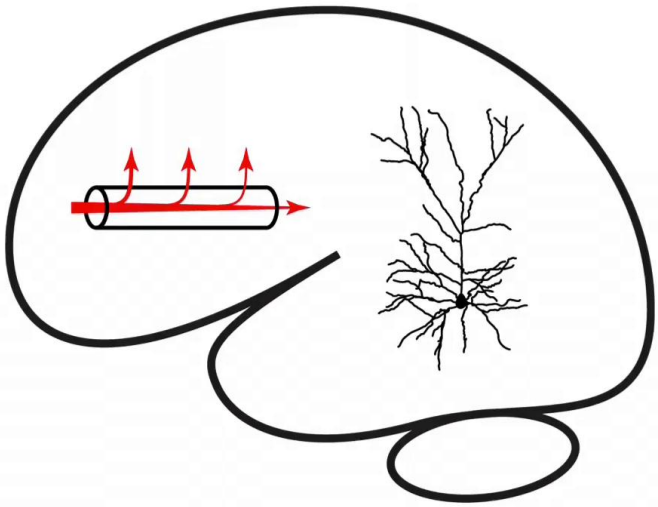
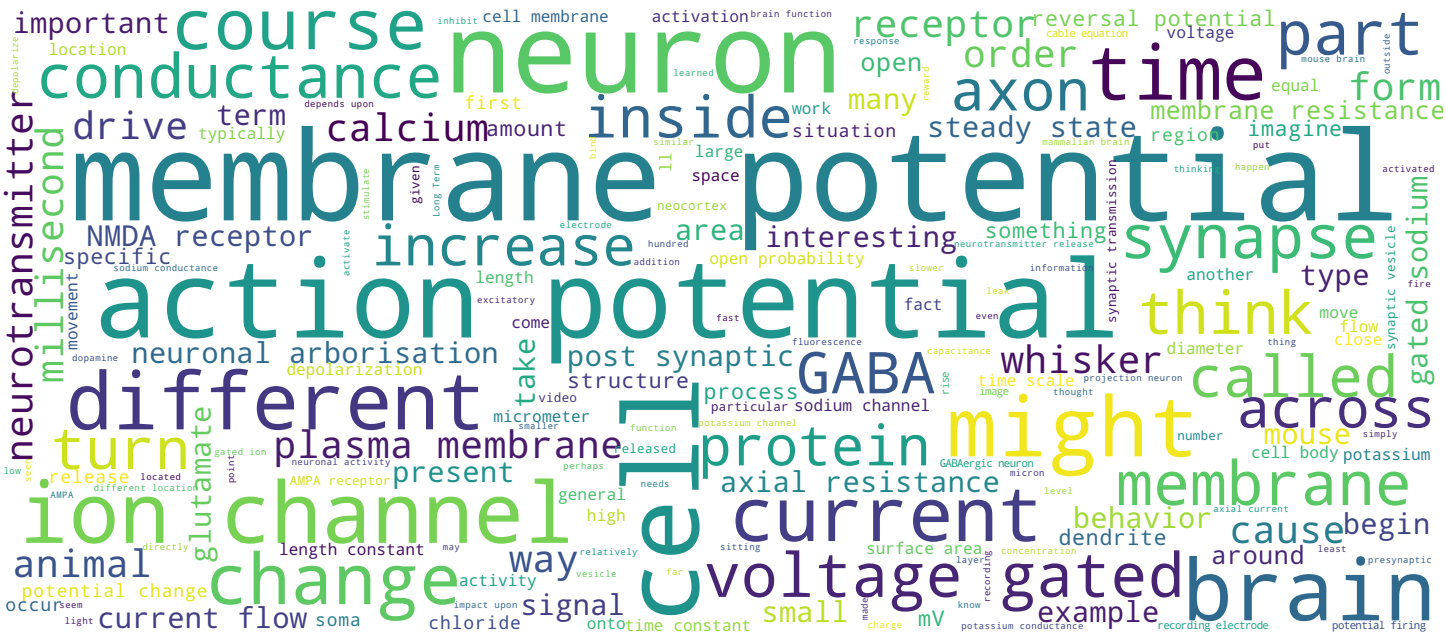


1.5 Cable properties

Cellular Mechanisms of Brain Function

Prof. Carl Petersen



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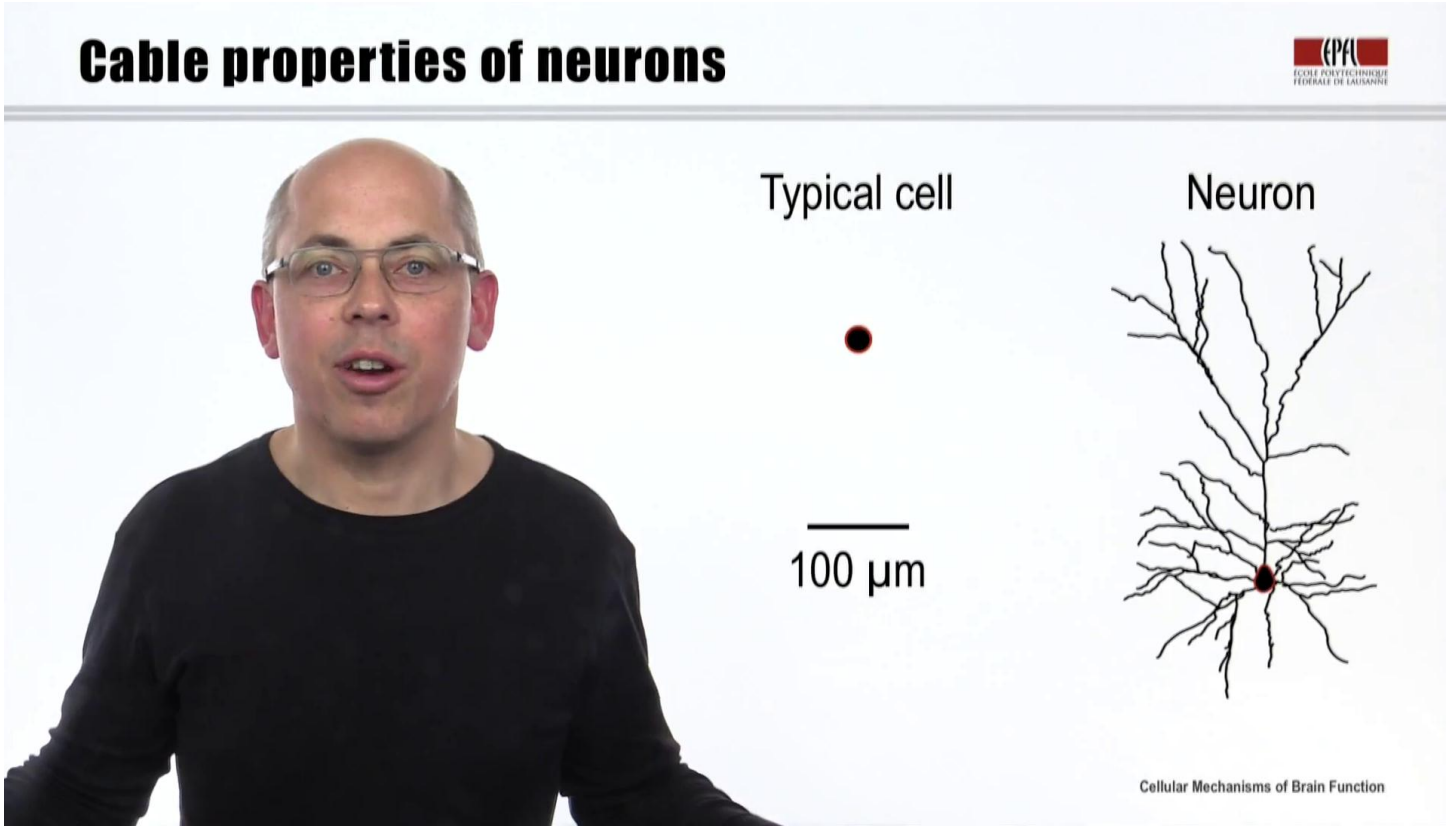


So far, we have learned that the cell membrane contains ion channels of selective permeability for specific ions. Ionic currents flowing across the cell membrane can then drive membrane potential changes that are filtered, in time, by the membrane capacitance. We've considered the cell to be small and round, and therefore, isopotential -- that is, all parts of the cell membrane have the same electrical potential. And, indeed, many types of cells in our body are small, round, and isopotential. However, this is very far from the situation when it comes to considering neurons. Neurons, in fact, have very extensive arborisations. These outgrowths from the cell body are filled with cytoplasm and covered by a plasma membrane, just like the cell body, but much thinner. Whereas the cell body typically has a diameter of 10 microns, your neuronal arborisations may have diameters of the order of one micrometer or less. Typically, these branches of the neuron extend for hundreds of microns. In the largest arborisations, the process can extend several meters. Think of neurons in the giraffe brain that need to communicate along the length of the spinal cord. It turns out that the neuronal arbors can be considered as leaky electrical cables with capacitance. These cables transmit and transform the electrical signals generated in one part of the neuron to other parts of the neuron.

