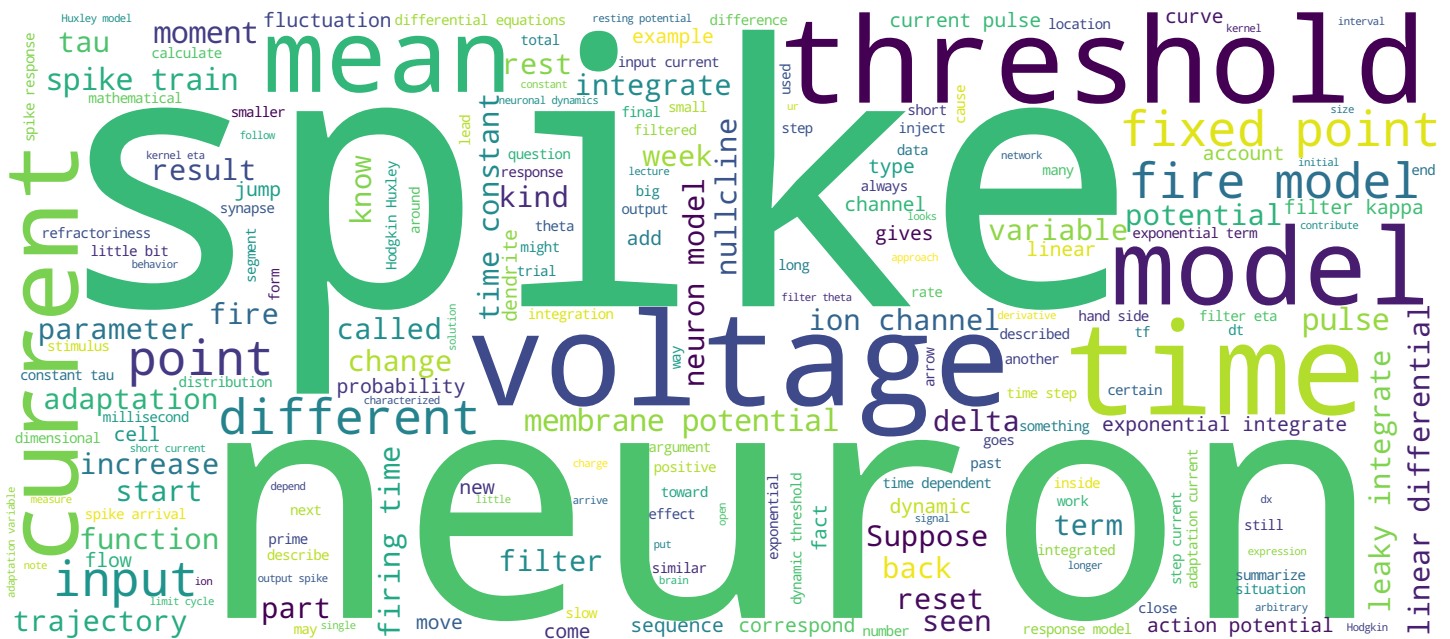


ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

EPFL, Lausanne, Switzerland

7.7. Helping Humans



EPFL



Week 7 – part 3 :Spike Response Model (SRM)



✓ 7.1 What is a good neuron model?

- Models and data

✓ 7.2 AdEx model

- Firing patterns and analysis

7.3 Spike Response Model (SRM)

- Integral formulation

7.4 Generalized Linear Model

- Adding noise to the SRM

7.5 Parameter Estimation

- Quadratic and convex optimization

7.6. Modeling in vitro data

- how long lasts the effect of a spike?

7.7. Helping Humans

Welcome to the third part of week seven of the class neuronal dynamics. We have seen that adaptation, together with an exponential integrate and fire, model can account for a variety of firing patterns, in particular for adaptation. Now let's move on and change to formulation a little bit.

