Biochemistry – I
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Lecture # 15
Membrane Transport

In the last two classes we spoke about lipids and membranes. We are going to consider today how we have the transport from the inside of the cell to the out side or vice versa. It is basically membrane transport that we are going to talk about today. If we look at the fluid mosaic model that we discussed in last class, we know that this lipid bilayer that comprises the membrane is interspersed with proteins and channels that allow the transport of the ions from one side to the other, whether it from the inside to the out side or from out side to the inside of the cell. This is extremely important for cellular processes is that are going on and you also realize that all types of molecules will not be transported into the cell not only because of the size but also because of the polarity, because the lipid bilayer has a polar head group on either ends but it is interspersed by this hydrophobic tails of the lipids.

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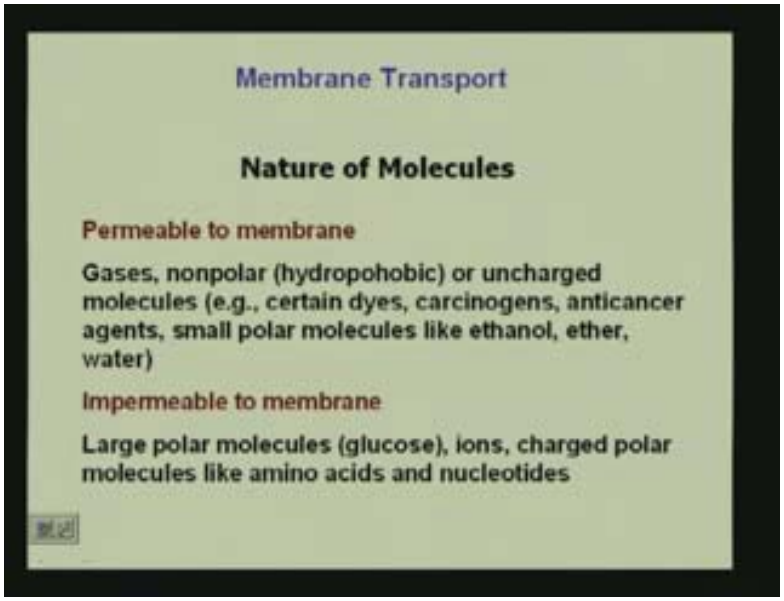

Because it is intersperse by the hydrophobic tails of the lipids, we have specific proteins that are going to allow the transfer of ions and molecules. Before we go into that, we will see the nature of molecules that are going to be transported. First of all, we consider those that are permeable to the membrane and those that are impermeable to the membrane.

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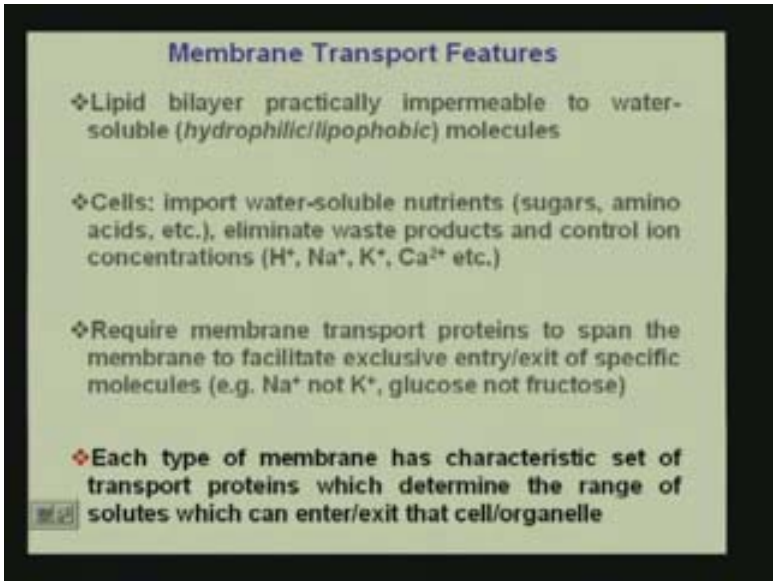

For example, if we look at small non polar hydrophobic uncharged molecules, small polar gases molecules would be permeable to the membrane because they would basically diffuse through the membrane. But if we look at other larger polar molecules for example, ions or charged polar molecules like amino acids nucleotides, adenosine monophosphate (AMP), adenosine diphosphate (ADP) or adenosine triphosphate (ATP), these would be impermeable to the membrane. As I mentioned, since we have hydrophobic lipid layer it is unlikely that is going to allow charge molecule to pass through.

You have to have some channel or some way that the molecule has to get through. Considering what could happen, let us see what some of the features. First the lipid bilayer practically impermeable to water soluble, that is, hydrophilic molecules the reason again the being it is a lipid bilayer. It would not allow this transfer to the favorable. Second, the cells import water soluble nutrients like sugars and amino acids, they eliminate waste products and control ion concentrations. This is extremely important in maintaining what is called sodium-potassium balance in our cells. This is what the cells actually have to do and to do this in the importing of the water soluble nutrients or the elimination of the waste products, which has to be done through these channels.

We have studied integral membrane proteins, peripheral membrane protein and anchor proteins. There is a specific requirement for membrane transport proteins that have to span the membrane to facilitate exclusive entry or exit of specific molecules. For the specific transfer, there is specific transport protein and because each of them has a specific molecule that they are going to bind and transport, each membrane activity is unique.

Each type of membrane therefore has characteristic set of transport proteins which will determine what is going to enter the cell. It is like a security control. Each of these

membrane proteins will exactly determine what types of ion molecules are going to enter the cell and when they are going to enter the cell. All this is controlled by these transport proteins.

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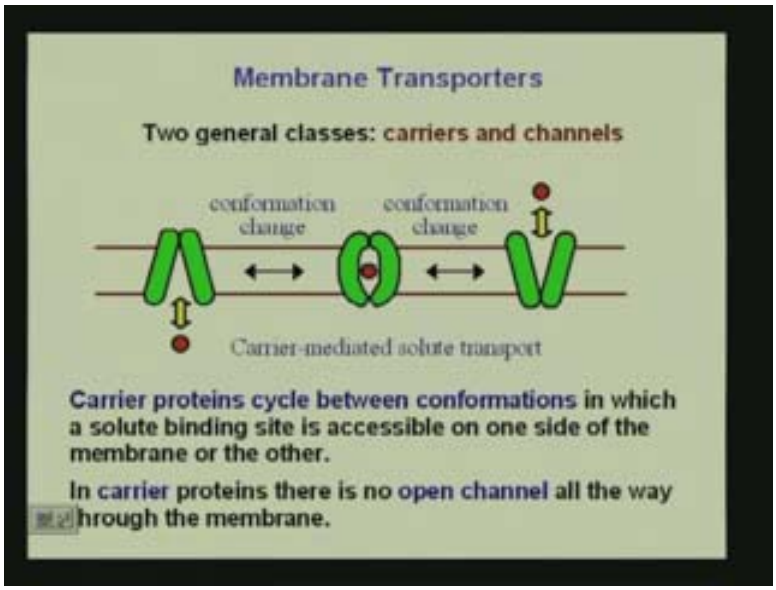

The membrane transporters are of two general classes; carriers and channels. what carriers do is, in a carrier mediated solute transport, because of the lipid bilayer, it is unlikely that this specific solute will be allowed to go from one side of the membrane to the other solely because of the lipid hydrophobic tails that are present here. So what happens is there is a specific carrier protein that cycle between conformations which allow the solute binding on one side and release on the other side.