Notes

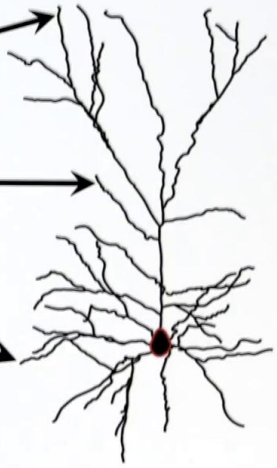
Summary

0m 04s

Spatiotemporal V_m dynamics

In general, membrane potential (V_m) differs according to location across the neuronal arborisation.

$V_m(x_1, y_1, z_1, t) \neq V_m(x_2, y_2, z_2, t) \neq V_m(x_3, y_3, z_3, t)$



Cellular Mechanisms of Brain Function

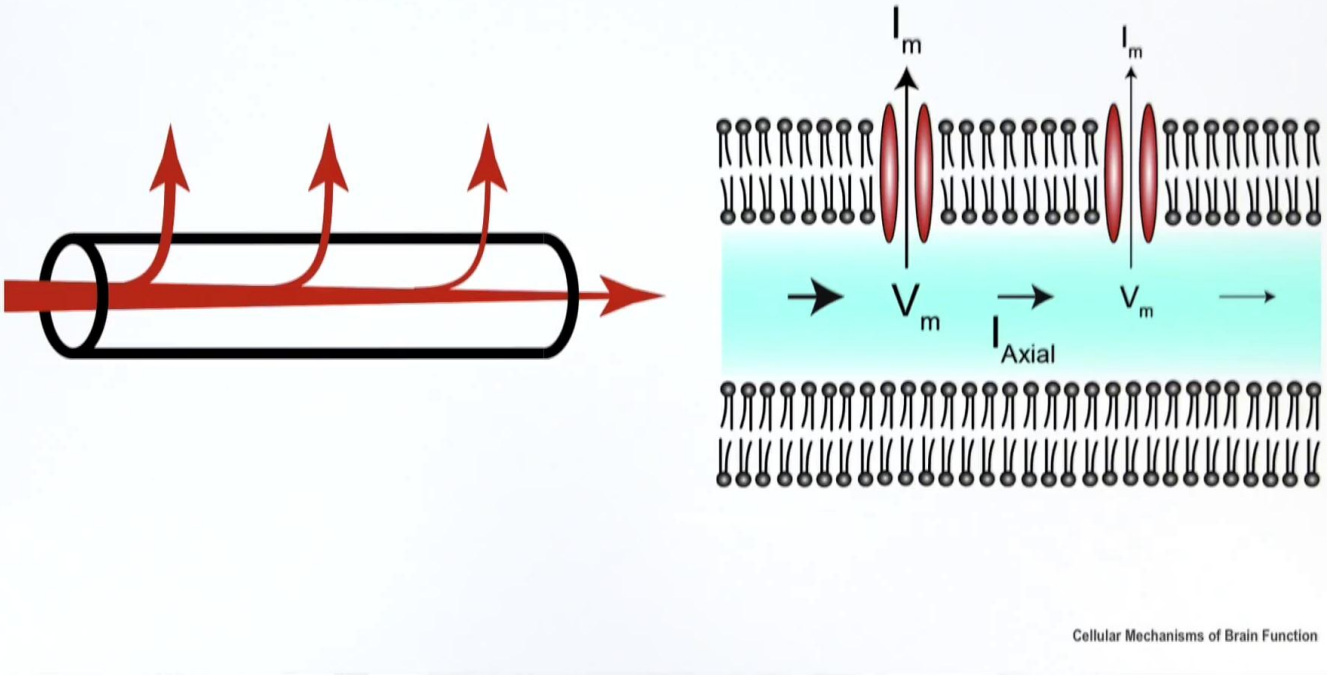
The most important point to realize is that the membrane potential at different locations across the neuronal arborisation will be different. Membrane potential can fluctuate strongly in one part of a neuron and might make little impact upon other regions of the neuron. To understand why, in this lesson we'll study the basic principles of leaky electrical cables with capacitance.

Notes

Summary

1m 48s

Leaky cables



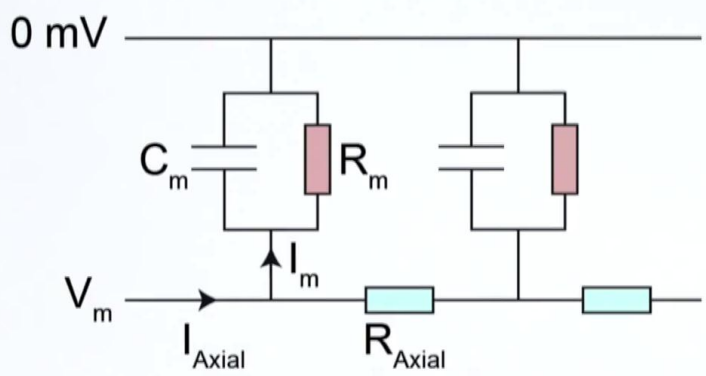
The simplest analogy to think about in terms of neuronal arborisations and ionic current flow in these arborisations is to think of a watering hose as you might use in your garden. Water influx across this leaky cable will be high at the input end, and if we make small holes in this garden hose, water will leak out along the length of this tube. The pressure at different points in the tube will differ. Here we'll have a high water pressure, and as the water leaks out, at the far end of the water hose you'll have a lower pressure. We can think of the same thing in terms of the arborisation. We have intracellular cytoplasm, we have axial current flow, ionic flow of electricity down the length of the center of the arborisation. This is flanked by lipid bi-layer membranes, and part of that current flow will leak out across the ion channels that are present in the plasma membrane. The current flow that enters here will therefore decrease in each part of the cable by the amount of current that leaks out across the plasma membrane. In addition, of course, we must remember that the lipid bilayer is an important capacitor, and we therefore need to think of capacitance of the axial current in part goes to flow across the ionic channels, in part charges the membrane, and in part drives the additional current flow down the length of the arborisation.