Notes

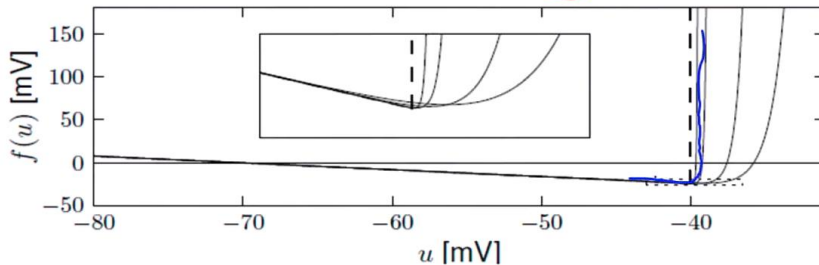
Summary



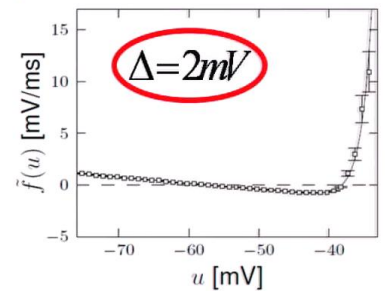
0m 04s

Exponential versus Leaky Integrate-and-Fire

$$\tau \frac{du}{dt} = -(u - u_{rest}) + \Delta \exp\left(\frac{u - \vartheta}{\Delta}\right) + RI(t)$$



Badel et al (2008)



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

Reset if $u = \vartheta$

Leaky Integrate-and-Fire

Let's focus, for the moment, on the exponential integrate and fire model. It has this linear term that was mentioned before and the exponential term. This exponential term is characterized by a parameter delta. Delta controls the rapidity and the sharpness of the kink, the sharpness of the bend down here. So you see here a zoom in this small region here with different values of this parameter delta. Now, this is a parameter of the model. If you measure the curve, the non-linearity, of the exponential integrate and fire, and you fit with this linear plus exponential term, you find a delta in the range of 2 millivolt. That's not a lot. That means it's really a sharp transition up here. Now, let's consider what it means, a sharp transition. Let's make it sharper and sharper. If it's really sharp, then it's like saying, the threshold sits right here where the kink is, where the curve bends upwards. Thus, the exponential term for very sharp delta can be replaced by just a sharp threshold. And that means we are back to the leaky integrate and fire model.

Notes

Summary



0m 34s

Neuronal Dynamics – 7.3 Adaptive leaky integrate-and-fire

$$\tau \frac{du}{dt} = -(u - u_{rest}) - R \sum_k w_k + RI(t)$$
$$\tau_k \frac{dw_k}{dt} = a_k (u - u_{rest}) - w_k + \underbrace{b_k}_{\text{after each spike}} \tau_k \sum_f \delta(t - t^f)$$

after each spike

w_k jumps by an amount b_k

↩ / ⇨ ⇩ ⇧

Now, we said earlier this week that an exponential integrate and fire model is fine, but you need to add adaptation variables. And the same holds for the leaky integrate and fire model. Just add some adaptation currents, w_k , maybe five different adaptation currents, and each adaptation current w_k is controlled by the linear differential equation that we have seen before where this parameter, b_k , controls the jump size at the moment of the reset.

Notes

Summary



2m 17s

Neuronal Dynamics – 7.3 Adaptive leaky integrate-and-fire

$$\tau \frac{du}{dt} = -(u - u_{rest}) - R \sum_k w_k + RI(t)$$

$$\tau_k \frac{dw_k}{dt} = a_k (u - u_{rest}) - w_k + b_k \tau_k \sum_f \delta(t - t^f)$$

SPIKE AND
RESET

after each spike

w_k jumps by an amount b_k

If $u = \vartheta(t)$ then reset to $u = u_r$

Dynamic threshold

The voltage itself is reset to u_r . So it's just like in our discussion of the adaptive exponential integrate and fire model, except that the non-linear term here has disappeared, and, instead, we've work with a sharper threshold. The threshold itself can be time dependent, as before.

Notes

Summary



2m 59s

Neuronal Dynamics – 7.3 Adaptive leaky I&F and SRM

$$\begin{aligned}\tau \frac{du}{dt} &= -(u - u_{rest}) - R \sum_k w_k + \underline{RI(t)} \\ \tau_k \frac{dw_k}{dt} &= a_k (u - u_{rest}) - w_k + b_k \tau_k \sum_f \delta(t - \underline{t^f})\end{aligned}$$

Adaptive
leaky I&F

Linear equation → can be integrated!

$$u(t) = \sum_f \eta \underbrace{(t - t^f)}_{\uparrow t^f} + \int_0^\infty ds \kappa(s) \underbrace{I(t - s)}$$

