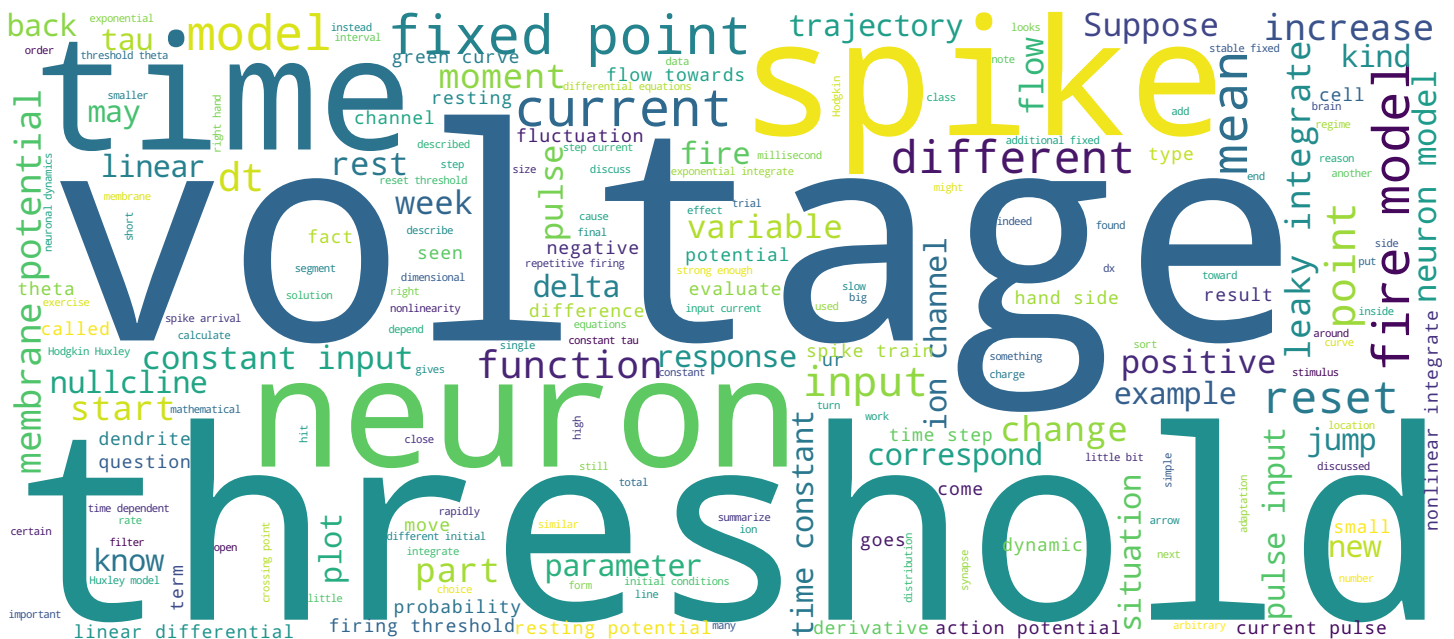


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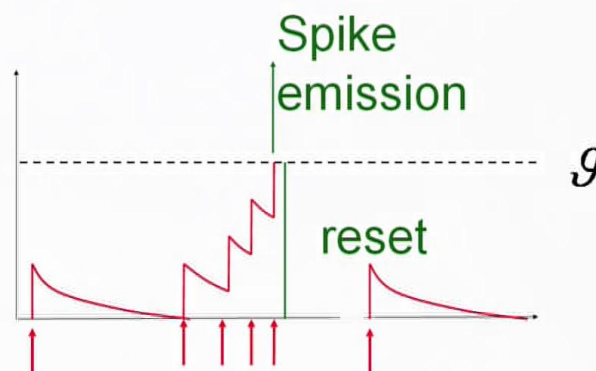
1.5. Quality of Integrate-and-Fire Models



EPFL



Neuronal Dynamics – 1.4. Generalized Integrate-and Fire



Integrate-and-fire model

LIF: linear + threshold

Welcome back to the class on neuronal dynamics. This is part four. In part three, we have discussed the leaky integrate-and-fire model. In the leaky integrate-and-fire model, everything is linear-- incoming pulses, course responses that are summed up linearly. Everything is linear except at the threshold. Now, in this class, I would like to generalize the idea of integrating file models to the case of nonlinear integrate-and-fire models. However, before we can do so, I would like to go back to the leaky integrate-and-fire model and look at it from a slightly different perspective.

