

Week 4 – part : Type I and Type II Neuron Models



Neuronal Dynamics: Computational Neuroscience of Single Neurons

Week 4 – Reducing detail:

Two-dimensional neuron models

Wulfram Gerstner

EPFL, Lausanne, Switzerland

✓ 4.1 From Hodgkin-Huxley to 2D

✓ 4.2 Phase Plane Analysis

✓ 4.3 Analysis of a 2D Neuron Model

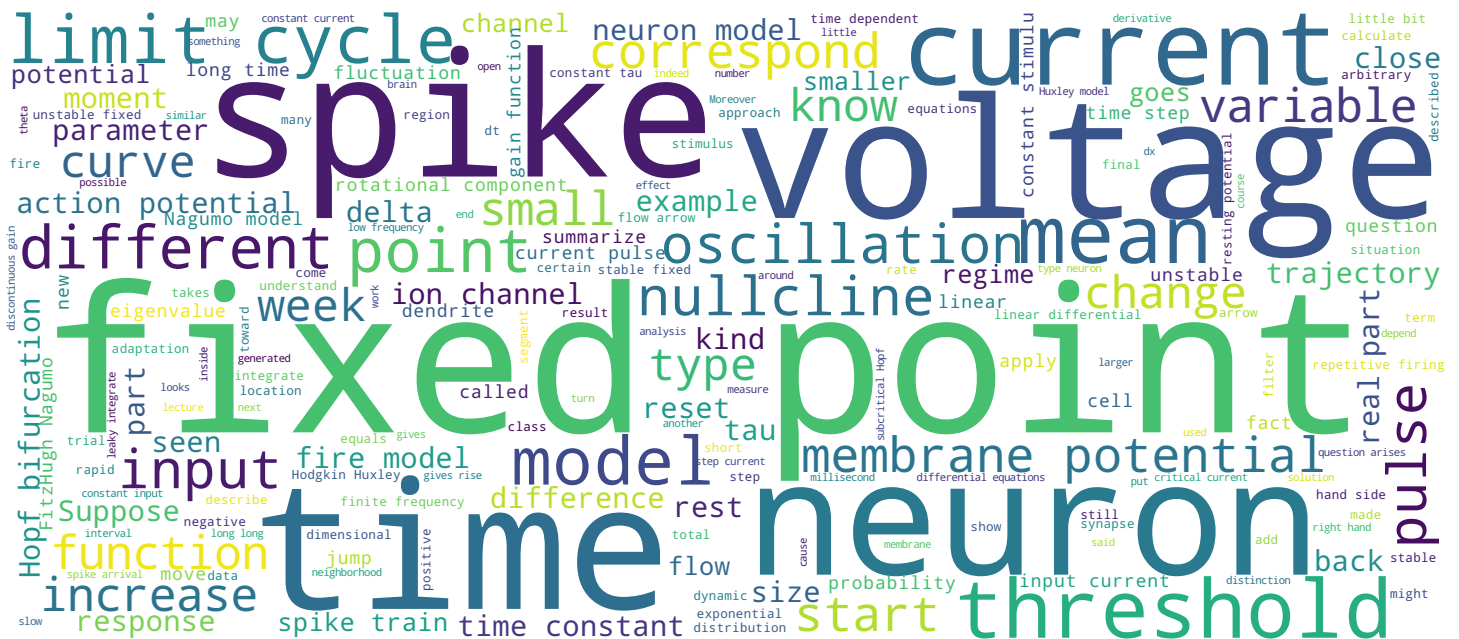
4.4 Type I and II Neuron Models

- where is the firing threshold?

- MathDetour 4: separation of time scales

4.5. Nonlinear Integrate-and-fire

- from two to one dimension



Week 4 – part 4:



✓ 4.1 From Hodgkin-Huxley to 2D

✓ 4.2 Phase Plane Analysis

✓ 4.3 Analysis of a 2D Neuron Model

4.4 Type I and II Neuron Models

- where is the firing threshold?
- MathDetour 4: separation of time scales

4.5. Nonlinear Integrate-and-fire

- from two to one dimension



Welcome to part 4 of week 4.

Notes

Summary



0m 04s

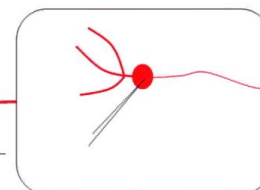
Neuronal Dynamics – 4.4. Type I and II Neuron Models



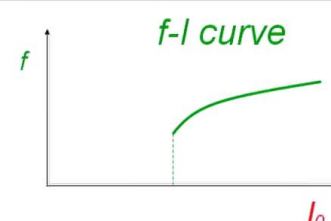
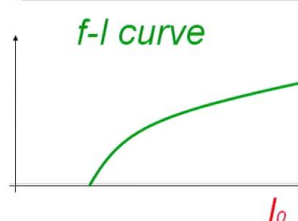
ramp input/
constant input



neuron



Type I and type II models



Biologists have made, for a long time, the distinction between continuous f-I curves called type 1 or class 1 and discontinuous f-I curves called type 2 or class 2. In fact, Hodgkin and Huxley introduced this distinction. But, of course, the question arises whether there are specific biological processes that make the differences between a type 1 or type 2 model, or whether we can understand this difference on some more general mathematical grounds.

