

Foundations of Cognitive Robotics
Prof. Bishakh Bhattacharya
Department of Mechanical Engineering
Indian Institute of Technology, Kanpur


Lecture - 09

Good morning students, welcome to the course on Foundations of Cognitive Robotics. In the last class, I have told you about the mathematical modeling of a neuron, I told you that how with the help of the classical Hodgkin-Huxley model we can actually mathematically model the action potential of a neuron.

Now, today we will go beyond this, today we will talk about how we can have some of the most recent theories to explain these kind of you know propagation of action potential. So, let us look into that what will be the outline of today's lecture.

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Today, we are first going to talk about the Hodgkin-Huxley model summary. So, that you can summarize and then we will talk about that, what are the properties which is still unexplained by the Hodgkin-Huxley model and then we will talk about the development of a new model.

We will then talk about the wave equations the development of solitons and the significance of the bilipid layer membrane, piezoelectric modeling and a co-propagation

model. So, these are the things that we will discuss today. So, first of all let us try to summarize the Huxley-Hodgkin's model.

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HH Model in a nutshell

Key equations:


1. Membrane Current Equation

$$I_m(t) = C_m \frac{dV_m}{dt} + g_{Na}(V_m - E_{Na}) + g_K(V_m - E_K) + g_L(V_m - E_L)$$

$$\frac{g_{Na}}{g_K} = \frac{g_{Na_0} m^3 h}{g_{K_0} n^4}$$

$g = \frac{1}{R}$
 $I = \frac{V}{R}$
 $= gV$

C_m = Membrane Capacitance, V_m = Membrane Voltage
 E_{Na} , E_K Membrane potential for different ions


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The HH model in a nutshell it starts with some of the key equations, the first equation that I told you is that is the membrane current equation. So, here the neurons are considered as you know kind of an assembly of capacitors and resistors. So, in that neuronal circuit and also the cell itself as a kind of a source of potential or a battery.

So, the neuronal current which is actually the membrane current is $I_m(t)$ and C_m is the membrane capacitance and V_m is the membrane voltage. Now, g_{Na} is the conductance with respect to sodium channel, g_K is the conductance with respect to potassium channel and g_L takes care of the leakage current which is mainly with chloride and other ion channels.

$$I_m(t) = C_m \frac{dV_m}{dt} + g_{Na}(V_m - E_{Na}) + g_K(V_m - E_K) + g_L(V_m - E_L)$$

$$g_{Na} = g_{Na_0} m^3 h,$$

$$g_K = g_{K_0} n^4$$

So, one thing we have to keep in our mind here that we are representing the resistance in terms of conductance g which is actually 1 over the R . So, it is the reciprocal of the resistance that we have to keep in our mind, ok.

So, just like we write say for example, when in terms of current if we have to write then it will help us, because we write usually current as what? Current we write as V/R and in this case we will write it the current as what we will write it as $g_x V$ conductance times the voltage. So, that is the difference that we have to keep in our mind.

And of course, the other part of the current that is related to the capacitor that is remaining the same, because it is in relation to the capacitance and that is $C_m dV/dt$. Now, the other important thing that I had discussed in the last class is that, this conductance like the conductance of sodium, conductance of potassium, it is found experimentally by Huxley-Hodgkin's is that they actually vary with respect to certain gate opening and they found out that there are essentially three types of gates, for sodium it is three types of m gate and one type of h gate.

So, three m type of three type of m and one h gate; this actually controls the conductance and for potassium this is actually four types of n gates which actually control the conductance of the potassium.

Now, if there are three of the m gates and if each one of them is having a probability of m, then it will be $(m \times m \times m)$ which is the $m^3 h$, that is the probability of opening up of the gates permitting the current to flow.

And similarly, in since there are four types of n gates. So, it is n into n into n into n. So, it is n^4 . So, that is what is the g_{Na} and g_K . Now, m, h, n these are having their own rate constant.

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HH Model contd.

Stage 2: Gate Kinetics

$$\begin{aligned}\frac{dm}{dt} &= \alpha_m(V_m)(1-m) - \beta_m(V_m)m, \\ \frac{dn}{dt} &= \alpha_n(V_m)(1-n) - \beta_n(V_m)n, \\ \frac{dh}{dt} &= \alpha_h(V_m)(1-h) - \beta_h(V_m)h\end{aligned}$$

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So, they have a simple kinetics which will be covered in the second equation, that is the gate kinetics equation in which we will be talking about dm/dt , that is the rate of change of this gate type m , then dn/dt and dh/dt .

$$\frac{dm}{dt} = \alpha_m(V)(1-m) - \beta_m(V)m,$$

Now, I told you also earlier that this depends on two things, one is what one for let us say for the first gate kinetics for the opening up of the m type of gates it will depend on α_m which is of course, intrinsically a function of the voltage itself.

So, it is α_m , where α_m will be the typical rate constant corresponding to m and $(1-m)$. So, $(1-m)$ is the probability that this n gates will be opened and then the opposite probability that it will be closed will be related to $\beta_m(V)m$, where β_m also is intrinsically a function of V_m .

$$\frac{dh}{dt} = \alpha_h(V)(1-h) - \beta_h(V)h,$$

$$\frac{dn}{dt} = \alpha_n(V)(1-n) - \beta_n(V)n$$

So, similarly there for n gate you need α_n, β_n and similarly for the h gate you need α_h, β_h , which means in order to solve these you need to have the six sets of coefficients. So, these are three pairs.

So, you need these six constants and these six constants are actually experimentally determined. So, this is something we have to keep in our mind.

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HH Model in a nutshell

Key equations:

1. Membrane Current Equation

$$I_m(t) = C_m \frac{dV_m}{dt} + g_{Na}(V_m - E_{Na}) + g_K(V_m - E_K) + g_L(V_m - E_L)$$

$$g_{Na} = g_{Na,0} m^3 h,$$

$$g_K = g_{K,0} n^4$$

C_m = Membrane Capacitance, V_m = Membrane Voltage

E_{Na}, E_K Membrane potential for different ions

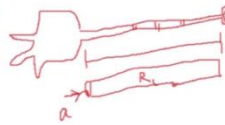
So, once we know these six constants, then we can go back to this equation and we can find out that what is g_{Na} , because then we know g_{Na} is 0; m h we can find out and similarly, we can find out g_K and we can put it back to this equation in order to get the membrane current. So, this is first of all the electrical part of the equation.

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HH Model: Cable Equation

Following Cable Equation for Action Potential for internal resistance R_i and cable radius a :

$$\frac{\partial^2 V_m}{\partial x^2} = \frac{2R_i}{a} I_m$$



By substituting Ion current:

$$\frac{\partial^2 V_m}{\partial x^2} = \frac{2R_i}{a} \left(C_m \frac{dV_m}{dt} + g_{Na}(V_m - E_{Na}) + g_K(V_m - E_K) \right)$$



If we now look into the HH model cable equation, then you can see here that in the cable equation we can actually keep the special variation of the membrane voltage. So, we can equate the special rate of change of the special variation of the membrane voltage with the membrane current by using the cable equation.

$$\frac{\partial^2 V_m}{\partial x^2} = \frac{2R_i}{a} I_m$$

So, essentially what this cable equation does is that, let us say we have a soma and which has some dendrites let us say and that is the soma and from that soma let us say we have the action. So, let us say this is the action going and which will be ending to some synapse.

