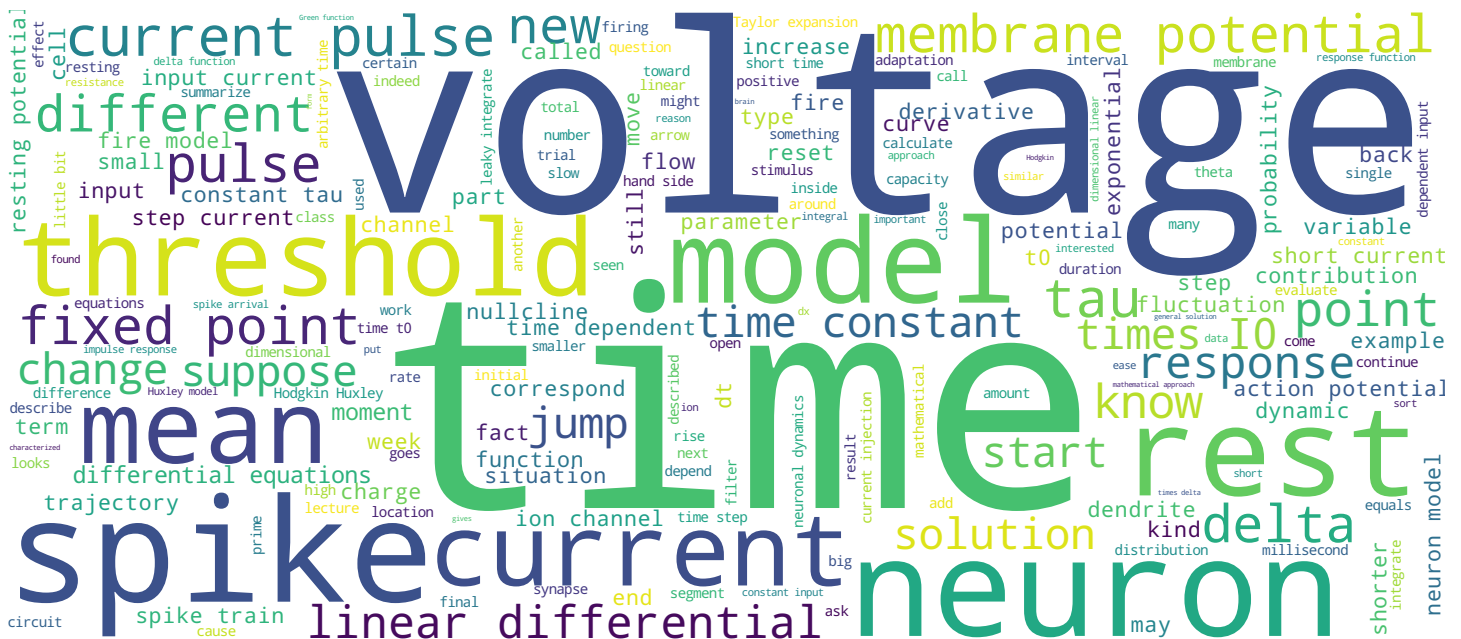


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EPFL, Lausanne, Switzerland

1.5. Quality of Integrate-and-Fire Models



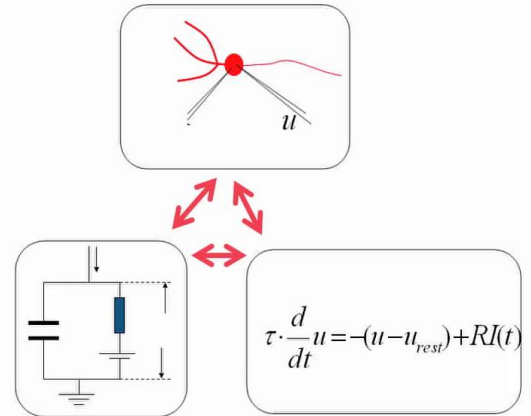
EPFL



Neuronal Dynamics – 1.2 Detour – Linear Differential Eq.



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



Welcome back to the class on neuronal dynamics. I hope that each of you have spent 10 or 15 minutes with the exercises 1.2. All those who had no problem solving those exercises can skip over this set of slides and go directly to lesson 1.3. For the others, I've prepared here some additional information just to remind you of the properties of one-dimensional linear differential equations.