So what actually happens is there is a specific conformational change that occurs bringing it into a fashion that will allow an opening on one end of the membrane only. It is not a channel; a channel is something that would be all through. This is what would you call a carrier protein. Therefore this carries the molecule from one side to the other and in doing this; it has to have a conformational change that occurs only on the ligand binding.

Once the ligand is bound what happens is it changes its conformation. Then a reaction is instigated where the molecule is then eliminated on the other side of the membrane, Then to come back to this, it probably takes a waste molecule from the cell and then changes its conformation again, then goes back where it started from, exactly like a normal enzymatic mechanism.

You know that it goes through a certain mechanism and then to revert back, it has to do just the opposite of what it had done. This is how a carrier protein would cycle between conformations in which the solute binding would be accessible on one side of the membrane or the other. There is no open channel all the way through the membrane.

These can be of different types. They are called uniport, symport or antiport. This can be shown in diagram and it will be easier to understand.

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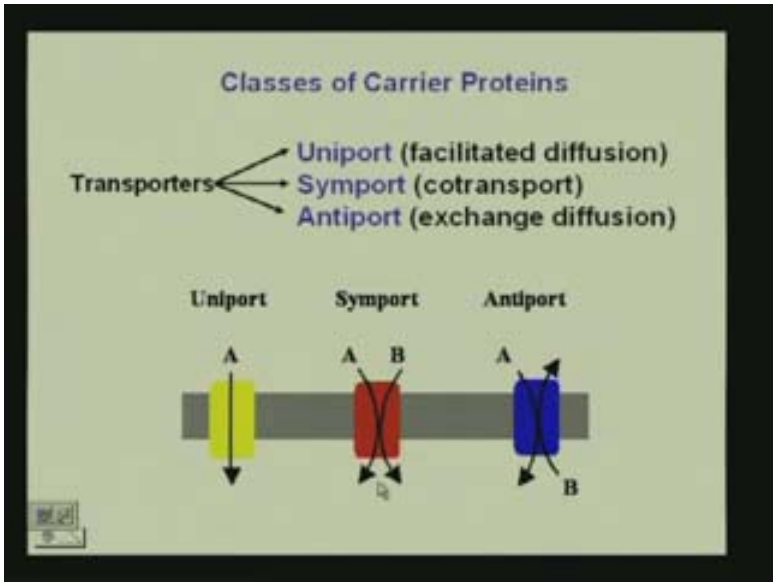

In a uniport transporter you have facilitated diffusion where A goes from one direction to the other. That's uniport. It has just one directional movement. Symport has bidirectional movement. It is co-transported where it transports A and B together. It is a synchronous process that occurs when you have a simport. In antiport, you have exchange diffusion and A going in one direction and B going in the opposite direction. The classes of carrier proteins, these transporters are uniport, symport or antiport. Uniport means you have just transfer of one set. Simport means you have simultaneous co-transport of A and B together and antiport means you have exchange diffusion where A is going in one direction and B in the opposite direction.

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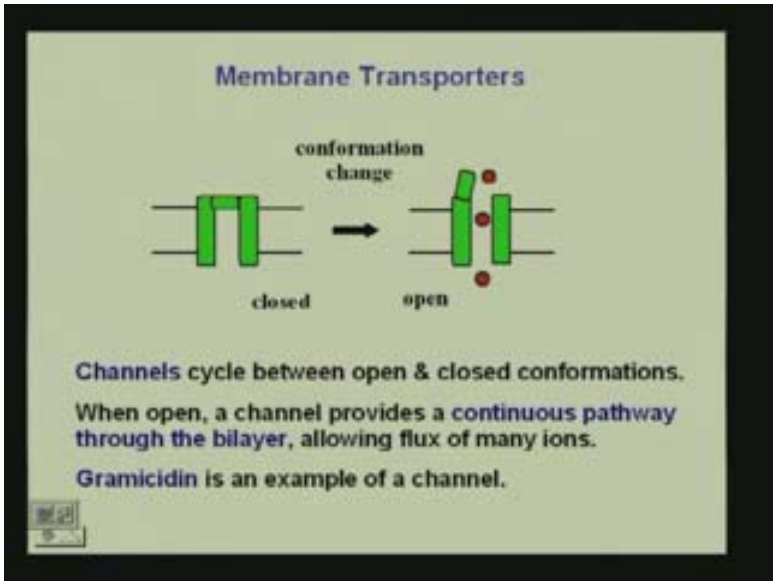

Ion channels are basically openings but these are also sometimes what are called gated ion channels. Gated means basically it has a gate. It opens and closes depending on concentration differences inside and outside the cell. Whether it is potassium or sodium would depend upon whether this ion channels is going to open or close. The channels basically cycle between open and close conformations and when open you recognize it is not like carrier protein where carrier protein does not allow anything else to get through. Once this channel is open, there is going to be flux of many ions going through because you have an open channel now.

An open channel is actually very sensitive to the flux, so what is going to happen is as soon as there's too many going through this, just like a security gate, it just shuts itself. This is unlike the carrier protein where you recognize that once the ligand is bound then what happens is there is a conformational change but nothing else can get through. But when we have this open channel it forms the continuous pathway through the bilayer. So it is open for everybody to get through. All the ions will just try and push themselves through but the cell might not require those ions. Then it will shut the gate so that it is not allowed. It is beautiful way that these membranes actually work and gramicidin is an example of such an ion channel. The structure of which was solved quite a few years ago which is a combination of D and L amino acids. This is one of the proteins that not only has L amino acids but also has D amino acids.

We find a conformational change in this case also but the cycling is between an open and closed conformations. So the differences between a carrier protein and an ion channel are quite clear here. How does this transport takes place? There can be diffusion, osmosis or they can be what is called facilitated diffusion.

