n-1}$ and $u_n - u_{n+1} = RI_n$. Introducing $Q_n = Cu_n$, it leads to

$$C \frac{du_n}{dt} + \frac{u_n - u_{n+1}}{R} - \frac{u_{n-1} - u_n}{R} + \sigma u_n (u_n - u_a)(u_n - u_b) = 0. \quad (4)$$

1(b) To arrive at the proposed dimensionless equation, divide the equation by σu_b^3 and put $U = u/u_b$.

$$\frac{C}{\sigma u_b^2} \frac{dU_n}{dt} - \frac{1}{\sigma R u_b^2} (U_{n+1} + U_{n-1} - 2U_n) + U_n \left(U_n - \frac{u_a}{u_b} \right) (U_n - 1) = 0 \quad (5)$$

A continuum approximation for the finite difference in U_n is made at this stage. If we note a the length of the axon "element", n the length along the axon, we end up at

$$\frac{C}{\sigma u_b^2} \frac{\partial U}{\partial t} - \frac{a^2}{\sigma R u_b^2} \frac{\partial^2 U}{\partial n^2} + U \left(U - \frac{u_a}{u_b} \right) (U - 1) = 0 \quad (6)$$

By introducing the quantities without dimensions $\tau = t\sigma u_b^2/C$ and $x = nu_b\sqrt{R\sigma}/a$, one arrives by posing $\alpha = u_a/u_b$ at the following result

$$\frac{\partial U}{\partial \tau} - \frac{\partial^2 U}{\partial x^2} + U (U - \alpha) (U - 1) = 0 \quad (7)$$

1(c) If $U = 0$, $U = \alpha$ or $U = 1$, we have an obvious solution of the equation, a stationary and homogeneous solution.

To study the stability, we develop around each solution.

For $U = 0 + v$, we obtain at the lowest order

$$\frac{\partial v}{\partial \tau} - \frac{\partial^2 v}{\partial x^2} + \alpha v = 0 \quad (8)$$

whose solution is $v = v_0 e^{i(qx - \omega t)}$ with the condition $-i\omega + q^2 + \alpha = 0$. So we have $v_0 e^{iqx - (q^2 + \alpha)t}$ with $-(q^2 + \alpha) < 0$. This solution is therefore stable

For $U = \alpha + v$, we get at the lowest order

$$\frac{\partial v}{\partial \tau} - \frac{\partial^2 v}{\partial x^2} + \alpha(\alpha - 1)v = 0 \quad (9)$$

whose solution is $v = v_0 e^{i(qx - \omega t)}$ with the condition $-i\omega = -q^2 - \alpha(\alpha - 1)$. As $\alpha < 1$, the quantity $-i\omega$ is positive for values of q small enough. This is a sufficient condition for this solution to be unstable.

For $U = 1 + v$, we obtain at the lowest order

$$\frac{\partial v}{\partial \tau} - \frac{\partial^2 v}{\partial x^2} + (1 - \alpha)v = 0 \quad (10)$$

We thus find a stable solution.

In summary, 0 and 1 are stable, while α is unstable.

1(d) We can have regions where $u = 0$ and $u = 1$ are stable. We can therefore design a solution which interpolates between these two regions.

Solution with a constant profile : we look for solutions in the form $U(z) = U(x - v\tau)$ where v is now the speed, not to be confused with the perturbation around the u solution as in the present question.

The equation (2) is written as follows

$$-v \frac{du}{dz} - \frac{d^2u}{dz^2} + u(u - \alpha)(u - 1) = 0. \quad (11)$$

It corresponds to the equation of motion of a fictitious particle, of unit mass, represented by the position U , the fictitious time z , moving in a potential V such that $\partial V / \partial U = U(U - \alpha)(U - 1)$ and subject to friction characterized by the damping coefficient v .

The potential is such that $\partial V / \partial U = U(U - \alpha)(U - 1) = -U^3 + U^2(1 + \alpha) - \alpha U$. We thus conclude that the potential is

$$V(U) = -\frac{U^4}{4} + \frac{1 + \alpha}{3}U^3 - \frac{\alpha}{2}U^2 + cste. \quad (12)$$

We'll take the constant equal to zero-zero.

We then obtain $V(0) = 0$, $V(1) = -1/4 + (1 + \alpha)/3 - \alpha/2$.

We notice that for $\alpha = 1/2$, $V(1) = 0$. Therefore, for $\alpha < 1/2$, $V(1) > 0$, while for $\alpha > 1/2$, $V(1) < 0$,

Moreover for $0 < U < \alpha$, the sign of $f(U)$ is negative. the potential is decreasing. It grows from α to 1. We therefore deduce its qualitative form.

1(e) Looking for soliton we study the motion of a particle that starts from one of the maxima (0 and 1) with a zero "speed" and must finish its motion at the other maximum with a zero speed. The motion of this pseudo-particle is damped with a coefficient v .

If $\alpha > 1/2$, for this to be possible, the particle must be in $U = 0$ for $z \rightarrow -\infty$. It will then move to $U = 1$ where it will stop if the dissipation is such that it loses in this movement exactly the difference in potential energy $V(0) - V(1)$. Since the solution propagates with $v > 0$, it moves with a tendency to enlarge the $u = 0$ domain.

On the contrary, if $\alpha < 1/2$, one must always start from the highest point, $U = 1$, and reach $U = 0$ in $z \rightarrow +\infty$.

Note that to study the case $v < 0$, we must change z into $-z$.

In any case, the area that grows is the one with the smallest potential : $U = 0$ for $\alpha > 1/2$ and $U = 1$ otherwise.

For the nerve impulse, one must pass from the resting potential $U = 0$ to the excited potential. The zone which enlarges must be the zone $U = 1$. This corresponds therefore to $\alpha < 1/2$.

1(f) For $\alpha = 1/2$, we have $V(0) = V(1)$ and we pass between these two states without "dissipating" energy. We must therefore have $v = 0$. It is therefore a static solution.

We can see that the potential $V(u)$ is then analogous to the one we get in the case of the model ϕ^4 whose equation of motion is $-\phi_{xx} - \phi + \phi^3$ with extrema in (-1) and (+1) for the potential V . We have

$$-\frac{d^2U}{dx^2} + U(U - 1/2)(U - 1) = 0 \quad (13)$$

with extrema in 0 and 1 for V . Let's put $U = (1 + \phi)/2$. The equation of motion becomes

$$-\frac{1}{2} \frac{d^2\phi}{dx^2} + \frac{(\phi + 1)\phi(\phi - 1)}{2} = 0 \quad (14)$$

By posing $y = x/2$, we end up à $-\frac{d^2\phi}{dy^2} - \phi + \phi^3 = 0$ which is formally analogous to the ϕ^4 model of which we know the solution $\phi = \tanh(y/\sqrt{2})$, which yields

$$U = \frac{1}{2} \tanh\left(\frac{x}{2\sqrt{2}}\right) + \frac{1}{2} \quad (15)$$