✎ ✎ ✎ ✎

Now let's look what this gives. I now have two coupled linear differential equations. If I know the jump size, if I know the moments of a spike, if I know the spike firing times, then this is just a sequence of short current pulses in a linear differential equation. But we have seen in week one that such a differential equation can be integrated, and then we have our expression for w_k , an explicit expression for w_k , which you can insert over here. The result is that the reset that's happening after each spike can be integrated up. First I integrate up the w equation. Then I insert it in here. This is again the linear differential equation which I can integrate. And the result of the sequence of two integrations gives the effect of the spike that has happened in the past at time t^f . Similarly, if you start with the input here, the input goes in this linear differential equation. And we know how to integrate such a differential equation. And the result is this term here. Note that the integration can be done despite the fact that there is a coupling between the voltage and the w variable.

Notes

Summary



3m 26s

Neuronal Dynamics – 7.3 Adaptive leaky I&F and SRM

$$\begin{aligned}\tau \frac{du}{dt} &= -(u - u_{rest}) - R \sum_k w_k + RI(t) \\ \tau_k \frac{dw_k}{dt} &= a_k (u - u_{rest}) - w_k + b_k \tau_k \sum_f \delta(t - t^f)\end{aligned}$$

Adaptive
leaky I&F

Linear equation → can be integrated!

$$\begin{aligned}u(t) &= \sum_f \eta(t - t^f) + \int_0^\infty ds \kappa(s) I(t - s) \\ g(t) &= \theta_0 + \sum_f \theta_1(t - t^f)\end{aligned}$$

Spike Response Model (SRM)
Gerstner et al. (1996)

As long as it's a linear differential equation, several coupled linear differential equations driven by spikes, driven also by the external input - as long as this is the case, we can do the integration. Moreover, we still have the dynamic threshold. The dynamic threshold means that, after each spike, the value of the threshold is higher than it would normally be. And this integral formulation has been called the spike response model. Why this name? Well, this is a spike, and the response of the spike-- if the neuron's own spiking is this refractory, an adaptation kernel, eta. Similarly, in a network, the input current would consist of spike arrival. Integrating this out means that this kernel kappa describes the response to spike arrival.