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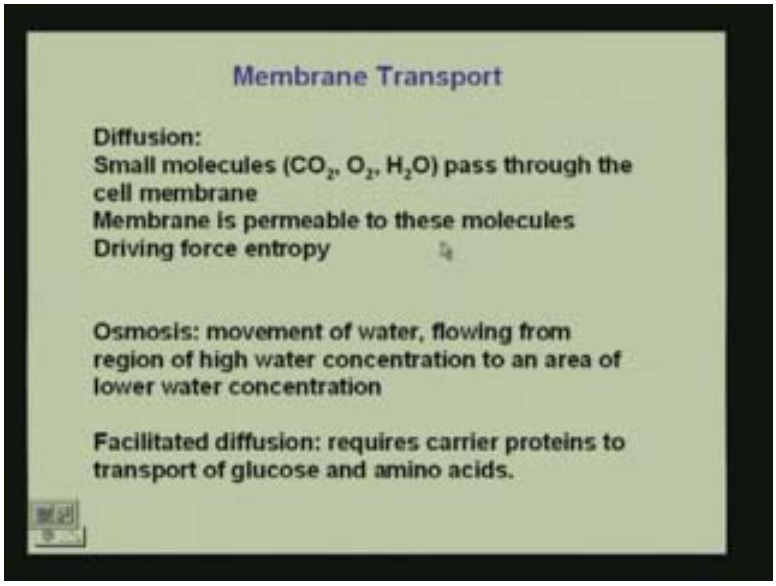

When we consider diffusion, it is just like small molecules that pass through the cell membrane because there is just enough interstitial space or intersperse space. But you see that none of these are charged in that sense. They just pass through the cell membrane and the membrane is basically permeable to these molecules. So it just an ordinary diffusion. You recognize that this is essential so that you have the CO_2 and O_2 because you have oxygen bound to hemoglobin or the CO_2 bound that has to be released. It has to be a normal diffusion in and out of the cell. Osmosis will allow the movement of water flowing from the region of high water concentration to a region of low water concentration.

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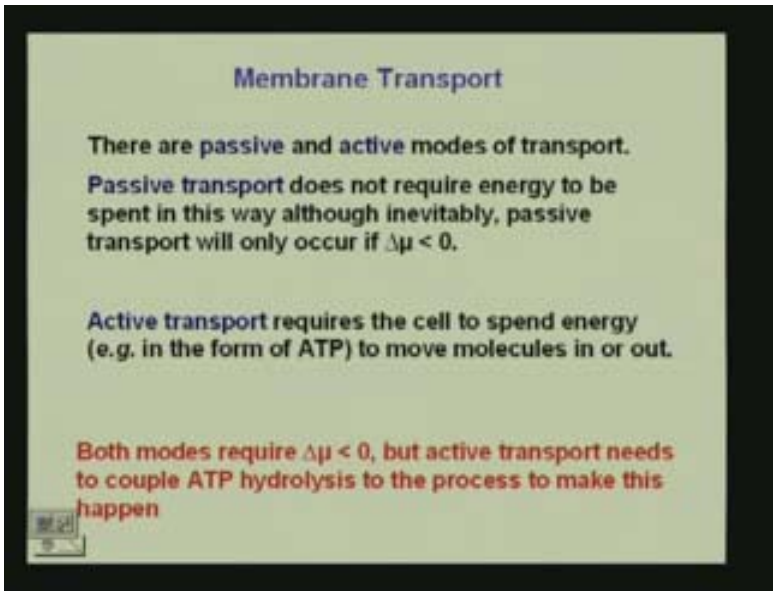

Facilitated diffusion is something that carrier proteins do. They help the diffusion of these certain proteins or certain ions or glucose or amino acids or whatever has to go through the membrane. It is diffusion but is facilitated by the presence of carrier of the proteins. We have diffusion, osomosis and facilitated diffusion.

We also have two other kinds of transport that are called passive and active modes of transport. When we have passive transport it means that there is no extra energy required for the transport of the solute from one end to the other. When we are speaking of energy, we speak about the free energy. It is a spontaneous movement of the solute molecules, be it from one side to the other the inside to outside or outside to inside. That is what is called passive transport.

When you have active transport, it means you are going against the gradient. If you are going against gradient you have to push a way through and in pushing your way through you have to expand energy that energy comes from ATP hydrolysis. It is coupled with ATP hydrolysis. When we have this membrane transport, we have two kinds of transport where we have passive transport that does not require any energy for the solute molecules to pass through and active transport where the cell has to spend energy and the place where it gets this from is from ATP hydrolysis. ATP hydrolysis, there is a high energy bond that breaks and energy is produced. It is beautiful in the way that there are two reactions that are always coupled together where one reaction needs the energy and ATP supplies that energy. It's not that ATP is just break up to provide the energy if it is not required. It is essentially for both the cases that the $\Delta\mu$, which is the free energy change, has to be less than zero because it has to be process where the spontaneous transport of the solute molecules are going to occur.

In the case of passive transport, this extra energy is not required so $\Delta\mu$ is less than zero. But for the active transport where one of the reactions is going to have a ΔG that is positive, the energy release from ATP is going to more than compensate for that ΔG positive value and give you an overall ΔG that is negative and this will be coupled. Therefore the two reactions will be coupled to give you an overall ΔG that is negative so that the transport can occur. If we look at the thermodynamics of membrane transport, speaking about free energy and how all these occur, basically we are looking at two chambers where we are transporting one solute say, from one side to the other.

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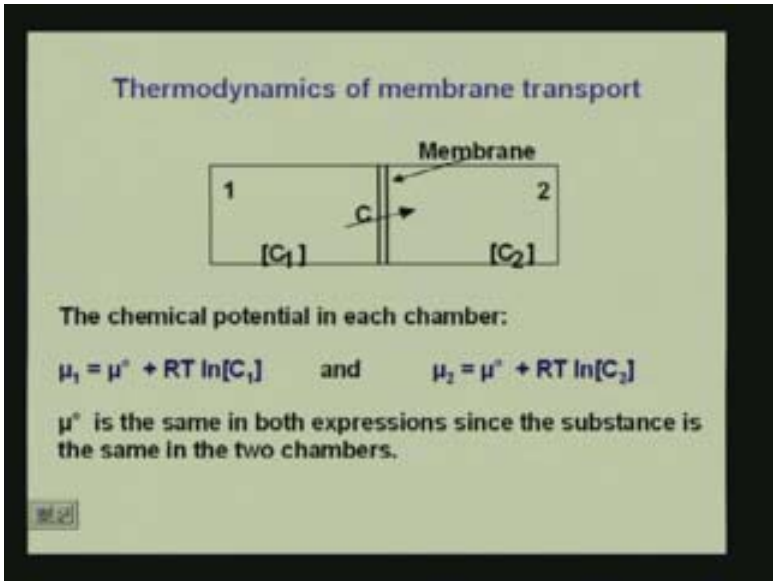

If we look at this generally, we have say just general membrane transport where we are looking at, say a box here (Refer Slide Time: 15:58) where we have one membrane and we are looking at a region say α going to β. α is a region of high concentration and β is the region of low concentration of say a solute X. In general, the chemical potential $\Delta\mu_X = \Delta\mu_X^0 + RT \ln X$. If we have this going from A to B, then we have to look at the change of $\Delta\mu_{XB}$ because that is our final state minus $(\mu_X)_\alpha$ which are in initial stage .that is going to give $R\Delta\mu$. So if we write out this for β and we write it for α the $\Delta\mu$ that is associated with this is going to be $RT \ln X$ because what happens is this cancels out because we are speaking about the same solute X. So we have $RT \ln X$ the concentration of X in the β low concentration side and the concentration of X in the α side.