Now, this action is essentially modeled like a cable and the radius of this cable. So, essentially this part it is this part which is modeled like a cable of some radius a . So, this is the cable. So, let us see this is the cable and the radius of the cable is modeled as a , that is one thing and the other thing here is this internal resistance. So, this internal resistance is the resistance inside this cytoplasm of these axon.

$$\frac{\partial^2 V_m}{\partial x^2} = \frac{2R_i}{a} \left(\frac{C_m dV_m}{dt} + g_{Na}(V_m - E_{Na}) + g_K(V_m - E_K) \right)$$

So, this internal resistance let us say that is denoted as R_i . So, if the internal resistance is R_i and these cable radius is a , then the cable equation which essentially considers that there

is this continuous membrane which is continuously between different points of nodes of ranvier, this can be actually segmented in terms of what you call a kind of a electronic systems.

So, in terms of let us say some voltage and this resistance and the capacitance of the i^{th} cell. So, then if any one of this this system can be modeled separately and then you know if you actually get the differential of it, then you will be coming to this particular equation which will equate between the membrane current and the voltage of the membrane.

Now, membrane current already we know that the membrane current itself can be written in terms of the current across the capacitance and then the across the sodium channels and across the potassium channels.

The leakage part is not considered it is just neglected here, but you can improve that. So, this is what you know if you substitute the I_m from the earlier relationship; that means, that we have done in equation 1.

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HH Model in a nutshell

Key equations:

1. Membrane Current Equation

$$I_m(t) = C_m \frac{dV_m}{dt} + g_{Na}(V_m - E_{Na}) + g_K(V_m - E_K) + g_L(V_m - E_L)$$
$$g_{Na} = g_{Na,0} m^3 h,$$
$$g_K = g_{K,0} n^4$$

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 E_{Na} , E_K Membrane potential for different ions



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So, if you substitute it, here you are going to get this complete relationship which is giving you the relationship between the special rate of change of the voltage membrane voltage with respect to the temporal rate of change of the membrane voltage.

So, the special versus temporal, but yet you can see here that, we still have the spatial variable and the temporal variable here. Ideally speaking, we would actually like to get equation which will be completely in terms of the temporal variable.

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Unified Equation for Action Potential

We know from wave equation, for a pulse with propagating speed θ ,

$$\frac{\partial^2 V_m}{\partial t^2} = \theta^2 \frac{\partial^2 V_m}{\partial x^2}$$


After joining the cable equation

$$\frac{a}{2R_i \theta^2} \frac{\partial^2 V_m}{\partial t^2} = C_m \frac{dV_m}{dt} + g_{Na}(V_m - E_{Na}) + g_K(V_m - E_K)$$


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Now, that can be done of course, so that is what we will be talking about in the next equation where we talk about the unified action for the action potential and here what we do is that, we acknowledge the fact that the pulse is the action pulse can be actually modeled in terms of a wave equation.

So, essentially if you remember that the action pulse if we try to model it is something like this that there is this time t and then there is this membrane voltage which will be basically starting say for example, from a negative state across the threshold go to a peak and then it will again come down come down and then it goes back.

So, that is something like this and this is the part which you remember is the depolarization part that is the depolarization part of it.

And, this is the part which is the repolarization part; that is the repolarization I am just abbreviating it as RP and this is the part which is the hyperpolarization part of it right. So, this kind of a signal now if you look at the action, so let us say this is what is my action which is model like a cable and then, this action at different points if you look at it you

will see that this signal is actually the nature of the signal and also the amplitude is remaining the same.

So, there are these loads of engaging between, which actually contain set of the intensity losses, but this is how it happens and this is the way the signal will propagate and the velocity of this wave velocity is what is theta here, ok.

So, then you know you can actually correlate between the voltage variation with respect to type and the voltage variation V is special variation of the voltage.

So, once we have this relationship all we need to do is to replace the left side as where it was $\frac{\partial^2 V_m}{\partial x^2}$ by $1/\theta^2 \frac{\partial^2 V_m}{\partial t^2}$. So, this part of it and also from the left hand side of the earlier equation we have just taken that $2 R_i$ by a , and we brought it in the left hand side.

$$\frac{\partial^2 V_m}{\partial t^2} = \theta^2 \frac{\partial^2 V_m}{\partial x^2}$$

$$\frac{a}{2R_i\theta^2} \left(\frac{\partial^2 V_m}{\partial t^2} \right) = C_m \left(\frac{dV_m}{dt} \right) + g_{Na}(V_m - E_{Na}) + g_K(V_m - E_K)$$

So, it becomes $\frac{a}{2R_i\theta^2} \left(\frac{\partial^2 V_m}{\partial t^2} \right)$ which equals to these current part of it that is $C_m \left(\frac{dV_m}{dt} \right)$ then the conductance related that sodium and the potassium current.


So, this is what you will get the final cable equation, by solving this as you can see now that this equation, it has been possible to bring everything with respect to the time domain variation.

Of course, it is a non-linear equation because the g_{Na} itself depends on m and m itself has a rate dependence etcetera, but you can still get the entire equation with respect to the temporal variation and that is a good point. So, it is easier to solve this kind of equation in order to get the action potential of the system.

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Properties unexplained by H-H Model

- Why nerves display thickness and length variations under the influence of the action potential?
- Why the action potential can be excited by a mechanical stimulus?
- Why during the first phase of the nerve pulse, heat is released from the membrane, while it is reabsorbed during the second phase
- It seems as if the mechanical and the heat signatures rather indicate that the nerve pulse is an adiabatic and reversible phenomenon such as the propagation of a mechanical wave.

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We now we will talk about the properties, which are actually unexplained by the HH model. For example, we know that as the action potential actually crosses the action, there is a change in the thickness and in the change in the length variation; in the length variation, under the influence of the action potential.

Also, we know that the mechanical stimulus can actually actuate the action potential, how whereas, the electrical model cannot explain that.

Also, during the first phase of the nerve pulse, heat is released from the membrane and it is reabsorbed during the second phase. Now, if these entire you know neuronal system is like a resistor then it will only dissipate the energy it will not you know release the heat and reabsorb it just like an adiabatic and reversible phenomena. So, that is something that also is not possible.

So, these are the some of the important things, which are not explained by the HH model and hence this drives us to think of a better model towards explaining these facts as well.