Notes

Summary



0m 05s

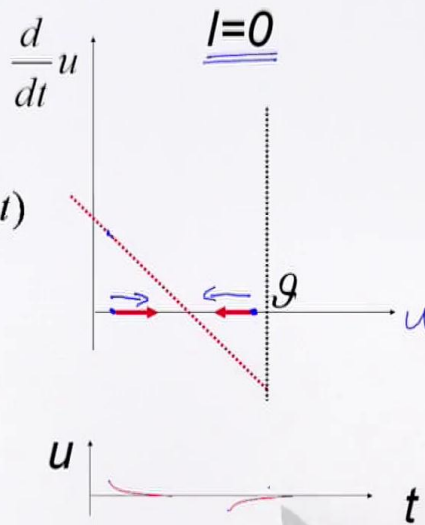
Neuronal Dynamics – 1.4. Leaky Integrate-and Fire revisited

LIF

$$\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t)$$

If firing:

$$u \rightarrow u_r$$



What we have here is a linear differential equation. And I've started a plot here which has on the vertical axis $d/dt u$, which is essentially the left hand side of the equation. And I can express this and I plot this as a function of the voltage u . So in order to know what the derivative $d/dt u$ is as a function of the voltage, I just have to evaluate the right hand side of equation. u minus u_{rest} is a linear function, so this gives this linear line over there. Suppose for the moment that the current is 0. Now, let's look at the following situation. Suppose that my momentary voltage is here. It's at a value above the crossing point. So now, what can I do with this plot? With this plot, I can look at the change. I evaluate $d/dt u$. $d/dt u$ is negative. It's below 0. The change is negative. That means u , to voltage, gets smaller. I go downward. Let's look at this in this plot here. If the voltage is high, it goes down. Now, let's look at the situation where the voltage is low. Say the voltage is here. $d/dt u$ is positive. Therefore, the voltage increases. The only point where it does not change is this point here, which is the resting potential.

Notes

Summary



0m 46s

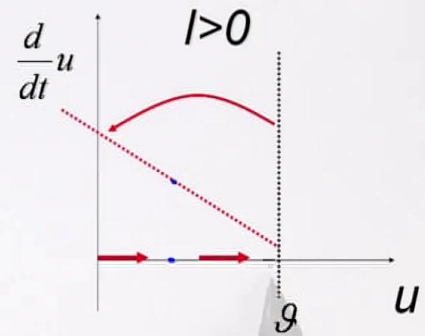
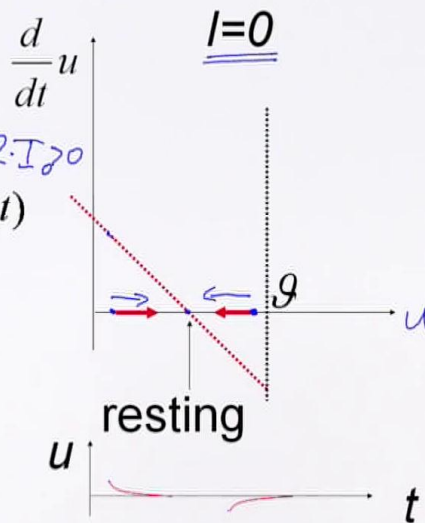
Neuronal Dynamics – 1.4. Leaky Integrate-and-Fire revisited

LIF

$$\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t)$$

If firing:

$$u \rightarrow u_r$$



So for the leaky integrate-and-fire model, you have already analyzed mathematically the properties of the neuron. We have found the fixed point. We have found the resting potential as the stationary solution in the absence of input. What I am doing here is a graphical solution. This kind of graphical solution is, of course, an overkill for a linear differential equation, because for a linear equation, we can write down the solution. However, it will allow us to go from the leaky integrate-and-fire model to nonlinear integrate-and-fire models. So far, we have looked at the case of constant input. The input was 0. Let's stick with constant input, but go to finite input. Again, on the vertical axis, I plot $d/dt u$. The right as a function of the voltage, $d/dt u$ is more or less the same, except that now I have a constant value, R time is $I0$, which is positive. As a result, this straight line is shifted vertically upwards. Suppose I have a certain voltage, like the voltage here. I can now evaluate the function. $d/dt u$ is positive. Therefore, it will flow. The voltage will increase further-- positive $d/dt u$, positive change, increase in the voltage.

