**Computational Neuroscience**
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**Week – 04**
**Lecture – 16**

Lecture 16 : Phase Plane Analysis - I

Welcome. So we will continue on with our discussions of the Morris-Lecar equations and in the phase plane, that is with the phase plane analysis, the tools that we are learning about. So we ended the last week's discussions with an example of the sensitivity to initial conditions, which is one of the behaviors of non-linear systems that you would not see in a linear system. So we showed that there is a threshold like behavior in the Morris-Lecar equations at a particular voltage, that is if we start the system in to the left of that particular voltage and to the right of that particular voltage, we will get two very different kinds of behavior. On the right that is with a voltage above that value, that is above the threshold, we get spikes and below that value, which is below the threshold, we do not get spikes. In both cases, the system ultimately moves in the phase plane and ends at the equilibrium point, that is its resting membrane potential.

So in that case, we were starting the system somehow with by moving the initial value of the voltage to a higher value by perturbing the system from the equilibrium point to a higher voltage value with the 'w' at the same point. So we can actually achieve that with a current impulse, which is a different discussion and the counter, another way of stimulating the system that we have been drawing before is by using a current injection, that is a current that will keep on going for a period of time. So let us say this is zero current, this is time and this has some particular value $I_0$ So in this particular case, when $I_0$ is approximately 95 micro amp per centimeter square. So I must say that these kind of numerical values that I am pulling, I am not pulling out of thin air, these are actually based on simulations, which you will be provided to study.

And the units of these are also, there is a discussion that you should have had beforehand about the units of this kind of systems of equations during the introduction to simulation of these systems. So when we have this kind of a current, this amount of current, how do we understand the behavior of the system? Let us say this is V and this is w. So here time, so let us say it is, if this is time zero, then $I_{external}$ is now becoming $I_0$ for a period of time as long as we want to simulate it, let us say. So that means if we have our nullclines, let us say our

V-nullcline was like this and our w-nullcline as drawn earlier is somewhat like this. So this is our w-nullcline, our V-nullcline.

Remember this is the original system that we had. Now we have an external current that is $I_0$, a fixed current, which means that now $I_{external}$ needs to be incorporated in the system and would it make any changes in whatever we have so far in the phase plane? Indeed it will because if you remember that our V-nullcline or w-nullcline is $CdV/dt = I_{external} - G_calciumm_infinity(V), V - E_calcium - G_Kw, V - E_k, -G_leakV - E_leak$. So now we have our $dV/dt = 0$ and now if we get the w values at the V-nullcline, that is by replacing this $dV/dt$ by zero and equating the rest to zero, we will see this w-nullcline is turning out to be $I_{external} - G_calciumm_infinity(V), V - E_calcium - G_leak, V - E_leak/G_kbarV - E_k$. So earlier this $I_{external}$ was zero. So that makes a difference in the nullcline and so now the equilibrium point is not at zero at the V rest that we had before, it has moved away from there.

Would anything be happening to our W nullcline? There is no $I_{external}$ in the W nullcline. The W nullcline was simply that W, W and C value, W nullcline values is $W_infinity(V)$. Then the $W_infinity(V)$ did not have any $I_{external}$ there. So the V nullcline remains the same and $I_{external}$ is positive, so which simply means that this will be shifting upwards, this entire V nullcline will be shifting upwards. So it will shift up to some point here, so it will shift upwards in this manner and the equilibrium point which was here has moved to this new point which is marked in cyan let us say.

So the equilibrium point is changed. So let us draw this new phase plane, I am sorry, let us draw this new phase plane with the new nullclines V and W and let us say that the V nullcline is like this and the W nullcline is going like this. So this is our new equilibrium point and the interesting thing is that under these conditions that is this $I_{external} = I_0$ which specifically let us say 95 microampere centimeter square and the system if is just outside this equilibrium point, what it would do is that it would start to move around it couple of times and then it would move in this direction and then it would move in this direction and keep on moving along the same trajectory all along. Which means if we look at the behavior of the system with time, so this is the solution of the system with $I_0$ equals 95 and the system being started just around the equilibrium point very close by. Remember if we start exactly at the equilibrium point it is going to stay there forever, theoretically it has to and if when we do this for simulations we simply start the V and W value slightly off the equilibrium point just a tiny little bit and then we see this kind of trajectory.

