

Week 1 – part 2: The Passive Membrane



Neuronal Dynamics: Computational Neuroscience of Single Neurons

Week 1 – neurons and mathematics:
a first simple neuron model

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1.1 Neurons and Synapses:

Overview

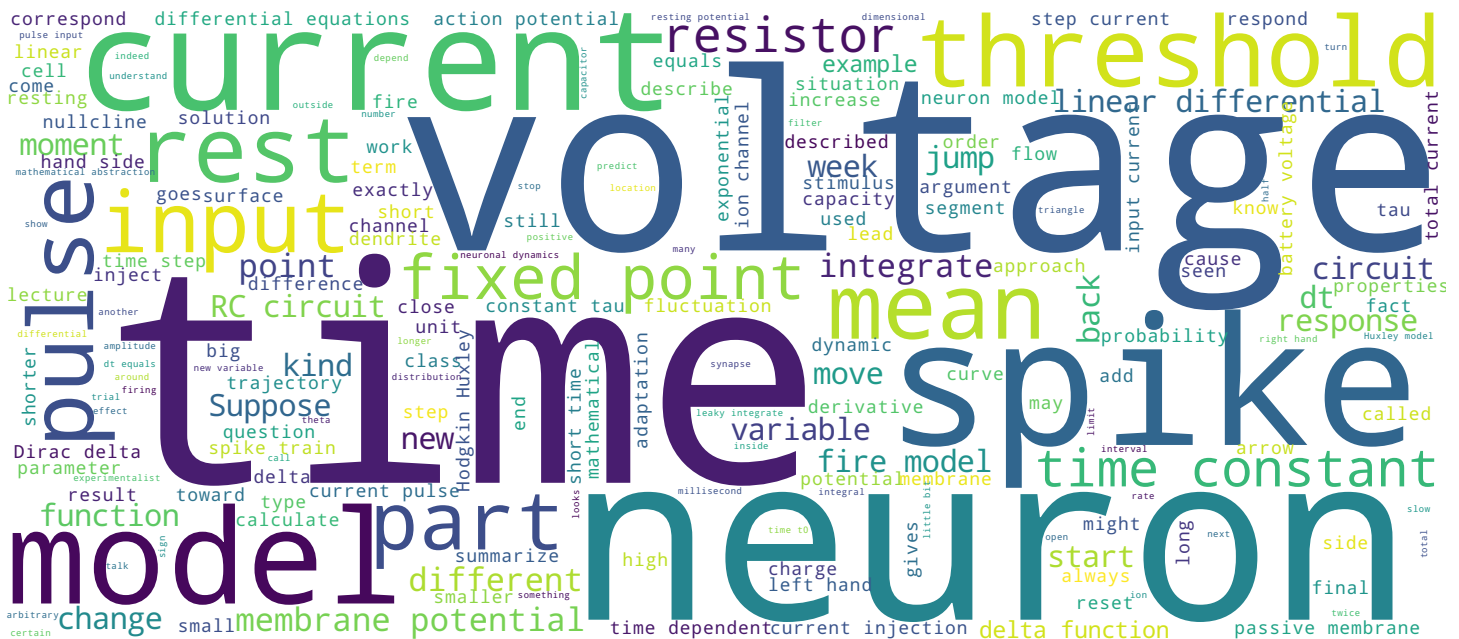
1.2 The Passive Membrane

- Linear circuit
- Dirac delta-function

1.3 Leaky Integrate-and-Fire Model

1.4 Generalized Integrate-and-Fire Model

1.5. Quality of Integrate-and-Fire Models

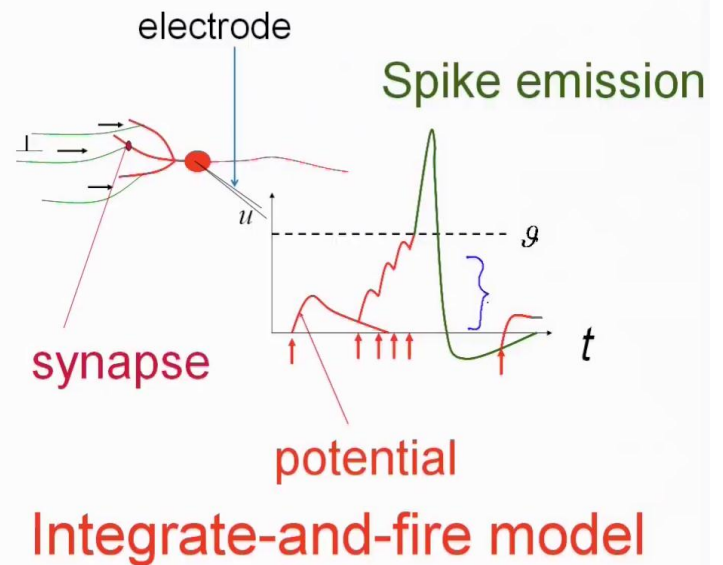


EPFL

Video



Neuronal Dynamics – 1.2. The passive membrane



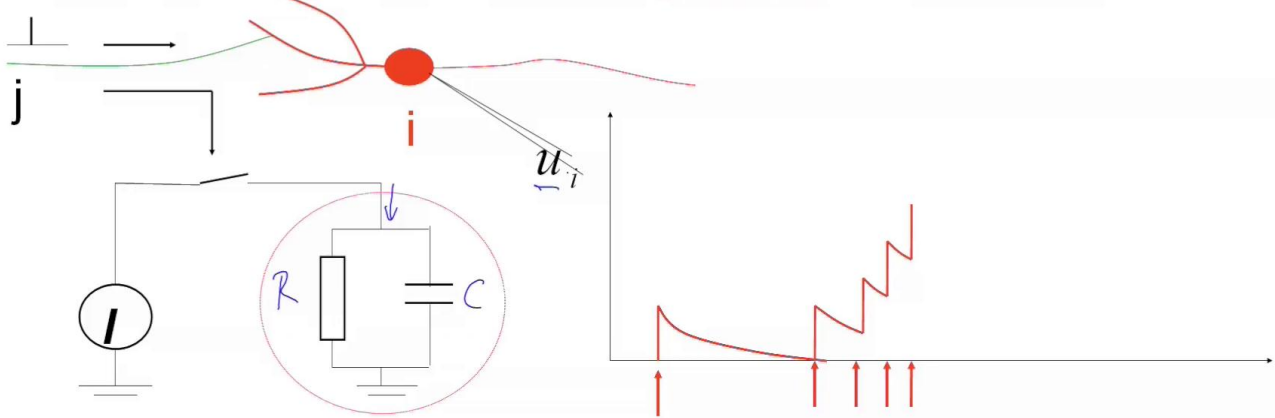
Welcome back to the class on neuronal dynamics. This is part two of week one. After the overview, we can now turn to the model of a passive membrane. In the previous lecture, we have already seen the case of an integrate-and-fire model as an example of a simplified neuron model. In an integrate-and-fire model, a pulse that comes in causes some response. This response can be measured with an electrode. If several pulses come in, these pulses add up linearly. The responses add up linearly. And at some point, in an integrate-and-fire model, the potential hits the threshold, and out goes a spike. If you talk about a passive membrane, we focus on the subthreshold regime, where everything is linear.

Notes

Summary



Neuronal Dynamics – 1.2. The passive membrane



Subthreshold regime

- linear
- passive membrane
- RC circuit

And the simplest example of a model of a passive membrane is the model of a linear circuit, and particularly, an RC circuit. An RC circuit is called RC because it has a resistor, R , and a capacity, C . Now suppose a pulse comes in. The pulse closes the lever for a very short moment of time so that a current pulse is delivered on to the RC circuit. As a result of this, the response of the potential, U , will be an exponentially decaying pulse. This is the impulse response function of the linear circuit-- of the RC circuit. If several pulses come in, these linear responses are simply added.