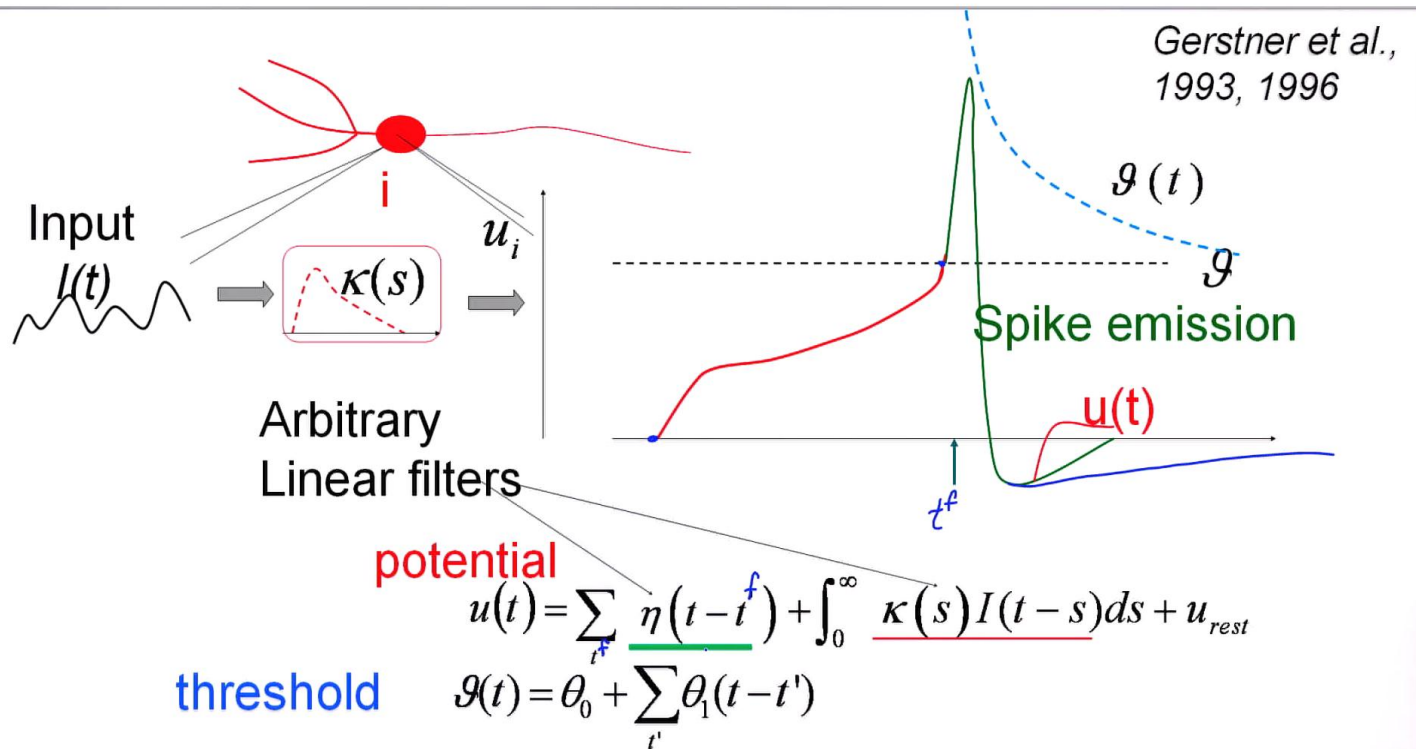
Notes

Summary



5m 06s

Neuronal Dynamics – 7.3 Spike Response Model (SRM)



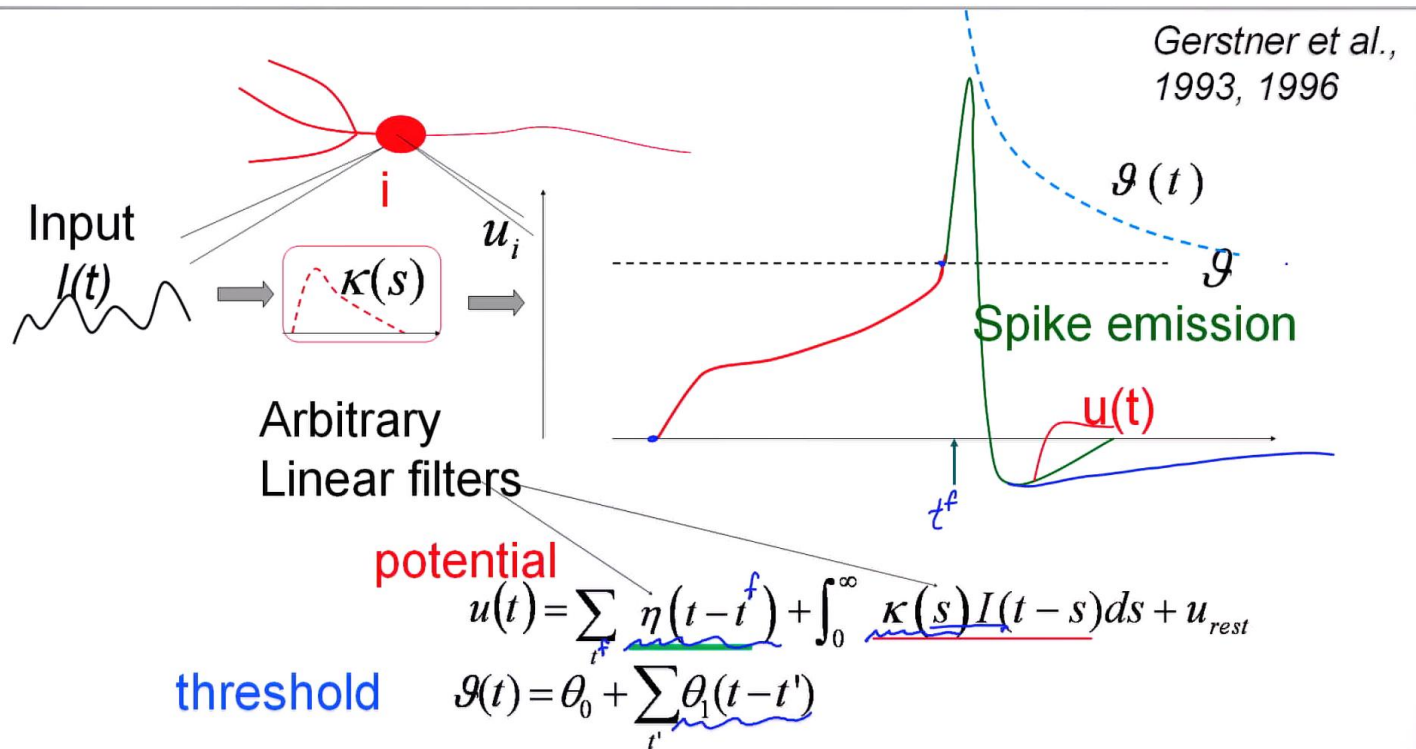
Now let's see how this model works. I apply some arbitrary input to some neuron. In the case of my model neuron, this means I filled out this arbitrary input kappa. That's this first term. And if I do this, starting from this initial condition, then the voltage will follow some trajectory, which I can calculate. That's this term here. And then at this point, point here, it hits the threshold. At the moment of the threshold crossing, we paste in the shape of the spike and, importantly, this spike after potential, which accounts for refractoriness. We add, over several past spikes, t prime, or t^f . These are the past firing times of this neuron. We add over the effects of several firing times in the past so that this term eta, which can be very long, will also account for adaptation. And then after the spike, the threshold is increased. We have a dynamic threshold. So this is the essence of the spike response model. And note that, even though we have come from the integration of the leaky integrate and fire model with adaptation, in the end, these kernels or filters here can be chosen completely arbitrarily in a way that they would best fit experimental data.