Now all we know that the concentration of X at the β side is less than the concentration of X on the α side. What can I say about $\Delta\mu$, it is negative so what do I have here. I have a spontaneous process that is going to allow the transport of X from the high concentration side to the low concentration side. This is something you have done before but it is just basic thermodynamics that all of you have studied but what we are looking at is normal spontaneous reaction that is going to occur here. $\Delta\mu$ is negative and we have the transport of X is going from α to β where the concentration of X in α is at at a high concentration and at a low concentration.

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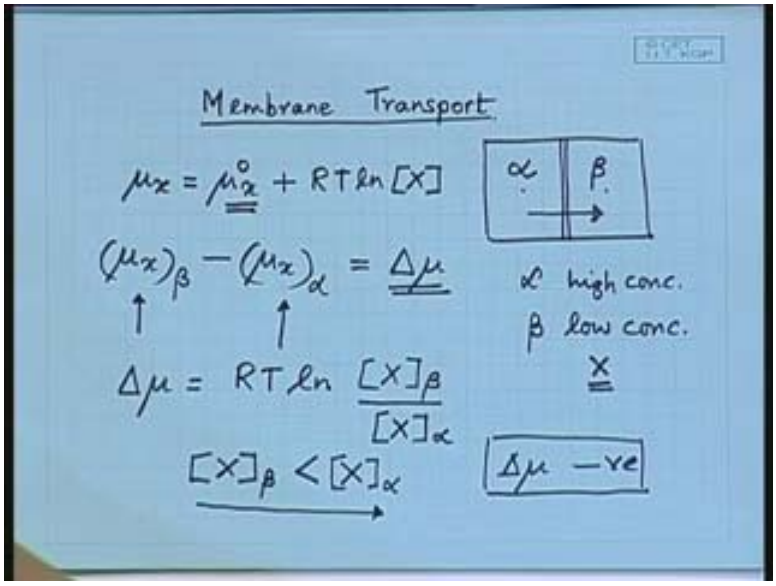

This is similar to what we have here where we are considering the concentration of the component c and we have again the chemical potential calculations where we can then determine what the transfer $\Delta\mu$ is going to be from 1 to 2. It is going to $\mu_2 - \mu_1$ once again. We have $RT \ln X \frac{C_2}{C_1}$. If you put in the correct value of R, you are going to get ΔG value in joules or kilojoules per mole.Now, if the concentration of C_2 is higher than C_1, then we have the positive value for ln which makes $\Delta\mu$ positive. The transfer from 1 to 2 is going to be unfavorable. So what do I have to do, in that case I have to have the transfer occur in terms of the membrane transport I have to couple it ATP hydrolysis.
ATP hydrolysis is going to give a huge amount of energy that is going to compensate for the positive amount of that I get here. We will see that very clearly when we do bioenergetics but for now what we need to know is for the transfer. if I have this C_2 greater than C_1 then $\Delta\mu$ is positive so that the transfer not going to be favorable.

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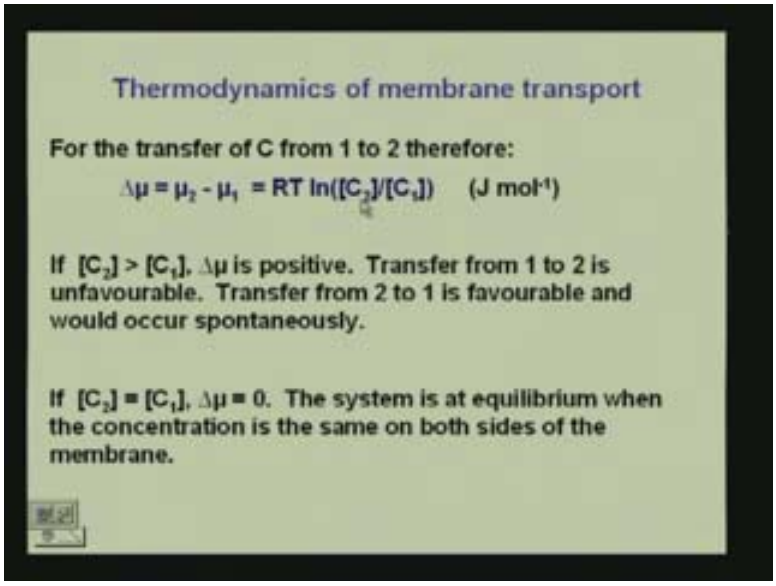

However, if C_2 is less than C_1 than my ln is negative and $\Delta\mu$ is negative. So the transfer of 2 to 1 would occur spontaneously because I have a negative and then when do I have an equilibrium when I have the same concentration on both sides. But this does not happen in membrane transport. You do not have continuous diffusion till the levels of concentration are same on the both sides.

For example; we will be considering sodium and potassium level in the cell which never gets to a constant level. If they do, we will be seriously in trouble with your health. Let us consider what we have here. Now when I speak about the sodium potassium channel or a sodium potassium transport, you understand that it is transporting ions. When I transport ions, I do not have a free energy only associated with the transport due to the chemical potential. Not only a concentration difference but also an electro chemical potential associated with it. So the free energy change is going to be associated ΔG.

Nerst equation ΔG has with an electro chemical potential which is equal to $-nFE$. So not only do you have the potential due to the concentration difference you also have a potential due to the electrochemical difference when you are transporting ions. When we have the movements of these charged species it will give arise to the potential difference across the membrane. Now due to the potential difference rise there is going to be an imbalance of ion concentrations across the membrane.