Notes

Summary



Neuronal Dynamics – 1.4. Leaky Integrate-and Fire revisited

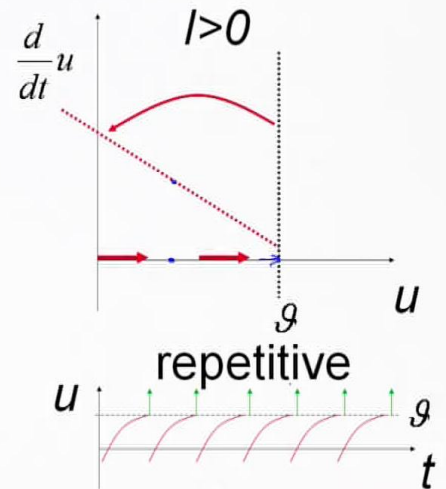
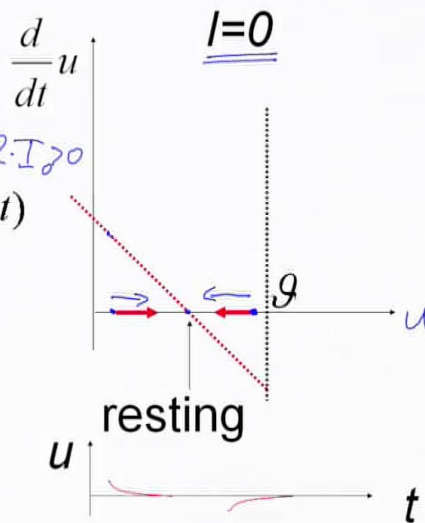
LIF

$$\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + RI(t)$$

R.I > 0

If firing:

$$u \rightarrow u_r$$



The voltage will increase further, but at some point, it will hit the threshold. At this point, it's reset to some reset value, which, say, could be 0 or some other value u_r . As a result, for positive voltage, I have a flow towards the threshold. It's a spike. It's reset, flowed towards the threshold, spiked, reset, and so forth. So the graphical picture allows us to discuss this linear differential equation in the presence of a threshold in a rather transparent fashion. So let's use this now for a generalization.

Notes

Summary



4m 23s

Neuronal Dynamics – 1.4. Nonlinear Integrate-and-Fire

LIF

$$\tau \cdot \frac{d}{dt} u = -(u - \underbrace{u_{rest}}_{\text{rest}}) + RI(t)$$

NLIF

$$\tau \cdot \frac{d}{dt} u = \underbrace{F(u)}_{\text{nonlinear}} + RI(t)$$

If firing:

$$u \rightarrow u_{reset} = u_r$$

So instead of a linear equation, we now have an arbitrary nonlinear function, f of u . As before, if the neuron is firing, it's going to be reset to some value, which I will call u_r , in the future.

Notes

Summary



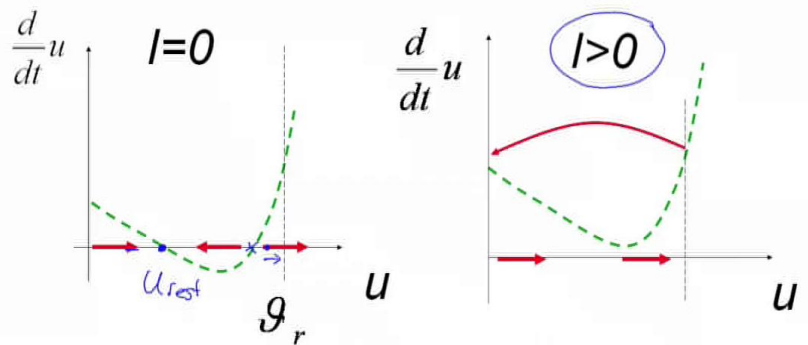
5m 05s

Neuronal Dynamics – 1.4. Nonlinear Integrate-and-Fire

Nonlinear Integrate-and-Fire NLIF

$$\tau \cdot \frac{d}{dt} u = F(u) + RI(t)$$

firing: $u(t) = \vartheta_r \Rightarrow$
 $u \rightarrow u_r$



So this is a similar picture as before, except that now, instead of a straight line, I have some curved function, f of u . For the case of input equal to 0, I still have a flow. The flow is positive. It's negative, which means this is a stable fixed point. Now, if I have a positive current, the green curve is shifted upwards, and now, I have the flow towards the threshold. Let's return to the case of current equal to 0. I said already I have a flow towards this value here, which is the resting value. And it's a stable, fixed point. Interestingly here, there's another point. Once the voltage is above this value, it will not flow back to the resting value, but it will flow autonomously towards the threshold. At the threshold it's going to be reset to some reset value, which may or may not be identical to the rest value.