Notes

Summary



Neuronal Dynamics – 7.3 Spike Response Model (SRM)



And there are three of these kernels, a filter for the external input, a filter that describes refraction as an adaptation, and the filter that accounts for the dynamic threshold, an increased threshold immediately after a spike.

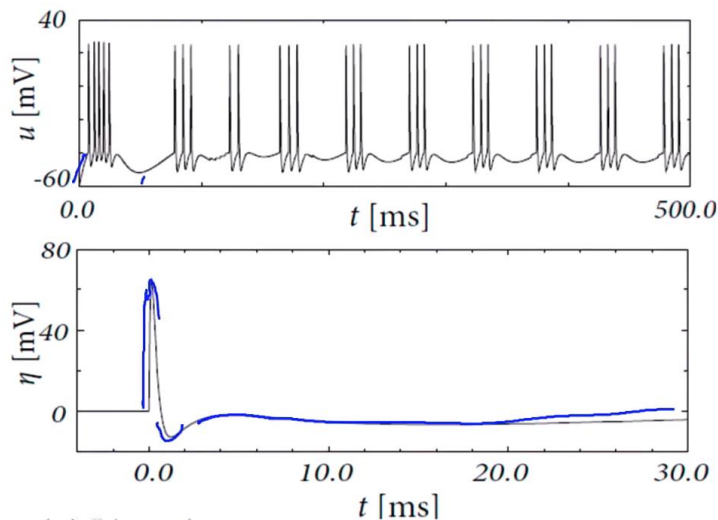
Notes

Summary



Neuronal Dynamics – 7.3 Bursting in the SRM

SRM with appropriate η leads to bursting



$$u(t) = \sum_f \eta(t - t^f) + \int_0^\infty ds \kappa(s) I(t - s) + u_{rest}$$

Navigation icons: back, forward, search, etc.

Suppose I take such a model, and I take a kernel η , the refractor-- the spike and refractoriness kernel, which has, first, the spike. And it has a downswing, important for refractoriness. And then it has a second bump and a much longer second downswing. And then I take a neuron, and as you inject a step current-- And the result of this step current integration is that we first integrate up to a threshold. That's this part here. And then we have our first spike. We paste in that spike. Immediately afterwards, firing is impossible. But then the membrane potential increases again. So we have a second spike. We have a third spike, a fourth spike, a fifth spike. And this burst of spikes stops only because there's some defect of all these negative contributions that are hyperpolarizing spike after potentials, it will finally turn firing off. And then it recovers. In the end, we have a sequence of bursts. We have constructed a bursting neuron model by an appropriate choice of this kernel η here.