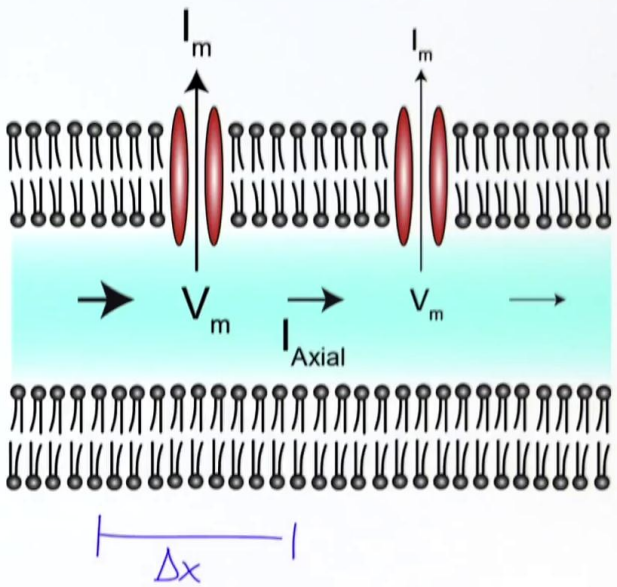
Notes

Summary

2m 16s

Leaky cables with capacitance





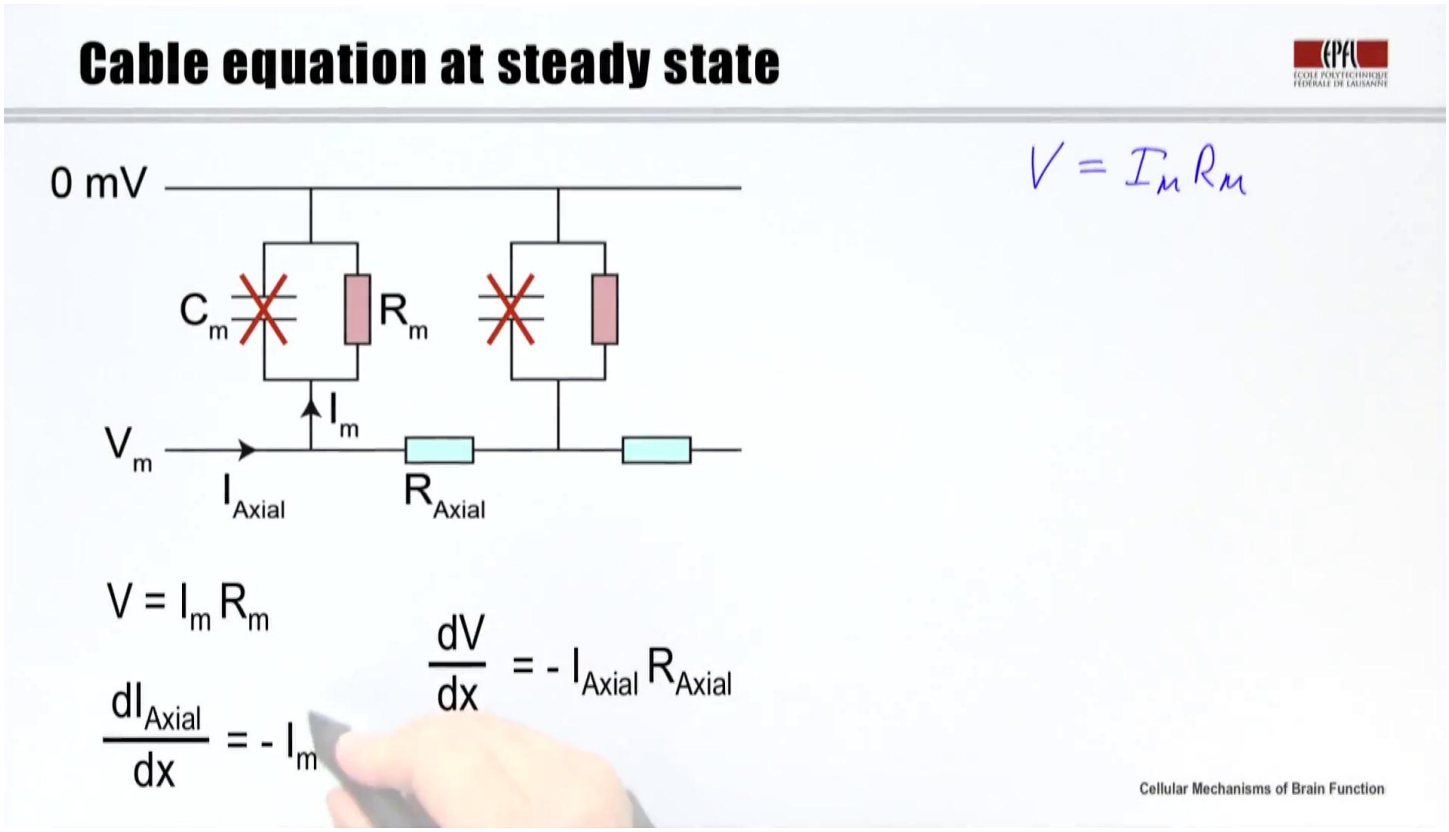
Cellular Mechanisms of Brain Function

We can draw the electrical equivalent of any small length of this cable through thinking about the capacitance across that unit length provided by the surface area of the lipid bilayer. There's the membrane conductance provided by the numbers and types of ion channels present in that part of the membrane, and of course, we have the axial current flow that flows down the length of the arborisation, changing potential depending upon the axial resistance that's offered to that current.

Notes

Summary

4m 03s



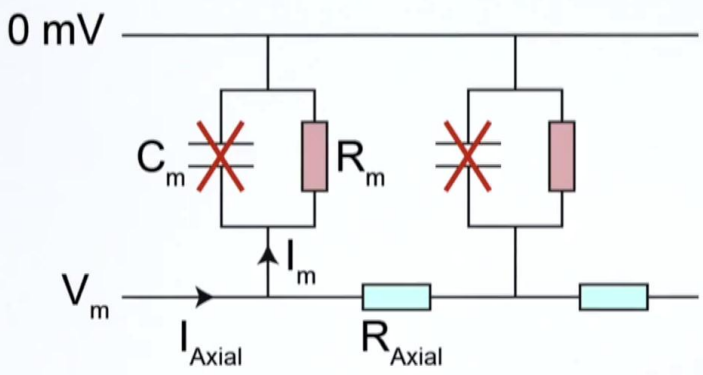
In general, we can write cable equations that describe this electrical situation. The simplest one is the steady-state cable equation where we forget about time-dependent changes and if we forget about time-dependent changes, we don't need to consider capacitance because current only flows into a capacitor during charging, when which is obviously not at steady state. The membrane potential at any given point in this cable is therefore given by the trans-membrane current multiplied by the trans-membrane resistance. Ohm's Law: V = IR. We can also see that the drop in potential between adjacent points in the cable depends upon the axial resistance, and the change in potential across arbitrarily small areas of the cable depend upon the current and the resistance, axially. Finally, we can see that the change in axial current depends upon how much of that current leaves across the plasma membrane, and so, the change in axial resistance is equal to minus the membrane current. We can take these three equations and solve it for the cable equation in one dimension at steady state. We begin by Ohm's Law. From this equation we can see that Im can also be written as minus dI Axial over dx.

Notes

Summary

4m 42s

Cable equation at steady state



$$V = I_m R_m$$

$$\frac{dI_{Axial}}{dx} = -I_m$$

$$\frac{dV}{dx} = -I_{Axial} R_{Axial}$$

$$V = I_M R_M$$

$$I_m = -\frac{dI_A}{dx}$$

$$V = -R_M \frac{dI_A}{dx}$$

$$I_A = -\frac{1}{R_A}\frac{dV}{dx}$$

$$\frac{dI_A}{dx} = -\frac{1}{R_A}\frac{d^2V}{dx^2}$$

$$V = \frac{R_M}{R_A}\frac{d^2V}{dx^2}$$

Cellular Mechanisms of Brain Function

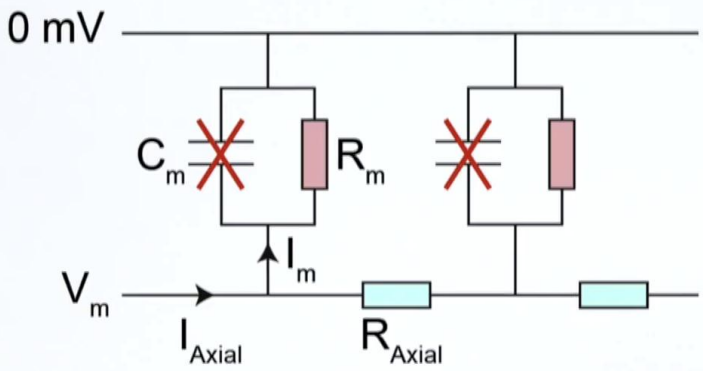
And so, the membrane potential is therefore equal to: minus Rm, dI axial by dx. The axial current we can rewrite here as being one over R axial, dv by dx. Differentiating this one more time gives us the second derivative here with respect to space. We can then put this equation in here, and finally we solve for Voltage as being the ratio of the membrane resistance to the axial resistance times the second derivative with respect to space.