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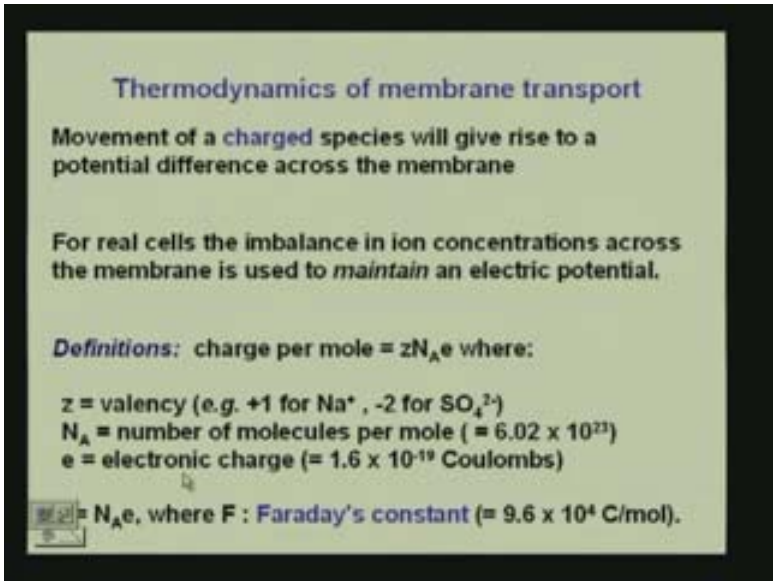

So we have to have an electric potential. Now we know this is just basic definition which we all know, you have z valency, N_A which is the Avogadro's number and *e* which is the electronic charge and F is Faraday's constant i.e., Avogadro's number into the electronic charge. Basically what we are saying now is when I do not have just concentration difference, but I also have the transport of a charged species, I have to consider an additional electrochemical potential.

So we have a membrane with the potential difference across it now. I also have a concentration associated with it. Because of the difference in the levels of concentration of sodium in side 1 and side 2 but since we have a charged species, now in addition I have an electrochemical potential and this is also going to contribute to my delta mu. So I have now, a system where at Na_1, the concentration of the sodium at side one it is 145 millimolars. The concentration at side 2 is 12 millimolars. Now when I consider the $\Delta\mu$, I also have to consider I am transferring from 1 to 2.

Let us go back to the system, make it clear so I have my cell and here (Refer Slide time: 24:40) I have chamber one here, I have chamber two in chamber one I have the concentration at 145 millimolar for sodium and the potential V_1. In chamber 2, I have 12 millimolar and V_2 which is the potential. so I am to calculate the $\Delta\mu$ value, I have to consider $\mu_2 - \mu_1$. So the contribution is going to come from RT ln and Na^+ at 2 because that is our final state over $Na^+{}_1$. I have ZF (V_2-V_1), the ΔV that I have. So if I calculate this actually, I am going to have 12 and145 both are in millimolar and I have a Z and F this V_2-V_1 is actually 70 millivolts.

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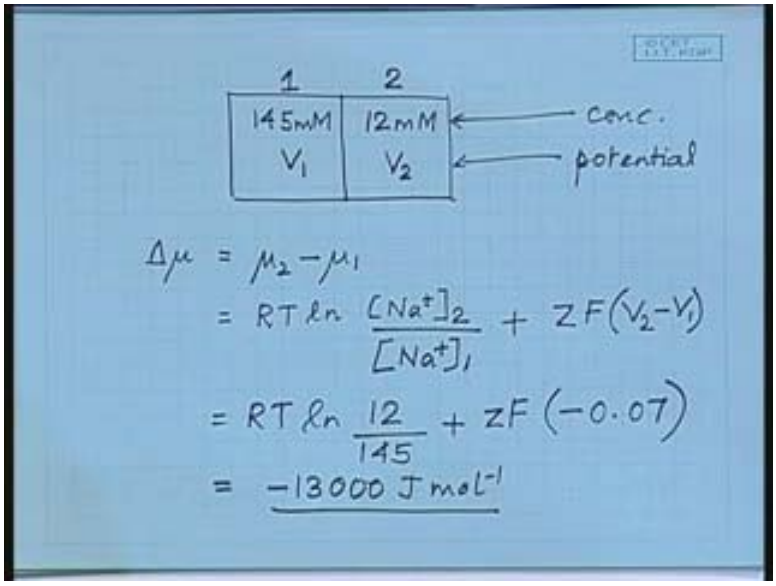

If I calculate this, it works out to -1300 J mol^{-1}. So what it is saying that the transport of sodium from this higher concentration side to the lower concentration side is a favorable process and you have a process that is a concentration that you have to consider and the potential that we have to consider. These are the two considerations that we have to make when you are transporting a charged species to the membrane. What we have is, we have the $\Delta\mu$ i.e, $(\mu_2 - \mu_1)RT \ln \frac{[N_a^+]_2}{[N_a^+]_1} + ZF(V_2 - V_1)$, When the system at equilibrium we can write this we turnout that $V_2 - V$ is 67 millivolts.

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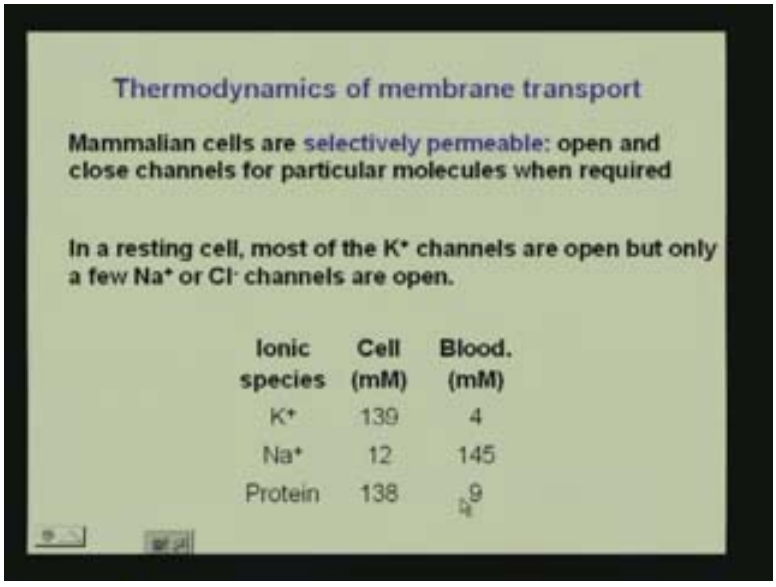

This is very important when we consider the ionic species in the cell a concentration in the cell and the concentration in the tissue oriented blood. If you notice the concentration of potassium in the cell is high and the concentration of sodium is low. In the blood it's just the opposite. This is an extremely delicate balance. You can have severe brain damage if this balance is even slightly distorted.

If the sodium level in the blood goes even if your say, potassium level goes down to 3 millimolar and your sodium level goes down 220 millimolar, you will have to be administer saline to get and be given potassium chloride to get your level back up and you cannot do that very drastically because your brain will be irreversibly damaged and it's extremely delicate. So even this 4 millimolar cannot go down to 3 millimolar this cannot even go down to 120 millimolar. This is extremely important because we have a specific carrier protein that can act on sodium and potassium. So what it does is it brings the potassium-sodium out of the cell and it is the same protein that will take the extra cellular potassium into the cell. If we consider these mammalian cells, they are selectively permeable and they open and close channel for particular molecules when they are required because you cannot have too much sodium and potassium in the cell which is bad.