So there is a spiraling out of the equilibrium point and then it starts to move

along the same sort of trajectory along with time. So the $V_T$ which is the solution here can be plotted and it will turn out to be, so let us say this is the particular V value this is 9, so this is the $V$ of the equilibrium point. So if you start here what we are seeing is a sort of movement in V like so and then all of a sudden it bursts into large oscillations. Since it will repeat the same trajectory it is oscillating. So again this kind of, so all these curves, all these oscillating trajectories are going to be identical to each other in the sense that they are repeating the same curve all along.

So this kind of behavior is what we call a limit cycle that shows oscillations. So in linear systems we would never see this behavior in the sense that now let us say if I start the system here then also it will if in a let us do it in a different color then also it will end up going on to this same trajectory and start to go into oscillations. If we start the system from outside this particular point even then the system will go and evolve to join that same limit cycle. So nowhere where you start in this phase plane actually within the limits of the possible V and W values we will end up on that same trajectory all the time which is that limit cycle. So this means that in spite of changes in the initial value in fact very large changes in the initial value there is no change in the final oscillating behavior of the system.

In other words in a linear system if we have to see oscillations then it becomes the size of the oscillations would become proportional to the input size. In this case it is going to converge on to the same sized oscillations and the same oscillations throughout. So this is another typical behavior of non-linear systems or another different kind of behavior of non-linear systems which make these systems so interesting to study and we will see that this kind of limit cycle behavior does exist in neurons where we have a small fluctuation that can then go into oscillations if we have a background current for a while. Now so both the things that we have seen so far they actually we presented it in a manner such that as if with simulations we came upon those phenomena like the limit cycle here or the threshold kind of behavior it is as if we said that if we keep on increasing V a point will come when all of a sudden there will be action potentials after a particular value. And here also it is simply that let us start near the equilibrium point and then try out other places and see that that is going into the trajectory all the time on the limit cycle.

So actually we can in fact have make predictions about these systems whether they will have a limit cycle or not or at least based on different conditions can predict whether they will necessarily have a limit cycle or not or otherwise or if there is going to be threshold behavior or not and so on that can be done based on simply looking at the equilibrium points the properties of the equilibrium points.

So as you may notice we did this earlier when the equilibrium point was here and if you remember if we started here the system would go back and come back into the equilibrium point. In this case it is actually going away from the equilibrium point and going on to this trajectory here in the on the limit cycle. So how do we know priori before hand given the system without simulating whether the system is going to go away from that equilibrium point or whether the system is going to come back into the equilibrium point. So for these very ideas it is formalized by looking at the stability of the equilibrium points.

So we can compute or we can determine the stability of the equilibrium point by linearizing the system close to the equilibrium point. In other words if we consider the entire system and then look at a very small neighborhood around the equilibrium point in the phase plane then we can change the system of differential equations into or rather the $dV/dt$ and $dw/dt$ into linear functions. And with those linear functions we can determine whether the system whether the equilibrium point is stable or unstable or something else which we are going to discuss in a little bit. So if the system is attractive in nature if the equilibrium point is attractive in nature that is how it was in the earlier case where there was no $I_{external}$ $I_{external}$ was 0 we found that the trajectories went and ended up at the equilibrium point. So those kind of equilibrium points are the stable equilibrium points that is they attract the trajectories to come and stay there.

And the kind of equilibrium point that we can talk about here is unstable equilibrium points. So in order to look at the stability and linearize the system we have to take into account little bit of mathematical treatment around of the equations. We will try to understand the stability of the equilibrium points based on linearization around a small in a small neighborhood around the equilibrium point. Let us say that for any system let us first consider an n dimensional system like this where we have our vector and a vector variable $\dot{X}$ which is a function of the vector X which can be let us say represented let us say X the vector X is given by the elements $x_1$ the variable $x_1$, $x_2$ up to $x_n$ and the derivative and these are the derivatives of that and $f(X)$ is basically going to be $f_1$ function of the elements $x_1$ up to $x_n$ and this is $f_2(x_1, .$

.. $x_n)$ this is $f_n(x_1...x_n)$. So if we were to linearize the system we have to replace this by a polynomial and consider only the up to the first order term.