Notes

Summary

6m 21s

Cable equation at steady state



$$\frac{d^2V}{dx^2} = \frac{R_{Axial}}{R_m} V$$

$$V = V_0 e^{-(x/\lambda)}$$

$$\lambda = \sqrt{(R_m / R_{Axial})}$$

$$V = I_m R_m$$

$$\frac{dV}{dx} = - I_{Axial} R_{Axial}$$

$$\frac{dI_{Axial}}{dx} = - I_m$$

Cellular Mechanisms of Brain Function

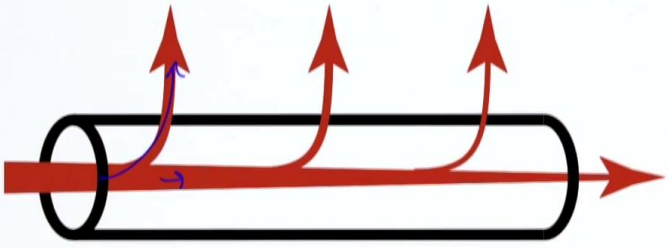
This second order differential equation has a solution with an exponential form with respect to space, length down the cable, and we introduce now the length constant which is equal to the square root of the membrane resistance divided by the axial resistance.

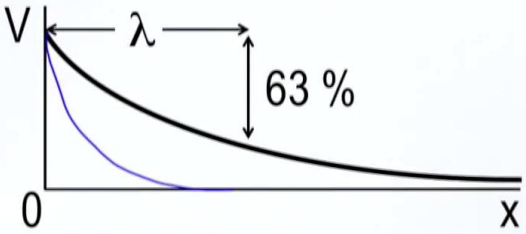
Notes

Summary

7m 09s

Spatial distribution of V_m at steady state





$$\frac{d^2V}{dx^2} = \frac{R_{Axial}}{R_m} V$$

$$V = V_0 e^{-(x/\lambda)}$$

$$\lambda = \sqrt{(R_m / R_{Axial})}$$

$R_A \uparrow$

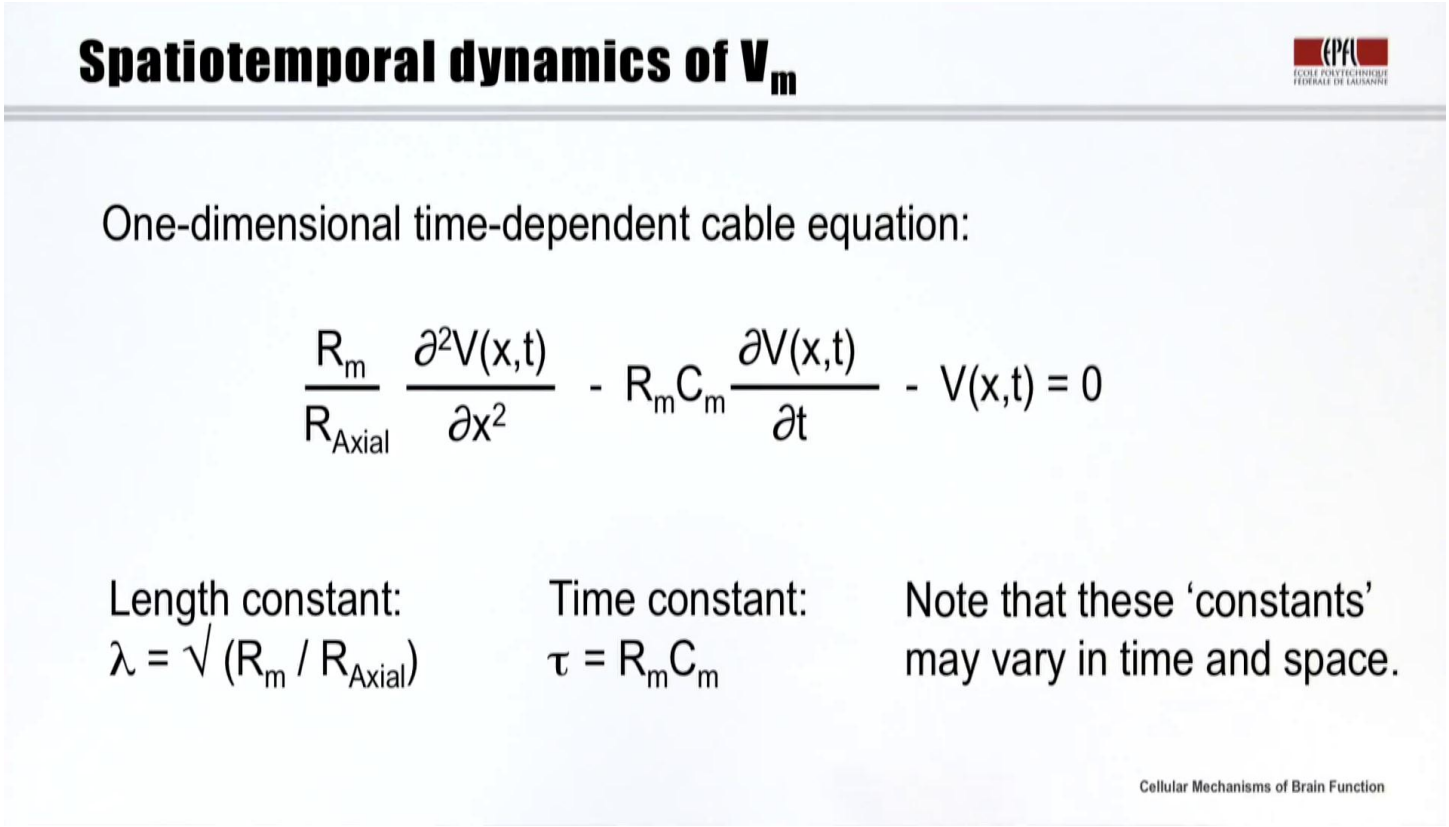
Cellular Mechanisms of Brain Function

We can plot the exponential drop-off of voltage across the length of the cable here as the exponential decay of the membrane potential as the current traverses this leaky cable at steady state. The distance where the potential has dropped to 63% -- that is, 1/e -- is equal to the length constant of the cell, Lambda. Lambda defined as the square root of membrane resistance divided by axial resistance has some obvious intuitive properties. If we were to increase the membrane resistance, there would be less leak of current across the length of the cable, and the voltage would therefore drop less across space. Conversely, if we had a very high axial resistance, then the amount of current that would leak out would increase and it would be more difficult for current to flow down here, and we would therefore get a more sharp drop in the membrane potential. Lambda would be low.

Notes

Summary

7m 33s



The steady-state cable equation can be rewritten to include the time-dependent charging of the membrane capacitance. As we saw last week, there's a time constant involved with charging the membrane that's equal to the product of the membrane resistance and the membrane capacitance, and that can then be included in this larger partial differential equation that describes the one-dimensional, time-dependent spread of voltage across space. We have two important constants: we have a length constant that indicates the length scale over which the membrane potential decreases, and we have another important constant, the time constant, that tells us over what time scale the membrane potential is filtered as it traverses the neuronal arborisation in space and time. It's worth noting that these constants are actually variable in time and space. The membrane resistance depends upon how many ion channels are open at any given time, and in general, the open probability of ion channels is something that's highly regulated, and so, the membrane conductance and membrane resistance varies considerably over time; in fact, that's what drives the membrane potential changes in a cell.

Notes

Summary

8m 46s

Spatiotemporal dynamics of V_m

One-dimensional time-dependent cable equation:

$$\frac{R_m}{R_{Axial}} \frac{\partial^2 V(x,t)}{\partial x^2} - R_m C_m \frac{\partial V(x,t)}{\partial t} - V(x,t) = 0$$

Length constant:
$\lambda = \sqrt{(R_m / R_{Axial})}$

Time constant:
$\tau = R_m C_m$

Note that these 'constants' may vary in time and space.