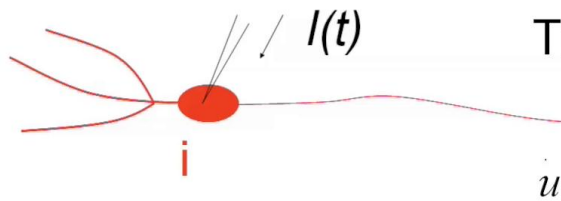
Notes

Summary

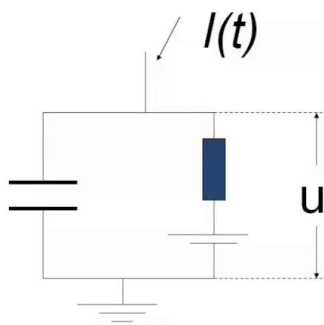


1m 02s

Neuronal Dynamics – 1.2. The passive membrane



Time-dependent input



*Math development:
Derive equation*

So far for pulse input. But you can also study this RC circuit for an arbitrary time-dependent input, which will cause some kind of voltage response. The question, then, is, are we able to predict the voltage response for any arbitrary time-dependent input. And the answer is yes. Because the RC circuit can be described mathematically by a linear differential equation, which I will derive now.

Notes

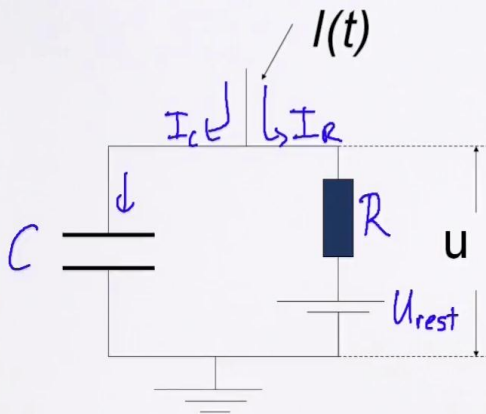
Summary



2m 10s

Passive Membrane Model

$$I(t) = I_R(t) + I_C(t)$$



$$C = \frac{Q}{U} \Rightarrow U \cdot C = Q$$

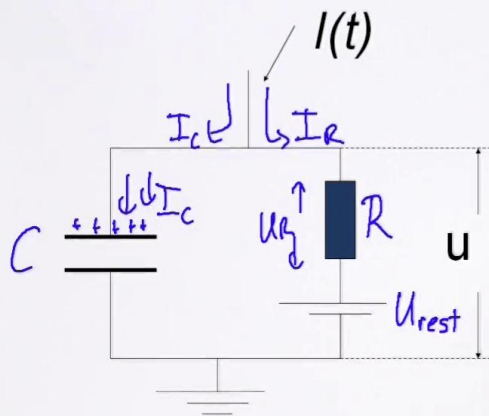
Let's look now at our RC circuit, and derive a mathematical equation in order to describe the properties of this circuit. So our RC circuit is called RC because it's characterized by a resistor, R, and a capacity, C. To keep the treatment slightly more general, I also introduced, here, the sign of a battery. This is a battery with voltage, which I call U rest. If there is no current injected into the circuit, the voltage measured across the circuit would be exactly U rest. U rest stands for resting voltage. OK. Now, let's inject some current. The total current will split up into a part that goes on to the capacitor and a part that goes on to the resistor. Let's try to write this down. So the total current is conserved. So the resistive current and the capacitive current, together, must add up to the current that is injected. So what can we say about the capacity of current? Let us recall that the capacity is defined as charge over voltage. Let me move the voltage to the other side. So I have U times C equals Q. Now what is a current? A current is charge divided by unit of time. So I will look at d dt Q.