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Development of a new model

Consider the well-known Euler wave equation for area density $\Delta\rho^A$ as:

$$\frac{\partial^2}{\partial \tau^2} \Delta\rho^A = \frac{\partial}{\partial z} \left(c^2 \frac{\partial}{\partial z} \Delta\rho^A \right)$$


However, close to the melting transition, the velocity of sound, c is not constant and it may be written as follows ('p', 'q' are material parameters). Also, considering dispersion of sound wave into account.

$$c^2 = c_0^2 + p\Delta\rho^A + q(\Delta\rho^A)^2 + \dots$$

$$\frac{\partial^2}{\partial \tau^2} \rho^A = \frac{\partial}{\partial z} \left[(c_0^2 + p\Delta\rho^A + q(\Delta\rho^A)^2 + \dots) \frac{\partial}{\partial z} \Delta\rho^A \right] - h \frac{\partial^4}{\partial z^4} \Delta\rho^A$$

Here,

$\Delta\rho^A$ = change in lateral density of the membrane
 ρ^A = lateral density of the membrane
 c_0 = velocity of small-amplitude sound



Now, when we will talk about the development of a new model consider first of all that it is based on the wave equation, because we already know that the wave equation is there in place.

However, in this case the wave velocity is c that is fine, and the x that we had earlier discussed is actually z here. So, z or x they are similar. So, this is the longitudinal direction of the action that we are talking about; so that is what, is the z direction. Please keep in mind just the symbols vary, but that part is the same.

Whereas, now these variation actually depends on something called $\Delta\rho^A$ and what is this $\Delta\rho^A$? That is the change in the lateral density of the membrane. This is something that is experimentally observed, that the membrane density that is if you consider that the neuron itself is like a membrane there are this that is the up some thickness, ok.

And, then I also told you that this membrane changes in the thickness direction as the action wave propagate. Now, let us say that that change is creating a change in terms of the variation of the area density and that variation of area density is $\Delta\rho^A$, then the wave equation I can write in a different way here now as $\frac{\partial^2}{\partial \tau^2} \Delta\rho^A$ and that is if provided if this c^2 does not vary, of course it varies along the length because of some other chemical changes inside the system, but it is essentially $c^2 \frac{\partial}{\partial z} \Delta\rho^A$.

$$\frac{\partial^2}{\partial \tau^2} \Delta \rho^A = \frac{\partial}{\partial z} \left(c^2 \frac{\partial}{\partial z} \Delta \rho^A \right)$$

So, you look at it carefully that in the last an expression, what was it? It was with respect to the membrane voltage right. So, the last equation was the wave equation was with respect to the membrane voltage.

Now, we say no, we are going to go to something more fundamental and we are going to look into it in terms of the membrane you know change of the area density of the membrane and in terms of that we are defining the wave equation that is the change a we have to keep in our mind.

$$c^2 = c_0^2 + p \Delta \rho^A + q (\Delta \rho^A)^2 + \dots$$

$$\frac{\partial^2}{\partial \tau^2} \Delta \rho^A = \frac{\partial}{\partial z} \left((c_0^2 + p \Delta \rho^A + q (\Delta \rho^A)^2 + \dots) \frac{\partial}{\partial z} \Delta \rho^A \right) - h \frac{\partial^4}{\partial z^4} \Delta \rho^A$$

Secondly, in the last equation we said that θ is not varying with respect to the length, but now we are telling no, this c is actually varying with respect to z , it is not constant.

In fact, the c itself has a kind of a dispersion relationship; that means, c^2 is something like $c_0^2 +$ it so, it is a; it varies with the density and some constant of it and it is a non-linear variation with respect to the area density.

So, if I put our model like this, then I can actually put this expression of c in this entire thing. So, we get this final model and what we will see is that, in this final model because of the dispersion we will get an additional dispersion term here.

This is very very important ok, that is we get in addition to that the c is variation because of the dispersion we get an extra variation here and this extra variation will be very important we will look into it so.

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Development of a new model

Non-dimensionalisation of the wave equation:

$$u = \frac{\Delta\rho^A}{\rho_0^A}, \quad x = \frac{c_0}{h} z, \quad t = \frac{c_0^2}{\sqrt{h}} \tau, \quad B_1 = \frac{\rho_0}{c_0^2} p, \quad B_2 = \frac{\rho_0^2}{c_0^2} q$$

Here, ρ_0^A = equilibrium lateral density of the membrane in the fluid phase

p and q are the parameters determined from density dependence of the sound velocity. These two constants parameterize the experimental shape of the melting transition of the membrane

h is a parameter describing the frequency dependence of the speed of sound, that is, the dispersion

$$\frac{\partial^2 u}{\partial t^2} = \frac{\partial}{\partial x} (B(u)) \frac{\partial u}{\partial x} - \frac{\partial^4 u}{\partial x^4}$$

$$B(u) = 1 + B_1 u + B_2 u^2$$

C_0 is approximately 176.6m/s



Now, certain non-dimensionalization let us do for the model; which means, that for the you know $\Delta\rho^A$ we can actually with respect to the equilibrium lateral density, let us have a variable u .

$$u = \frac{\Delta\rho^A}{\rho_0^A}, \quad x = \frac{c_0}{h} z, \quad t = \frac{c_0^2}{\sqrt{h}} \tau, \quad B_1 = \frac{\rho_0}{c_0^2} p, \quad B_2 = \frac{\rho_0^2}{c_0^2} q$$

Then, let us have x as a non-dimensional variable now, with respect to this thickness and then let us have the time itself as another non-dimensional variable and we have these two constants B_1 and B_2 . So, this is the thing that will require to non-dimensionalize the last equation.

So, if I do that and here, the h is a parameter which describes the frequency dependence of the speed of sound ok. So, if I do that we are going to get that last equation in a much more neat and clean form, which is that the non-dimensional variation of area density is now u . So, that is $\frac{\partial^2 u}{\partial t^2}$ will be $\frac{\partial}{\partial x}$ of these velocity itself is with respect to a new non-dimensional quantity B .

$$\frac{\partial^2 u}{\partial t^2} = \frac{\partial}{\partial x} (B(u)) \frac{\partial u}{\partial x} - \frac{\partial^4 u}{\partial x^4}$$

$$B(u) = 1 + B_1 u + B_2 u^2$$

So, it is like $\frac{\partial}{\partial x} (B(u)) \frac{\partial u}{\partial x}$ and then that h factor is accommodated here in we get this relationship the dispersion part of is as $-\frac{\partial^4 u}{\partial x^4}$ and the B(u) you can take up to two terms as $1 + B_1 u + B_2 u^2$. So, this is how we can actually get this whole expression in a non-dimensionalized mode.

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Development of a new model

Modified equation considering the propagation of density pulse:

Consider the propagation of the density pulse 'u' with a constant velocity. We can use a coordinate transformation $\xi = x - \beta t$, where β is the dimensionless propagation of velocity which gives us the modified equation as:


$$\beta^2 \frac{\partial^2 u}{\partial \xi^2} = \frac{\partial}{\partial \xi} \left(B(u) \frac{\partial u}{\partial \xi} \right) - \frac{\partial^4 u}{\partial \xi^4}$$

The analytical solution of the density propagation equation becomes:

$$u(\xi) = \frac{2a_+ a_-}{(a_+ + a_-) + (a_+ - a_-) \cosh(\xi \sqrt{1 - \beta^2})}$$

$$a_{\pm} = -\frac{B_1}{B_2} \left(1 \pm \sqrt{\frac{\beta^2 - \beta_0^2}{1 - \beta_0^2}} \right), \quad \beta_0 < |\beta| < 1$$

The value of non-dimensional velocity, β generally lies between 0.6 to 1.