Cellular Mechanisms of Brain Function

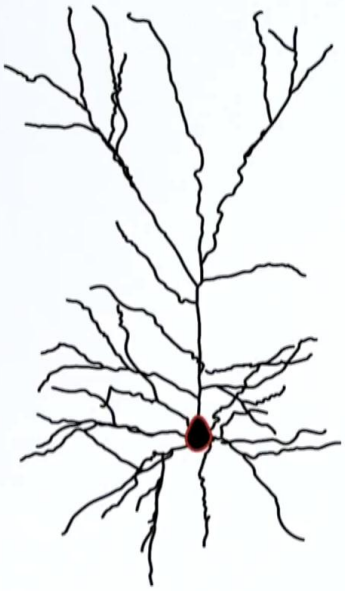
The axial resistance may not change over time, but it certainly changes over space, and so, very thick arbors of the neuron which have large diameters have low axial resistance, whereas the very thin arborisations that might be far from a neuron might have much higher axial resistances and so the membrane time constants are not constant across the neuronal arborisation in space or time, leading to a great deal of complexity.

Notes

Summary

10m 09s

Spatiotemporal dynamics of V_m



In general, there are no analytical solutions to the cable equations for real neuronal structures and numerical computer simulations are therefore typically used.

For example NEURON
www.neuron.yale.edu

Cellular Mechanisms of Brain Function

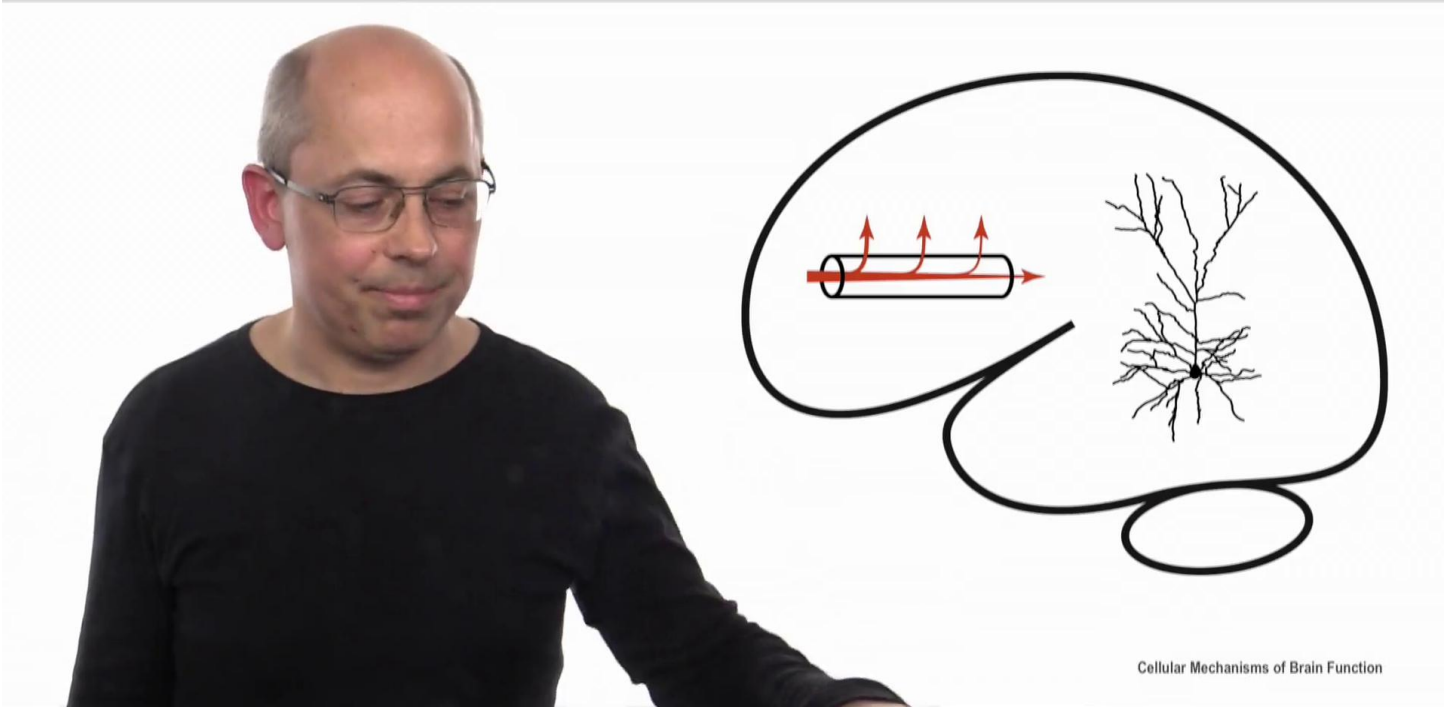
In general, it's fair to say that there are no analytical solutions to the cable equation for real neuronal structures, and therefore, numerical computer simulations are therefore typically used, and one that's particularly used often is the one called Neuron, which is freely available for download at this World Wide Web address, and you can download it and play with these simulations and see for yourself how complicated and interesting the spread of neuronal membrane potential is within individual neurons.

Notes

Summary

10m 45s

Cable properties of neurons

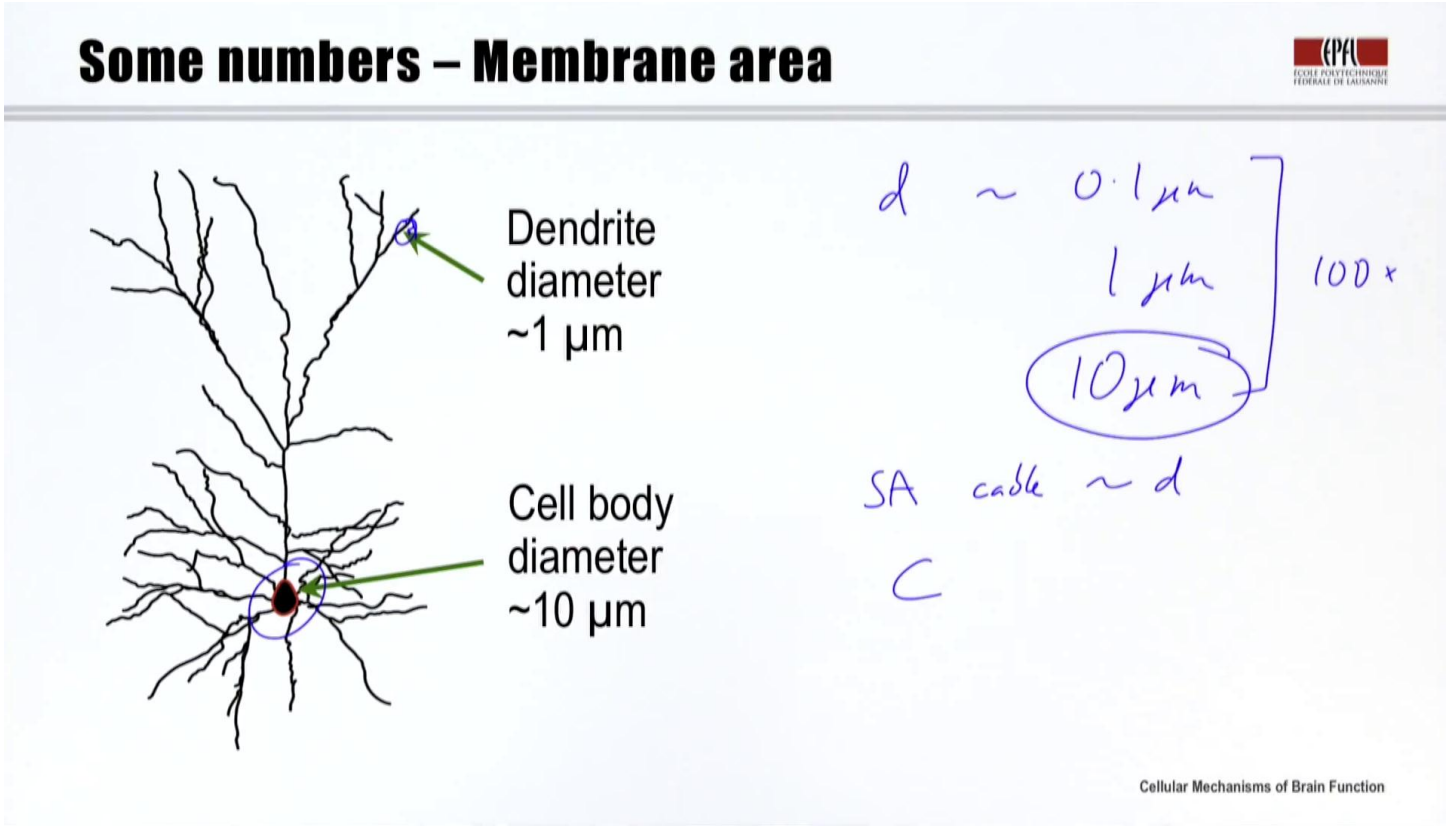


So in terms of membrane potential distributions, neurons are rather complicated. The membrane potential at one point in a neuron differs from that in a different point of a neuron. The membrane potential is filtered as current flows down the neuronal arborisations because there's some leak across the plasma membrane. Equally, membrane potential changes are highly filtered in time. A membrane potential change that occurs rapidly at a distal part of a neuronal arborisation may have very little impact upon the cell soma. In order to get a better feel for how this works, let's have a look at some example neurons and how membrane potential varies across the neuronal arborisation.