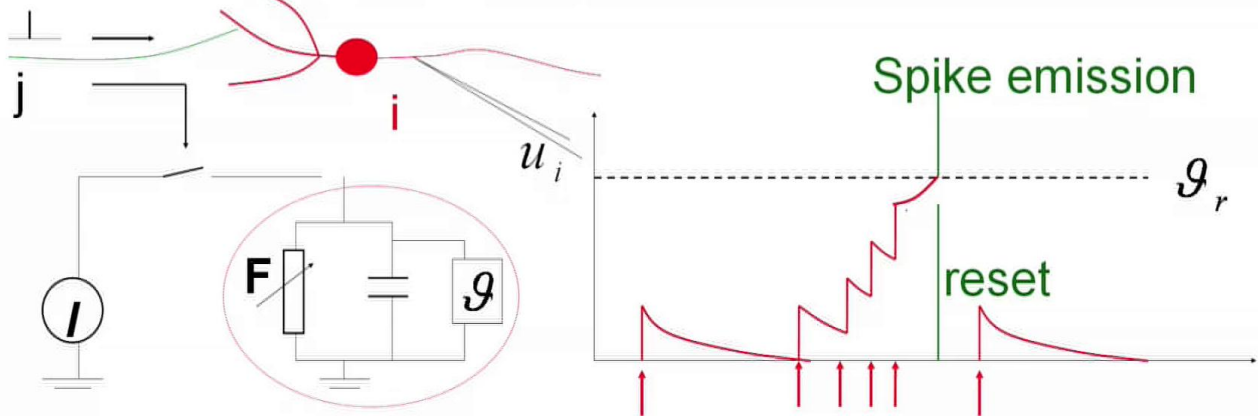
Notes

Summary



5m 25s

Nonlinear Integrate-and-fire Model



$$\tau \cdot \frac{d}{dt} u = F(u) + RI(t)$$

NONlinear

$$u(t) = g_r \Rightarrow \text{Fire+reset threshold}$$

Now, the fact that we have this additional fixed point-- I have a first fixed point corresponding to the resting potential, and then I have this additional fixed point-- means that the summation is no longer linear. At some point, if the voltage is beyond this value, it will autonomously flow towards the threshold, where it's reset. And then the whole process starts again. Now, let's discuss this a little bit further.

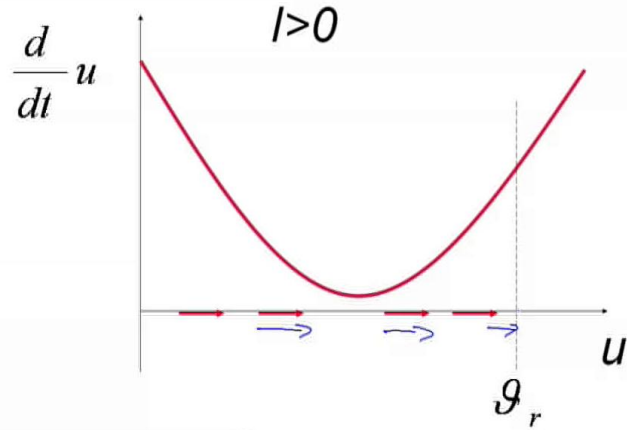
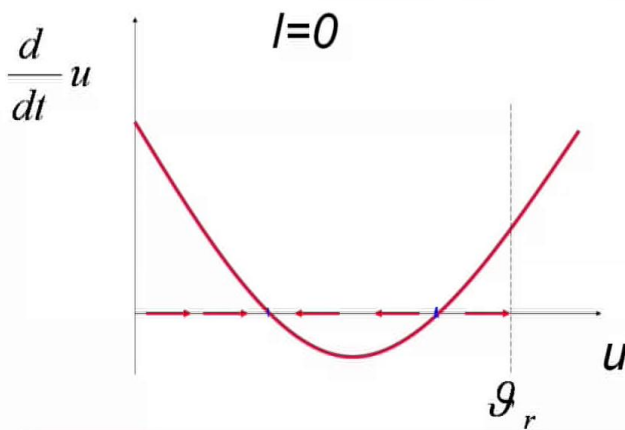
Notes

Summary



6m 46s

Nonlinear Integrate-and-fire Model



$$\tau \cdot \frac{d}{dt} u = F(u) + RI(t) \quad \text{NONlinear}$$

$$u(t) = \vartheta_r \Rightarrow \text{Fire+reset threshold}$$

Quadratic I&F:

$$F(u) \equiv c_2(u - c_1)^2 + c_0$$

What are typical choices for this function, f of u of the nonlinearity? A first choice is the quadratic function, which has a resting value here and this additional fixed point over there. This is the flow pattern. If the voltage reaches the threshold ϑ_r of a reset ϑ_r , then the voltage is reset to some value u_r . Now, for the case of constant input, the whole curve shifts upward. And if the input is strong enough, I have a flow of the voltage towards the threshold, at which point it's reset to u_r .