Notes

Summary

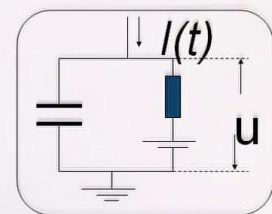


0m 04s

Neuronal Dynamics – 1.2 Detour – Linear Differential Eq.

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

*Math development:
Response to step current*



So this is the kind of equations we have. We have here a linear differential equation. And we want to apply some arbitrary input current. And we are interested in coagulating the response, the voltage u of t . And as a first step, we are going to do this for a step current.

Notes

Summary



0m 36s

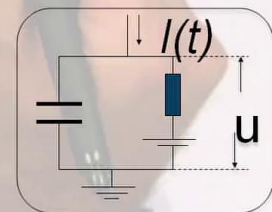
Neuronal Dynamics – 1.2 Detour – Step current input

fixed point $\frac{du}{dt} = 0$

$(I=0) \Rightarrow$
 $0 = -(u - u_{rest})$
 $u = u_{rest}$

$(I=I_1) \Rightarrow$
 $0 = -(u - u_{rest}) + R \cdot I_1$
 $u = u_{rest} + R \cdot I_1$

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



So here is the step current. How can we proceed? So at beginning, the step current is zero, which means this current here is zero. And, now, we can take two different approaches. Let's take the mathematical approach first. The mathematical approach is to look for a stationary solution, a fixed point you find as a derivative, which vanishes, $\frac{du}{dt}$ equals 0. Now, if $\frac{du}{dt}$ is equal 0, then we are in the case that I equals 0. That means 0 is equal to u minus u_{rest} , or u is equal to u_{rest} . u_{rest} is the resting potential-- say it's here, u_{rest} -- so we knew that while the current is 0, u equal u_{rest} is a solution. So supposing that we started at zero, at u_{rest} , there's no need that the evolution changes, so we stay fixed at the level u_{rest} . Now, we applied a step current. After the switch, the step current has a new value, I_1 . So let's do the same thing again. We look for a fixed point, but now I is equal to I_1 . Therefore, we have 0 equals u minus u_{rest} , plus R times I_1 . Or u is equal to u_{rest} plus R times I_1 . So I know that for a constant input, there exists a solution for the voltage, which is constant as well. Let me draw it like this here. So this is my voltage, which I call, now, u_1 , to keep things simple.

Notes

Summary



Neuronal Dynamics – 1.2 Detour – Step current input

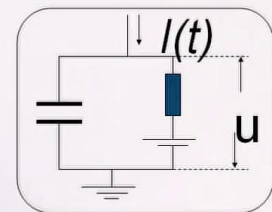
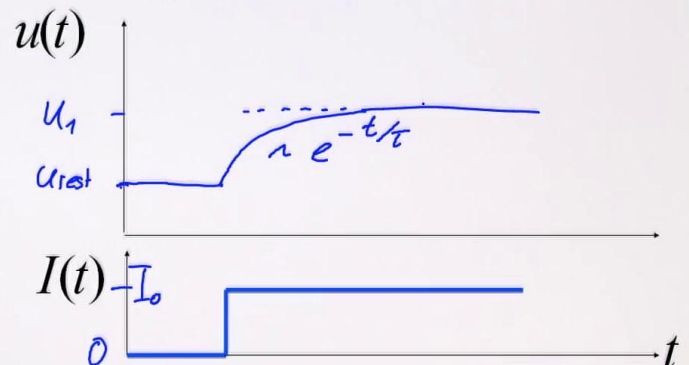
fixed point $\frac{du}{dt} = 0$

$(I=0) \Rightarrow$
 $0 = -(u - u_{rest})$
 $u = u_{rest}$

$(I=I_0) \Rightarrow$
 $0 = -(u - u_{rest}) + R \cdot I_0$
 $u_1 = u_{rest} + R \cdot I_0$