Notes

Summary

11m 21s

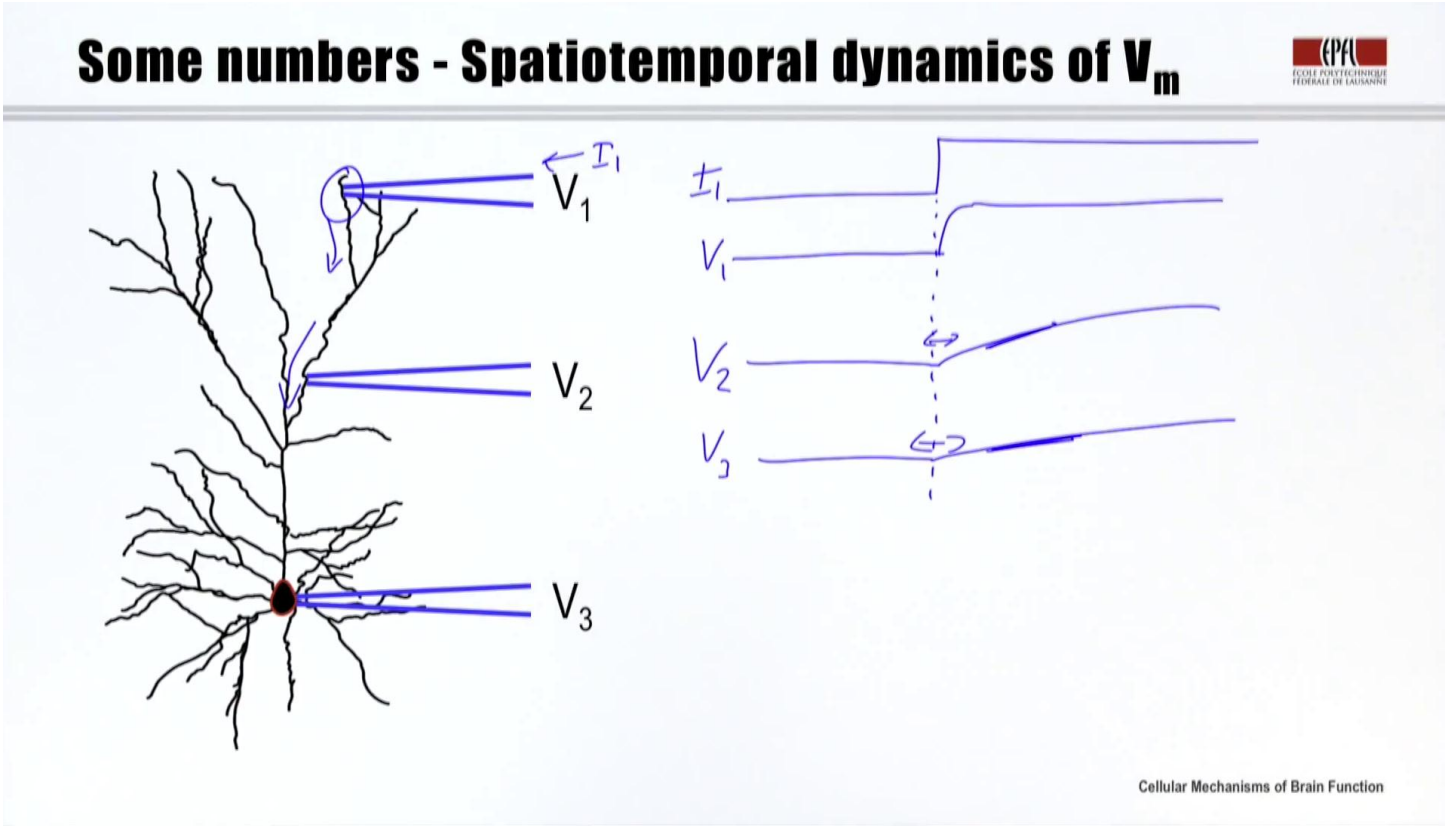


Let's first think about membrane area. In the distal processes of a neuron, the diameter might be 0.1 micrometers or one micrometer, or somewhere in between. The largest diameters are present at the cell body, where the nucleus and the genetic material is also located, and there we have diameters of around ten micrometers. So there's an approximately hundredfold difference in the diameter of the structures that are located at different points across a neuron. The surface area of a cable is approximately proportional to the diameter of that structure. and the surface area, of course, also for a capacitor, tells us how much capacitance there is, and so, the local capacitance at the soma might be a hundred times higher than the local capacitance sitting here in a dendrite. A given amount of current or charge flowing into a small dendrite here with a small amount of capacitance might then give rise to a very large voltage change, whereas the same charge flowing into the cell body will give rise to a smaller change in membrane potential. One might, therefore, imagine very large potential differences across time and space here as conductances open here, compared to slower and smaller membrane potential changes at the cell body, where there's considerably larger filtering due to the large amount of surface area immediately available to this region.