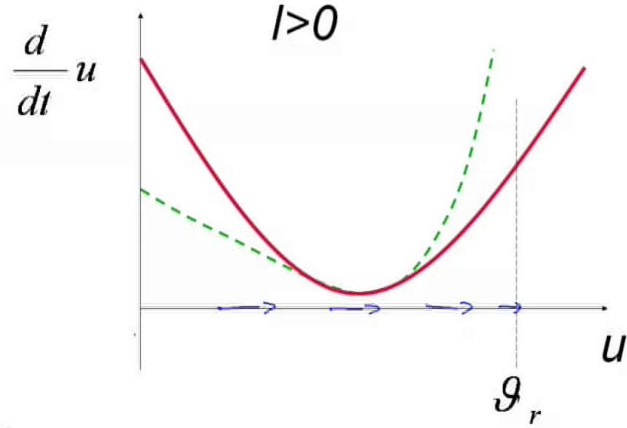
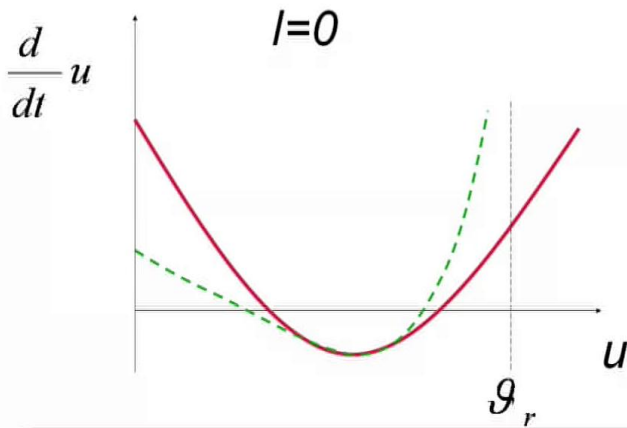
Notes

Summary



7m 17s

Nonlinear Integrate-and-fire Model



$$\tau \cdot \frac{d}{dt} u = F(u) + RI(t)$$

$$u(t) = g_r \Rightarrow \text{Fire+reset}$$

Quadratic I&F:

$$F(u) = c_2(u - c_1)^2 + c_0$$

exponential I&F:

$$F(u) = -(u - u_{rest}) + c_0 \exp(u - g)$$

This is a first choice-- the quadratic integrate-and-fire model. Now, here comes the second possibility. It's the exponential integrate-and-fire model. It's a linear function over here. And then it bends over. And it bends over rapidly. Exponentially fast, it will go towards infinity. Now, let's look at the situation for constant input. Basically, as before, if the input is strong enough, I will have a flow towards the threshold. If the threshold is hit, the membrane voltage is reset to a lower value, and the whole process restarts. A quadratic integrate-and-fire and the exponential integrate-and-fire are two famous neuron models which have both been studied in the field of computational neuroscience.

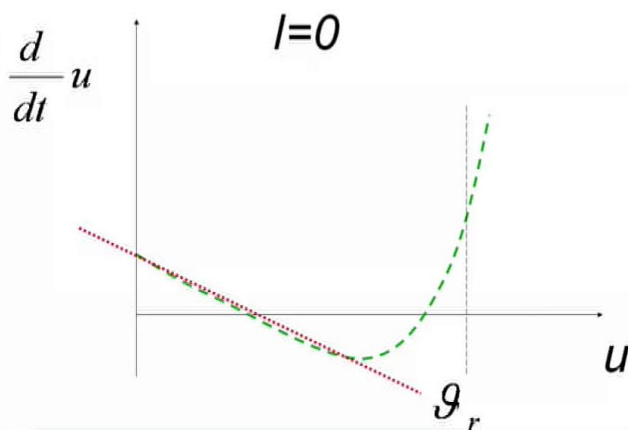
Notes

Summary



8m 05s

Nonlinear Integrate-and-fire Model



$$\tau \cdot \frac{d}{dt} u = F(u) + RI(t) \quad \text{NONlinear}$$

$$u(t) = g_r \Rightarrow \text{Fire+reset threshold}$$

exponential I&F:

$$F(u) = -\frac{(u - u_{rest})}{\tau} + c_0 \exp(u - g_r)$$

So here again, the linear or leaky integrate-and-fire model replaced by some arbitrary nonlinearity-- in the case of the exponential integrate-and-fire model, this nonlinearity has a linear part, which is identical to the situation of the leaky integrate-and-fire model. But then comes the nonlinearity, which means that the curve bends over rapidly. If the reset threshold is hit, then the voltage is put back to a value u_r .

