

ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

EPFL, Lausanne, Switzerland

- stochastic resonance



EPFL



Week 6 – part 3 : Likelihood of a spike train



✓ 6.1 Escape noise

- stochastic intensity and point process

✓ 6.2 Interspike interval distribution

- Time-dependent renewal process
- Firing probability in discrete time

6.3 Likelihood of a spike train

- generative model

6.4 Comparison of noise models

- escape noise vs. diffusive noise

6.5. Rate code vs. Temporal Code

- timing codes
- stochastic resonance

Welcome to the third part of week six. In the previous lecture I've explained how to calculate things like the Interspike interval distribution, how to calculate the survivor function. We'll now use these notions to look at the likelihood of an observed spike train.

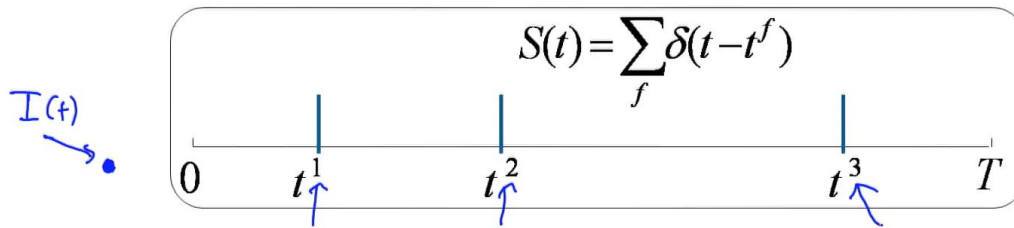
Notes

Summary



0m 04s

Neuronal Dynamics – 6.3. Likelihood of a spike train



Measured spike train with spike times $t^1, t^2, \dots, t^N$

Explanation now: Likelihood L that this spike train could have been generated by model?

$$L(t^1, \dots, t^N) = \exp\left(-\int_0^{t^1} \rho(t') dt'\right) \rho(t^1) \cdot \exp\left(-\int_{t^1}^{t^2} \rho(t') dt'\right) \dots$$

Suppose an experimentalist has injects a signal into a neuron. And he observes spike times. Suppose a first spike at time t^1 , a second time at time t^2 , a third spike at time t^3 . The upper index indicates the firing times. Firing times are events. And the spike train as a whole is a sequence of events we presented as a sequence of delta pulses. Now, you as a modular have a model. You inject the same current. And you add its [INAUDIBLE] noise so that your model also generates spikes. Now you ask what's the likelihood that this spike train with defined times at t^1 , t^2 and t^3 could have been generated by your model? Now, here's the answer. You can write down the likelihood. Now of course, this needs some explanation. That's what I will do now.

