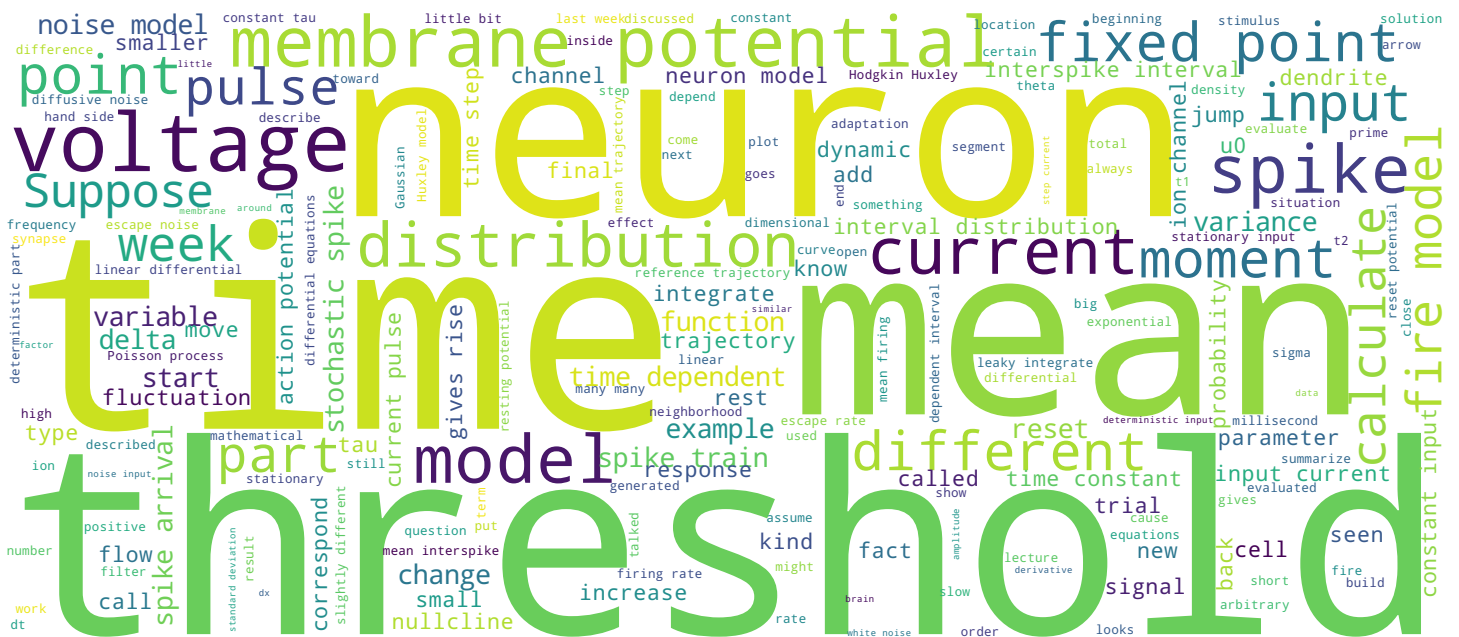


ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

EPFL, Lausanne, Switzerland

- stochastic resonance



EPFL



Neuronal Dynamics – 6.4. Comparison of Noise Models

Diffusive noise

- represents stochastic spike arrival
- easy to simulate
- hard to calculate

Escape noise

- represents internal noise
- easy to simulate
- easy to calculate
- approximates diffusive noise
- basis of modern model fitting methods



Welcome to part four of week six. Last week, I talked about a noise model that represents stochastic spike arrival. This week so far, I talked about an escape noise model. So what's the relation between those two noise models?

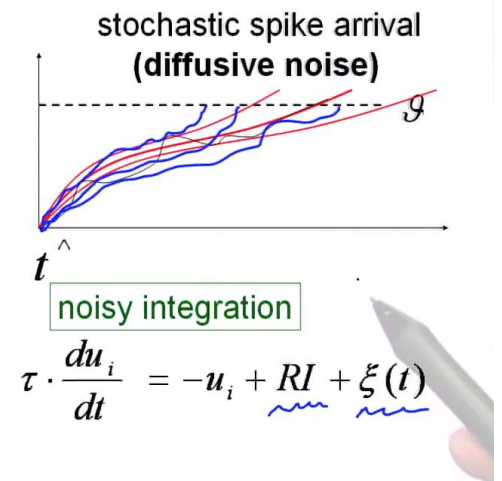
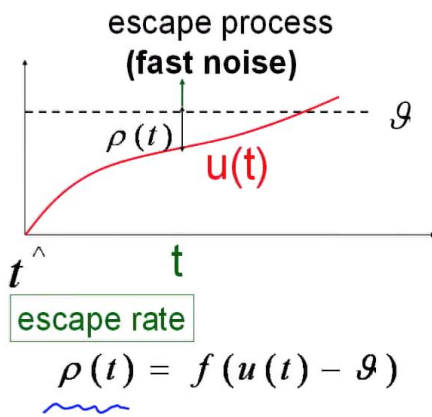
Notes