Notes

Summary



Passive Membrane Model



$$I(t) = I_R(t) + I_c(t)$$

$$I(t) = \frac{1}{R}(U - U_{rest}) + C \cdot \frac{dU}{dt}$$

$$C \cdot \frac{dU}{dt} = -\frac{1}{R}(U - U_{rest}) + I(t)$$

$$C = \frac{Q}{U} \Rightarrow U \cdot C = Q$$

$$C \cdot \frac{dU}{dt} = \frac{d}{dt}Q = I_c$$

$$U_R = R \cdot I_R \quad ; \quad U = U_{rest} + U_R$$

$$U - U_{rest} = R \cdot I_R$$

The change of the charge on this capacitor-- this will be, exactly, my charging current, my capacitive current, I_c , which I can now calculate as C times du/dt . Let me block this into the equation. So I_c is C times du/dt . What can I say about the resistor? Well, a resistor is defined by Ohm's law. The voltage is the resistance times the current. Now we have to be a little bit careful here. With current, I mean the current flowing through the resistor. And with voltage, U mean the voltage across the resistor. But this is not the total voltage. The total voltage, U , is the battery voltage, plus the voltage across the resistor. In other words, the voltage across the resistor is U minus U_{rest} . So I can take the result for I_R . The resistive current is 1 over R , U minus U_{rest} . So this is the total current. Now it's convenient to move this to the left hand side, but keep the sign. So it's the same as moving this term here, to the outside. But let me copy this, move this to the left hand side. C times du/dt equals minus 1 over R , U minus U_{rest} plus I of t . Sometimes the equation is written in a slightly different form.

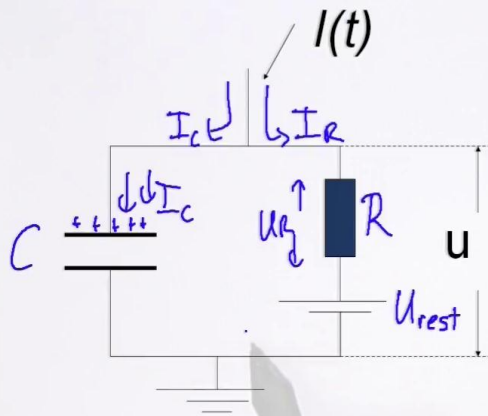
Notes

Summary



4m 52s

Passive Membrane Model



$$I(t) = I_R(t) + I_c(t)$$

$$I(t) = \frac{1}{R}(U - U_{rest}) + C \cdot \frac{dU}{dt}$$

$$C \cdot \frac{dU}{dt} = -\frac{1}{R}(U - U_{rest}) + I(t)$$

$$\left\| \underbrace{R \cdot C}_{\tau} \cdot \frac{dU}{dt} = -(U - U_{rest}) + R \cdot I(t) \right\|$$

$$C = \frac{Q}{U} \Rightarrow U \cdot C = Q$$

$$C \cdot \frac{dU}{dt} = \frac{d}{dt}Q = I_c$$

$$U_R = R \cdot I_R$$

$$U - U_{rest} = R \cdot I_R$$

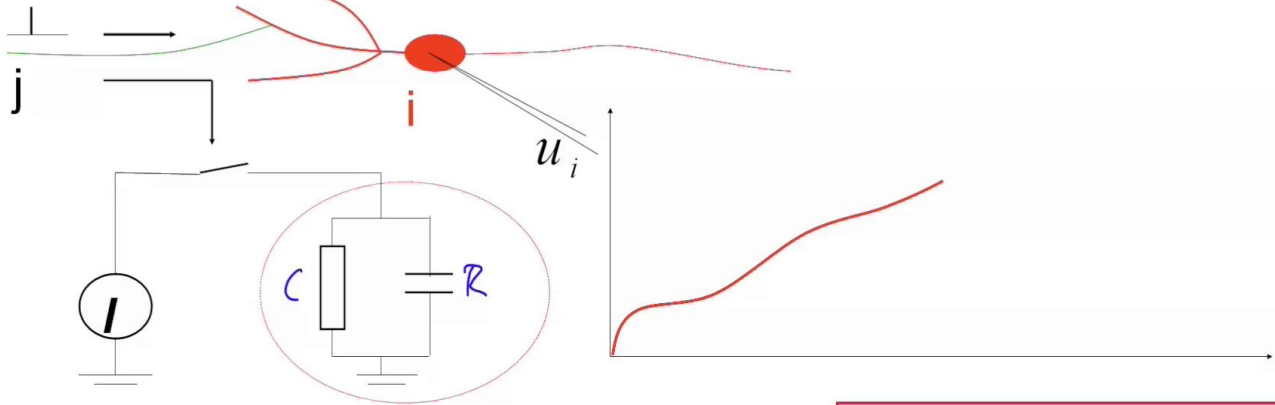
If you multiply both sides of the equation by R, by the value of the resistor, we get R times C du dt equals minus U minus U rest plus R times I of t. This is the final equation. Let's look at the units of this equation. This is voltage. So the equation on the right hand side has units of voltage. This is the battery voltage. R times I-- look back at Ohm's law-- is, again, units of voltage. So the left hand side also has units of voltage. This part here is voltage divided by time. That means R times C, together, must have units of time. And this is why I introduce a shorthand notation, Tau, or "Tao", the time constant of this differential equation. RC equal Tau is the time constant of this RC circuit.