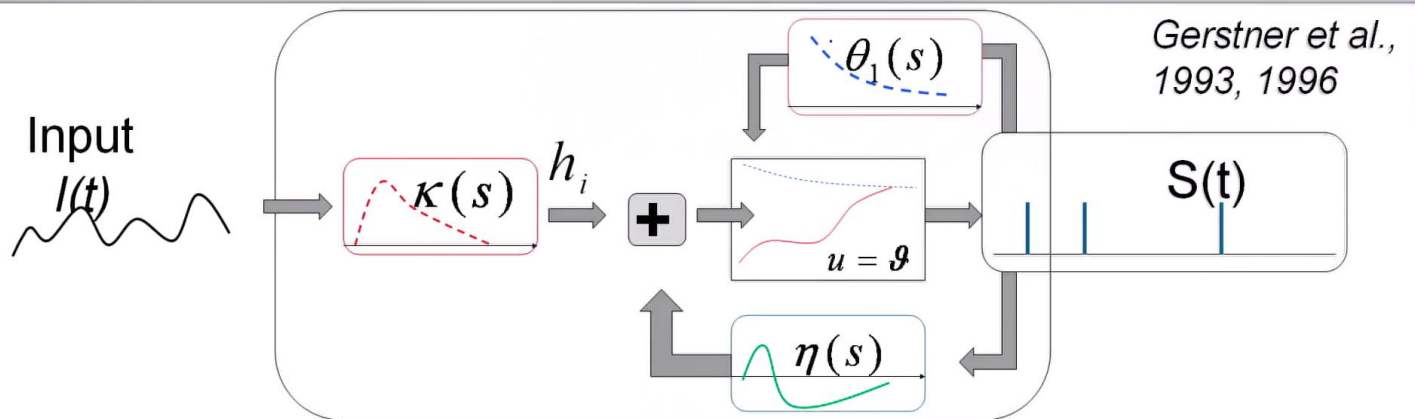
Notes

Summary



8m 16s

Neuronal Dynamics – 7.3 Spike Response Model (SRM)



potential $u(t) = \sum_{t'} \eta(t - t') + \int_0^\infty \kappa(s) I(t - s) ds + u_{rest}$

threshold $\mathcal{G}(t) = \theta_0 + \sum_{t'} \theta_1(t - t')$

firing if $u(t) = \mathcal{G}(t)$

The spike response model can be described as a sequence of filters. Input is filtered with the filter kappa. Comes here. This leads to an integration towards the threshold. If the threshold is crossed, we have a spike during the output. And this spike train causes two different effects. It contributes to a spike after potential that shapes adaptation and refractoriness. And it also contributes to an increase in the threshold that, again, shapes adaptation.

Notes

Summary



Neuronal Dynamics – 7.3 Spike Response Model (SRM)

potential

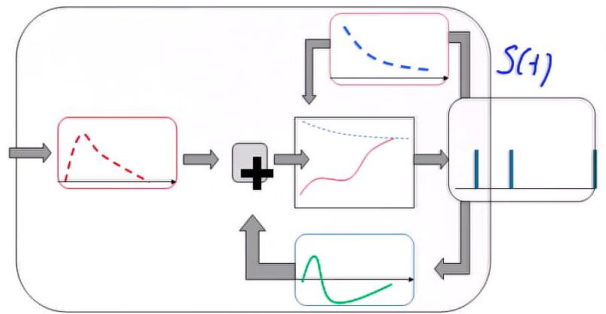
$$u(t) = \sum_f \eta(t - t^f) + \int_0^\infty \kappa(s) I(t - s) ds + u_{rest}$$

$$S(t) = \sum_f \delta(t - t^f)$$

$$\downarrow$$

$$= \int \eta(s) \underbrace{\sum_f \delta(t - t^f - s)}_{S(t-s)} ds$$

$$= \int \eta(s) S(t-s) ds$$



Linear filters for

- input
- threshold
- refractoriness

Now, let me work a little bit on this potentially equation. I set this as the filter eta here that gives the feedback of an output spike on to the dynamics of this neuron, the very same neuron. Now, let's rewrite this term in a slightly more complicated fashion. I write it as eta of s delta t minus t f minus s. t prime are the firing times, and a sum of all these different firing times. Sum over f, integral ds. Now, I admit that after these manipulations, this expression looks much more complicated than it was before. Let's just check that it gives the right result. So I have direct delta function. I will integrate over s. Thus, the argument after the integration, t minus t f minus s, that means whatever is not s, and is t minus t f has to be inserted where we had the s before. And so we are back to this term here. So the two expressions are completely equivalent. Now, the advantage of writing it this way is that this really is the spike train. This is my spike train, s of t. What is s of t? s of t is the sum of all spikes, over all spike events. So let me write this up in a more concise form. I can write this as integral eta of s, s of t minus s, ds. And the integral goes from zero to infinity.