Notes

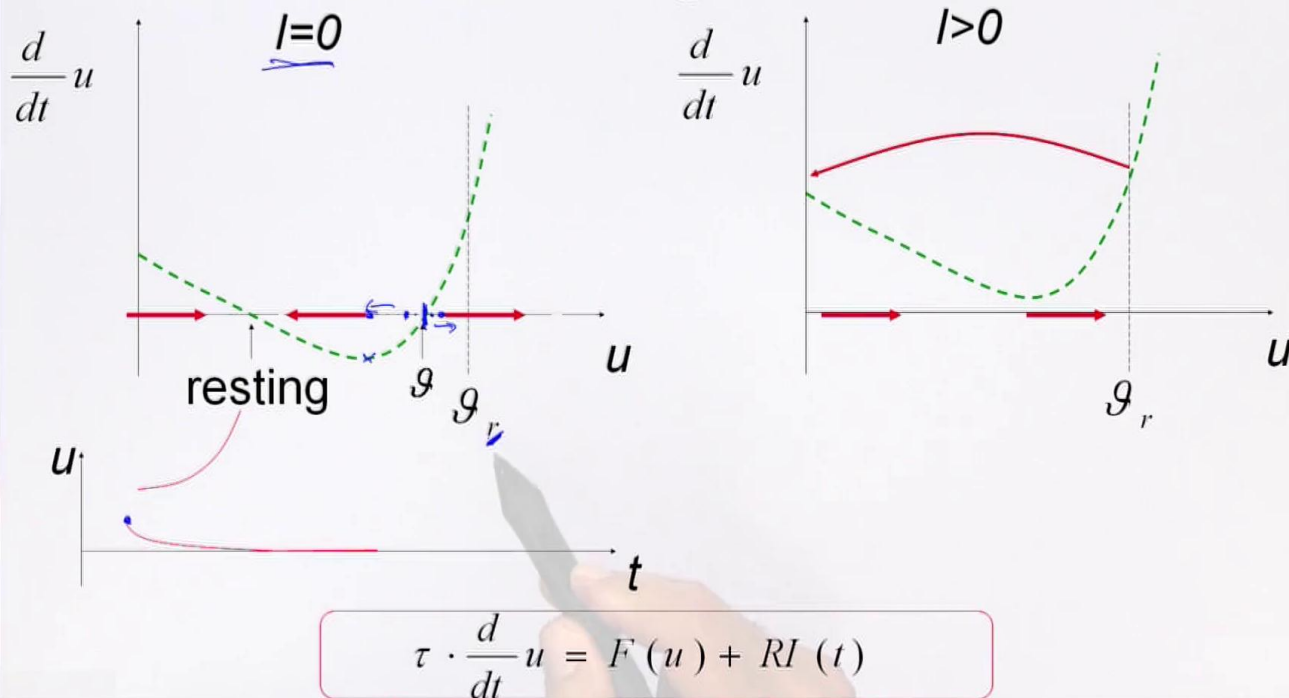
Summary



9m 08s

Nonlinear Integrate-and-fire Model

Where is the firing threshold?



Now, I've changed the notation slightly. I added this little r to the threshold, theta reset. And the reason is that we need to talk about the notion of threshold in this model. So I would like to pose the following question. Where is the firing threshold in this nonlinear integrate-and-fire model? So suppose I start with some voltage-- for example, a voltage here. Voltage here means I evaluate the change. $d/dt u$ is negative. It will flow backwards towards the resting potential. That's what we see here. If I have a voltage on this side, the crossing point, then it will automatically flow towards the threshold, which means the voltage will on its own increase further. Now, you can repeat the argument. Suppose I start here. The voltage will still flow down. If I start here, it will flow up. So this value here is critical. This crossing point defines a sort of firing threshold-- the firing threshold for different initial conditions. If the voltage is here and there is no further current, I is 0. If it's here, it will go up. If it's here, it will go down. So this is like a firing threshold, theta, for the voltage. And this is different from theta r. Theta r is the numerical threshold for the reset.