In a resting cell, most of the potassium channels are open because it can have a large amount of potassium in the cell, not outside. The ion gated channel will in this case what happens for the resting cell, most of the potassium channels are open so that the potassium ions can come through but only a few of the sodium channels are open because we don't want too much sodium in the cell.

If we look at some interesting features of the sodium and potassium ions, then what we have here is if we look at the radius of the sodium and potassium ions we have K^+ ions that has the radius of 1.33 Å. We have Na^+ ions that have the radius of 0.98 Å. Now if we consider that the sodium ions are small so it is likely that they are going to go through more easily that is not true you know that when you have hydration.

The hydration sphere is different from sodium and potassium but when it enters the cells it is stripped of this hydration sphere because what you have to do is; now you have to traverse this membrane. There is a certain molecule that is very cleverly designed called valinomycin. This is a circular molecule made of 6 aminoacids. So we have some amino acid chains. There are valin amino acids valin side chains rather that are out side here. The valid chain is $-CHCH_3CH_3$ it is a hydrophobic group. We have a hydrophobic cell now and this hydrophobic cell in here (Refer Slide Time: 32:25) has 6 oxygen atoms here. These 6 oxygen atoms are spaced in such a way that this fits the potassium ions exactly and because of this hydrophobic surface that you have what happens it can pass through the membrane very easily.

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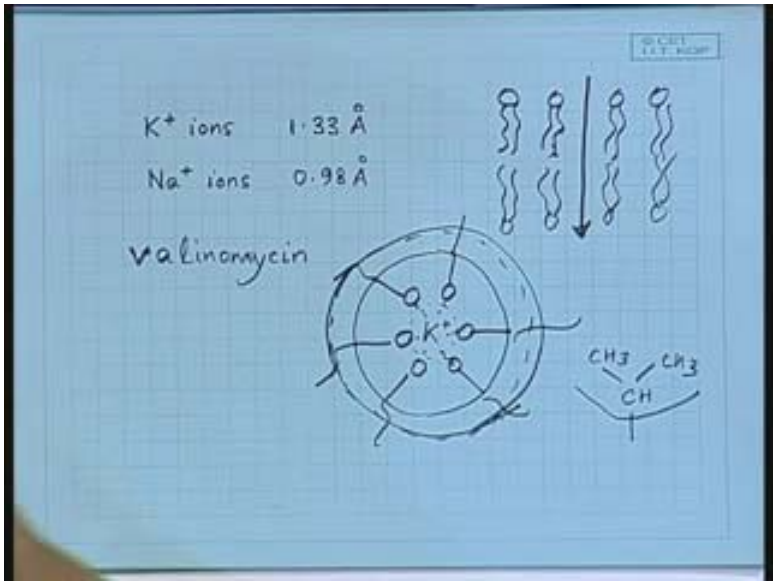

The size is such that the interaction between the oxygen and the potassium charges is unique. Now because sodium is too small it does not sit here and does not have the specific interaction that the potassium has. It does not transfer as efficiently. This is useful because the concentration of K^+ in this cell has to be high. The factor that valinomycin actually binds K^+ with much higher affinity than sodium is useful for the transfer of the potassium ions in the cell. The reason for having these specific types of hydrophobic type amino acids on the surface is so that it can be just pass through the lipid bilayer.

It can interact with these lipid hydrophobic tails and pass through. so nature has designed everything. What we have here is, in a resting cell, the K^+ channels open where it is transported using this valinomycin also but few of the sodium channels open. The membrane potential which I used in the expression for the sodium potassium where we have minus 70 millivolts which is why we calculated the $\Delta\mu$ which was found to be -1300 J mol^{-1}. That was due to sodium concentration and also the potential difference which is the membrane potential.

We have a membrane potential because we have different amount of charged species on either side of the membrane. So that is going to give rise to a membrane potential. It is also going to give rise to concentration gradient and in the calculation of the ΔG. We have to utilize not only the concentration gradient but also the membrane potential and later on when we study about ATP hydrolysis and the ATPAs pump, we will have what is called proton gradient, so not only we are going to have a concentration change, we are also going to have a membrane potential and a proton concentration gradient which is going to give rise to a pH gradient. That is also important. We are going to have then the ΔG contribution which will be from 3 levels concentration, membrane potential and pH. We will do that later when we consider ATP transfer. This is what we have for the potassium. We worked it out for the sodium this is what we have for the potassium. For

the sodium it came out to be 67 millivolts. It is -95 millivolts at 310 K i.e. 37 ^{0}C, which is normally where you would all your biological calculations.

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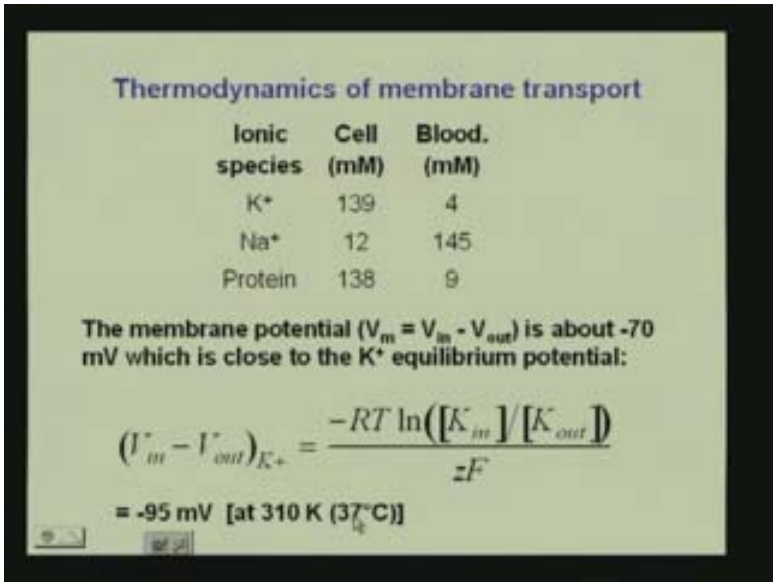

The pH 7.4 and 37 ^{0}C which in some books and most of the books where you will read bio chemistry, the ΔG_0 has a prime to it which means that it is a biological standard. In the normal ΔG^0 we consider 298 K, when it's the prime it means it's 37^{0}C i.e. 310 K and the pH is 7.4. If we consider our sodium gradient, we had a 145 millimolar. We know that the inside of the cell has high potassium and low sodium. So the sodium gradient is such that you are going from the outside to the inside of the cell. The tissue fluid has 0 millivolts, the cytoplasm has -70 millivolts. Now where this -70 millivolts come from, it is come because of the ion concentration being different on either side of the membrane.

