# Computational Neuroscience

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**Week – 04**
**Lecture – 18**

Lecture 18 : Phase Plane Analysis - III

Welcome. We had discussed about the equilibrium points and how with the saddle node we can show threshold behavior or we can understand threshold behavior of neurons using the Hodgkin-Huxley system of equations or version of the Morris-Lecar equations. And we had one other property of non-linear system that we had discussed which is limit cycle behavior. As you may recollect for the Morris-Lecar equations with a current injection of about 95 microampere centimeter square, we see a shift in the V-nullcline and there is one equilibrium point that is created or that stays, but it is not a stable node anymore or a stable equilibrium point anymore. It becomes an unstable equilibrium point. So, just for a recap, if we consider the MLE Morris-Lecar equations with V and w and an $I_{external}$ that is not 0 and about 95 microampere centimeter square, then the w-nullcline would be something like this and the V-nullcline turns out to be like so, where this kind this equilibrium point is created which is unstable.

And we said that this system shows limit cycle behavior in the sense that if we start the system very close to this equilibrium point, then it does spiraling and then it breaks out into a limit cycle behavior. So, and oscillation start. If we start outside of the limit cycle, we end up being on the limit cycle. So, the question is so, it is essentially saying that the system will keep on oscillating or produce keep on producing action potential.

So, if we plotted the V over time along this limit cycle or along this whole trajectory, we would see so, if this is our voltage and this is our time and let us say we are starting from this value of V, this is our let us say $V_0$, this is our $V_0$, then we see this behavior where it then emerges into an oscillatory behavior like this and keeps on producing action potentials. And as we were saying that no matter where we start inside that limit cycle or outside that limit cycle, the system ends up being on the limit cycle. So, in a linear system we can have multiple sizes of oscillations and it is dependent on the initial values. So, the large change in initial value will cause a large change in the oscillation size. But in this non-linear system, a large change in initial values gives the same behavior ultimately over time that is they converge on to the same oscillating system or oscillating behavior.

So, just like we had extreme sensitivity to initial conditions in the earlier case, where we saw threshold behavior with a very small change, we have drastic change in behavior. Here we have a big change in the initial values, yet we converge on to the same behavior. So, just conceptually just the opposite kind of thing that this kind of these non-linear system can possess. So, in terms of the analysis of the system, we need to be able to predict whether this kind of a non-linear system can have a limit cycle or not or how do we know whether a limit cycle would exist in that system. So, for this we have to take help of a few ideas from mathematics, we will not go into the details of it, but we will introduce the concept of an index.

So, what we know is any closed curve on the phase plane has an index that is if we have this, if this is a closed curve does not have to be a trajectory any closed curve. So, I should actually remove the arrows, so that it is not confusing. So, let us say this is any closed curve and this is one of the state variables let us say $x_1$ as we had and this is $x_2$. So, this any of these curves will have a index and that is given by how by if we go along the trajectory along the curve anticlockwise and at each of these points we will have an angle for the resultant flow at that point from the horizontal axis. The cumulative effect of this angle across the entire curve if we go once divided by 2 pi is the index of the curve.

So, it is not trivial to say that the angle is not trivial to prove a few things about this index, but what we will say is that we correspondingly for equilibrium point we will say that their equilibrium points also have an index in the sense that let us say this is the phase plane $x_1$ $x_2$ and let us say this is the one of the equilibrium points. Then if we draw a closed curve right around it infinitesimally close to that equilibrium point then the index of that curve is essentially going to represent the index of an equilibrium point. It is not entirely correct to say index of an equilibrium point, but this is what we will mean that index of an equilibrium point is basically the index of the closed curve right outside the equilibrium point. And this index for stable and unstable equilibrium points turns out to be plus 1 and so this is stable and unstable equilibrium points it is plus 1 and for saddle nodes it is minus 1. How if we take the same example for saddle node consider let us say this is a saddle node let us say this is a stable node then the trajectories around this equilibrium point would be pointing in this direction very close by they are all going to come into this stable node all of them.

So, now if I draw a circle around it and now try to see how the angle of the flow along the curve when I go counter clockwise how the angle changes and adds up till when we go the full circle what we will see that let us start from this particular point and then we are going on that is on the other side what we see that the arrow or the flow starts from minus pi or I mean we can actually pi that is how it is starting then it is going to the negative side then it is going to minus 3 pi by 2 and then along this it is going to minus 3 pi by 2 and then it if we go here it goes along this. So, the angle that it has traversed up to here is pi and so at we are at this point now which is that the arrow is going into the stable node and then if we carry on along this direction the arrows are going to go this way and ultimately comes back to the full circle point and so it is traversing 2 pi in the positive direction that is counter clockwise. So, the index is this 2 pi divided by 2 pi. So, that is equal to plus 1 I leave it for you as a thought exercise for to see that for an unstable equilibrium point also this is going to be plus 1 and similarly in the same way you can easily see that for stable and unstable spirals which is when we have complex Eigen values they turn out to be plus 1 again. So, now the for the saddle node why is it minus 1 is if we go here remember if this is the saddle node nearby the trajectories are doing a behavior like this where this is the unstable manifolds and this is the stable manifolds.