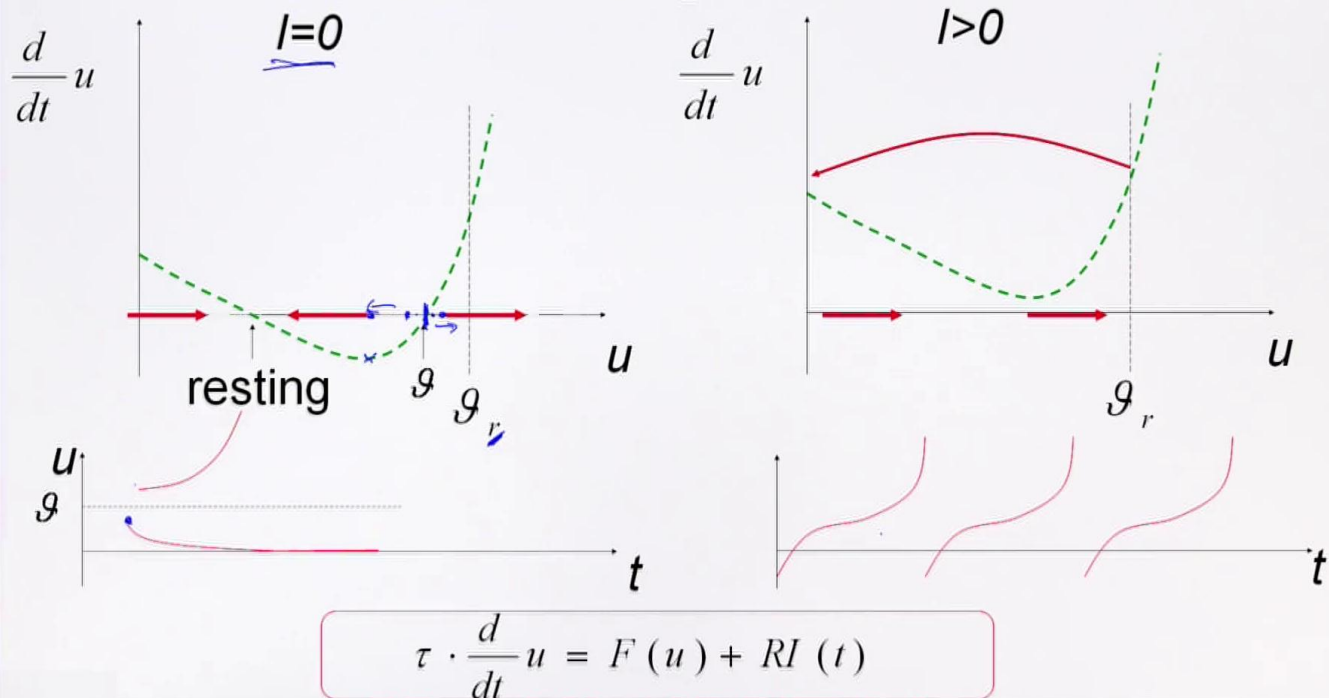
Notes

Summary



Nonlinear Integrate-and-fire Model

Where is the firing threshold?



Its value is somewhat arbitrary. I could put it further up. I can put it slightly further down. It doesn't really matter, because the increase of the voltage is so rapid that it will blow up very rapidly. It's a fraction of a millisecond, the difference between a threshold here or there. So you can say that if I have different initial conditions, then this acts like a threshold. Different initial conditions corresponds to a short pulse input. As we have seen in an earlier part of this week's lecture, a pulse input just makes the jump of the membrane potential to a new value. If this jump is to a value below θ , it will go back. If the jump is to a value above θ , the voltage will increase further until it's reset numerically. Now, let's look at the situation of constant input. If the input is strong enough, the curve is shifted upwards so that there's no crossing point. Therefore, the flow is always towards the right. Again, there is a reset threshold. And the trajectory will move regularly towards the reset threshold, and then it's reset. So the question now is at which point will the neuron enter in the regime of repetitive firing?