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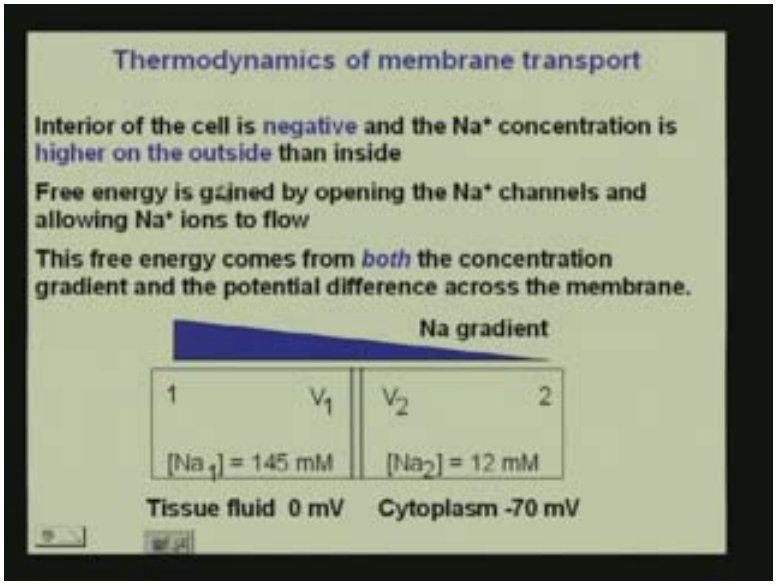

The interior of the cell is negative and the sodium concentration is higher on the outside than the inside. The free energy is gained by opening the sodium channels and allowing the sodium ions to flow why because your concentration on the other side is low. If you are going from high concentration to a low concentration then that is favorable. We calculated that the $\Delta\mu$ is going to be negative for such a case because the ln is going to be negative. We gain free energy by opening the sodium channels and allowing the sodium ions to flow but we know the free energy comes from both the concentration gradient and the potential difference across the membrane. When we have H^+ case, in addition to this we are going to have a pH gradient as well that has to be considered in our calculation for ΔG.

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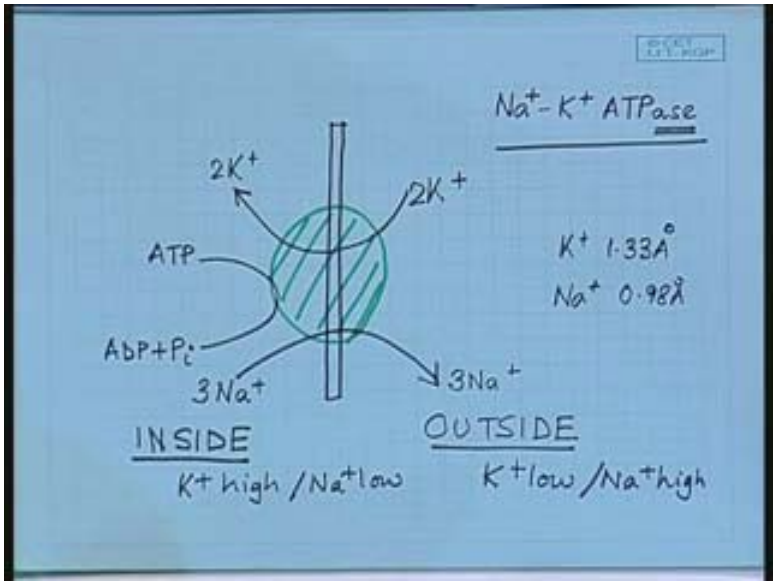

What happens is as I was mentioning the sodium and the potassium sets are actually coupled together. This is our membrane what is called sodium potassium Na^+ K^+. It acts so much like an enzyme that is being given a name Na^+ K^+ ATP ase. This "ase" suffix is usually used for an enzyme but this sodium potassium pump acts so efficiently that this is being given this name. This is occupying region where our Na^+ K^+ ATPase is. What happens is, if this is the outside and this is the inside (Refer Slide Time: 39:58) what happens here is there is a certain get it channel here where we have ATP hydrolysis because this has to be given it's an ATP is pump, so we have ADP we will be studying all these when we do bio energetic in more details. Potassium is high inside and low outside. Na^+ is low inside and Na^+ is high outside. So whatever is going out is Na^+ from the inside to the outside and what is coming in is K^+.

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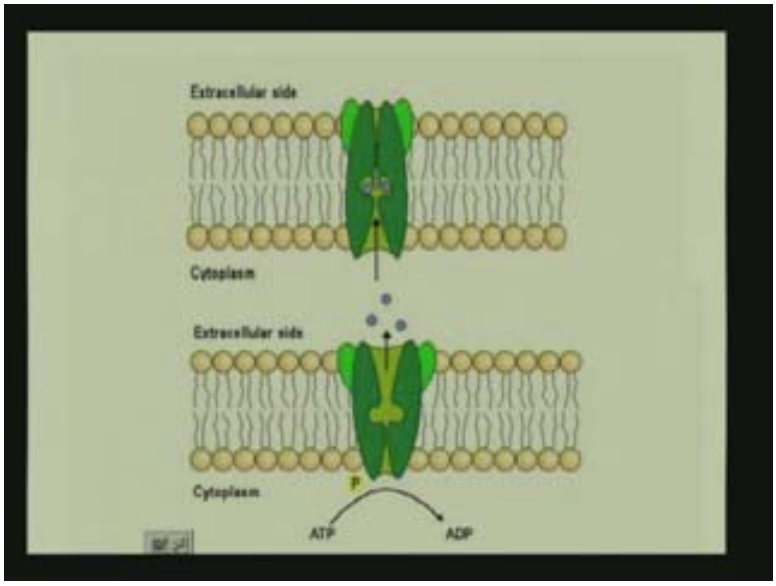

What happens is the carrier protein is such that it takes out 3 Na^+ ions and brings in 2 K^+ for every cycle that it goes through. Because it built in such a manner you understand the K^+ ions are larger inside. The size of K^+ is about 1.3Å and the Na^+ is 0.99 Å. Three of these Na^+ apart from the inside to the outside and two of the K^+ are taken from the outside to the inside and then what happens is this is then ready to take the sodium outside again. Because you have to get back where it started from just like an enzymatic reaction so let us see how this works.

Now what happens is we have the extra cellular side which we mean the outside and we have the cytoplasm which is the cell matrix inside the cell. So what we have here is the cytoplasm and the extra cellular side. These are the three sodium ions. The sodium ions are going from the cytoplasm; they have to be taken outside because we do not need a large amount of sodium inside the cell so what is going to happen is these three sodium ions get embedded in this protein, this carrier and defect in quite strongly this point.