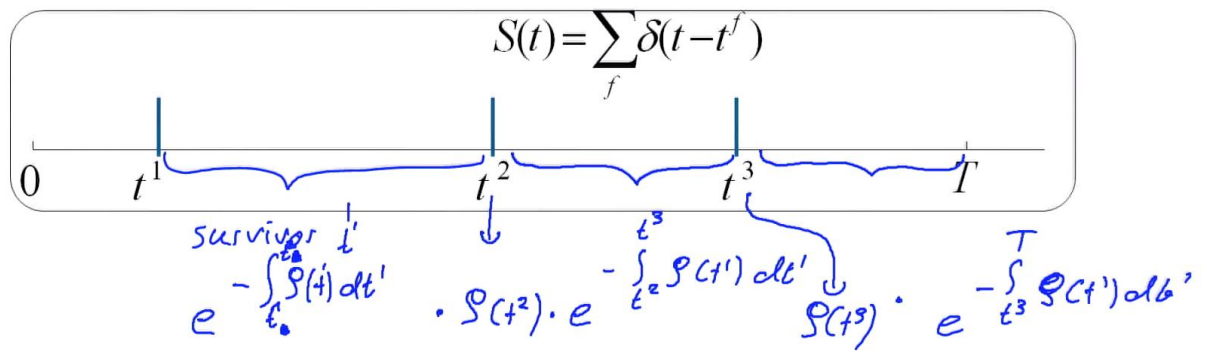
Notes

Summary



0m 27s

Neuronal Dynamics – 6.3. Likelihood of a spike train



So here again, my sequence of spikes. We have seen in part two that we can discuss the question what's the likelihood that a neuron would survive a certain interval from t_1 to t_2 without firing? So what's the probability to survive? Well, it's given by the survivor function. At each moment the neuron has a certain rate of firing. At this moment, say, t , it has a certain rate r of t . But we observe that it did not fire. The probability to survive without firing decays exponentially. And it doesn't fire in the whole interval from t_1 to t_2 . So we integrate this instantaneous rate from t_1 to t_2 . And then again, the neuron should stay silent. It should survive from t_2 to t_3 without firing. t_2 is this firing time here. t_3 is the next firing time. Firing times are the upper index. So this must be in upper index here and there. But then the neuron actually has to fire at time t_2 . Well, it does so with a firing intensity r or t , evaluated at time t_2 . Similarly, it has to fire here, at t_3 . And then it doesn't fire again between t_3 and T , capital T . So it's, again, times e to the minus from t_3 to the end of the measurement period, r of t prime, dt prime. And note it stays silent at the beginning.

Notes

Summary



Neuronal Dynamics – 6.3. Likelihood of a spike train

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

$$\mathcal{L}(t^1, t^2, t^3) = e^{-\int_0^{t^1} g(t') dt'} \cdot g(t^1) e^{-\int_{t^1}^{t^2} g(t') dt'} \cdot g(t^2) \cdot e^{-\int_{t^2}^{t^3} g(t') dt'} \cdot g(t^3) \cdot e^{-\int_{t^3}^T g(t') dt'}$$

So I have e to the minus, 0 too t^1 , row of t prime, dt prime. And it did fire at time t^1 . So the likelihood that within this period, from 0 to t , we would observe just three spikes at times t^1 , t^2 , and t^3 is, therefore, this.

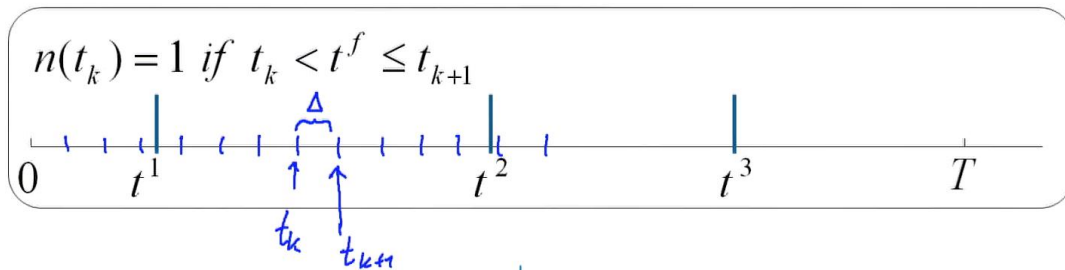
Notes

Summary



4m 22s

Neuronal Dynamics – 6.3. Likelihood in discrete time



Prob. to fire in $t_k < t \leq t_{k+1}$

$$P_{t_k}^{\Delta}$$

Prob. to be silent in $t_k < t \leq t_{k+1}$

$$S^{\Delta} = e^{-\int_{t_k}^{t_{k+1}} s(t') dt'}$$



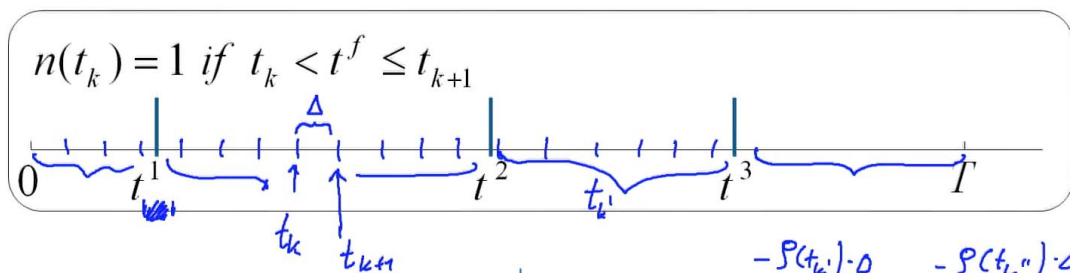
Now, working with these instantaneous rates, stochastic intensities with [INAUDIBLE] rates in continuous time sometimes causes problems. It's hard to imagine this. And sometimes it's easier to think in discrete time. Moreover, any computer implementation has to happen in discrete time. So let's introduce some discrete time bins. So I introduce my time bins like this. And let's look at this time bin, at this moment of time here. I call this t_k . Now, let's look at this moment here. This would be t_k plus 1. The lower index k is an index of the time bin. The upper index, f , is an index for the firing times. Now, let's look at the probability to survive this interval, Δ -- the time step Δ -- without firing. The probability to be silent in this interval Δ is given by the survivor function. I integrate from t_k to t_k plus 1, row of t prime, dt prime. Now, suppose that this is the time dependence of my functioned row of t , which I need to evaluate at these different moments in time. This would be at t_k . This would be at t_k plus 1. And you see that it changes only slowly. The difference between the value here and the value here is marginal. Whereas at some other times you might have a completely different value.