Notes

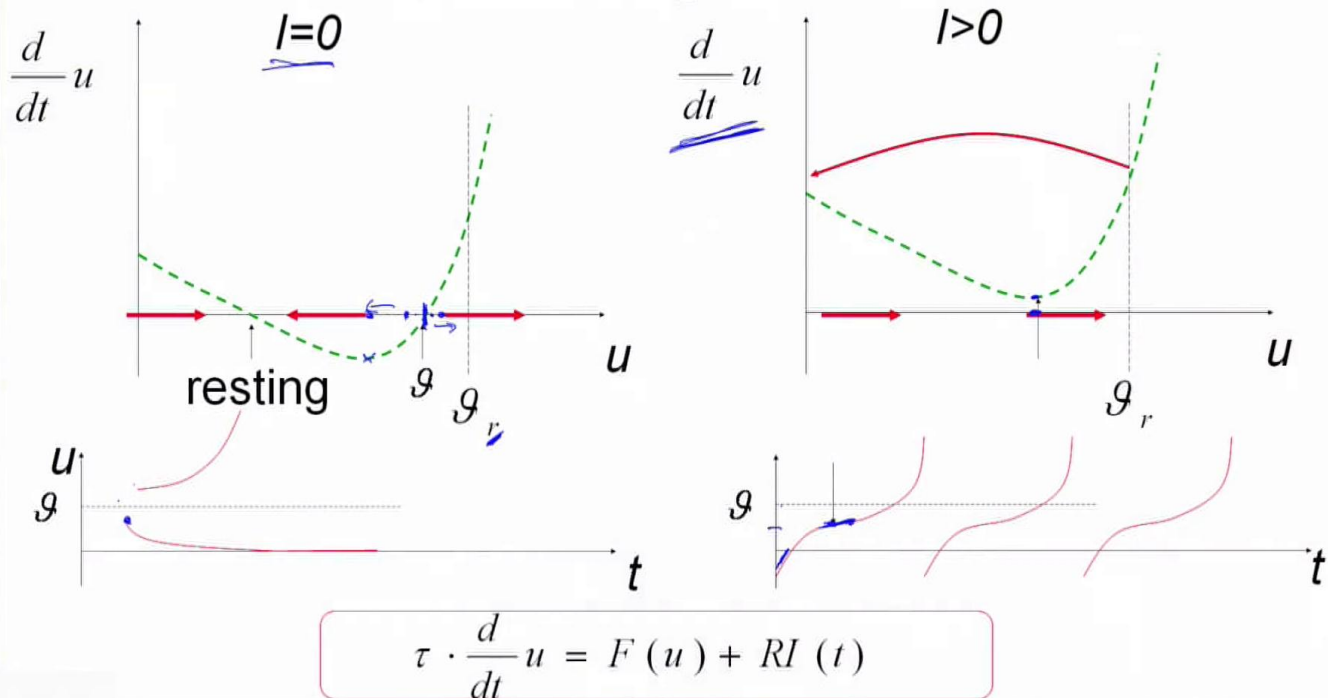
Summary



11m 41s

Nonlinear Integrate-and-fire Model

Where is the firing threshold?



Well, it will enter in the regime of repetitive firing as soon as no fixed point remains-- as soon as the green curve is above the 0 line. Imagine we increase the current from 0 to some positive value. The green curve shifts up at the beginning of a fixed point here, another one there. I shift the green curve up at some point. The fixed points move together. They merge. And then that is up here. And this is the moment when repetitive firing starts. Just before the fixed points disappear, they will still touch the 0 line, about here. So this is the critical value of the voltage for which repetitive firing sets in under a constant but positive input curve. Now, in this figure, where does it correspond to? Well, note that the green curve gives du/dt . It skips the derivative. If you get down here, the derivative is big-- large slope upwards. Now, this is the point where the slope is minimal-- about here-- before it turns up again and will take up speed. So this value is about here in this region here, minimal slope. That would correspond to the threshold for constant input. Now, note that this threshold here for constant input is different from the threshold I found over there-- the threshold for pulse input, or threshold for initial conditions.

Notes

Summary



13m 26s

Neuronal Dynamics – 1.4. Nonlinear Integrate-and-Fire

Where is the firing threshold?

Leaky integrate-and-fire (LIF)

Strict voltage threshold

- by construction
- spike threshold = reset condition



Nonlinear integrate-and-fire (eIF)

There is no strict firing threshold

- firing depends on input
- exact reset condition of minor relevance

To summarize, where is the firing threshold? Well, for leaky integrate-and-fire model, it's simple. There is only one threshold. The threshold for the reset is the same as the threshold for pulse input. It's the same as the threshold for constant input. For nonlinear integrate-and-fire models, the picture is more complicated. The neuron has a formal threshold for the reset, which is of minor importance. What is important is the intrinsic threshold. And this intrinsic threshold is different for the case of pulse input, initial condition. It corresponds to the crossing point at the intersection point of the green curve. It's different for pulse input and for constant input. Therefore, a nonlinear integrate-and-fire model does not have a unique firing threshold. The concept of a threshold is an abstraction. And if, in this class, we often talk about the threshold, then this is indeed a simplification. Real neurons will have a different threshold if we observe them under pulse injection or constant current injection and yet a different threshold if you use a slow current ramp.

Notes

Summary



15m 18s

Neuronal Dynamics – Homework 1.3



Take 10 minutes!

I invite you to spend some time with the exercises that should trigger some thinking about the different versions of nonlinear and neuron models. So please spend five to 10 minutes with the exercises, and then move on to the last part of this week's lecture.

Notes

Summary



16m 45s