Notes

Summary



0m 09s

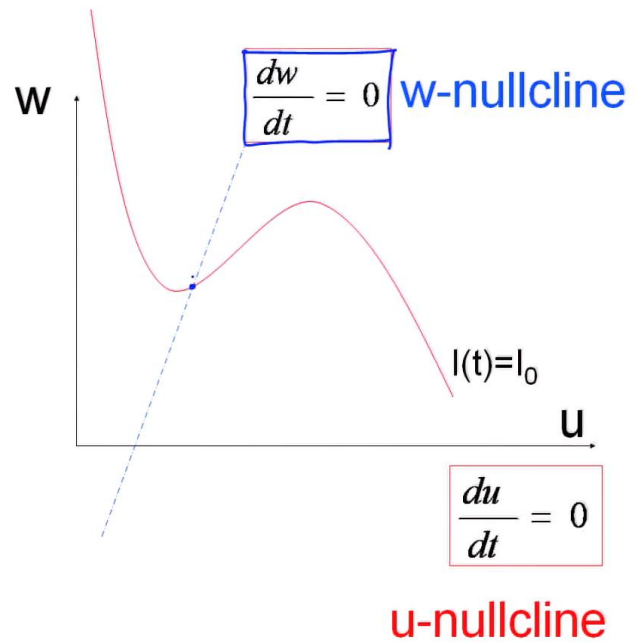
2 dimensional Neuron Models

$$\tau \frac{du}{dt} = F(u, w) + I(t)$$

stimulus
↓

$$\tau_w \frac{dw}{dt} = G(u, w)$$

apply constant stimulus I_0



So let's start the discussion with our two-dimensional neuron model. And we have seen, for the type of FitzHugh-Nagumo model, that the w -nullcline would be a straight line, while the u -nullcline the red nullcline would have some more interesting shape. Now, let's apply a stimulus. Let's apply a constant stimulus. A constant stimulus, as we have seen for the FitzHugh-Nagumo model, will shift up the curve. And if the curve is shifted upwards, what happens is that at some point the fixed point loses stability.

Notes

Summary



0m 49s

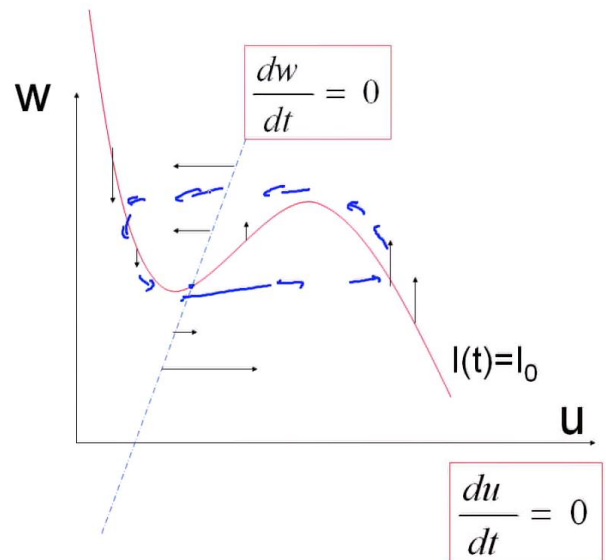
FitzHugh Nagumo Model – limit cycle

$$\tau \frac{du}{dt} = F(u, w) + I(t)$$

stimulus
↓

$$\tau_w \frac{dw}{dt} = G(u, w)$$

- unstable fixed point
- closed boundary
with arrows pointing inside
- limit cycle



⌂ / ☐ ➡

Now if the fixed point is unstable and, moreover, we can construct a close boundary around it such that all arrows point inwards, then we know that there must be a limit cycle which corresponds to repetitive firing of the neuron. So the neuron fires repetitively, periodically while on this limit cycle.

Notes

Summary

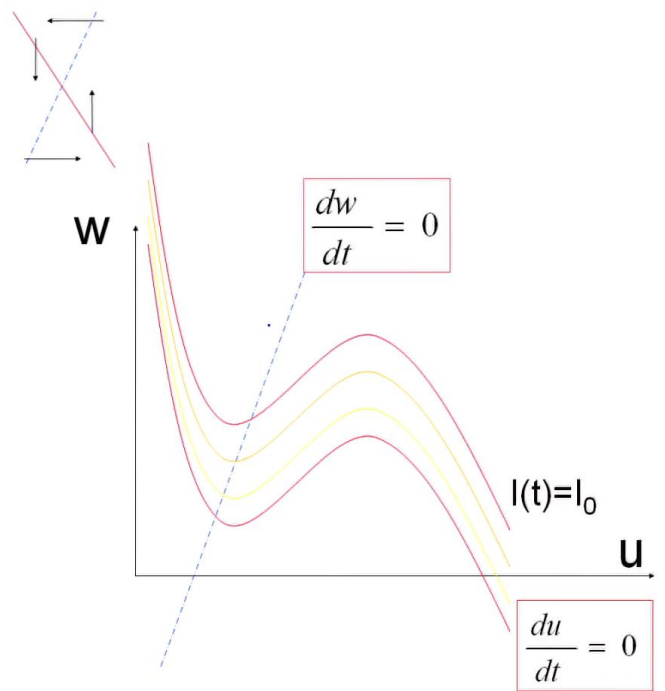


1m 37s

Type II Model constant input

$$\tau \frac{du}{dt} = F(u, w) + \overset{\text{stimulus}}{\downarrow} I(t)$$

$$\tau_w \frac{dw}{dt} = G(u, w)$$



I_0

So let's apply our constant stimulus.