The three sodium ions have come from, which have come from the inside of the cell are bound here and they have to be pushed outside. Once the sodium ions bound, they sit in here, that is the conformational change that occurs and we have ATP go to ADP, releasing a phosphate. We have an energetic procedure that has to occur here, that is going to release the three sodium ions to the outside of the cell. Now to have this proteins back to where it has to come back to this conformation. It is now open conformation. It has released the sodium ions and bound to it. So in the next step what happens is from the extra cellular side, it takes up to 2 potassium. The 2 potassium then sit in this side in the protein and bring about such a conformational change that potassium ions are released on the cytoplasmic side.

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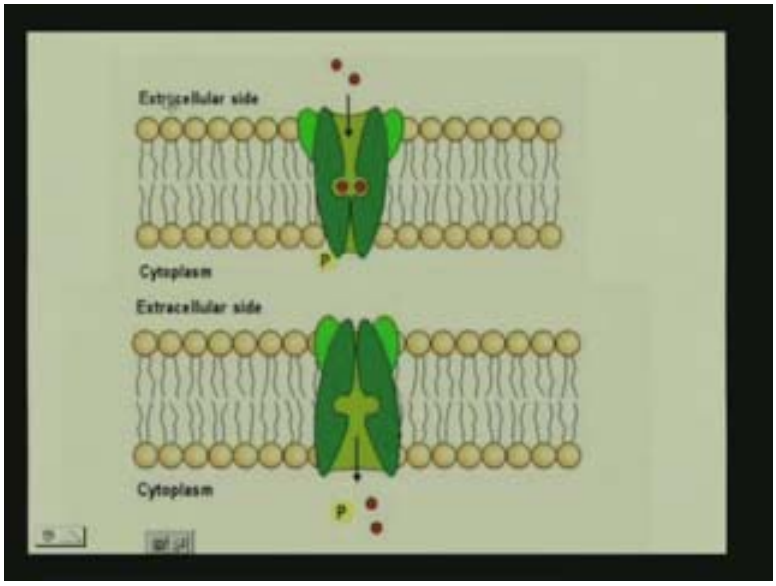

Just like you would expect to happen because you want the K^+ to be high inside and the K^+ level to be low outside. This is ensured by, let us look at the previous one what happens here we have these three sodium ions the three sodium ions came in from the cytoplasmic side and were released on the extra cellular side on the out side of the cell. But to get the conformational aspect of the protein back to where it's started from so it can accept another set of three sodium ions, it has to get back to the same conformation. Because what happens in these carrier protein is you have a conformational change that occurs and in this conformational change you have to get it back to it's original conformation so that it can perform the procedure once more. It has to keep on doing this as constantly, so we have the three sodium ions that go through and they are released on the extra cellular side then you have the potassium ions that bind to the protein that are eliminated on the cytoplasmic side to maintain this.

Na^+ K^+ ATPase pump, also known as sodium potassium pump is extremely important. It is also known as a sodium potassium pump now what we have. This is extremely important in nerve cell signaling which is why if you have an imbalance, your brain gets affected and you have what is called confusion. You do not remember things because of the imbalance of the sodium potassium. You do not have proper cell signaling which affects your brain.

Then what you have in these cases is what are called voltage gated ion channels. So in this voltage gated ion channels when we have a lipid membrane, for example; in gramicidin in what happens, you have say a single channel for gramicidin. Initially it has part of the lipid membrane. So just put the gramicidin in different color and one of them is here (Refer Slide Time: 48:08). They have pores half way through the membrane. What happens is, when it has to form an ion channel, the movement that can occur for these lipid membrane is you have lateral diffusion and you have flip flop as well.

When lateral diffusion occurs in this case what happens is at one point there is a dimer formation. What happens is this channel, this is your gramicidin half and this is the gramicidin monomer and this is another monomer. And now when there is a lateral diffusion, at one point what happens is it forms the channel through and through. Then because, what is going to happen is even though an ion may get in here, it will not get to the other side because the lipid hydrophobic tail is there. The same thing for this case(Refer Slide Time: 49: 10), an ion can come from which ever way you are talking about inside or outside extra cellular intra cellular and ion can get through but it will not come to the other side because there is no channel through it. But due to the lateral diffusion, at one point what is going to happen is you are going to get a channel.

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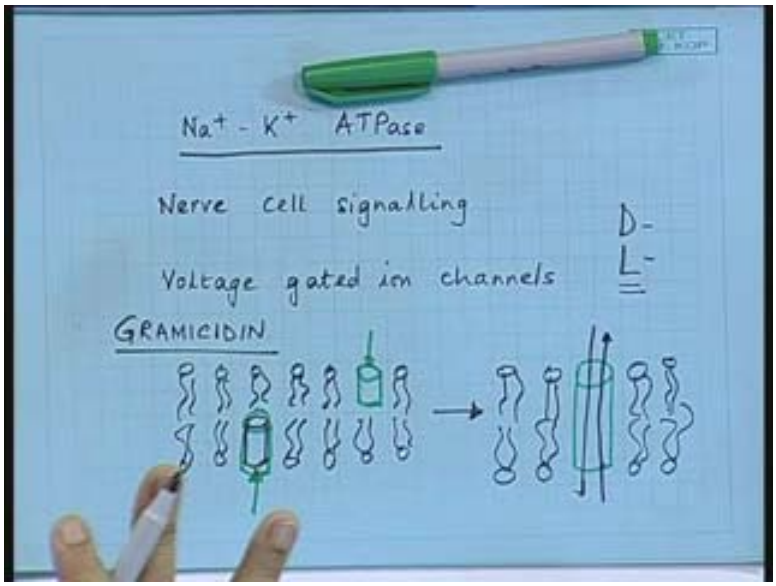

This is what you see when you form gramicidin. This is what gramicidin is and gramicidin is unique, in that it has as I mentioned D amino acids in. apart from L amino acids which are common, it has D amino acids as well. So what happens in this case you have the monomers that are present and it forms a dimmer. What happens in this case is then you have an ion channel that will allow the flux of ions through in. It is possible because your whole membrane is fluid in nature. Because of the fluidity of the lateral movement, it is possible that you have these ion channels that allow the transfer of ions inside and outside.

So what we have studied today is membrane transport. Basically what we understand is that for the membrane transport to occur we have concentration gradient. We have specific types of transport active transport that requires energy, passive transport that is just going to allow the permeability of the molecules solute molecules and we have specific molecules that have to be have specific concentration inside and outside the cell as a result of which there is going to be a potential develop because of the charge species that have to be transfer and we have the concentration gradient as well. And went on do

some free energy thermodynamics the thermodynamics of membrane transport where we calculated what the free energy changes were.