$u(t) = u_{rest} + R \cdot I_0 [1 - e^{-t/\tau}]$

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



So this is u_1 . u_1 is the stationary state. And it will be reached after some time. But it does take some time to reach this new stationary state. I told you earlier that all differential equations-- linear differential equations, one-dimensional linear differential equations-- are characterized by a time constant. Here's my time constant τ . The solution always is exponential. The solution of a one-dimensional linear differential equation is an exponential. So supposing that this is the new solution and we start from here, we have to fit in some exponential to connect the two solutions. And here is how you can construct this. So we know that before the switch, in this version, u was equal to u_{rest} . Afterwards, it has a new value u_1 , which is $u_{rest} + R \cdot I_0$. So the new value, $R \cdot I_0$, will not be approached immediately but exponentially. So let's try this. $e^{-t/\tau}$. So the result, now, is that the approach is, exponentially, this new value, $u_{rest} + R \cdot I_0$. And this gives exactly this kind of curve an exponential approach. You can check that this is, indeed, a solution of the differential equation by checking the derivative. So let's take the derivative.

Notes

Summary



3m 43s

Neuronal Dynamics – 1.2 Detour – Step current input

fixed point $\frac{du}{dt} = 0$

$(I=0) \Rightarrow$
 $0 = -(u - u_{rest})$
 $u = u_{rest}$

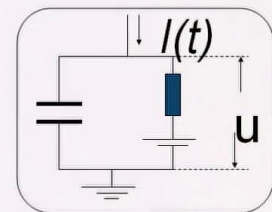
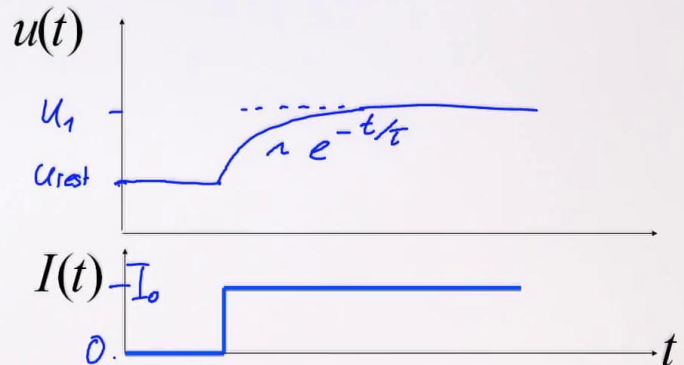
$(I=I_0) \Rightarrow$
 $0 = -(u - u_{rest}) + R \cdot I_0$
 $u = u_{rest} + R \cdot I_0$

$$u(t) = u_{rest} + R \cdot I_0 [1 - e^{-t/\tau}]$$

$$\left[\frac{d}{dt} u = R \cdot I_0 \frac{1}{\tau} \cdot e^{-t/\tau} = u - u_{rest} + R \cdot I_0 \right] \checkmark$$

$$u - u_{rest} = R \cdot I_0 - R \cdot I_0 e^{-t/\tau}$$

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



$\frac{d}{dt} u$ is u_{rest} has no derivative, it's a constant. $R \cdot I_0 \cdot 1$ is also a constant. So I have $R \cdot I_0$, derivative of this exponential gives me a $1/\tau$, $e^{-t/\tau}$. You have to compare this with the differential equation up here. So I have $u - u_{rest}$ of t minus u_{rest} is $R \cdot I_0$ minus $R \cdot I_0 e^{-t/\tau}$. u of t is this. I subtract u_{rest} . I have those terms, which I'll write as two terms. And now you see that-- let's go back to differential equation-- this is, indeed, the correct solution. Because I can write this as $u - u_{rest}$ plus $R \cdot I_0$. Therefore, I am OK.