Notes

Summary

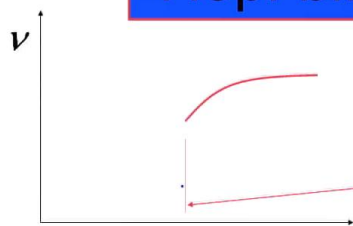


Type II Model constant input

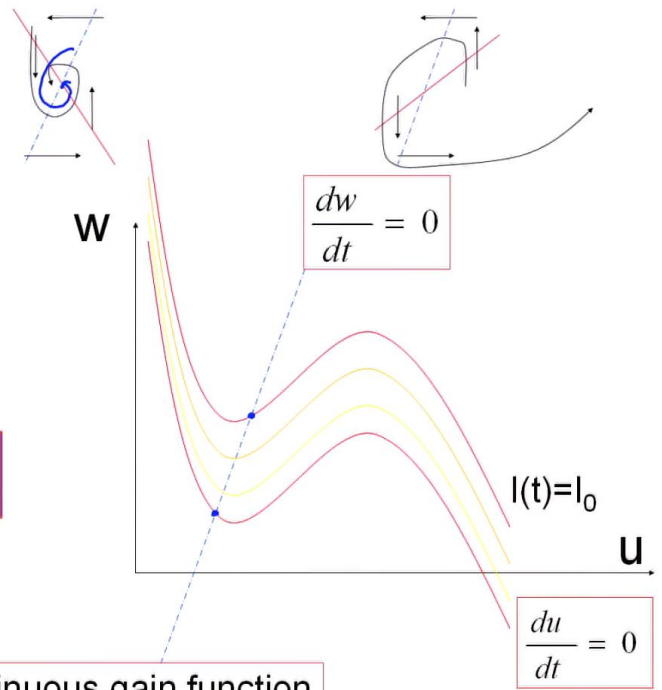
$$\tau \frac{du}{dt} = F(u, w) + I(t)$$

$$\tau_w \frac{dw}{dt} = G(u, w)$$

Hopf bifurcation



Stability lost $\rightarrow$ oscillation with finite frequency



If we are down here, then we have a situation that corresponds to a stable fixed point with a invert circling trajectory. If you have a larger input, then we have an unstable fixed point with an outward circling trajectory. At some point there's a transition. And this transition corresponds mathematically to a Hopf bifurcation. The stability is lost at some finite frequency. There will be oscillations at some finite frequency that correspond to this rotational component here. Moreover, for the kind of FitzHugh-Nagumo model that we have considered here, the oscillation will be big. Importantly, it generates a discontinuous gain function out of this Hopf bifurcation.