Notes

Summary



Passive Membrane Model



Math Development:
Voltage rescaling

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

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

And this is the equation we have here, on the next slide. This is the equation I just derived. R is the resistor, C is the capacitor. But R times C is now summarized as the membrane time constant. You see that, in this electrical diagram, the battery, U_{rest} , is no longer there. Indeed, it's possible, mathematically, to make it disappear, and have a simplified equation where I introduce a new variable, V, as U minus U_{rest} . Again, let me show you how this works.

Notes

Summary



8m 37s

Passive Membrane Model

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

$$V = u - u_{rest}$$

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

$$\frac{dV}{dt} = \frac{du}{dt} - \cancel{\frac{du_{rest}}{dt}}$$

$$\tau \cdot \frac{d}{dt} V = -V + RI(t);$$

$$V = (u - u_{rest})$$

Mathematically, I set V equals U minus U rest. Now if I take the derivative of V, dV dt, this is du dt minus the derivative of U rest. But U rest is a constant parameter, so the derivative disappears. Therefore, I have dV dt equals du dt. Or I can set, here, Tau d dt V is the same as du dt. But du dt is this equation. This equation has U minus U rest-- by definition, this is V-- plus R times I of t. So in the new variable, V, the battery voltage U rest has disappeared.

Notes

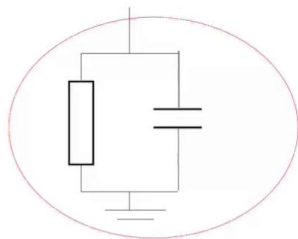
Summary



9m 23s

Passive Membrane Model/Linear differential equation

$$\tau \cdot \frac{d}{dt} V = -V + RI(t);$$



Free solution:
exponential decay

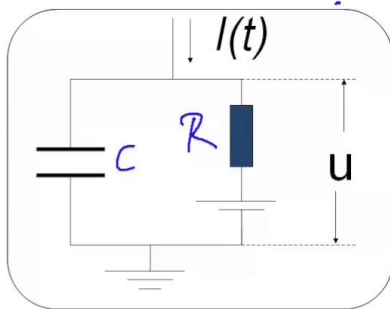
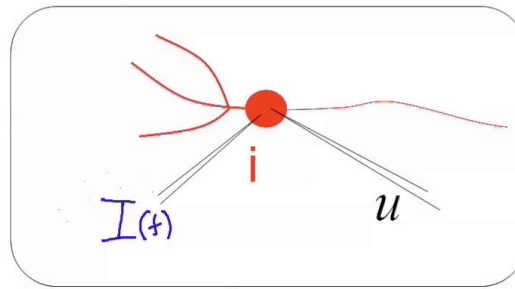
To summarize, the passive membrane is described by a linear differential equation, which describes the evolution of a voltage. A potential battery voltage is included in the derivative definition of this new variable, V, which appears in both sides of the equation. Now let's look at the type of solutions that this equation may have. Suppose, for the moment, that there is no input. So this is gone. And now the question is, what's the solution. Well, this is a linear differential equation with a time constant Tau. Suppose that, for some reason, I start at a value V0. There's no further input. Some input may have brought me to V0. But now it's just freely evolving in the absence of any further input. The solution of such a linear differential equation is an exponential decay back, with a time constant Tau, which is exactly this membrane time constant, the time constant of the linear differential equation than I have introduced before. Quite generally, linear differential equations occur in many areas of science, of physics, of chemistry. A famous example is radioactive decay. Exponential decay is the solution of a one-dimensional differential equation.