So if we use the Taylor series expansion then with $f_1(x_1$ up to $x_n)$ we will see that we have the 0th order term which is $f_1$ at 0 or here we are evaluating it at the equilibrium point which is let us say our $x_0$ and this $x_0$ as a vector is $x_10x_20$ up to $x_n0$. So this $f_1$ at $x_0$ is going to be the first term and then plus $\partial f_1/\partial$ the entire vector then we can sum it up with $\partial x_1$ up to $x_1 - x_10$ plus $\partial f_1/\partial x_2 x_2 - x_20$ and

so on. So these are the only first order terms for this n dimensional system. So we now $f_1(x_0)$ where $x_0$ is the equilibrium point we know is going to be 0 $f_1(x_0)$ is equal to 0 and here I am sorry the $\partial f_1$ is evaluated at x equal to $x_0$ in each of these cases. So this term goes to 0 so we are only left with the derivatives or the partial derivatives of $f_1$ with respect to $x_1$, $x_2$ and up to $x_n$.

Similarly for $f_2$ we can replace it by $f_2(x_0)$ and then $\partial f_2/\partial x_1$ and so on with the multiplication of $x_2 - x_20$ and so on. So now again $f_2(x_0)$ is also going to be 0. So with this we can extend the idea and see that this is turning out to be $\dot{x_1}$ $\dot{x_2}$ up to $\dot{x_n}$ is by setting these terms to 0 we will have $\partial f_1/\partial x_1$ and this is multiplied by $x_1 - x_1naught$ and $\partial$ plus $\partial f_2/\partial x_2 x_2 - x_2naught$ and so on will not extend these terms. Now we if we substitute x is equal to or x as the change $\Delta x$ let us say is $x_1$ is $x_1 - x_1naught$ then our $\dot{x_1}$ is also simply $\Delta\dot{x_1}$ this is simply the coordinate of the equilibrium point along $x_1$ axis. So these $x_1 - x_10$, $x_2 - x_20$ can be replaced by a single variable let us say little x and this can be replaced similarly by the single variable little $\dot{x}$ for the entire vector.

So let us go one step further that is we have $\dot{x_1}$ $\dot{x_2}$ up to $\dot{x_n}$ and now we convert the earlier functions we can write it as simply a matrix multiplied by a vector where we have $\partial f_1/\partial x_1$ as the first term along the first row $\partial f_2/\partial x_2$ as the second term in the first row and so on multiplied by the vector $x_1 - x_10$ is the first term $x_2 - x_20$ is the second term and so on. So here we will see that we can replace it with $\partial f_1/\partial x_1$ evaluated at the equilibrium point $\partial f_1/\partial x_2$ evaluated at the equilibrium point and then $\partial f_n/\partial f_1/\partial x_n$ multiplied by $x_1 - x_10$ $x_2 - x_20$ up to $x_n - x_n0$. So by multiplying this row with this vector we get the term that we had written earlier which is this sum. Similarly for the next function the next variable $\Delta x_2$ $\partial f_2/\partial x_1$ evaluated at $xnaught$ and $\partial f_2/\partial x_n$ evaluated at $xnaught$. So now if we replace $x_1$ x by or capital X by little x then this whole equation can simply be written by $\dot{x}$ equals this matrix which is a Jacobian times x where x is a vector which is where x is representing the variation from the equilibrium point.

That is we had this in our case V and M in the two dimensions and this is let us say the equilibrium point then the 0 of this x is at the equilibrium point and x is representing any position with respect to this particular as an axis. So it is this $x_1 - x_1naught$ is the deviation from the equilibrium point along this axis and $x_2 - x_2naught$ is the deviation along the equilibrium point on this axis. So and this matrix that we have written here is called the Jacobian matrix and it simply is the first order derivatives partial derivatives evaluated at the equilibrium point. So now that we have linearized the system so this is as you can see is simply a linear system where we have only first order derivatives and we have removed all the second order terms. So this neighborhood is such that this system has to be

valid this linearization has to be valid.