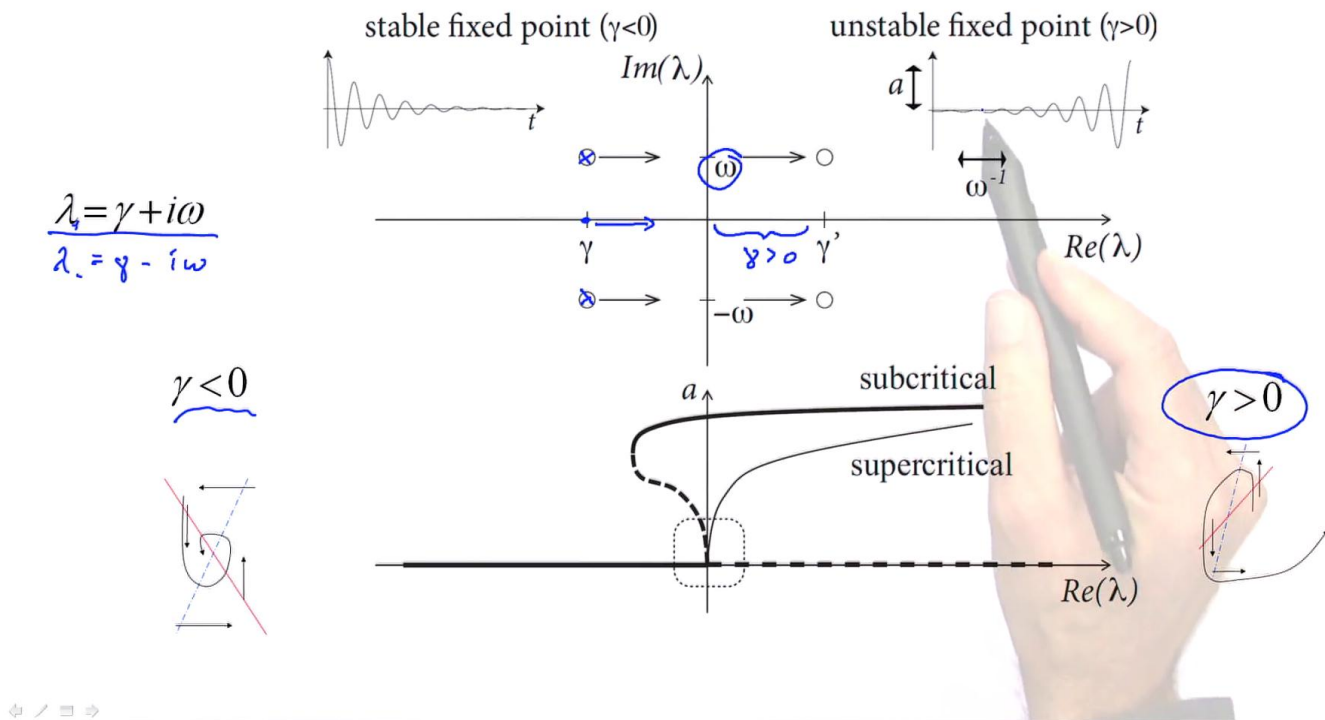
Notes

Summary



2m 16s

Neuronal Dynamics – 4.4. Hopf bifurcation



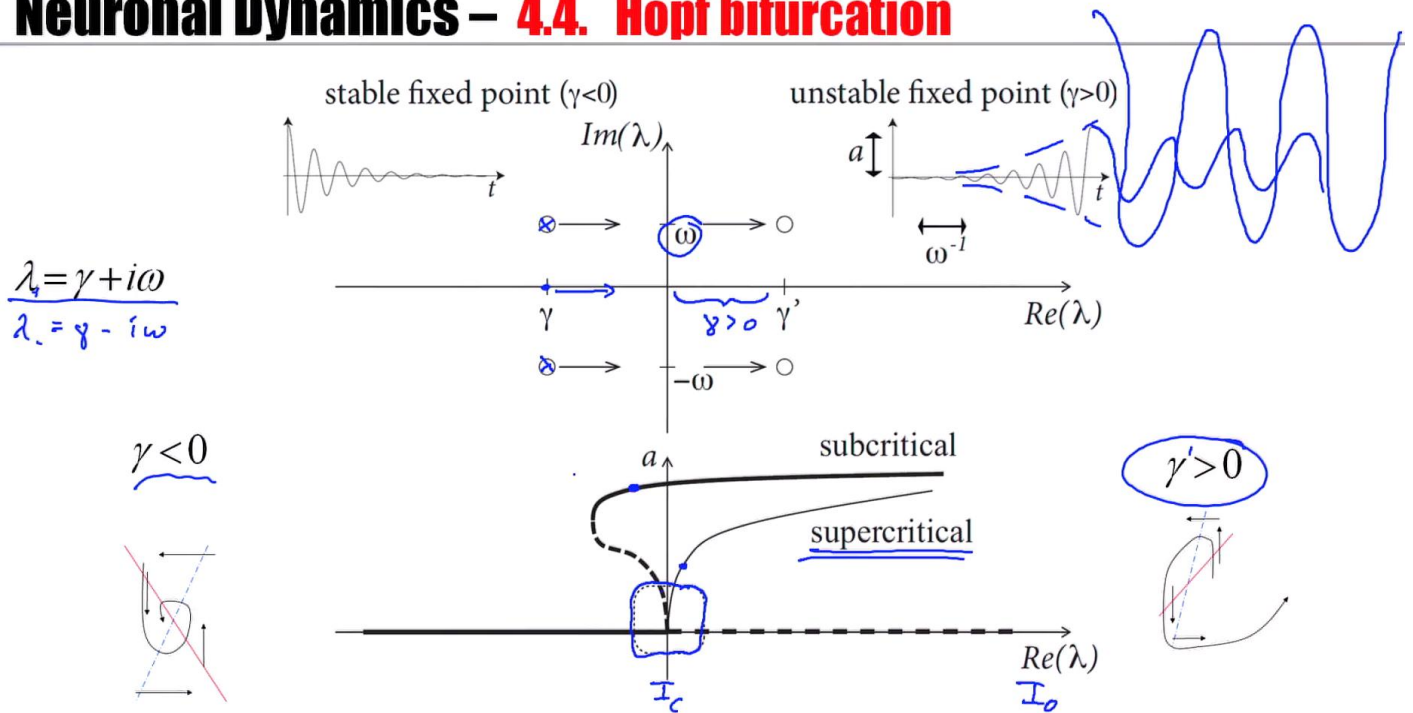
So let me discuss this in more detail. If you analyze the stability of the fixed points, they are first for 0 input in a regime where you have a rotational component corresponding to the imaginary part of the eigenvalue value. And we have a real part of the eigenvalue which is negative. This corresponds to this invert circling. If you just look at the voltage, it will show some oscillation and oscillations. Why? Because gamma, the real part of the eigenvalue is negative. Now, we increase our current. If we increase our current, then the real part of this eigenvalue increases. The eigenvalues sit at gamma plus I omega. That's this eigenvalue. And then there's another one, gamma minus I omega. It's down here. If I increase the constant external current, the real part increases, which means the eigenvalues move in the complex plane. And at some point, they're past 0. And, suddenly, we have here a positive real part, gamma larger than zero. In this case, any small [? third ?] perturbation will blow up. We have the oscillatory component corresponding to the imaginary part, omega. And we have a blow up of the envelope, which corresponds to the real part of the eigenvalue, to gamma prime.

Notes

Summary



Neuronal Dynamics – 4.4. Hopf bifurcation



Now, the bifurcation picture holds only in the direct neighborhood of this transition point. So as I increase my constant input, I've frozen the state of regime. Then there's a critical value of the input. And then I'm in the regime where the fixed point is no longer stable. The linearization, the tail expansion around the fixed point is only possible in the direct neighborhood of the fixed point. And the analysis, the Hopf bifurcation is only valid if we are in the neighborhood of this critical point. Now two possibilities exist. One is that the oscillation itself is stable. And then this would correspond to an oscillation of finite size. So this amplitude of the oscillation would stabilize at some final value. The fixed point is unstable. And oscillation develops. But the oscillation itself is stable. This is called a super critical Hopf bifurcation. Or the other possibility, an oscillation develops. But this oscillation itself is unstable. However, there is, in the case of the FitzHugh-Nagumo model, another limit cycle further out. We know that there is a stable limit cycle. And this limit cycle corresponds to a large amplitude, to a much larger amplitude of the oscillation. This amplitude of the oscillation itself cannot be found through this linear stability analysis that we do here.