Notes

Summary



Triangle: neuron – electricity - math



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

So quite often, in this class, we will work along the triangle. On the top of the triangle, we have the experimentalist, which injects some current I of t into a neuron. And he might be able to record, with a different electrode, the voltage of the neuron-- the potential-- the membrane potential of the neuron. Now we can try to predict the membrane potential by using an equivalent electrical circuit. The simplest case would be a circuit with just a resistor, R , and the capacity, C . But we will see more complicated circuits later on in this class. Now the circuit itself can be analyzed mathematically. And it's often possible to write down a differential equation that describes the properties of the circuit, and ideally, also, the properties of the neuron. So in this first class, I just talked about the passive membrane, and we went around the triangle for the case of the passive membrane. But in other lectures, over the next weeks, we will consider more complicated models of a neuron, which leads to more complicated circuits, which leads to slightly more complicated differential equations. So if we want to understand the properties of a neuron, we can use arguments from electricity, and we can use arguments from math.

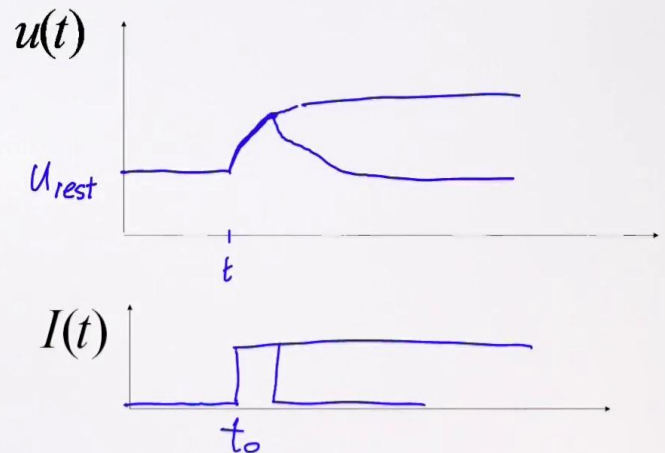
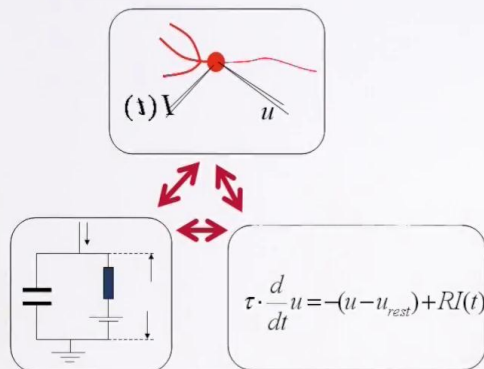
Notes

Summary



12m 04s

Pulse input – charge – delta-function



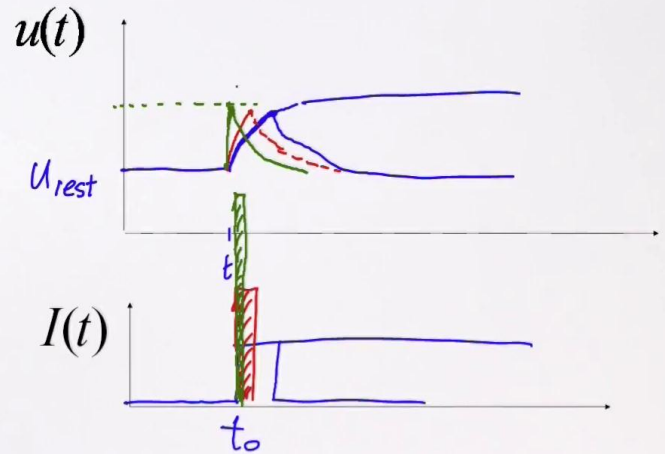
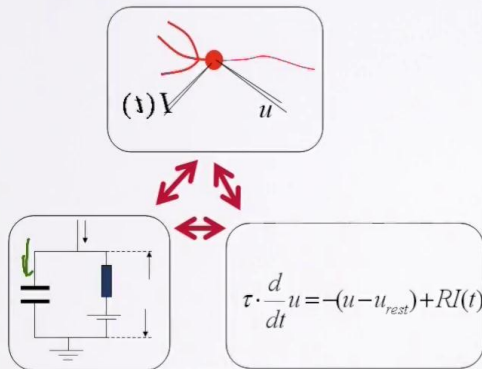
Let's see how this works. Let's look at pulse input. So for the moment, as input, I use a step current. The current is 0. At some time t_0 -- it "naught"-- it switches to a new value. The question then, is, how is the voltage of this RC circuit going to respond, or equivalently, how is the differential equation going to respond, or-- plus, in neuroscience-- how is the neuron going to respond to a step current input. The voltage, in response to the step current input, will be a constant at the battery voltage U_{rest} . It's just sitting there. And then, at time t_0 , it will jump, like the input current. But it will move to a new value. It will approach a new value. And the approach is, again, going to be exponential with time constant τ , the time constant of the differential equation. Now suppose I stop the stimulation after some time, say, here, and we go back to 0. In this case, the voltage trajectory will be the same. The differential equation of the neuron, or the circuit, does not know that the input is about to change. But then, when you change, the two curves become different, it will return, exponentially, back to the resting value U_{rest} . Now let's do the following.