Now, if I get this whole expression in a non-dimensionalized mode the only thing now is that, we can actually you know apply another parameterization in terms of the density pulse we can use a coordinate transformation now and we can put a new coordinate $\xi = x - \beta t$, where β will be the dimensionless propagation of velocity.

So, we can get the new equation in terms of not in terms of x, but in terms of $\beta^2 \frac{\partial^2 u}{\partial \xi^2} = \frac{\partial}{\partial \xi} \left(B(u) \frac{\partial u}{\partial \xi} \right) - \frac{\partial^4 u}{\partial \xi^4}$, which is what is the dispersion part again.

We have to keep in your mind; that this dispersion if it is not there, then the system will be a conservative system and it will not give you the relationship which is very important for us in terms of the propagation of the wave.

$$u(\xi) = \frac{2a_+ a_-}{(a_+ + a_-) + (a_+ - a_-) \cosh(\xi \sqrt{1 - \beta^2})}$$

So, the analytical solution of this density propagation if you solve this equation you will get it, in this $u(\xi)$ in terms of two constants- a , one a_+ and a_- where a_+ and a_- can be expressed in terms of the B_1, B_2 's β, β_0 's.

$$a_{\pm} = -\frac{B_1}{B_2} \left(1 \pm \sqrt{\frac{\beta^2 - \beta_0^2}{1 - \beta_0^2}} \right), \beta_0 < |\beta| < 1$$

So, we will get it and the β itself please keep in mind that it is a non-dimensional velocity, which generally varies between 0.6 to 1.

Now, we will see something very interesting in terms of the behavior of the β , we will see that this solution actually takes us to a very well-known wave solution which is in terms of solitons.

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Soliton

The solution to the density propagation equation gives->

A soliton is a self-reinforcing solitary wave packet that maintains its shape while it propagates at a constant velocity.


These are caused by a cancellation of nonlinear and dispersive effects in a medium.

Solitons are the solutions of a widespread class of weakly nonlinear dispersive partial differential equations describing physical systems.

The soliton phenomenon was first described in 1834 by John Scott Russell who observed a solitary wave in the Union Canal in Scotland.

Calculated solitary density pulse as a function of lateral position calculated using experimental parameters for a synthetic membrane. The pulse travels with about 100 m/s.

Ref. T. Holmberg, A.D. Jackson, Thermodynamics of the nervous impulse. In: K. Nag (Ed.), Structure and Dynamics of Membranous Interfaces, Wiley, Hoboken, NJ, 2008, pp. 317-339



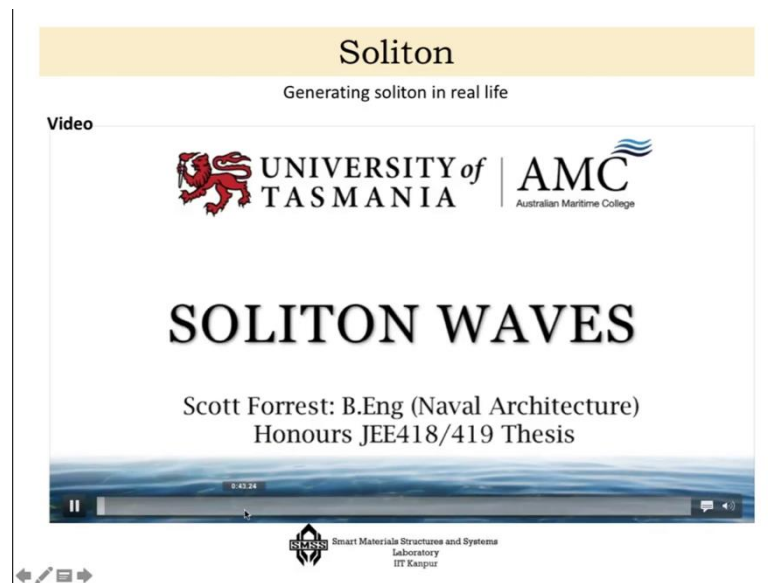
Well, the solution in that last equation will actually give you what I was just telling you that is soliton, ok. And, what is the soliton? It is a self-reinforcing solitary wave packet and which will maintain its shape, remember the action potential maintaining same. While it propagates at a constant velocity imagine that, this is what is the direction of the, action potential.

So, there is a soliton that is propagating if that wave equation if we solve that will give us a soliton and these are caused how by a cancellation of non-linear and dispersive effects in the medium.

That is why I said that the dispersive effect is important because it is going to cancel out the non-linear part. Now, solitons are the solutions of a wide spread class of weekly non-linear dispersive PDEs describing the physical system.

As far as in 1834, John Scott Russell observed first a solitary wave in a canal in Scotland. And, it is only late and you know the researchers like Heimburgs, Jacksons they have found out that you know in terms of the neuronal voltage such a solution actually matters. Now, let us look into that, how does a soliton actually behaves?

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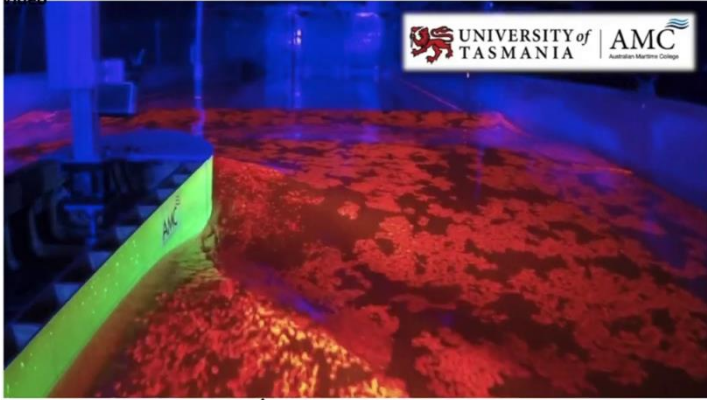



I will take you through a small animation from University of Tasmania and of its Scott Forrest, I will show you the video which will explain you beautifully that, how does a soliton propagates? Let us look into the soliton wave.