Notes

Summary



Neuronal Dynamics – 6.3. Likelihood in discrete time



Prob. to fire in $t_k < t \leq t_{k+1}$

$$P_{t_k}^{\Delta} = 1 - S^{\Delta} = 1 - e^{-\int_{t_k}^{t_{k+1}} s(t') dt'}$$

Prob. to be silent in $t_k < t \leq t_{k+1}$

$$S^{\Delta} = e^{-\int_{t_k}^{t_{k+1}} s(t') dt'} = e^{-\int_{t_k}^{t_{k+1}} s(t_k) dt'}$$

$$\prod_f P_{t^f}^{\Delta} = e^{-\sum_{k'} \int_{t_k}^{t_{k+1}} s(t_k) dt'}$$

↑
silent bins



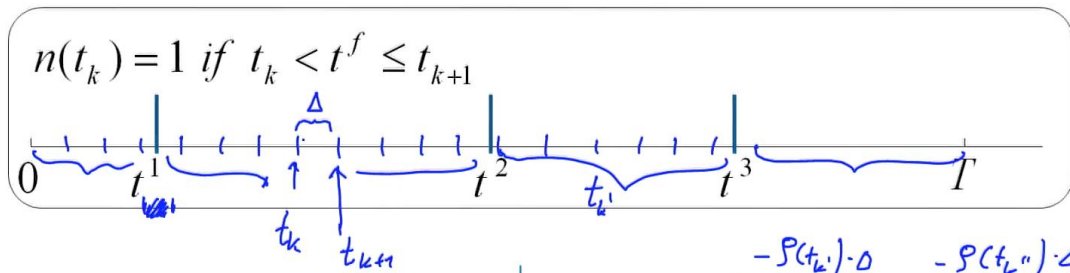
So if I say that row changes little in a small time step then I can approximate this by the following expression. I just evaluate at time t_k . And then I multiply for the duration of this integral. So the probability to stay silent in these different time steps here, time steps, time moments, k prime, would be you need to stay silent in one time step. Say row of t_k prime times Δ . And then you have to stay silent again in the next time step. t_k double prime times Δ would be the next time step. I have exponentials here. The product of exponentials can be written as a sum, row of t_k prime, a sum over all k prime times Δ . Now, a sum of all t_k primes that lie in between t_2 and T_3 . I do something similar for the interval from t_3 to capital T for this interval and for this interval here. So far, for the periods where the neuron does not fire. But then there are these moments and the neuron does fire. For example, in this interval here. Well, the probability to fire is 1 minus the probability of staying silent. So this is 1 minus e to the minus, row of t_k times Δ , in the approximation I made here. And I have to add all these different moments, P of $t^f \Delta$, for all the moments where I have firing. Product of all firing times. This is the sum of all bins where the neuron stays silent. So this is the discrete time construction of a likelihood.

Notes

Summary



Neuronal Dynamics – 6.3. Likelihood in discrete time



Prob. to fire in $t_k < t \leq t_{k+1}$

$$P_{t_k}^{\Delta} = 1 - S^{\Delta} = 1 - e^{-\int_{t_k}^{t_{k+1}} s(t') dt'}$$

Prob. to be silent in $t_k < t \leq t_{k+1}$

$$S^{\Delta} = e^{-\int_{t_k}^{t_{k+1}} s(t') dt'} = e^{-\int_{t_k}^{t_{k+1}} s(t_k) dt'}$$

$$\prod_f P_{t^f}^{\Delta} = e^{-\sum_{k'} \int_{t_k}^{t_{k+1}} s(t_k) dt'}$$

↑
silent bins

how about $\Delta \rightarrow 0$??

Now, let's ask the following question-- what happens if I make this bin size, delta, smaller and smaller?