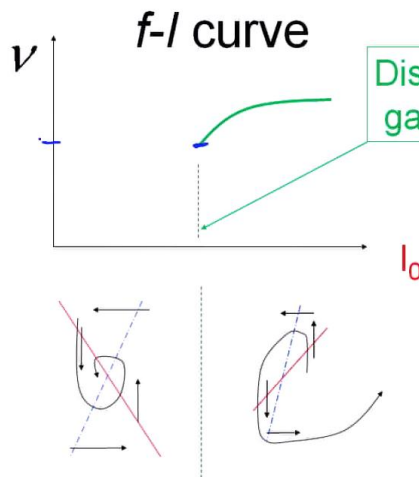
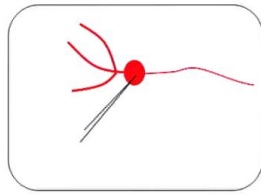
Notes

Summary



Neuronal Dynamics – 4.4. Hopf bifurcation: f - I curve

ramp input/
constant input



Stability lost $\rightarrow$ oscillation with finite frequency

To summarize, with the Hopf bifurcation, you have a transition from a stable fixed point with a rotational component to an unstable fixed point with a rotational component. For a subcritical Hopf bifurcation, this unstable rotational component leads to a limit cycle of large amplitude, correspond which we can interpret as sequence of action potential as repetitive firing. And repetitive firing sets in as a finite frequency, at a finite frequency. We have a discontinuous f - I curve of this continuous gain function.

Notes

Summary

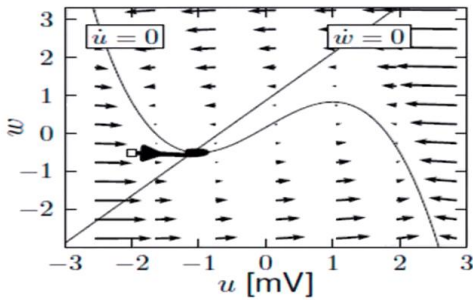
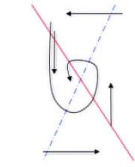


7m 21s

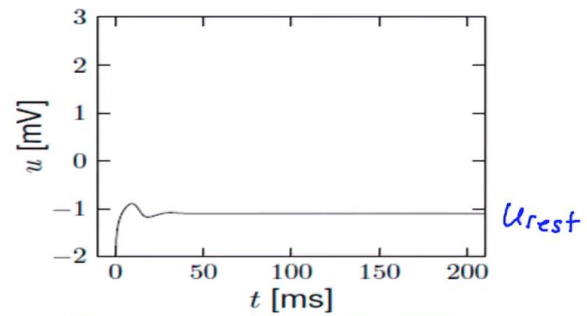
FitzHugh-Nagumo: type II Model – Hopf

bifurcal'

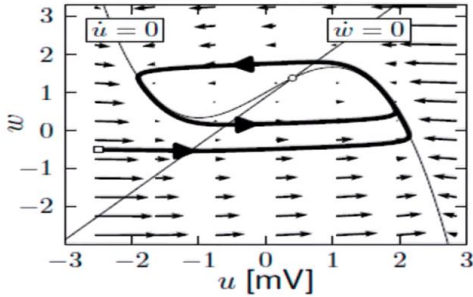
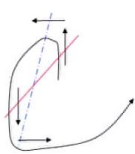
$I=0$



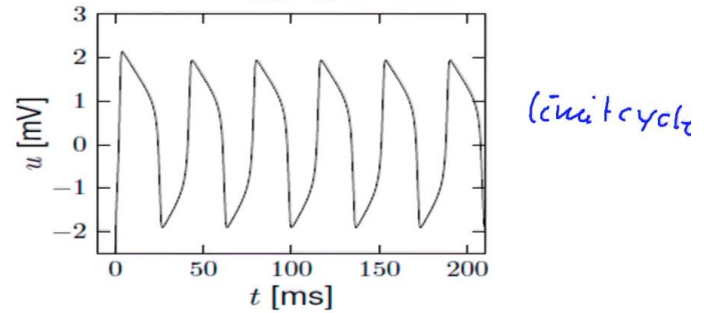
B



$I > I_c$



D



8m 08s

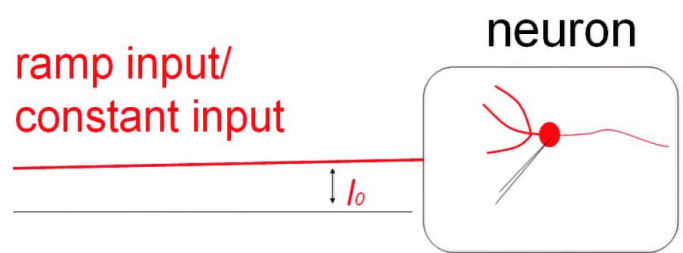
So if you apply this in our case for no current, I have the rotational component. I see it here, a little bit of oscillation. And the system goes towards a resting state for I equals 0. With a current larger than the critical current, the system is locally unstable. This fixed point is unstable. And there's a limit cycle. And if you start with this initial condition, you go on to the limit cycle, which corresponds to periodic firing.

Notes

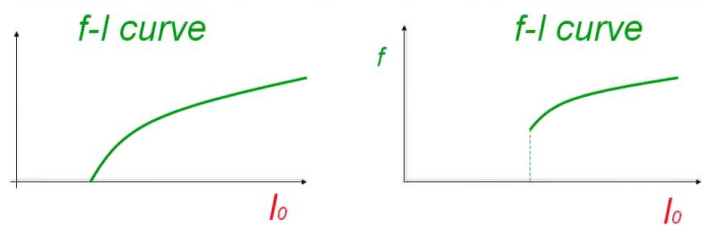
Summary



Neuronal Dynamics – 4.4. Type I and II Neuron Models



Type I and type II models



To summarize, a subcritical Hopf bifurcation, as we have it the FitzHugh-Nagumo model, gives rise to a discontinuous frequency current curve. Now what about type 1 models?