Notes

Summary

12m 12s

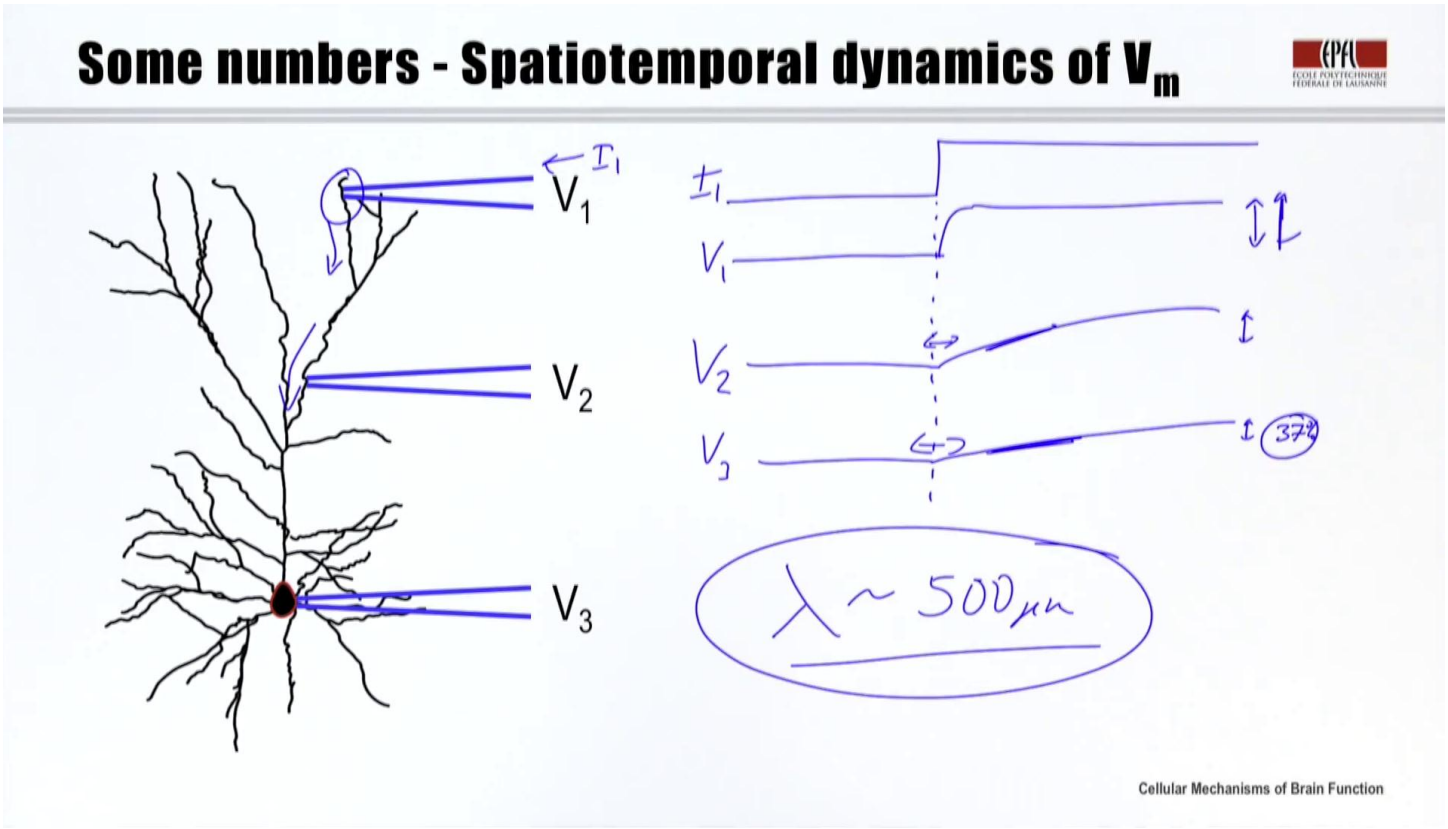


Let's consider a situation where we have three recording electrodes placed across the arborisation of a given neuron. At each electrode we could record the membrane potential at that location, and let's see what happens if we inject current into Location One. Let's take a given point in time where we begin to inject current. At recording electrode one, location one on the dendritic arborisation we're very close to where the current is being injected. There's only a small surface area here. The membrane is rapidly charged and reaches steady state. Current then begins to flow and charge the capacitors along the way and gradually, we charge location two and location three. And each time, there's some delay that increases as the current needs to flow down here, and the rate of charging slows down because the overall amount of surface area that needs to be charged has increased. The steady-state voltage that's reached at these different locations is described by the steady-state cable equation as we saw before, where we have our length constant Lambda that tells us how much of a drop in membrane potential we might expect.

Notes

Summary

14m 07s

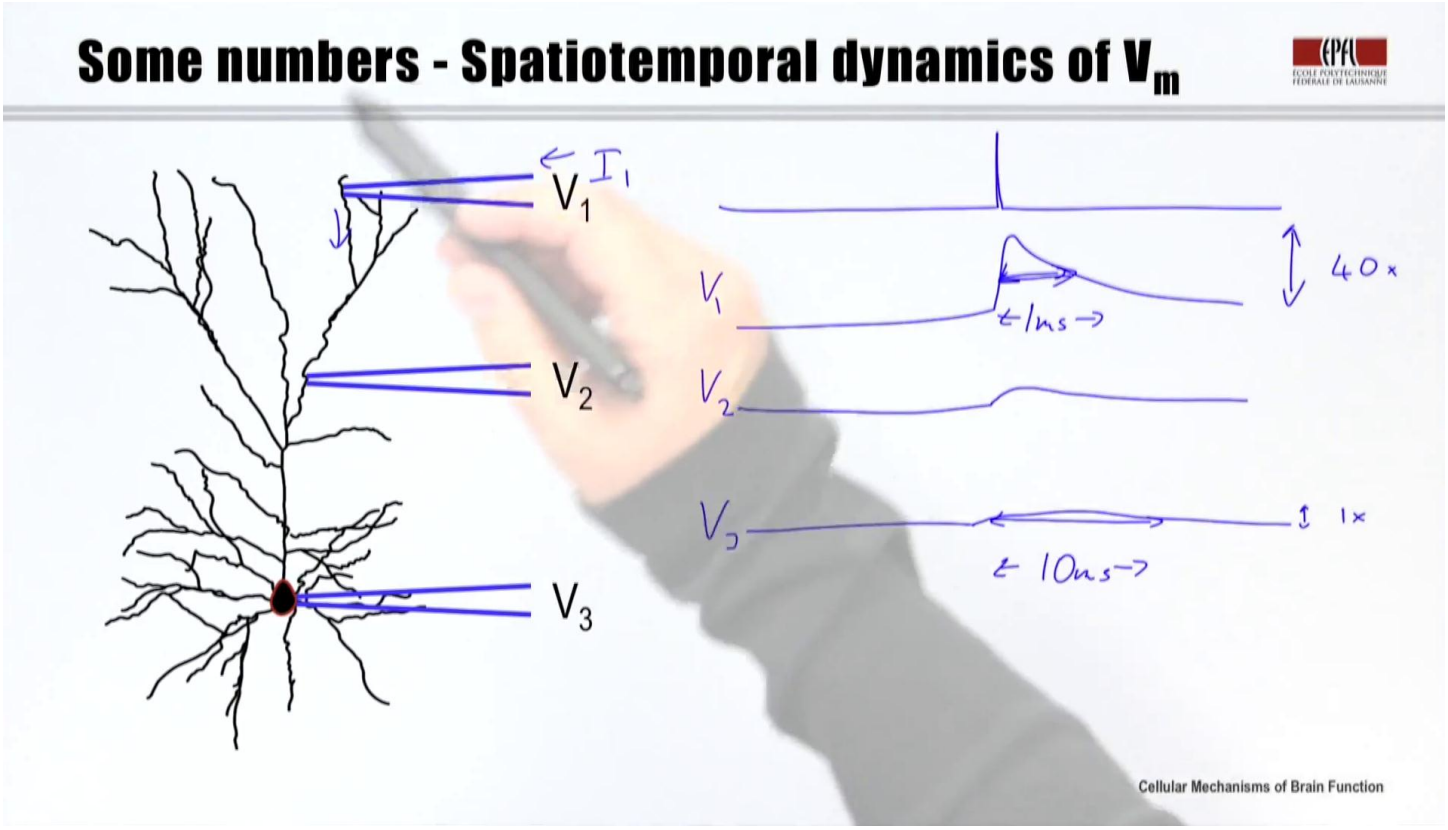


Now, in real neurons, the sizes of this dendritic arborisation might be hundreds of micrometers, and that's exactly the length scale that also the membrane length constant has. And so if we imagine that there's 500 microns between recording electrode one and recording electrode three, we can then say that this change in membrane potential will just be 37% of the steady state membrane potential reached here at this point in the neuronal arborisation. The length constant of neurons, then being on the same scale as the arborisation of a neuron, we realize that there's a considerable impact upon the steady-state membrane potential across this neuronal arborisation.