Notes

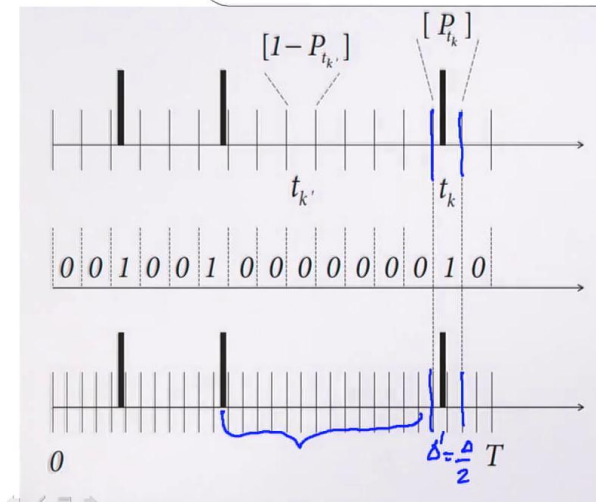
Summary



Neuronal Dynamics – 6.3. Likelihood in discrete time

$$n(t_k) = 1 \text{ if } t_k < t^f \leq t_{k+1}$$

$e^x = 1 + x + \dots$



$$P_{t_k}^\Delta = 1 - e^{-S(t_k) \cdot \Delta} = S(t_k) \cdot \Delta$$

$$\Delta \rightarrow 0$$

$$e^{-\sum_{k'} S(t_{k'}) \cdot \Delta} \rightarrow e$$

So for this bin size here I said, I for sure know probability, which is 1 minus e to the row of t_k times delta. Now, the Taylor expansion of e to the x is something like 1 plus x plus a term, x squared, and so forth. So if x is small-- and that's the case-- [INAUDIBLE] take delta very small. So this is going to be very small. I can use this Taylor expansion. And I arrive at row of t_k times delta, which becomes developed if delta gets very small. So now, consider the transition from time steps of duration delta to time steps of half the size, delta prime equals delta over 2. Well, now, I had a certain probability to fire in that time step. I must have a smaller probability to fire in the short time step. Because the total duration to fire between here and here, the total probability to fire between here and there should not change. And that's true for this firing probability that is proportional to the step size delta valid in the limit delta to 0. Now, all the survival terms that I have for the silent periods have to form into the minus sum over k prime row of $t_{k'}$ times delta. If I take the limit of delta to 0 then this transforms back into our [? unknown ?] integral, row of t prime, dt prime.

Notes

Summary

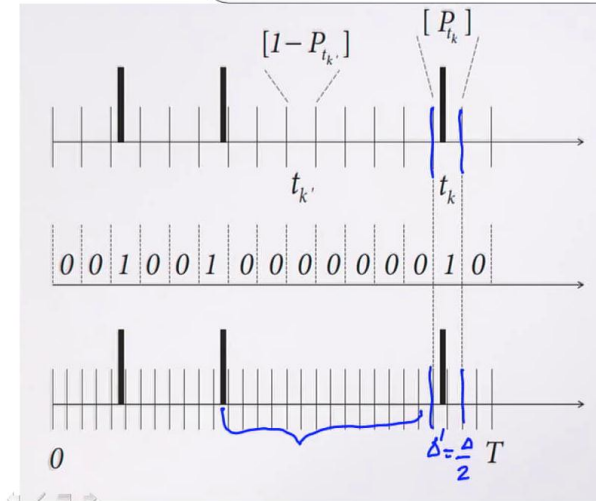


10m 08s

Neuronal Dynamics – 6.3. Likelihood in discrete time

$$n(t_k) = 1 \text{ if } t_k < t^f \leq t_{k+1}$$

$e^x = 1 + x + \dots$



$$P_{t_k}^{\Delta} = 1 - e^{-S(t_k) \cdot \Delta} = S(t_k) \cdot \Delta$$

$$\Delta \rightarrow 0$$

$$e^{-\sum_{k'} S(t_{k'}) \cdot \Delta} \rightarrow e^{-\int_{t^f}^{t^{f+1}} S(t') dt'}$$

$$\mathcal{L}^N = \Delta^N \left\{ \prod_{t^f, f=1}^N (S(t^f) \cdot \Delta) \cdot e^{-\int_{t^f}^{t^{f+1}} S(t') dt'} \right\}$$

$$\mathcal{L}(t^1, \dots, t^N)$$

And the intervals go over all these silent periods from a first firing time to the next firing time. Now, if you write down the likelihood in discrete time for a situation with exactly end spikes then we would have the product of all these different firing times, f equal 1 to N , row evaluated at t^f times Δ , multiplied with the survivor function going from t^f to t^f plus 1 of t prime, dt prime. The product is of these different firing times. Plus I should add the intervals at the beginning, at the end. I don't have the space to do so. And it's not important for the argument that I'm going to make. Now, what you see is that in this discrete time formulation of the likelihood I have this term, Δ . I have a term Δ for each firing time. So overall, I can move that in front. The script $\mathcal{L}$, for the discrete time likelihood is related to the factor Δ to the N , that Δ is the step size to the continuous time likelihood. $\mathcal{L}$ continuous time likelihood is really a density. And you have to integrate it N times to get a quantity that's related to a probability. So it's this continuous timed likelihood is an N -fold density.