Notes

Summary



Pulse input – charge – delta-function



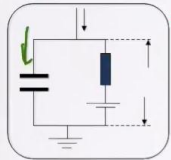
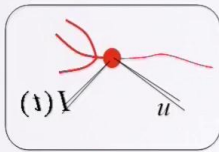
Let's consider a pulse which is shorter. It's half as long, but twice as high, like this. So the surface under the pulse is the same as before. Now what's the surface under the pulse? The surface under the pulse corresponds to the charge-- the total charge delivered onto the circuit. Now with a pulse twice as high, the response will go up twice as fast. And then, it stops here until it turns, exponentially, to the resting value. Now imagine that I make the pulse even shorter-- again, half as long as the red one-- but twice as big. So it's now a really huge pulse, in a very, very short amount of time. The rise is, again, much faster. And it will end here. And then afterwards, I have exponential decay. So what you see is that, if I make the pulse shorter and shorter while keeping the area under the pulse the same-- which means, while keeping the total charge deposited on the circuit the same-- the voltage response always has to same amplitude. And in the limit that the pulse becomes very short, it's just a jump-- a jump from the previous value to a new value. In the limit that the pulse becomes very, very short, I can say the total charge, Q , which corresponds to the surface under the pulse, is deposited in a very, very short time.

Notes

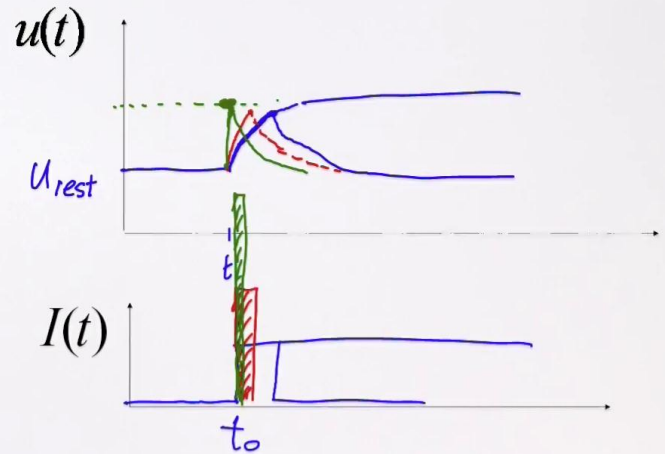
Summary



Pulse input – charge – delta-function



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



$$I(t) = q \cdot \delta(t - t_0)$$

Pulse current input

And this notion of a given charge deposited in a very short time is denoted by the so-called Dirac delta function. So the Dirac delta function is a mathematical abstraction. It's a mathematical abstraction because no experimentalist is able to deposit a certain amount of charge in an infinitely short time. It's a mathematical abstraction. However, the mathematical abstraction makes sense because the jump is always to the same value, however short the pulse is, as long as it's short enough.