Notes

Summary



Neuronal Dynamics – 1.2 Detour – Short pulse input

$$u(t) = u_{rest} + RI_0 \left[1 - e^{-(t-t_0)/\tau} \right]$$

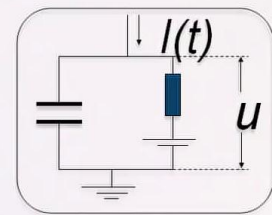
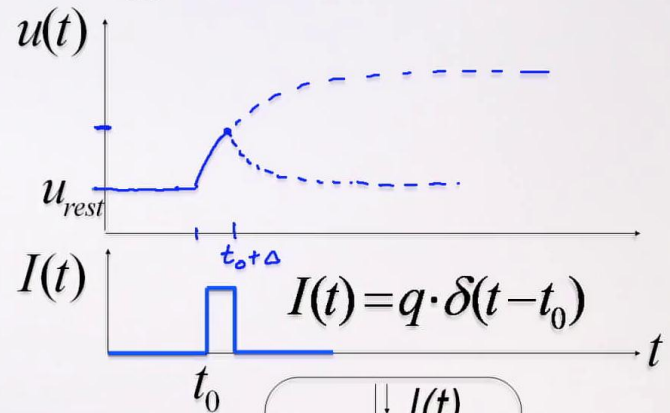
short pulse: $\Delta \cdot (t - t_0) \ll \tau$

at $t_0 + \Delta$

$$u(t_0 + \Delta) = u_{rest} + R \cdot I_0 \left[1 - e^{-\frac{\Delta}{\tau}} \right]$$

$$\Delta \ll \tau$$

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



So what we have found is that the solution to a step current input is the resting potential plus a change. And the change is not step-like, but it's approached. A new value is approached exponentially. So the solution for the step current, indeed, looks like this. Now, let's continue and look at the case of a short current pulse. If there's a short current pulse, then it's not going to continue. Because the current stops. So at this point here, it's going down again to the new value. I'm interested in calculating this new value here. The moment we need to reach is the maximum, the moment when the current stops and returns back to 0. So if this is t_0 , then this point is t_0 plus Δ , where Δ is the duration of the current pulse. So this is the solution which we have found before. Let's evaluate this solution at t_0 plus Δ , and this point in time. So u at t_0 plus Δ is $u_{rest} + R \cdot I_0 \left[1 - e^{-\frac{\Delta}{\tau}} \right]$ and now, evaluate the time t at t_0 plus Δ -- so I have, here, minus Δ over τ . Now, suppose that Δ is really short. Suppose that Δ is much shorter than the time constant. That's the condition that I've written down here. Δ , defined as t minus t_0 , is much shorter than τ .

Notes

Summary



7m 27s

Neuronal Dynamics – 1.2 Detour – Short pulse input

$$u(t) = u_{rest} + RI_0 \left[1 - e^{-(t-t_0)/\tau} \right]$$

short pulse: $\Delta = (t - t_0) \ll \tau$

at $t_0 + \Delta$

$$u(t_0 + \Delta) = u_{rest} + R \cdot I_0 \left[1 - e^{-\frac{\Delta}{\tau}} \right]$$