Notes

Summary



8m 46s

Neuronal Dynamics – 4.4. Type I and II Neuron Models

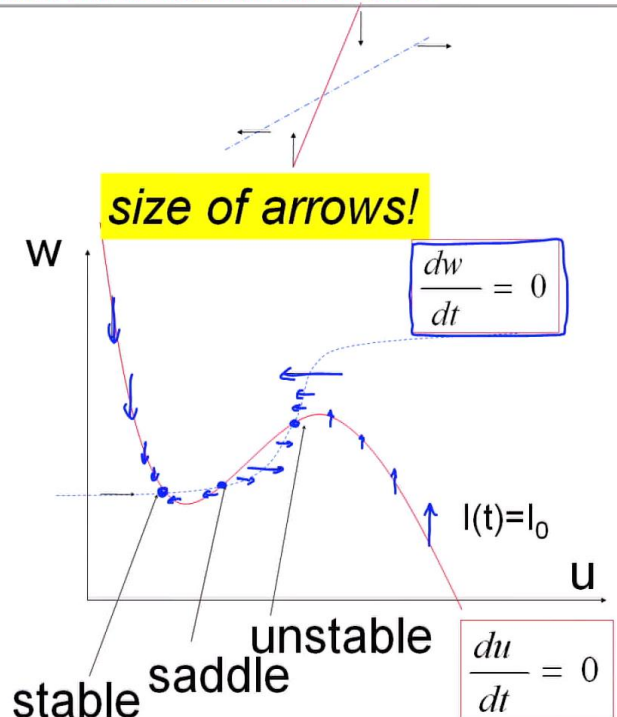
type I Model: 3 fixed points

$$\tau \frac{du}{dt} = F(u, w) + \overset{\text{stimulus}}{\downarrow} I(t)$$

$$\tau_w \frac{dw}{dt} = G(u, w)$$

apply constant stimulus I_0

Saddle-node bifurcation



Let's consider a slightly different scenario. The red nullcline, u-nullcline, is the same as before. However, the w-nullcline is different now. Before it was just a linear function. Now it's a function which itself bends and curves. And in this case, we would have three fixed points-- a first fixed point here, a second fixed point here, and a third fixed point. It turns out that this one is stable. The middle one is a saddle. And this one is unstable. Now, I've drawn some errors. Here we have vertical arrows upwards. Here I have vertical arrows downward. Now the size of the arrows get smaller and smaller as we approach one of the fixed points. The same is true for the horizontal arrows. The size of the arrows gets smaller when we approach the fixed point. In the vicinity of the fixed point, the speed of the flow, the size of the arrows is very small. Now we apply constant stimulus. A constant stimulus will shift the curve upwards. It might be a slight change in the shape of the nullcline. But, essentially, it's a shift upwards.

Notes

Summary

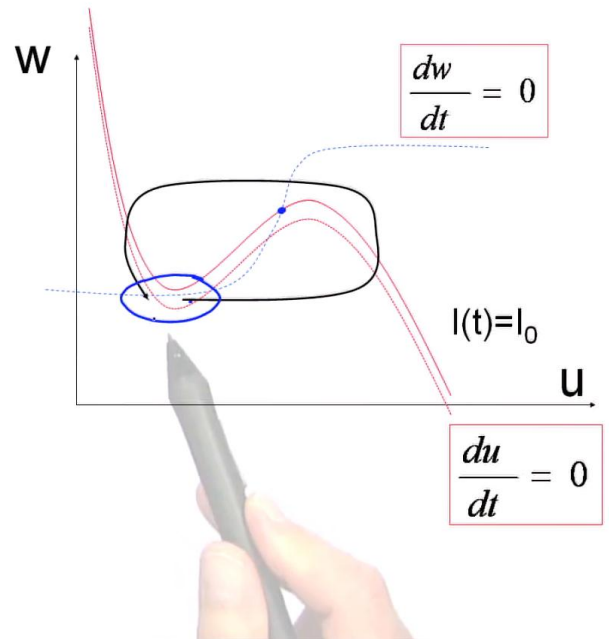
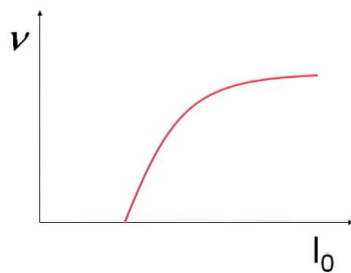


8m 58s

type I Model – constant input

$$\tau \frac{du}{dt} = F(u, w) + \overset{\text{stimulus}}{\downarrow} I(t)$$

$$\tau_w \frac{dw}{dt} = G(u, w)$$



And if you shift a nullcline upwards, what we see is that these fixed points, they disappear. They disappear. Now, what about the flow arrow? Previously, we said I have big flow arrows here. I have big flow arrows there. I have big arrows there. However, close to the fixed point, the arrows, they're very small, very, very small. What does that mean? It means that if we are on a trajectory-- so this is the new situation-- arrows are small. If the system is now on that trajectory, this is the remaining unstable fixed point. I have a boundary box with flow arrows inside. So I know there's a limit cycle. However, the limit cycle passes through this regime where the size of arrows is very small. They have been fixed point before. The fixed points have disappeared. But there's still something left, like the ruins of the fixed point. Now we make this minor change in the applied current, a minor shift to direct curve. The size of the arrows does not change substantially. That means the flow is extremely slow in this region. And, therefore, it takes a long time, a long, long time to close the limit cycle.