Summary



0m 05s

Neuronal Dynamics – 6.4. Comparison of Noise Models



In the first lectures of this week, we mainly looked at the escape rate, which describes the instantaneous rate that the neuron may fire despite the fact that the deterministic trajectory has not yet reached a threshold. Now in the previous week, we looked at a model describing stochastic spike arrival. If you start with a leaky integrate-and-fire model, there's an input current which has a deterministic part which gives rise to the red trajectory here. But then, because of additional noise that represent stochastic spike arrivals, there would be a real trajectory which is slightly different, which fluctuates around the reference trajectory. And in each trial, the actual trajectory is slightly different. So this actual trajectory stays in some neighborhood of the reference trajectory. If you want to link the two noise models, we need to look again a little bit at this model of stochastic spike arrival.

Notes

Summary



Poisson spike arrival: Mean and autocorrelation of filtered signal

signal

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

$F(s)$

Filter

$$x(t) = \int F(s) S(t-s) ds$$

Assumption:
stochastic spiking
rate $\nu(t)$

mean

$$\langle x(t) \rangle = \int F(s) \langle S(t-s) \rangle ds$$

$$\langle x(t) \rangle = \int F(s) \langle \nu(t-s) \rangle ds$$

Poisson rate

Autocorrelation of output

$$\langle x(t)x(t') \rangle = \left\langle \int F(s) S(t-s) ds \int F(s') S(t'-s') ds' \right\rangle$$

$$\langle x(t)x(t') \rangle = \int F(s) F(s') \langle S(t-s) S(t'-s') \rangle ds ds'$$

Autocorrelation of input

As we have seen last week, a spike train, described as a sequence of delta pulses, is filtered. And this gives rise to a signal. The signal at the end will be the membrane potential, but let's keep the mathematical treatment general right now. The stochasticity is in the spike train. If you look at the mean, then the mean is just over the stochastic spike train. No in the case that the stochastic spike train is generated by a Poisson process, then this just gives the instantaneous rate of the Poisson process. You can also look at the correlations. So this is the correlation of the signal x at time t with its value at time t prime. And again, the expectation signs can be moved inside. And so we see that the autocorrelation of the input is linked to the autocorrelation of the output. Now here, x was some arbitrary signal.

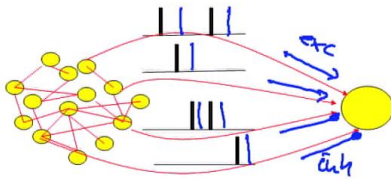
Notes

Summary



1m 43s

Diffusive noise (stochastic spike arrival)



Stochastic spike arrival:

excitation, total rate R_e

inhibition, total rate R_i

Synaptic current pulses

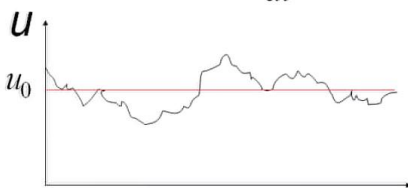
$$\tau \frac{d}{dt} u = -(u - u_{rest}) + \sum_{k,f} \frac{q_e}{C} \delta(t - t_k^f) - \sum_{k',f'} \frac{q_i}{C} \delta(t - t_{k'}^{f'})$$

EPSC

IPSC

$$\tau \frac{d}{dt} u = -(u - u_{rest}) + R I(t) + \xi(t)$$

Langevin equation,
Ornstein Uhlenbeck process



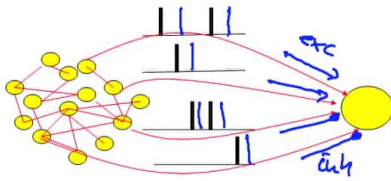
Let's consider now the case of a membrane potential, u , generated by a differential equation where the drive are spike arrivals. Suppose that there are some synapses that are excitatory, and there are other synapses that are inhibitory. An excitatory spike arrival causes a charge delivered to the membrane called q_e . This instantaneous delivery at that spike arrival time of the charge q_e gives rise to a positive jump of the membrane potential. Inhibitory synapses would deliver a negative charge, q_i . Now suppose that these spikes arrive at some frequency. Excited are rate μ_e . Inhibitors are rate μ_i . Now this mean drive causes a mean input current, a time-dependent, deterministic input current characterized by the rates μ_e and μ_i , the two different synapse types. Now let's suppose that we increase the frequency. We double the frequency in each of the input channels while decreasing the jump size, decreasing the charge delivered per pulse. Now if we increase by a factor of 10 and decrease the jump size by a factor of 10, then there are many, many jumps. The frequency is very high, but each jump makes only a very small contribution. And it's this limit that gives you a white noise input of some characteristic amplitude.