$\Delta \ll \tau$

$$= u_{rest} + R \cdot I_0 \frac{\Delta}{\tau} + \dots$$

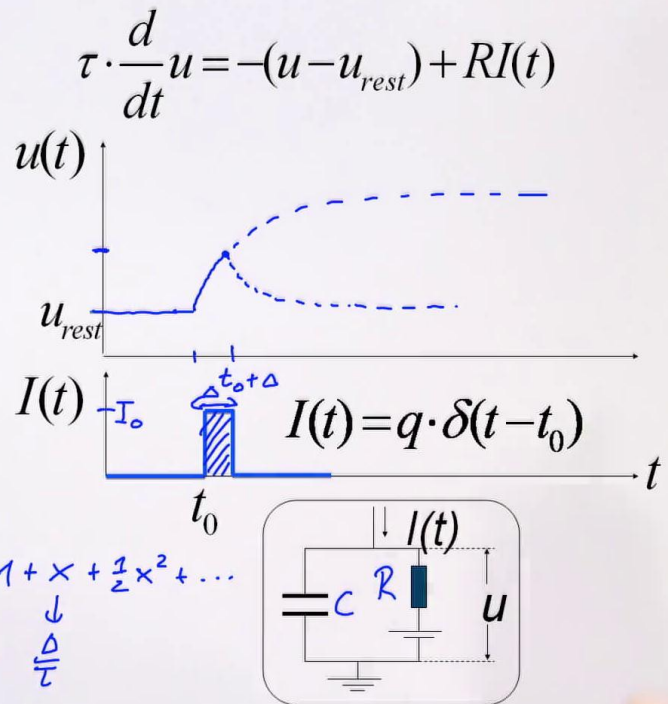
$$\tau = R \cdot C$$

$$= u_{rest} + I_0 \frac{\Delta}{C}$$

$$= u_{rest} + \frac{q}{C} \leftarrow \text{charge}$$

$$e^x = 1 + x + \frac{1}{2}x^2 + \dots$$

$\downarrow$
 $\frac{\Delta}{\tau}$



That's sort of the end of the pulse. Delta much shorter than tau. Now, I can use the Taylor expansion of an exponential. So the Taylor expansion of the exponential is 1 plus x plus 1/2 x squared, and so forth. So x is small. x is delta over tau, in my case. So let's write this down. I have u_{rest} plus R times I_0 . The first term of the exponential is 1. It kills this one here. The next term is x, which is delta, over tau plus other terms, which we are going to neglect. Now, remember that we defined the time constant, tau, as R times C . Tau is the time constant of the circuit with a resistance R , and the capacity, C . I insert tau in this expression here. And I get u_{rest} plus I_0 delta over C . Tau is RC , the R is canceled. Now, what does this tell us? Well, I have, here, the capacity, C . I have, here, my current, I_0 . This current, I_0 , is applied for a duration delta. That's the duration delta. Therefore, I_0 times delta is the surface under the pulse, or the charge. I can write this as u_{rest} plus q over C , where q is the charge deposited by my current pulse. And now, you see what's going to happen if I keep the charge the same but make the pulse shorter and shorter.

Notes

Summary



Neuronal Dynamics – 1.2 Detour – Short pulse input

$$u(t) = u_{rest} + RI_0 \left[1 - e^{-(t-t_0)/\tau} \right]$$

short pulse: $\Delta = (t - t_0) \ll \tau$

at $t_0 + \Delta$

$$u(t_0 + \Delta) = u_{rest} + R \cdot I_0 \left[1 - e^{-\frac{\Delta}{\tau}} \right]$$

$\Delta \ll \tau$

$$= u_{rest} + R \cdot I_0 \frac{\Delta}{\tau} + \dots$$

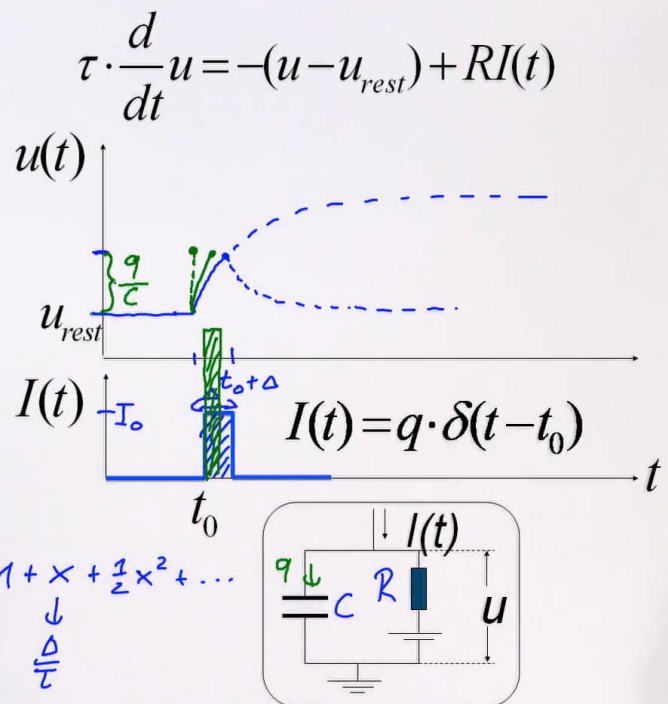
$$\tau = R \cdot C$$

$$= u_{rest} + I_0 \frac{\Delta}{C}$$

$$= u_{rest} + \frac{q}{C} \leftarrow \text{charge}$$

$$e^x = 1 + x + \frac{1}{2}x^2 + \dots$$

$\downarrow$
 $\frac{\Delta}{\tau}$



So let's now consider a pulse which is twice as high, but half as long. It has the same charge. The rise will be faster. The rise will be like this. But it will, essentially, stop at the same value. If I make the pulse even shorter but keep the charge the same, in the end, I will have a jump to the new value. And this distance here is just the charge over C . So this is the mathematical approach. We use the Taylor expansion. Now, let's go back at a more physical interpretation. For a more physical interpretation, we can look at the circuit and we say, a positive current for a very short time. Now, if it's for a short time, the current does not have the time to go through the resistor. Instead, the current will, basically, just go on the capacity. That means, if I have a very short current pulse, this short current pulse deposits charge on the capacitor. But if I deposit a charge, Q , on the capacitor, then I have a change in voltage, which corresponds to q over C .