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Soliton
Generating soliton in real life

Video



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Soliton
Generating soliton in real life


Video


Wave Speed

$$V = \sqrt{gh}$$

← wave speed ← water depth

↑
gravity (9.81ms⁻¹)



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Soliton

Generating soliton in real life


Video


Froude Depth

$$Fr_h = \frac{V}{\sqrt{gh}}$$

vessel speed
water depth

gravity (9.81ms⁻¹)



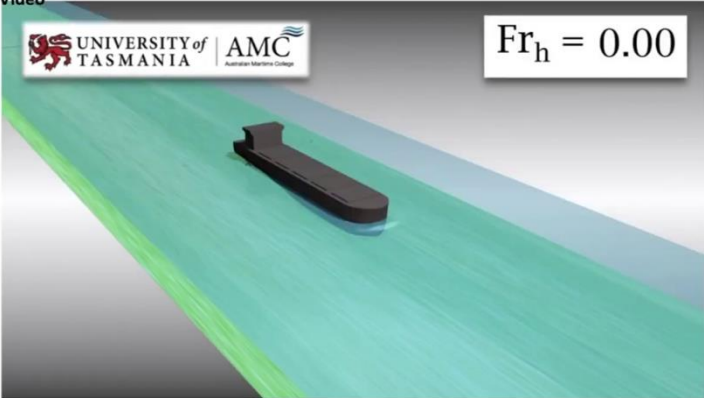
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Soliton


Generating soliton in real life

Video



$Fr_h = 0.00$


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Soliton
Generating soliton in real life

Video

$Fr_h = 0.05$


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Soliton
Generating soliton in real life

Video

$Fr_h = 0.40$


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Soliton
Generating soliton in real life

Video

$Fr_h = 0.45$


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Soliton
Generating soliton in real life

Video

$Fr_h = 0.50$


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Soliton
Generating soliton in real life

Video

$Fr_h = 0.75$


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Soliton
Generating soliton in real life

Video

$Fr_h = 0.80$

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Soliton
Generating soliton in real life

Video

UNIVERSITY of TASMANIA | **AMC**
Australian Maritime College

$Fr_h = 0.90$

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Soliton
Generating soliton in real life

Video

UNIVERSITY of TASMANIA | **AMC**
Australian Maritime College

$Fr_h = 0.95$

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Soliton

Generating soliton in real life

Video

$Fr_h = 1.00$

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Soliton

Generating soliton in real life

Video

Trim

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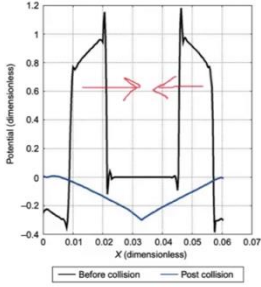
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Soliton


What happens when the Solitons collide:

- It has been shown by Tasaki that Nerve pulses are blocked upon collision.
- According to HH model, propagation of a nerve pulse generate a refractory period which is governed by the relaxation times of the protein conductance.
- A simulation of HH model shows the blocking -->

Ref: Revati Appali et. Al., A Comparison of the Hodgkin-Huxley Model and the Soliton Theory for the Action Potential in Nerves, **Advances in Planar Lipid Bilayers and Liposomes**, Volume 16



Collision of nerve pulses calculated with the FitzHugh-Nagumo equations. Two pulses traveling in opposite directions are shown before (black) and after the collision (blue). The pulses are annihilated after the collision.

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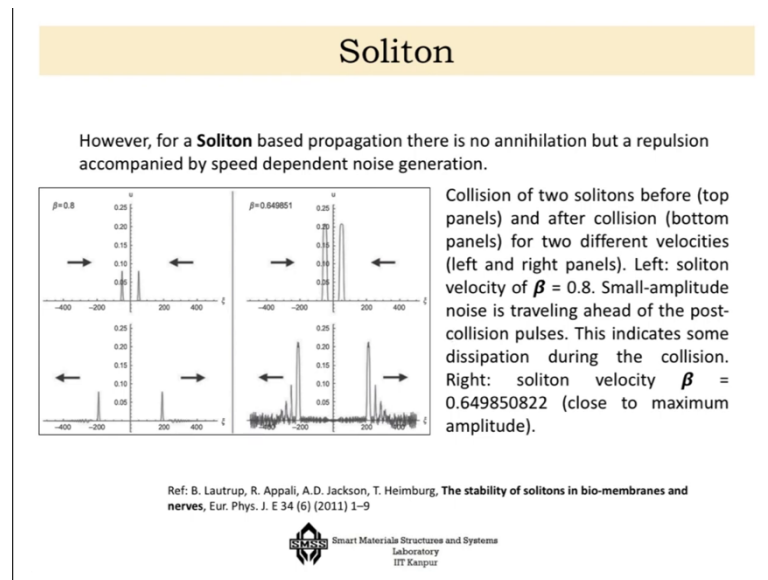
Now, of course, there is one point that, what happens when two solitons will collide from the opposite direction? Then, in such a case it actually any you know this there is a blocking of heat that you can see that as this is what is the before the collision these two waves are approaching you can see.

This is something that is still is to be actually checked with respect to the normal pulse and you can see what is happening you know if post collision and that is what is the post collision part of it. So, you cannot see either of the solitons here.

Now, if you use on the other hand a simpler form of collision which is a Hodgkin-Huxley equation, which is Fitzhugh-Nagumo equation. Then, two pulses traveling in opposite directions before and after you can see that you may see that the pulses are going to annihilate after the collision.

Whereas, for these kind of a system this kind of annihilation does not actually happen, they can actually pass through each other.

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So, that is something that is still you know not explainable through the soliton model. So, you can see that this is what is happening for a soliton that two solitons are approaching and you can see that after they are collision; they are actually with a lesser much lesser amplitude, but they are just going back to both the directions.

So, this is something that does not happen in this particular case whereas, in the case of the you know simpler version of the HH model that is the Hodgkin that is the Fitzhugh-Nagumo model you can see that there is a complete annihilation that is happening. So, the point is that these Hodgkin-Huxley model predicts a complete annihilation of two waves whereas, for soliton collision this does not happening.

Now, in reality; that means, the action you know a potentials in terms of waves if it reflects back from the synapse, then it will once again pass through without this you know this proceeding directions the propagation direction of the action wave we and both of them will come down, but there will be no annihilation.


On the other hand, in the last model we have seen that there will be an annihilation. So, that disparity is still existing in the system.

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Soliton

Does Soliton model support anesthesia?

- It is known that all general anesthetics lowers the melting point of lipid membrane.
- Reduction of melting point implies increase of required pressure to generate the density wave (as it only propagates in a liquid crystal phase of the lipid membrane).
- In the presence of anesthesia, free energy requirement increases which inhibits the soliton formation (remember: the soliton formation is possible only within a range of propagation velocity).
- In fact by increasing the ambient pressure level one can restart the nerve impulse. This is well known from a Tadpole experiment where about 50 bar pressure allowed the tadpoles to overcome the effect of ethanol-based anesthesia.
- The soliton model provides a mechanism for general anesthesia.



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Does soliton model support anesthesia? Well, that is another point that, it is known that well known that general anesthetics actually lowers the melting point of the lipid membrane and you know that the neuronal membranes are actually of lipid membrane.

So, reduction of melting point because of these drugs or anesthetics; that means, that there has to be a increase of the required pressure to generate the density wave. And, that means that, you know these density waves will not be able to get generated so easily. So, in the presence of anesthesia, the free energy requirement will increase which will inhibit the soliton formation and that explains that why an anesthesia would work.