Notes

Summary



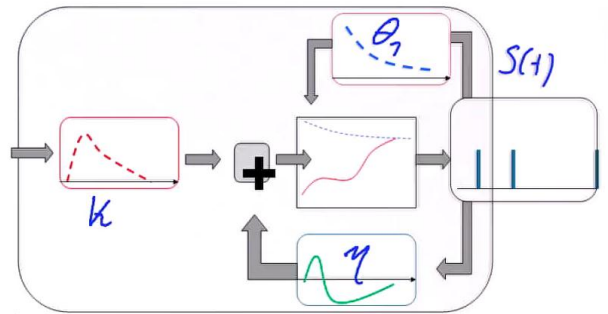
Neuronal Dynamics – 7.3 Spike Response Model (SRM)

potential

$$u(t) = \sum_f \eta(t - t^f) + \int_0^\infty \kappa(s) I(t - s) ds + u_{rest}$$

$$= \int_0^\infty \underbrace{\eta(s) \sum_f \delta(t - t^f - s)}_{S(t-s)} ds + \int_0^\infty \kappa(s) I(t - s) ds + u_{rest}$$

$$= \int_0^\infty \eta(s) S(t - s) ds + \int_0^\infty \kappa(s) I(t - s) ds + u_{rest}$$



Linear filters for

- input
- threshold
- refractoriness

threshold

$$\theta(t) = \theta_0 + \sum_{t^f} \theta_1(t - t^f)$$

$$= \theta_0 + \int_0^\infty \theta_1(s) S(t - s) ds$$

The integral goes over the past spike train. And now this term is suddenly very similar to the way we treat the input. And then I always have the u_{rest} . So the input is filtered with the filter κ . The output s is the output spike train. The output is filtered with a different filter, η . And this is then combined with the threshold equation, which has this form here. Again, it's a sum over all firing times. And analogously to the argument I made here, I can write this as θ_0 plus integral, θ_1 of s , spike train of the neuron in the past, and I integrate over the past. So the three filters-- the filter κ here, the filter η here, the filter θ_1 here-- all are treated in a parallel fashion. These filters are used in convolutions-- convolutions of the input with the filter κ , convolutions of the output spike train with the filter η and with the filter θ_1 .

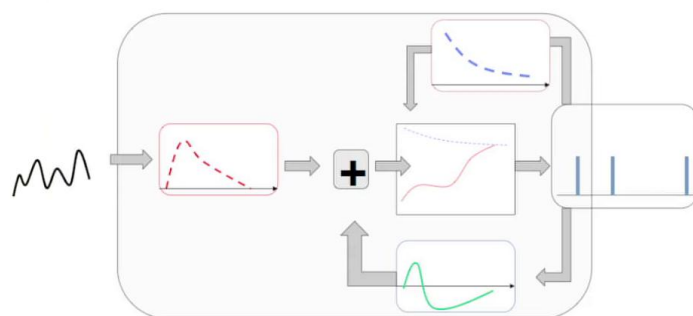
Notes

Summary



12m 34s

Neuronal Dynamics – 7.3 Spike Response Model (SRM)



Linear filters for

- input
- threshold
- refractoriness

Let me summarize what we have seen. The spike response model can be interpreted in two different ways. First, we can start from a leaky integrate and fire model with an arbitrary number of adaptation variables. If the adaptation and the leaky integrate and fire have both linear equation, it can be integrated, and we arrive at some kernel or filters. Alternatively, you can just start with these kernels or filters and state that there are three different filters, a filter κ convolved with the input and two filters that are convolved with the output, a filter θ for the threshold and a filter η for the subthreshold membrane potential after a spike. And these output filter contribute to refractoriness in adaptation. Now, the model is still deterministic, and the next lecture, I will add noise.

Notes

Summary



14m 11s