Notes

Summary



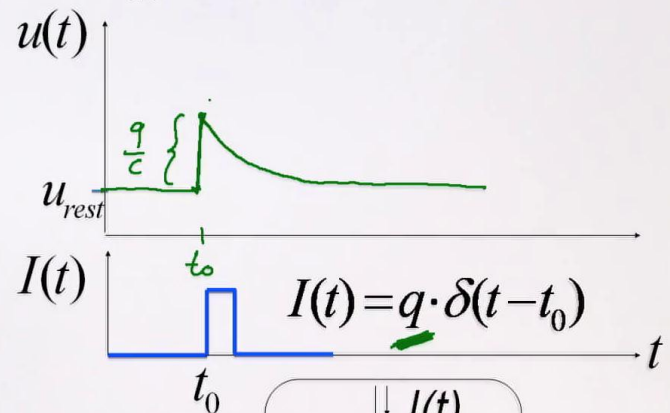
12m 29s

Neuronal Dynamics – 1.2 Detour – Short pulse input

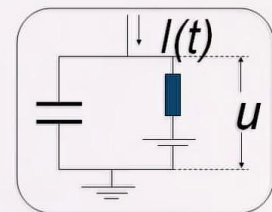
$$u(t) = u_{rest} + RI_0 \left[1 - e^{-(t-t_0)/\tau} \right]$$

short pulse: $(t-t_0) \ll \tau$

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



$$u(t) = u_{rest} + \frac{q}{C} e^{-(t-t_0)/\tau}$$



So in summary, a short current pulse that's made really short deposits a charge, Q , in a very short time. And the membrane potential will, at time t_0 , simply jump to a new value. And afterwards, there's no current anymore. The current is, again, 0. So we just have an exponential decay back to the resting value. And the jump size is q over C . The fact that we have a very short current pulse-- infinitely short current pulse-- that deposits a fixed amount of charge, mathematically, this effect is described by the so-called, Dirac delta function, which needs to be integrated to make sense. Physically, it has its meaning because-- with the Taylor expansion we see that whatever the duration of the pulse, it's short enough. It no longer matters. The jump is by an amount q over C . So the elegance of the Dirac delta function is that you don't need to work with short current pulses of finite duration. We can take the limit of a very short pulse and, then, forget the transient, and just say, it corresponds to a jump. This is a little bit like working with a somewhat lower time resolution. If your current pulse is shorter than the time course of the membrane potential, then what appears is just a jump.