In fact, there is an experiment that Heimburg's group have carried out, where the ambient pressure level of a of tadpole which is under anesthesia that is increased to about 50 bar pressure and they found that the effect of anesthesia is overcome and these tadpole is able to move again. So, thus the soliton model provides a mechanism for general anesthesia that is something that happens in terms of the soliton model.

Let us now carry out a brief summary between the Hodgkin-Huxley model and the soliton model and let us try to see that where we are with respect to both the models, as I told you that both the models are partially successful in explaining something and in not explaining something. So, which may actually generate further scope of research in this field.

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Brief summary of H-H and Soliton model

In H-H model:

- The action potential is based on the **electrical cable theory** in which the pulse is the consequence of voltage- and time-dependent changes of the conductance for sodium and potassium.
- The model is consistent with **quantized ion currents** attributed to opening and closing of specific channel proteins.
- It is consistent with the **channel-blocking effects** of several poisons, such as tetrodotoxin.
- The HH model is based on **ion currents through resistors** (channel proteins) and is therefore of dissipative nature.
- Reversible changes in heat and mechanical changes are not explicitly addressed, but heat generation would be expected.
- The HH model generates a **refractory period**.

In Soliton model:

- The nerve pulse is a **solitary electromechanical soliton wave** coupled to the lipid transition in the membrane.
- The solitary character is a consequence of the **nonlinearity of the elastic constants** close to the melting transition of the lipid membrane and of dispersion.
- It does not contain an explicit role of poisons and protein ion channels.
- However, the theory is consistent with **channel-like pore formation in lipid membranes** that is indistinguishable from protein conductance traces
- In agreement with the experiment, the propagating pulse does not dissipate heat because it is based on **adiabatic processes**.



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In the HH model, we can see that the action potential is based on the electrical cable theory in which the pulse is the consequence of voltage and time dependent changes of the conductance of sodium and potassium.

So, it is purely electrical in nature. The model is consistent with quantized ion currents that is proved. It is consistent with the channel-blocking effects also of several poisons, such as tetrodotoxin.

This model is based on ion currents through resistors that is a problem because it is therefore dissipative in nature. The reversible changes in heat and mechanical changes are not explicitly addressed, but heat generation would be expected, but why the heat is reabsorbed that is not explained. And, the model generates a refractory period.

On the other hand for the soliton model, which is a newer model the nerve impulse is considered to be an outcome of electromechanical soliton wave that is coupled to the lipid transition in the membrane.

And, the solitary character is considered to be a consequence of the non-linearity of the elastic constants. It of course, does not contain an explicit role of poison's and protein ion channel. So, that is something that is to be checked state.

And, the theory is consistent with channel-like pore formation in lipid membranes that part is consistent. And, the temperature part and it is it does not dissipate heat, but it actually shows the whole model as an adiabatic process.

So, that is something that happens of course, it still does not explain, the change in terms of the thickness for which possibly we need a more refined model.

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Bilayer lipid membranes (BLM)

Are Bilayer lipid membranes (BLM) piezoelectric or electro-active?

- Response of the Neurons to Nerve impulses is generally in the millisecond region which supports the existence of **piezoelectricity**.
- However, the **ionic motion** is more feasible due to the movement of Na and K ions.

EAPs are broadly classified into two groups – **Electronic EAP** and **Ionic EAP**

Electronic EAP (EEAP)	Ionic EAP (IEAP)
Dielectric EAP	Ionic Polymer Gels (IPG)
Electrostrictive Paper	Ionic Polymer Metal Composite (IPMC) Nafion & Flemion
Ferroelectric Polymers	Conducting Polymers Ppy, PA
Liquid Crystal Elastomer	Carbon Nanotubes (CNT)


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In order to look into a more refined model, we have to first know that the bilayer lipid membrane that is you know basically they are in the neuronal walls. So, if you consider the neuronal wall each wall of this neuronal wall is actually consists of bilayer lipid membranes.

Now, these bilayer lipid membranes they are known to be piezoelectric in nature. Now, the ionic motion whether the piezoelectricity is happening due to electro-active polymer or due to ionic motion that is something we need to still focus on. I have already told you about the characteristics of electronic EAPs and ionic EAPs when we have discussed about this kind of things in terms of active muscles.

So, in electronic EAP like dielectric EAPs, electrostrictive papers, ferroelectric polymers or liquid crystal elastomers these are all electronic EAPs and they are capable of actually these kind of motions, but it is slightly slower.

On the other hand ionic EAPs like ionic polymer gels, IPMCs, conductive polymers or CNTs they are actually faster. So, they are faster and these are slightly slower. So, because this nerve impulse is happening in the millisecond region so, this is millisecond region. So, that kind of tells that it could be because of these thing.

So, well, this I need to change. So, this is ionic EAP. So, this part is slower. So, ionic EAPs are slower and this is faster the electronic EAPs this is faster. So, because of these you know millisecond region this actually sort of tells us that maybe this phenomenon is because of the electronic EAPs, which are actually faster in nature. It is also possible that this kind of a thing is actually happening because of an electro-thermal mechanical system.

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Bilayer lipid membranes (BLM)

Or are they Electro-thermo-mechanical System?

Ref: Jakli et Al. Piezoelectricity of phospholipids: A possible mechanism for mechano- and magneto-receptions in biology. Electronic-Liquid Crystal Communications

Illustration of the molecular structure of phospholipid L- α -Phosphatidylcholine and of the piezoelectricity of a lipid bilayer. A tilt of the average molecular orientation (director) with respect to the layer normal, induced by mechanical shear and/or layer compression, leads to a SmC* configuration with polarization normal to the tilt (shear) plane.

The experiments claim to verify Piezoelectric nature of the liquid crystal

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If you consider the bi lipid layer people, have shown through experiments that the lipid layer can be actually modeled in terms of piezoelectric system. So, then it will be you know electro thermo mechanical system because any piezoelectric system consists of three things together. So, there is this piezoelectric effect and there is this pyroelectric effect and there is the mechanical effect.

So, that is why you know there is the temperature comes in the pyroelectric effect and the voltage comes in the piezoelectric effect and the mechanical force occur. So, all the three things together can be actually observed in this type of phospholipid layers. So, that may actually verify the piezoelectric nature of the liquid crystal.

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Bilayer lipid membranes (BLM)

Or are they Electro-thermo-mechanical System?

Ref: Jakli et Al. Piezoelectricity of phospholipids: A possible mechanism for mechano- and magneto-receptions in biology. Electronic-Liquid Crystal Communications

The frequency dependence of the induced electric polarization P calculated from the piezo-current I as $P=I/(A \cdot \omega)$, where $A \sim 0.6 \text{mm}^2$ is the area of the electrode and ω is the angular frequency.

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Now, this kind of piezoelectric nature will also show that there is a frequency dependent and a temperature dependent variation. As you can see here that, the electric polarization P is actually vary with respect to the frequency of propagation and with respect to temperature both.