So, if we again start with a circle through these trajectories let us say and let us say we are starting from this particular point and going counter clockwise as you can see initially the arrow is going to be horizontal that is at 0 and as it go as we go forward the arrow actually goes in the negative direction and finally, it goes on to the stable equilibra, the stable equilibra stable manifold which is in this direction. So, it has travelled minus pi by 2 and after that it will go along the along this direction here it is vertical and next it is going to from the vertical it is going to go to the left side and then finally, go in this direction when it is at this particular point. Now, if we keep on moving forward what we will find is that the arrow keeps travelling in the opposite direction in the similar manner up to the final point when it is reaching here. So, that angle it has gone through is minus 2 pi and normalized by 2 pi we have minus 2 pi is the cumulative angle and so in terms of how many factors of 2 pi it is going to be minus 1. So, the saddle node has an index of minus 1 and the stable and unstable nodes have index of plus 1.

Now, if you consider limit cycle as the closed curve let us say we have a limit cycle like this it would not matter in which direction we are going this is $x_1$ this is $x_2$ the two state variables. Now, if we in the on the limit cycle what we have is the arrows or in the flow the direction of flow along the points on a limit cycle are simply the tangent along that point because that is the direction it is going. So, when the limit cycle is being traversed by the system or if the trajectory is the limit cycle then the direction of flow at each point is essentially tangential and it continues that path throughout. So, you will now clearly see that if we start with this kind of an angle and go through the entire cycle the index of a limit cycle will turn out to be plus 1 very easily you can see that. So, the we have the equilibrium points and their corresponding circles around them or closed curves right around them those indexes are plus 1 and for saddle node it is minus 1 and for a limit cycle the index is plus 1.

Now, there comes two basic theorems here which will not prove, but just assume is that when we change when we distort a curve in the phase plane or a closed curve without overlapping anywhere without intersecting obviously. Let us say this same the one that we have drawn here that is being basically reshaped into this form and if it is in doing so it is not traversing we are not crossing any equilibrium points in the phase plane that is there are no equilibrium points in this region. So, we are reshaping the closed curve without intersecting itself anywhere and there are assumptions about how the system behaves in the sense of that smoothness conditions that is the derivatives are continuous and the second derivatives are also present and so on. Basically, a well behaved system and here we are not crossing any equilibrium points then the index of the curve does not change that is the white closed curve and the red closed curve have the same index if the cyan region the cyan striped region does not have any equilibrium points and the derivatives I mean the force field there is smooth and so on. So, thus the consequence of this particular idea is that the index of a closed curve is the same as the index of the equilibrium points or some of the indexes of the equilibrium points that are within the curve region.

So, again if we have a closed curve and we are close curve like this and let us say we have three equilibrium points. So, we have a closed curve like this and let us say we have three equilibrium points. So, we have a closed curve this is $e_1$ $e_2$ and $e_3$ and there is nothing else no other equilibrium points within this loop. Then if the index of $e_1$ is $I_1$ let us say index of $e_2$ is $I_2$ index of $e_3$ is $I_3$ then the index of this curve c is $I_1 + I_2 + I_3$ it is a it is a straight forward extension of the theorem that we discussed here. If you now basically reshape the curve let us do this we are reshaping the curve to be infinitesimally close to this equilibrium point and then like this and like this then also around this equilibrium point and then go back and this.

So, this is the point where so, we have reshaped the curve to be just around the equilibrium points with connection points along with connecting parts along the almost the same line or direction they are just. So, this is infinitesimally close to each other we can reshape the curve to be like that like almost the full circle around each of the equilibrium points and the gap in those full circles are points which are connected to the next equilibrium point and next equilibrium point. So, it essentially becomes if we now traverse this curve whatever we get as the index is the index of c. So, from c we deformed it to c prime and so the index of c is going to be whatever is the index of c prime from the previous theorem. So, now what how do we calculate the index of c prime we can easily do that.

So, we have to traverse in the anticlockwise direction along the c prime curve and so basically whatever angle is being traversed here will be cancelled out when we come back and traverse in the opposite direction exactly cancel out. Similarly, over here it is going to cancel out when we are traversing forward and then backward. So, the cumulative angles will simply be turned back by the same amount along those straight paths and what we are left with is basically loops around the equilibrium points almost full loops there is only a very small infinitesimal gap from which there are connections to the other equilibrium point that is what we have said. So, essentially we are left with the sum of all those together and that is $I_1$ plus $I_2$ plus $I_3$. So, the index of equilibrium point 1 equilibrium point 2 and equilibrium point 3 is going to be the index of c prime and hence from the first theorem the index of c.