Notes

Summary

15m 37s

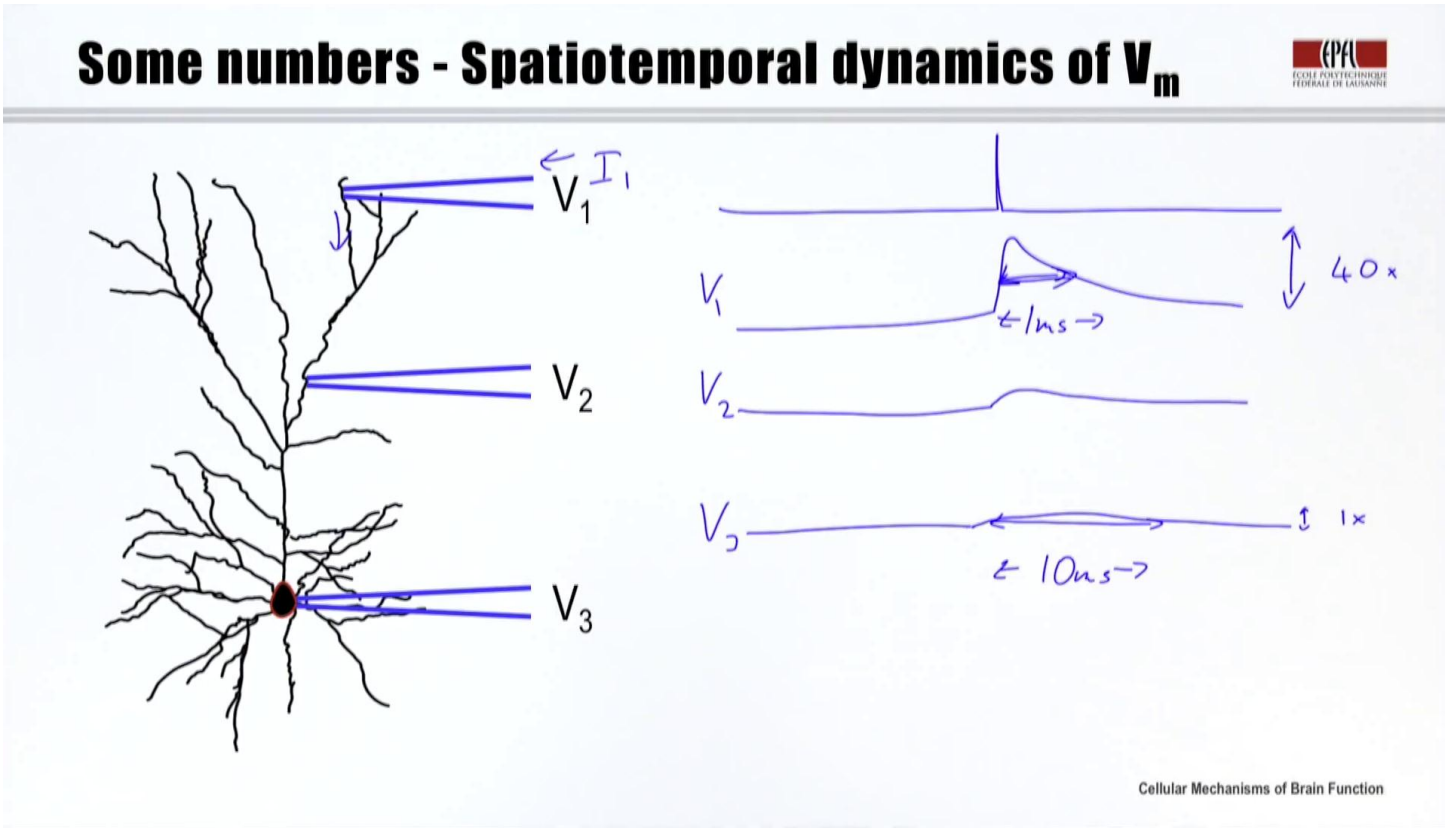


The situation, however, becomes even more extreme when we think about brief current pulses. Again, we consider injecting current here into electrode one, but now just a brief current pulse. We charge the membrane, and then it relaxes, because of the current spread rapidly flowing away from that location. What we see at electrode two, however, is a highly filtered version of this which is much slower, and electrode three, if we see anything at all, is again slower and smaller. The half-time of these membrane potential changes is very different comparing these different locations. The amplitude might be forty times larger at distal dendrites compared to what we see at the soma, and equally, the time course here, which is fast, will be much more extensive at these small membrane potential fluctuations. Here at the soma, we may have around ten milliseconds in terms of the half-width of membrane potential changes, whereas here, at the distal dendrites, we probably have time constants that are much closer to one millisecond. When currents and conductances are opening at different times across different locations of a neuronal arborisation, you can see that there will be very complex spatiotemporal dynamics where the fast, large signals taking place here are strongly filtered, giving rise to smaller amplitude, longer duration potentials at the soma.

Notes

Summary

16m 27s

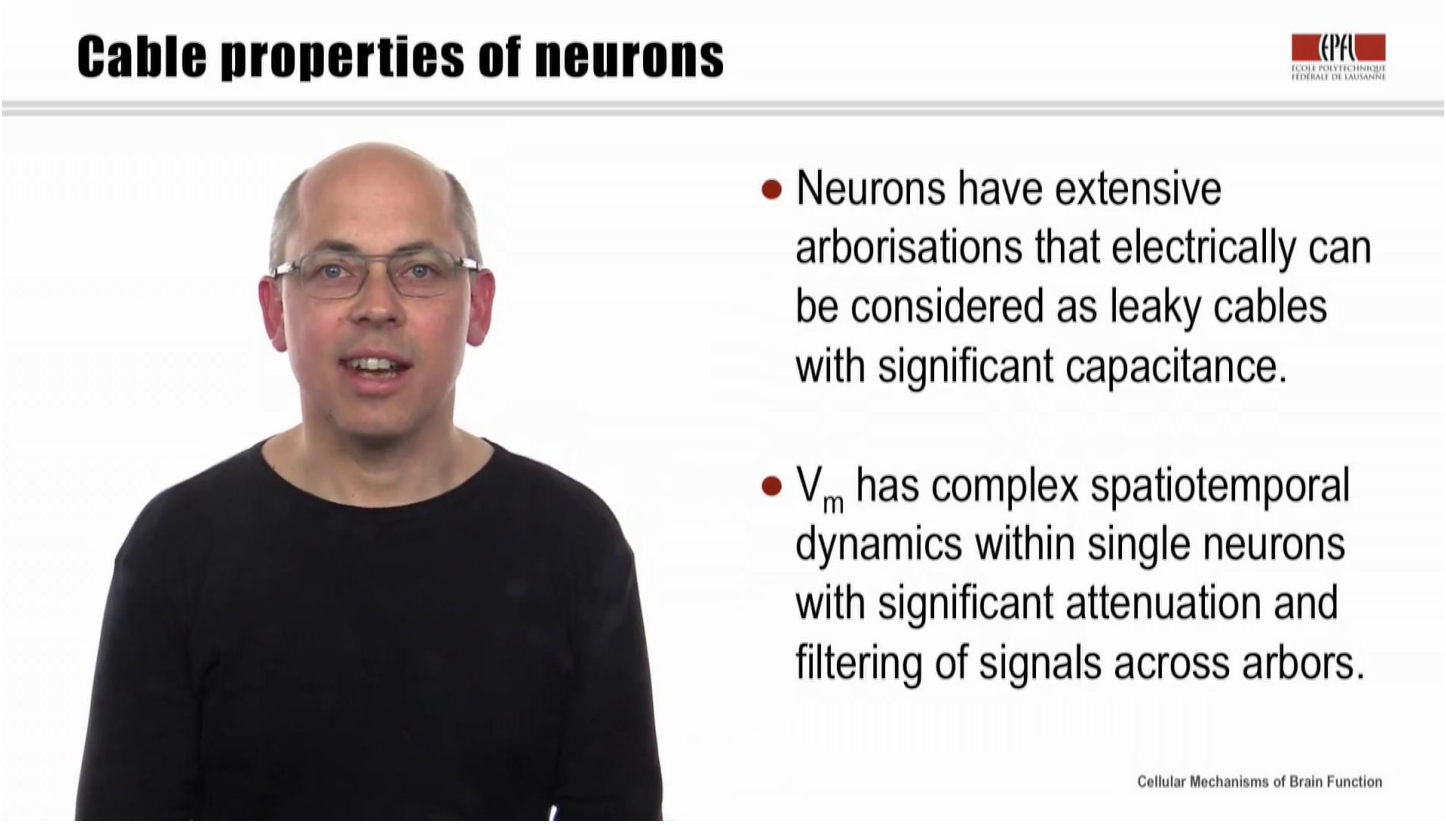


Membrane potential is, therefore, clearly very complex in real neurons.

Notes

Summary

18m 19s



So in this lesson we've learned about the complexity of neuronal membrane potential. Neurons have extensive arborisations that electrically can be considered as leaky cables with significant capacitance. Membrane potential, therefore, has complex spatiotemporal dynamics within single neurons, with significant attenuation and filtering of the signals across the arbors. In general, this leads to a complicated situation in terms of information processing, and next week we'll see that the nervous system has come across at least one solution as to how to make reliable signaling across large distances in the form of the axon potential. That, we'll discuss next week.

Notes

Summary

18m 25s