Notes

Summary

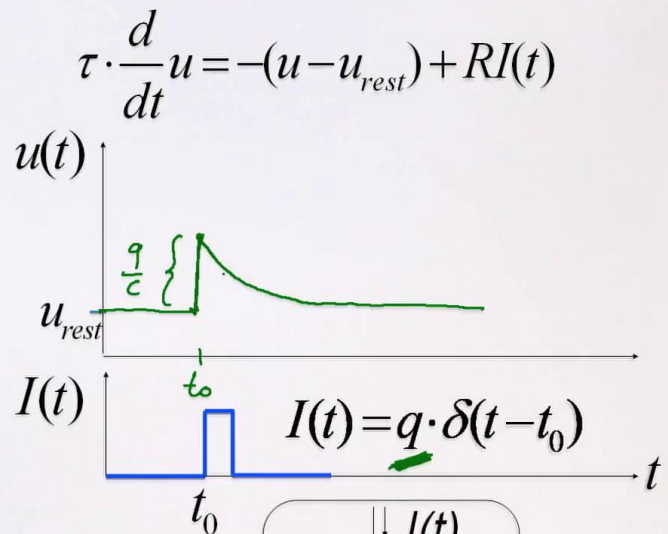


14m 07s

Neuronal Dynamics – 1.2 Detour – Short pulse input

$$u(t) = u_{rest} + RI_0 \left[1 - e^{-(t-t_0)/\tau} \right]$$

short pulse: $(t-t_0) \ll \tau$



$$u(t) = u_{rest} + \frac{q}{C} e^{-(t-t_0)/\tau}$$

In a physical situation, if you were to zoom in and say, well, the pulse, in the end, does have some finite width-- it's very short but still finite-- then it would not be a direct jump. But it will still have a tiny little slope to the right. The mathematical abstraction gives us a lot of ease of talking about solutions of linear differential equations and other differential equations, as well.

Notes

Summary



16m 01s

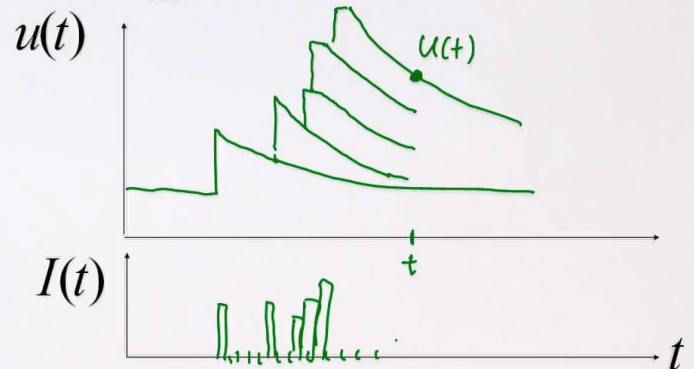
Neuronal Dynamics – 1.2 Detour – arbitrary input

Single pulse

$$u(t) = u_{rest} + \frac{q}{C} e^{-(t-t_0)/\tau}$$

Multiple pulses:

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



$$u(t) = u_{rest} + \int_{-\infty}^t \frac{1}{C} e^{-(t-t')/\tau} I(t') dt'$$

So now, we know that a single pulse leads to a jump of the membrane potential. So if I have a single current pulse here, then the response of the membrane potential will be a jump and it will go exponentially back to the resting value. Now, suppose that I have more pulses. Suppose I have another pulse here. So this pulse will also cause a change, a jump in the membrane potential. And the jump will leap be by the same amount. This is a linear differential equation. The elementary solutions add up linearly. Now, suppose that I have many more current pulses of different amplitudes. Each one will make it's little contribution. And in the end, I can sum up all the contributions of the different pulses and say, well, what's the response at time t? The response is the response to the first pulse plus the response to the second pulse, plus the response to the third pulse, plus this response to the forth pulse and the fifth pulse, and so on. And the net result, u of t, is the sum of all those responses. Now, mathematically, you can now consider the situation where, at each moment in time, you have a different current pulse coming in. And this is the current pulse at some time, t prime.

Notes

Summary



16m 27s

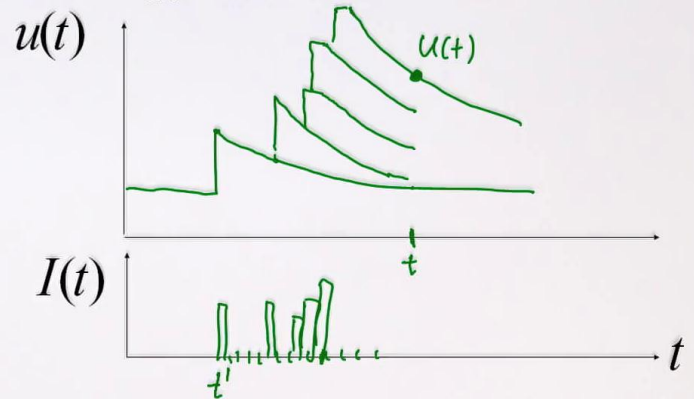
Neuronal Dynamics – 1.2 Detour – arbitrary input

Single pulse

$$u(t) = u_{rest} + \frac{q}{C} e^{-(t-t_0)/\tau}$$

Multiple pulses:

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



$$u(t) = u_{rest} + \int_{-\infty}^t \frac{1}{C} e^{-(t-t')/\tau} I(t') dt'$$

And you ask, what's the contribution of this pulse to the voltage at time t ? Well, the contribution of this pulse at t' was biggest here. But then it has decayed exponentially. So its relative width is less than a pulse who came in here, and still has a strong contribution. Now, interestingly, this is a solution to the linear differential equation, so arbitrary time dependent input current. And what you have here inside the integral is just the response to a single pulse. That means, once you have constructed the impulse response function, you have, also, at hand, the general solution of the differential equation.