Notes

Summary



12m 31s

Neuronal Dynamics – 6.3. Likelihood of a spike train

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

$$L(t^1, \dots, t^N) = \exp\left(-\int_0^{t^1} \rho(t') dt'\right) \rho(t^1) \cdot \exp\left(-\int_{t^1}^{t^2} \rho(t') dt'\right) \rho(t^2) \dots \exp\left(-\int_{t^N}^T \rho(t') dt'\right)$$

$$L(t^1, \dots, t^N) = \exp\left(-\int_0^T \rho(t') dt'\right) \prod_{f=1}^N \rho(t^f)$$

And here it's again, our density. This is the first interval. Then I have my spike. This is the second interval. Then I have my spike and so forth, until I have the last interval. I can rewrite this in a slightly different form. We see that this integral here goes up to t^1 . But the next integral starts at t^1 . It goes up to t^2 . The next integral would start at t^2 , go up to t^3 and so forth, until the final one, which goes from t^N to capital T . So all these terms give rise to one single integral over the whole period, the whole measurement interval, from 0 to T . The moments of firing for end spikes that equal 1 to N , I have N instantaneous firing rates.

Notes

Summary

15m 09s



Neuronal Dynamics – 6.3. Log-likelihood of a spike train

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


$$L(t^1, \dots, t^N) = \exp\left(-\int_0^T \rho(t') dt'\right) \prod_f \rho(t^f)$$

$$\log L = -\int_0^T \rho(t') dt' + \sum_{f=1}^N \log \rho(t^f)$$



Now, sometimes the likelihood is not written in this form but is transformed to a log likelihood. So if I take the logarithm, of this likelihood L , well, the logarithm of the exponential is just determine the argument of the exponential. Then I have a product. The logarithm of a product gives a sum. In fact, I have many products that turn into a sum over all spikes row of t^f .

Notes

Summary



16m 18s

Neuronal Dynamics – 6.3. Log-likelihood of a spike train

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


$$L(t^1, \dots, t^N) = \exp\left(-\int_0^T \rho(t') dt'\right) \prod_f \rho(t^f)$$

log L

$$= -\int_0^T \rho(t') dt' + \sum_{f=1}^N \rho(t^f)$$

Obviously, a 'log' sign is missing in the handwritten formula. The typed formula is correct.

$$\log L(t^1, \dots, t^N) = -\int_0^T \rho(t') dt' + \sum_f \log \rho(t^f)$$

Thus the likelihood can be rewritten as a log likelihood. And the two formulations are completely equivalent. I can also go back from the log likelihood to the likelihood. The reason for concentrating the log likelihood is simple. It looks nicer if you have sums compared to products.

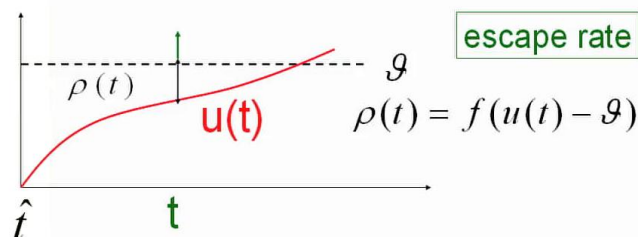
Notes

Summary



17m 03s

Neuronal Dynamics – 6.3. generative model of a spike train



generative model of spike train

- generates spikes stochastically
- calculated likelihood that an **observed** experimental spike train **could have been generated**

$$\log L(t^1, \dots, t^N) = -\int_0^T \rho(t') dt' + \sum_f \log \rho(t^f)$$

Let me summarize this. An integrated fire model with [INAUDIBLE] noise can be seen as a stochastic spike generator. It can be seen as a generative model, a model that can generate spike trains. If you have observed a spike train we can ask what would be the likelihood that this spike train could have been generated by my model? And the nice thing is you can write down. You can calculate this likelihood. Now, a model such as the [? integrated ?] fire model will have parameters, for example, the threshold. We are able to calculate this likelihood for different values of the threshold. And as we will see next week, this is the basis for optimizing parameters of such a neuron model.

Notes

Summary



17m 32s