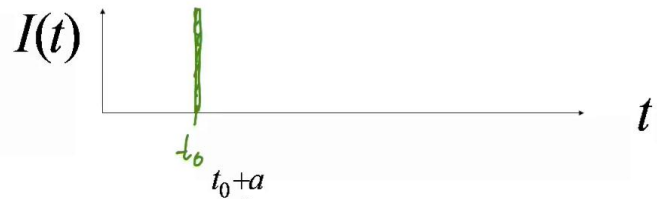
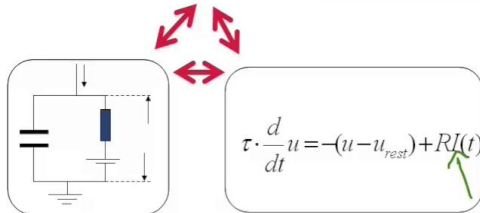
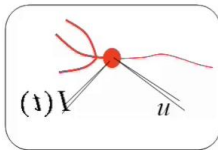
Notes

Summary



Dirac delta-function

$$I(t) = q \cdot \delta(t - t_0)$$



$$1 = \int_{t_0-a}^{t_0+a} \delta(t - t_0) dt$$

$$f(t_0) = \int_{t_0-a}^{t_0+a} f(t) \delta(t - t_0) dt$$

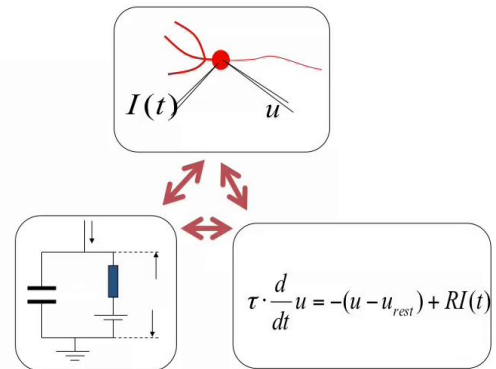
So this pulse-- the delta function at time t_0 cannot really be drawn, because the pulse should be very, very high and very short. That's impossible. So as such, the object-- Dirac delta function-- it's really an operator-- does not make a lot of sense. However, it does make sense, because we use this Dirac delta function in the differential equation, which we need to integrate. And once you integrate over the current pulse, you get back the charge. Once you integrate over the Dirac delta function, you get very useful results. And one of the two parts of the definition is that, if you integrate over the Dirac delta function from a value before t_0 to after t_0 , then the integral is always normalized to 1. And the more interesting property is that, if you integrate over the Dirac delta function, together with some other function, f -- some arbitrary function f of t -- then it just peaks out the time point t_0 as a result.

Notes

Summary



Passive membrane, linear differential equation



*Spend 10-15 minutes on Homework 1.1 now!
If you have difficulties, watch lecture 1.2detour.*

Now with this, let me come to the end of this part. In this class, we will quite often walk around the triangle from experimental neuroscience, to circuits, to math. And the famous example is the Hodgkin-Huxley model, that we will see next week, or the integrate-and-fire model, that we will talk about this week. And the first example has been the passive membrane. In order for you to get used to working with these kinds of differential equations, please spend, now, 15 minutes on the following exercise. Some of you are used to working with these kinds of linear differential equations. Others need to be reminded. So everybody, please try to get a solution of the following differential equation in the case of some current injection.

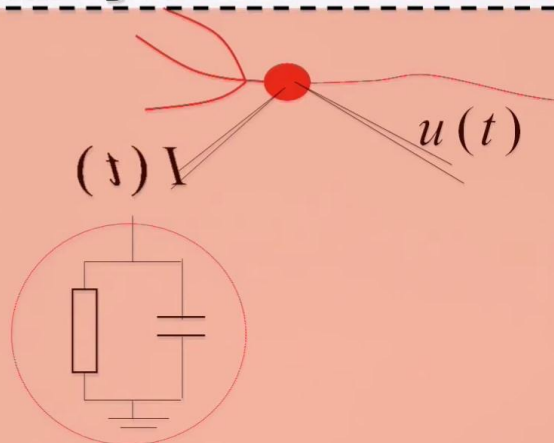
Notes

Summary



19m 37s

Neuronal Dynamics – Exercises 1.2 = Homework 1.1



$I_1(t)$

Step current input:

$I_2(t)$

Pulse current input:

$I_3(t)$

arbitrary current input:

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

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

**Calculate the voltage,
for the
3 input currents**

And the current injections we consider are, first, a step current injection, a pulse current injection, and finally, an arbitrary current injection. And in the context of this pulse current injection, I would like you to work through this iteration that the surface of the pulse is always the same, but the pulse becomes shorter and shorter. So please spend some time with the exercises before we continue with the lesson.

Notes

Summary



20m 36s