Notes

Summary



Neuronal Dynamics – 1.2 Detour – Greens function

Single pulse

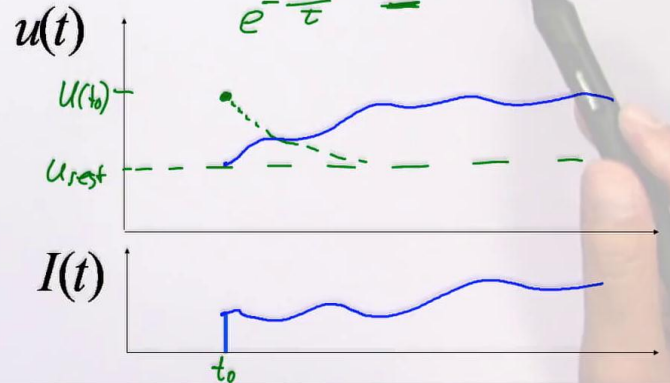
$$\Delta u(t) = q \frac{1}{C} e^{-(t-t_0)/\tau}$$

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

Multiple pulses:

Impulse response function,
Green's function

$$u(t) = u_{rest} + [u(t_0) - u_{rest}] e^{-\frac{t-t_0}{\tau}} + \int_{t_0}^t \frac{1}{C} e^{-(t-t')/\tau} I(t') dt'$$



$$u(t) = u_{rest} + \int_{-\infty}^t \frac{1}{C} e^{-(t-t')/\tau} I(t') dt' \quad ||$$

Technically, this is also called the Green's function of the equation. So once we have this impulse response function, we know the general solution of the differential equation. The assumption here is that the input current started a long, long time back in the past. The situation is somewhat different if the whole current injection starts at a fixed time, t_0 . So suppose we don't know what happened in the past. But what we do know is at time t_0 , current injection starts. And it starts at a new value, u of t_0 . For some reason-- say, we have measured the voltage-- we know, at time t_0 , the voltage was here. The resting potential is somewhere here. Now, you have two contributions. You have this part here with the Green's function or the impulse response function. And you have the effect of the initial condition. At the start, we know we have a value of t_0 . And this contribution will-- this difference, here, will decay exponentially. So we need to add an extra t minus t_0 over τ for this contribution. It will go down with a membrane time constant, τ . Now, the additional current, which starts here, will make an additional contribution to the membrane potential, which I can calculate by this term here. The total voltage is the exponentially decaying pulse caused by the initial condition plus the contribution of the input current convolved with the Green's function.

Notes

Summary



Neuronal Dynamics – 1.2 Detour – arbitrary input



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

Arbitrary input

$$u(t) = u_{rest} + \int_{-\infty}^t \frac{1}{c} e^{-(t-t')/\tau} I(t') dt'$$

Single pulse

$$\Delta u(t) = \frac{q}{c} e^{-(t-t_0)/\tau}$$

you need to know the solutions of linear differential equations!

This linear differential equation can be solved for arbitrary, time-dependent input. We can write down the general solution for arbitrary time-dependent input. Particularly interesting cases, in the context of neuroscience, are indeed the step current and the short pulse current. So if you have problems with these kind of differential equations, please work this out for yourself. It's important that you are at ease with linear differential equations. You will need that throughout the class at many occasions. And we have also prepared additional exercises for you, so that you can check whether you are at ease now with these kind of linear differential equations in one-dimension.

Notes

Summary



21m 39s

Neuronal Dynamics – Exercises 1.2-bis



*If you don't feel at ease yet,
spend **10 minutes** on these
mathematical exercises*

And now, we can move on to lesson 1.3.

Notes

Summary



22m 37s