So, we have to the basic point here is that the closed curve any closed curve c has an index which is the same as the sum of the indices of the equilibrium points inside the closed curve that it encloses. So, and we have said that the limit cycle has an index of plus 1. So, this brings us to the idea of the necessary and sufficient conditions for existence of limit cycles. So, we have said that the limit so from here since the index of a closed index of a limit cycle is plus 1 we get a necessary condition that a limit cycle must enclose equilibrium points whose sum of the whose indices sum to 1. So, in other words they must have odd number of equilibrium points with 1 more stable or unstable equilibrium point than the number of saddle nodes.

So, because the saddle node is minus 1 we will have an we will subtract out 1. So, if we have 1 stable node and 1 saddle node limit cycle cannot be formed around them because the sum of those is coming out to be 0. So, we need to have another stable or unstable node in there always. So, there has to be 1 extra stable or unstable node whenever there are saddle nodes it is going to cancel out 1 of the equilibrium points indices which are stable or unstable and so we need 1 more to make the plus 1 stable or unstable equilibrium point for the index of the limit cycle. So, now that we have the necessary condition there is also a sufficient condition and that is given by the Poincare Benediction theorem.

So, again we have we will assume the well behaved nature of the plane. So, we have the green or the face plane and so let us say this is $x_1$ and this is $x_2$ let us say we have a region R which is let us say marked by this green region. So, this is the green region. So, this is a region R in the face plane where the derivatives are smooth and continuous and so on that is the well behaved conditions and R does not contain any equilibrium points and we will say that if there is a trajectory that begins with a point $x_1$ and begins in R and stays in R then. So, let us say we have a trajectory C and let us do it in white with this green point is the initial point and it let us say it roams around and we know we can prove that this with that starting point this is never going to go outside of R then the trajectory must end up on a limit cycle in R or it itself is the limit cycle.

So, this is what the Poincare Benediction theorem says and this is basically the sufficient condition for existence of a limit cycle that is we have to find a bounded region R such that if a trajectory can be shown at a even just one trajectory can be shown to start in R and stay in R till t goes to infinity then it must end up on a limit cycle or a periodic orbit. So, this now gives us the basic idea of how to prove that the limit cycle would exist. So, we had the case where in the Morris-Lecar equations V and W for the current injection $I_{external}$ is equal to 95 micro ampere centimeter square we said that this is the W null line and the V null line ended up being like this and this was this is an unstable node. So, now if we consider an upper side of W that is 1 and lower side of W that is 0. So, the trajectories must stay within 0 and 1 because W can be since it is a probability must be between 0 and 1 also from the Morris-Lecar equations you can show that the E calcium on the positive side and E potassium on the negative side serve as bounds for the system because if you calculate the $dV/dt$ along the E calcium point for any W they are always negative and similarly for E k for any W is always positive.

So, what we now have is a limit bound on the phase plane such that trajectories must remain within the 0 and 1 along W and E calcium and E potassium on the V axis, but and we are satisfying the necessary condition that there must be an equilibrium point at least one equilibrium point and actually odd number of equilibrium points must be around the enclosed by the limit cycle here we have one equilibrium point which is not a saddle node it is a stable node. So, odd number of equilibrium points and that is plus 1. So, the index is plus 1. So, now if we define now we have to show that if we have a trajectory in some bounded region it the trajectory stays within that region forever then we are done then we can prove that we can conclude that there has to be a limit cycle because we have the necessary condition and the sufficient condition met. So, now if we consider an R to be bounded by this box that we have drawn and we take out a very small region around the unstable node that we have.

So, the green region that we had marked here marked earlier is this region. So, we also know that the inner bound encloses an unstable node. So, we have a stable node and the trajectory is very close by to that unstable node. So, this is the trajectory of the node. So, we also know that the inner bound encloses an unstable node which means that the trajectory is very close by to that unstable node cannot go out into that very small tiny circle or infinitesimally small circular space just around that unstable node.

So, a trajectory that starts in the green striped region cannot go outside into that region into that small region and it cannot go outside of any of the boundaries along V and w that we have marked which means that any there is at least one trajectory. In fact, any trajectory in there which if started in the region R which is the region R which is the green striped region it will forever stay inside R. So, it needs the sufficient condition. So, that essentially proves that a limit cycle must exist. So, this behavior can be shown in many cases when we will when you discuss about oscillations in a very small neurons this idea is used to prove that when a limit cycle exists.

So, we have also now shown how limit cycle behavior can be found in a neural system that is oscillations can be determined to be exist in such non-linear systems or in models of neurons or in actual neurons. So, we have covered the necessary things about a neurons limit cycle limit cycle behavior and a neurons threshold behavior which are the two most important things of non-linear system description of neurons and we will continue on in the next lecture with more phenomena that we encounter in neurons that can be explained by the Hodgkin-Huxley equations and we will continue with phenomena like relative refractory phenomena like anode break excitation and so on. Thank you.