Notes

Summary



Diffusive noise (stochastic spike arrival)



Stochastic spike arrival:

excitation, total rate R_e

inhibition, total rate R_i

Synaptic current pulses

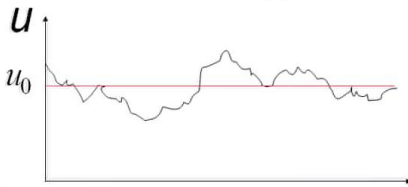
$$\tau \frac{d}{dt} u = -(u - u_{rest}) + \sum_{k,f} \frac{q_e}{C} \delta(t - t_k^f) - \sum_{k',f'} \frac{q_i}{C} \delta(t - t_{k'}^{f'})$$

EPSC

IPSC

$$\tau \frac{d}{dt} u = -(u - u_{rest}) + R I(t) + \xi(t)$$

Langevin equation,
Ornstein Uhlenbeck process



Let's call it sigma. And a differential equation with a deterministic part plus this white noise input is called the Langevin equation. The specific linear differential equation with this noisy input is called the Ornstein Uhlenbeck process. Now normally in this Ornstein Uhlenbeck process we don't have a threshold. A real integrate-and-fire model, however, does have a threshold.

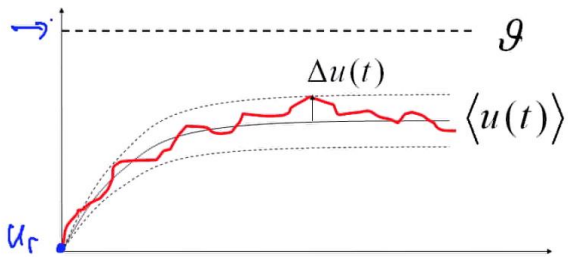
Notes

Summary



5m 05s

Diffusive noise (stochastic spike arrival)



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

$$\langle \Delta u(t) \Delta u(t) \rangle = \langle u(t) u(t) \rangle - \langle u(t) \rangle^2 =$$

$$\langle \Delta u(t') \Delta u(t) \rangle = \langle u(t) u(t') \rangle - \langle u(t) \rangle \langle u(t') \rangle =$$

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Suppose now that we simulate an integrate-and-fire model. After its spike, we start at a reset potential, u_r , and we integrate up to the threshold θ .

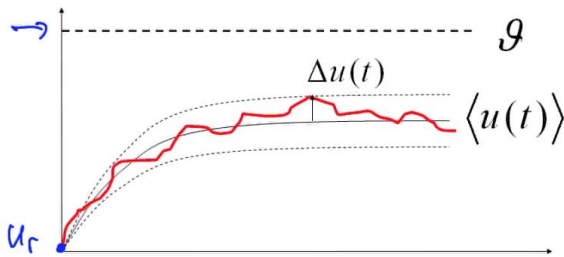
Notes

Summary



5m 36s

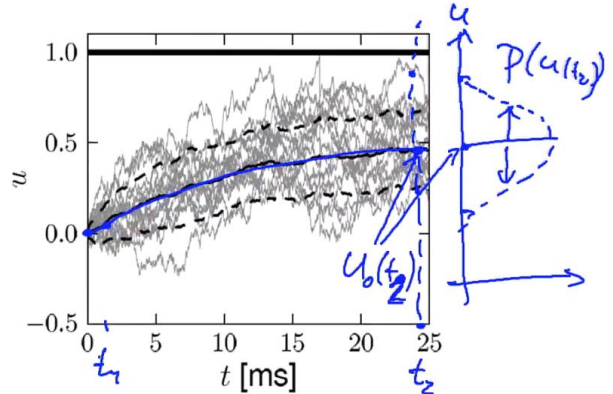
Diffusive noise (stochastic spike arrival)



$$\langle \Delta u(t) \Delta u(t) \rangle = \langle u(t) u(t) \rangle - \langle u(t) \rangle^2 =$$

$$\langle \Delta u(t') \Delta u(t) \rangle = \langle u(t) u(t') \rangle - \langle u(t) \rangle \langle u(t') \rangle =$$