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Bilayer lipid membranes (BLM)

A Bi-layer Lipid System supporting a Potassium Channel Protein

Schematic diagrams of a phospholipid (A) of the KscA potassium channel protein embedded in a lipid membrane (B) and the biomembrane in the presence of proteins and compositional separation of lipids into domains (C).

Ref: T. Heimburg, Die Physik von Nerven, Phys. J. 8 (2009) 33–39. Note: English translation: "The physics of nerves". arXiv:1008.4279v1 [physics.bio-ph].

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So, this is something like a bilayer system lipid system with a potassium channel protein and you can see the lipid layer and you can see the potassium channel proteins. So, this is something that, these is still to be explained that how this entire dynamics of the movement

of the potassium through the bilayer you know lipid layer happens with the help of the piezoelectricity.

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Piezoelectricity


Origins of Polarization

The diagram illustrates the origins of polarization and their corresponding response times. It shows four types of polarization:

- Electronic Polarization:** Occurs at 10^{12} Hz. It involves the displacement of electrons within atoms.
- Ionic Polarization:** Occurs at 10^9 Hz. It involves the displacement of ions in ionic crystals like NaCl.
- Dipolar Polarization:** Occurs at 10^6 Hz. It involves the alignment of dipoles, such as in HCl.
- Space Charge Polarization:** Occurs at 10^3 Hz. It involves the accumulation of charges at interfaces or grain boundaries.

A vertical blue arrow on the right indicates the response time, with a red arrow pointing to the left for higher frequencies and a red arrow pointing to the right for lower frequencies. A schematic at the bottom shows a capacitor with a dielectric layer, labeled "Total Charge = bounded + Free".

Ref. S. G. Kim, MIT

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Now, as I told you about the piezoelectricity that the electronic polarization in piezoelectricity is very fast in terms of the frequency 10^{12} hertz, ionic is about 10^9 hertz, dipolar is 10^6 and space charge is even slower 10^3 hertz or 1000 hertz or in the kilo hertz level.

So, accordingly the response time is going to be varying the response time will be more here. So, this will be more here the response time and the response time will be very very less here.

Now, depending on what type of a polarization is happening in the lipid layer we will be able to actually say that, what type of polarization is happening in the lipid layer.

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Piezoelectric Modelling


What does Piezoelectric modelling predict?

Consider a Piezoelectric periodic structure with impedance mismatch zones
(zone A with Piezo, zone B without Piezo)

$$\frac{\partial^2 U(x)}{\partial x^2} + k_i^2 U(x) = 0 ; \dots i = A, B$$

Here, $U(x)$ = Longitudinal displacement
 k = wave number

Ref: O Thörn et al., Attenuation and localization of wave propagation in rods with periodic shunted piezoelectric patches, 2001 Smart Mater. Struct. 10 979

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So, if we consider an action to have this kind of you know kind of a patches of piezoelectric patch then, what will that motion predict? So, here is an equation of motion as you can see which is different from the earlier two equations that we have seen because, now we have the longitudinal displacement $U(x)$ the spatial variation of it with respect to the wave number and we can get the equation and this longitudinal displacement and similarly you can also get for thickness wise displacements, but these changes are happening because of the piezoelectricity that is there in the piezoelectric patches.

$$\frac{\partial^2 U(x)}{\partial x^2} + k_i^2 U(x) = 0 ; \dots i = A, B$$

So, in every piezoelectric patch you will see this kind of a change that is happening in the system and that can also generate a kind of a pulse in the system.

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Piezoelectric Modelling

Solution of the wave equation:

State vector:

$$Y_{k_r} = [U_{k_r} \ ; \ N_{k_r}]^T$$

$$T_k = T_k^{(B)} T_k^{(A)}$$

Cell Transfer Matrix:

$$T_k^{(i)} = \begin{bmatrix} \cos(k_i L_i) & \frac{\sin(k_i L_i)}{z_i \omega} \\ -z_i \omega \sin(k_i L_i) & \cos(k_i L_i) \end{bmatrix} \dots i = A, B$$

Impedance:


$$z_B = \sqrt{(\rho_A A_A + \rho_P A_P)(E_A A_A + \bar{E}_{jj}^{SU} A_P)}$$

Wave Constant:

$$k_B = \sqrt{(\rho_A A_A + \rho_P A_P) / (E_A A_A + \bar{E}_{jj}^{SU} A_P)}$$

Note E_{jj}^{SU} is complex and hence, the Eigen values of the Transfer Matrix will be complex, where the real part indicates wave attenuation and imaginary part indicates wave propagation.

Ref: O Thorp et al., Attenuation and localization of wave propagation in rods with periodic shunted piezoelectric patches. (2001) *Smart Mater. Struct.* **10** 979



$$Y_{k_r} = [U_{k_r} \ ; \ N_{k_r}]^T$$

$$T_k = T_k^{(B)} T_k^{(A)}$$

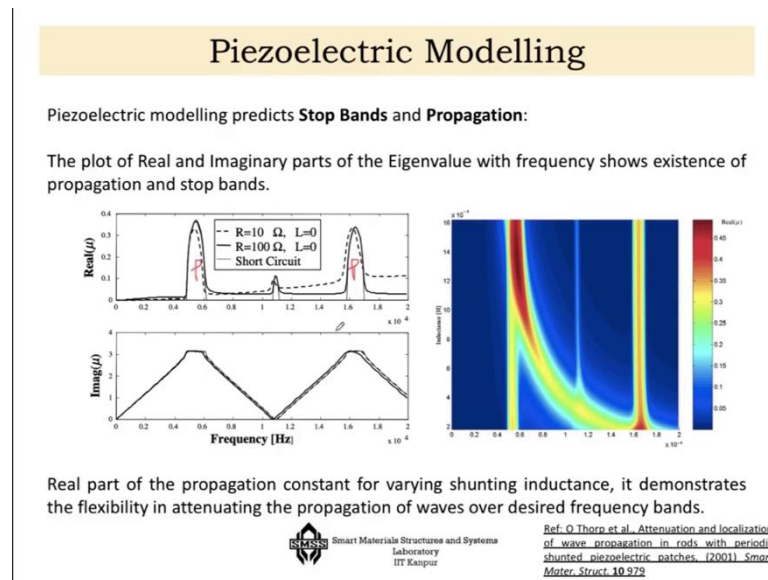
$$T_k^{(i)} \begin{bmatrix} \cos(k_i L_i) & \frac{\sin(k_i L_i)}{z_i \omega} \\ -z_i \omega \sin(k_i L_i) & \cos(k_i L_i) \end{bmatrix} \dots i = A, B$$

$$z_B = \sqrt{(\rho_A A_A + \rho_P A_P)(E_A A_A + \bar{E}_{jj}^{SU} A_P)}$$

$$k_B = \sqrt{(\rho_A A_A + \rho_P A_P) / (E_A A_A + \bar{E}_{jj}^{SU} A_P)}$$

So, in order to solve this wave equation, I can actually use a traditional transfer function matrix. So, where you actually put all the longitudinal displacements in terms of a state vector and you can develop the transfer function and you can find out the impedance and the wave constants and you can actually solve this in terms of finding out the wave propagation of the system.