So the behavior of the system what we will derive from this final form $\dot{x} = jx$ must be valid only in a very tiny region around the equilibrium point. As soon as the system goes out of the equilibrium point or out of that neighborhood tiny neighborhood the system will start I mean it will not follow this linear behavior anymore and we will have to linearize the point again and so on. So near the equilibrium point the $\dot{x} = jx$ this system of equations is going to predict the behavior of the system. So for a equation of this form equals $jx$ there is only there is one solution to this equation which is if I mean it with the initial conditions can be come about later. Let us say if x is made up of $x_1$ and $x_2$ equals $j$ and $x_1$ and $x_2$ then if $j$ has eigenvalues $\lambda_1$ and $\lambda_2$ and eigenvectors corresponding eigenvectors $v_1$ and $v_2$ then the behavior of the system.

So this is the general solution for two dimensional system with the matrix $j$ having eigenvalues $\lambda_1$ and $\lambda_2$ with eigenvectors corresponding eigenvectors $v_1$ and $v_2$. You can check yourself that this is the solution by plugging it into the $x$ dot here and x there and you will find that this is indeed the trajectory. So the behavior of the system near the equilibrium point let us say here this is $x_1$ this is $x_2$ will be determined actually now by these eigenvalues $\lambda_1$ and $\lambda_2$ because if we have and $v_1$ let us say $v_1$ is this direction and $v_2$ is in this direction what this equation is showing is that at very close by the system will move along the eigenvector $v_1$ and will have an exponential trajectory $e^{\lambda_1 t}$ and at the same time it will move along $v_2$ the eigenvector $v_2$ exponentially with $e^{\lambda_2 t}$ as the function. So obviously if our $\lambda_1$ and $\lambda_2$ are less than 0 when we say less than 0 we are already implying that $\lambda_1$ and $\lambda_2$ are real. Then we can see that if the system is around the equilibrium point then because the $\lambda_1$ and $\lambda_2$ are negative over time this term $e^{\lambda_1 t}$ and also $e^{\lambda_2 t}$ is going to go to 0 which means that both along $v_1$ and $v_2$ it will finally die down into the equilibrium point.

So when $\lambda_1$ and $\lambda_2$ are going to be less than 0 this would be a stable equilibrium point. Similarly if $\lambda_1$ and $\lambda_2$ are both greater than 0 then the system is going to be an unstable equilibrium point is going to be unstable which means that based on this solution that over time the system is going to go diverge out in along $v_1$ the first eigenvector and also along $v_2$ the second eigenvector and so it is not going to come back into the equilibrium point which would be so its behavior would be to push out the system from the from near the equilibrium point because of simply the sign of the real eigenvalues in this case and we will see that even for complex $\lambda_1$ and $\lambda_2$ if the real part is negative then it will be a stable equilibrium point but with an additional property of being a spiral then that will be called a stable spiral. Similarly when $\lambda_1$ and $\lambda_2$ are both positive then also it will be again unstable with

an additional property that it will be a unstable spiral which means that if this is the equilibrium point and this is $v_1$ and this is $v_2$ for a stable spiral it is going to go like this and gradually end up into the equilibrium point. So this is the final direction and obviously for the unstable spiral if this is the equilibrium point and this is $v_1$ $v_1$ and $v_2$ then if we start the system near here it will gradually move out of the equilibrium point of or from the vicinity of the equilibrium. So remember that these are only valid to valid only close by but that is sufficient to predict the behavior of the trajectories that are going to come around it close by it and we will see that indeed with this analysis we can conclude a number of things about the systems properties and the phenomena that the system can show.

So we will stop here by next going on to another kind of equilibrium point which is the last obvious case that is remaining that is $\lambda_1$ and $\lambda_2$ being of opposite signs that is let us say $\lambda_1$ is positive $\lambda_2$ is negative that has a very different kind of behavior and that is called a saddle node. So if I can write it down $\lambda_1$ is less than 0 $\lambda_2$ is greater than 0 or vice versa then this is called a saddle node whose properties we will be discussing in the next lecture. Thank you.