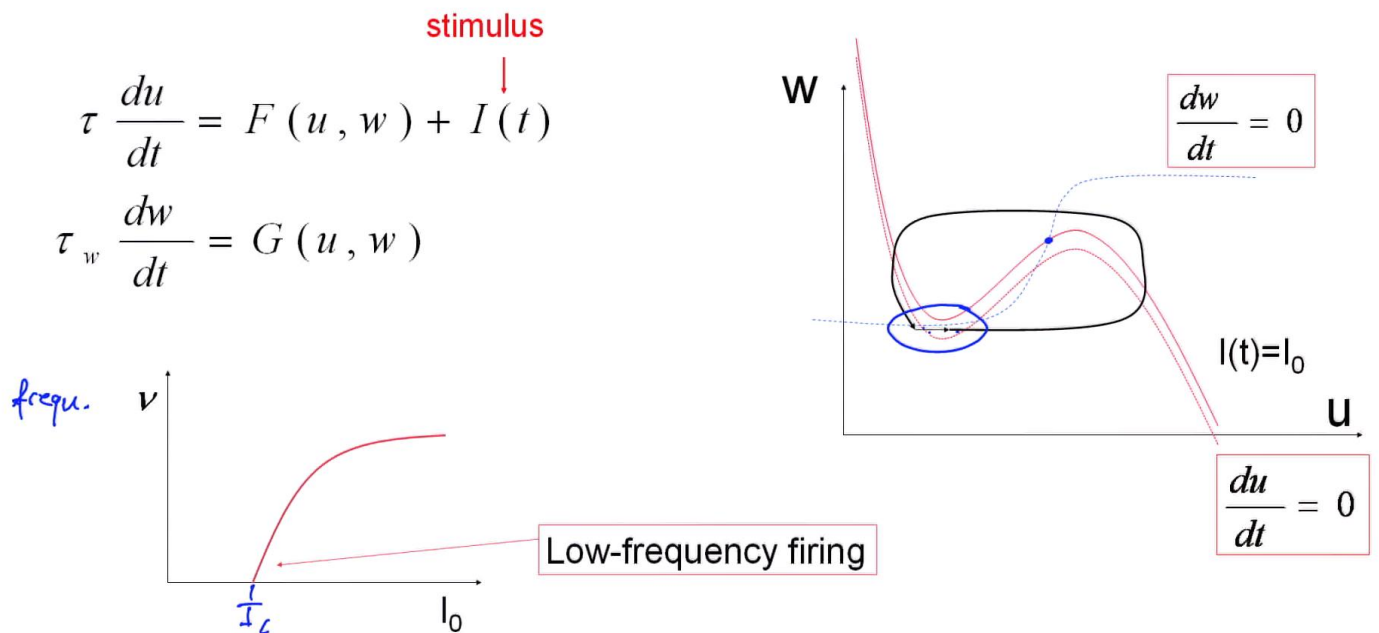
Notes

Summary

10m 30s



type I Model – constant input



Now, this means that while the upswing of the action potential is rapid, while the downswing of the action potential is rapid, the neuron spends a lot of time in this region here. Therefore, the total time to complete the limit cycle is very long. The period after limit cycle is long. That means the frequency of the limit cycle is very small. And right at the bifurcation point, at this critical current, the frequency goes to 0. The system spends a very, very, very long time in the neighborhood of the ruins of the fixed point. So the fixed points here have gone. But the ghost of the fixed point is still around. Now, this low frequency firing is characteristic for a type 1 neuron model.

Notes

Summary

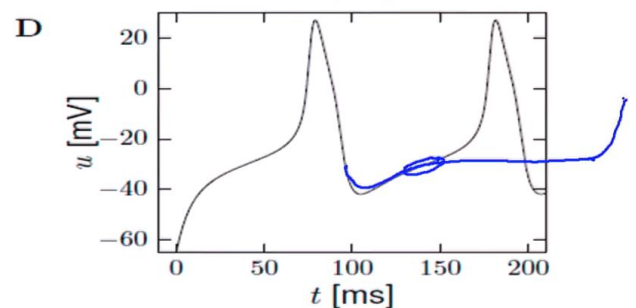
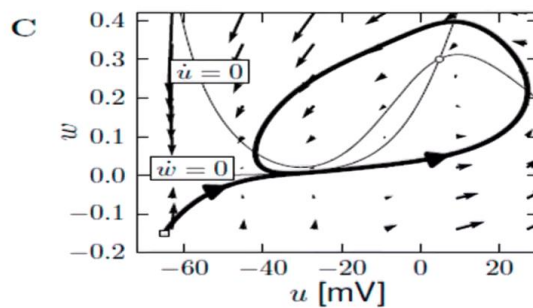
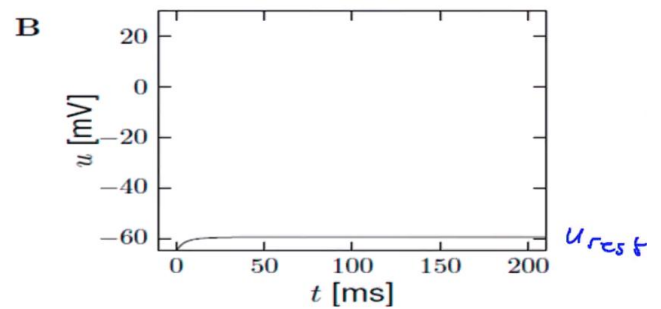
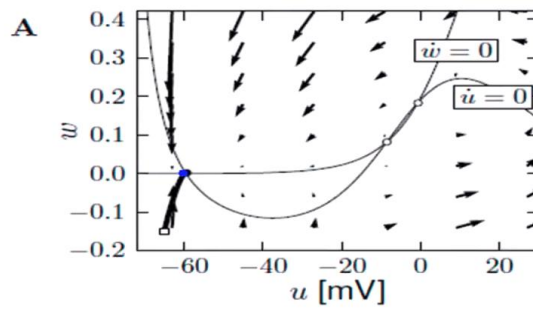


12m 02s

Morris-Lecar, type I Model – constant input

$I=0$

$I > I_c$
 $I \rightarrow I_c$



Now, here is an application, a concrete model if the input current is 0, I have a stable fixed point here. And, indeed, the voltage trajectory goes to the stable resting potential. Now, I've input larger than the critical input starting from the same value. It goes on the limit cycle. And the limit cycle is fairly slow here. The fairly slow means that there is not a lot of change in the immediate regime. If I make I larger than I_c but slowly approaching the critical current, then the system would spend a long, long, long time in this regime before it goes off to the next spike.