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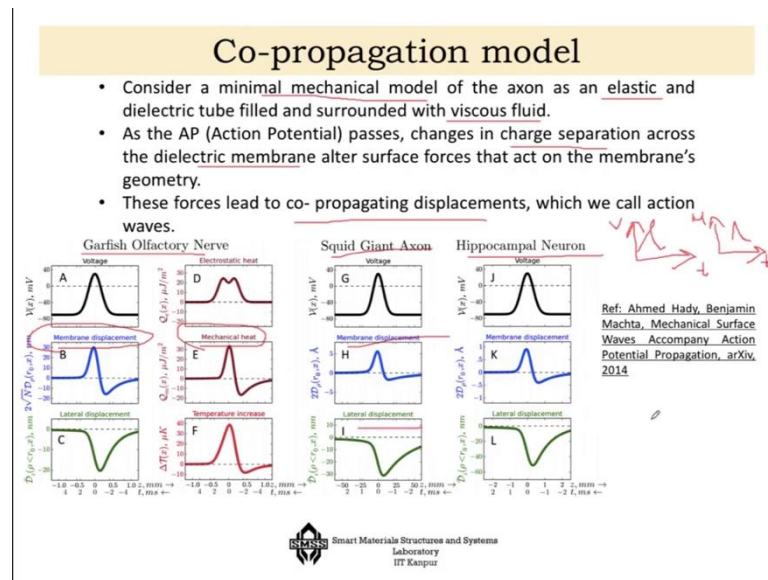
The interesting thing that you will note from these is that, there will be in such a system invariably certain bands where the wave constants will be actually real in nature whereas, certain bands where it will be imaginary in nature. So, these are the plot of the real and the imaginary parts.

Now, real part of the propagation constant actually is telling that there is a kind of a pass band. So, this is a pass band and this is a pass band. So, there are two pass bands, there is a very small pass band here.

Whereas, wherever the imaginary constant will come into picture then you may say that there are these stop bands which will be there. So, the creation of the pass band and the stop band is actually telling us that, only certain frequencies are allowed through these channels and certain frequencies are not allowed through these channels.

Now, based on this piezoelectric model and our earlier knowledge there is a new model which is coming up which is called a co-propagation model.

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I will just very briefly for your reference I will mention this model to you. In the case of a co-propagation model which is something like you know an advanced version where the piezoelectricity is considered, you can see that it is considering a minimal mechanical model of the action, which has an elastic and a dielectric cube filled with viscous fluid.

And, the action potential as it is passing, it changes the charge separation across the dielectric membrane, because the thickness change and that is altering the membranes geometry and that will create the electrical voltage.

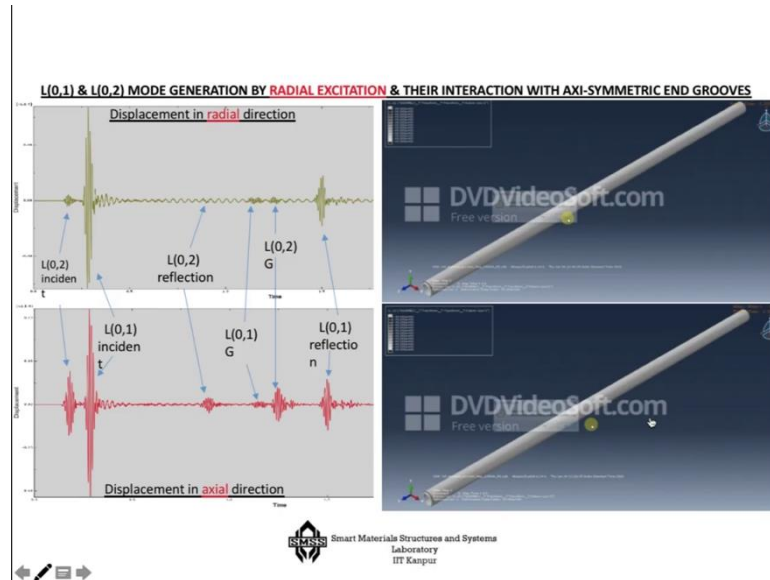
So, there is a co-propagation of displacement, because that voltage will again change the thickness. So, there is a co-propagation of displacement wave along with the electrical pulse. So, this theory is telling that there will be let us say with respect to time, there will be a voltage change, there will be a voltage pulse.

So, there will be a voltage pulse and also with respect to time as well as with respect to you know the direction of propagation there will be something like a displacement change. So, that also will be happening and they will be actually co-propagating both the models.

So, this is checked with the Garfish Olfactory Nerve, that there is this voltage propagation and the change in the membrane displacement, both are happening and you can also see that there is a mechanical heat that is happening and there is a change in the temperature increase and decrease.

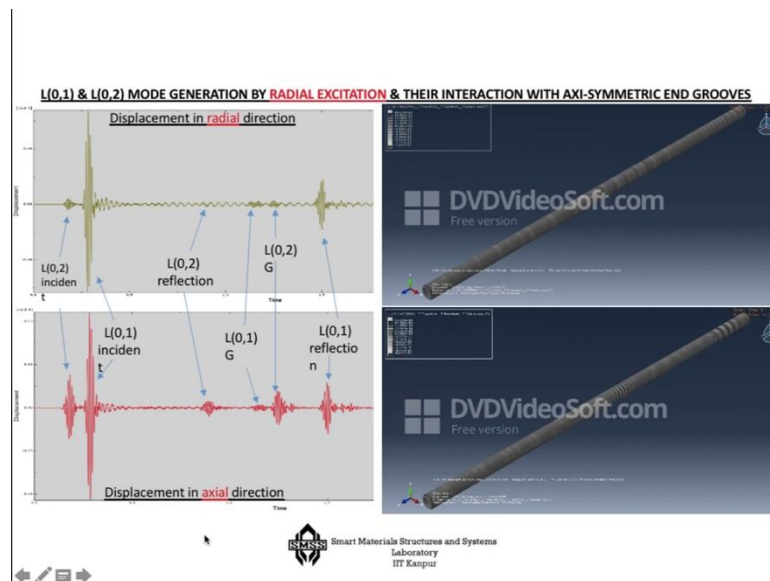
Similarly, the same thing is obtained from Squid Giant Axon, Hippocampal Neuron in all the cases they see that there is a membrane displacement and that is happening and there is a lateral displacement that is happening in the system.

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I will now show you a typical simulation where you can see that how this wave can propagate, imagine this is what, is your action.

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So, you can see first that how this radial propagation of wave is happening it is starting from one point how it is happening.

And, similarly you can see that how in axial direction also the wave is propagating, this is where is axially it is propagating. So, thus it is actually possible to propagate the wave both in the radial and in the axial direction under two different frequency bands.

Now, this is where we will put an end. In the next lecture, we will talk about different types of you know the ways experimentally how we can actually obtain the electrical signals from the brain, which is very important from the human robot interaction point of view.

Thank you.