Notes

Summary



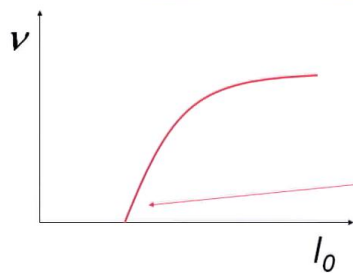
12m 59s

type I Model – constant input

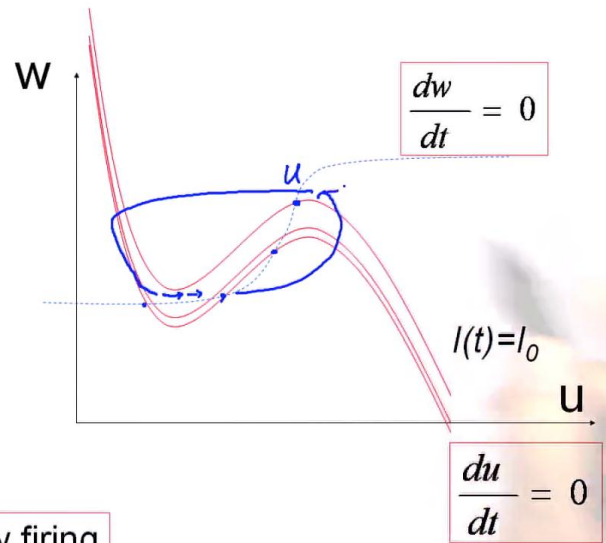
$$\tau \frac{du}{dt} = F(u, w) + \overset{\text{stimulus}}{\downarrow} I(t)$$

$$\frac{dw}{dt} = -\frac{w - w_0(u)}{\tau_{\text{eff}}(u)}$$

$$w_0(u) = 0.5[1 + \tanh(\frac{u - \theta}{d})]$$



Low-frequency firing



Now, all this was theoretical. I just hand drawn some curve for the w-nullcline. However, if you think of some activation dynamics, some gating dynamics, it'd be quite natural to write down something like this here. And that would correspond more or less to the blue curve that I've shown on the right hand side. So you have a bifurcation. You start off with three fixed points. You increase the current. The red curve shifts upwards. Only one fixed point is left. If this fixed point is unstable, you have a limit cycle. And the limit cycle is very, very slow in this region before it takes off again.

Notes

Summary



13m 46s

Type I and type II models

Response at firing threshold?

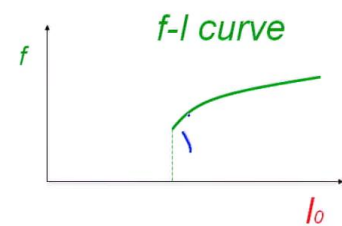
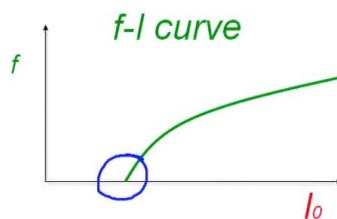
Type I

type II

Saddle-Node
Onto limit cycle

For example:
Subcritical Hopf

ramp input/
constant input



Thus, we can identify a type 1 f-I curve with a saddle-node bifurcation onto limit cycle, a type 2 curve, which mean a discontinuous gain function can, for example, be generated by a subcritical Hopf bifurcation. How would you measure these curves? You use a constant current, nearly constant current, a very slowly increasing ramp current so that you move very, very slowly along this axis. You see your firing starts at a very low frequency. Firing starts at some finite frequency.

Notes

Summary



14m 37s

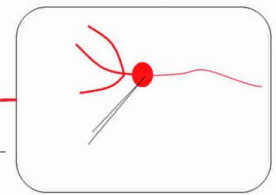
Neuronal Dynamics – 4.4. Type I and II Neuron Models



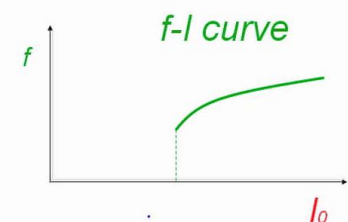
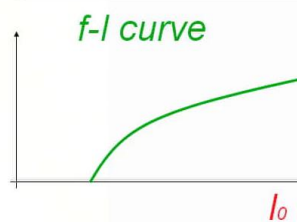
ramp input/
constant input



neuron



Type I and type II models



To summarize, biologists have made a distinction between type 1 neurons, those that have a continuous gain function, those that are able to fire at very low frequency on one side, and type 2 neurons, those that have a minimal [? fine ?] frequency and which a discontinuous gain function. Well, of course, the question arises whether such a difference must be attributed to specific ion channels. Now, the mathematical analysis that I have presented raised a long line of research of theoretical neuroscience. The analysis I've presented suggests that there are basic mathematical, as opposed to biological, properties that allow us to explain this distinction.

Notes

Summary



15m 19s