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



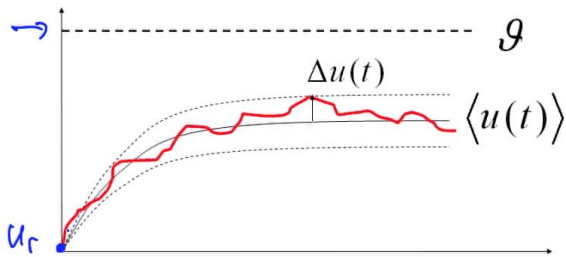
And we do this several times. Each time, we start at the reset value r , here equal to 0. And then we have many, many sample trajectories. Now this is the mean trajectory evaluated at different moments in time. And you see that, if you look at this moment here-- let's call it t_1 -- then the mean is different than at the later moment-- say, t_2 -- over here. So this trajectory, this value here would be u_0 , the mean at time t_2 . Now let's look at this time. Let's just do a vertical cut across all these different samples of membrane potentials. I put here the vertical axis, which is the axis of membrane potentials, and then I build a histogram of how many values do I see here. For example, I see a value here. I see a value here. And if I build this up, I will get some distribution of membrane potentials. Now if I have many, many, many different trajectories, many trials, all starting at the same reset potential, all driven by the same deterministic input i of t , then I can build up this distribution of membrane potentials, which is p of u . Now evaluated at this specific point, u of t_2 , it has a mean. And this mean is this value here. You zero the mean at time t_2 . And it also has some variance. And the variance is what we can calculate mathematically.

Notes

Summary



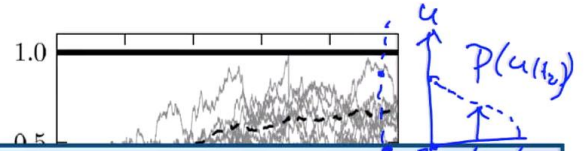
Diffusive noise (stochastic spike arrival)



$$\langle \Delta u(t) \Delta u(t) \rangle = \langle u(t) u(t) \rangle - \langle u(t) \rangle^2 =$$

$$\langle \Delta u(t') \Delta u(t) \rangle = \langle u(t) u(t') \rangle - \langle u(t) \rangle \langle u(t') \rangle =$$

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



Math argument:

- no threshold
- trajectory starts at known value

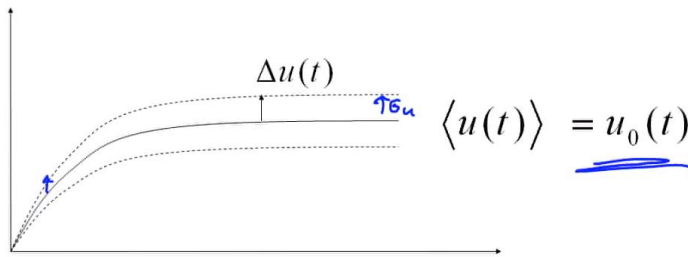
Now in order to do this mathematical calculation, we assume for the moment that there is no threshold. So this could be achieved simply by removing the threshold or by putting the threshold to such a high value that, in practice, it's never reached. And then we assume, as before, that the trajectory starts at some known value, for example, the reset potential.

Notes

Summary



Diffusive noise (stochastic spike arrival)

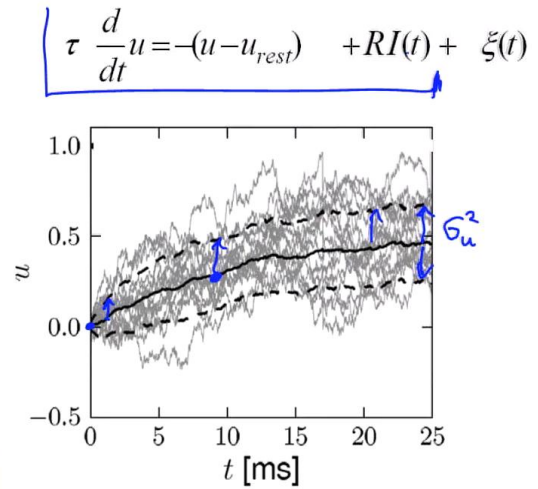


$$\langle \Delta u(t) \Delta u(t) \rangle = \langle u(t) u(t) \rangle - \langle u(t) \rangle^2 =$$

$$\langle \Delta u(t') \Delta u(t) \rangle = \langle u(t) u(t') \rangle - \langle u(t) \rangle \langle u(t') \rangle =$$

Math argument

$$p(u, t) = \frac{1}{\sqrt{2\pi \langle \Delta u^2(t) \rangle}} \exp \left\{ -\frac{[u(t) - u_0(t)]^2}{2 \langle \Delta u^2(t) \rangle} \right\}$$



$$\langle [\Delta u(t)]^2 \rangle = \sigma_u^2 [1 - \exp(-2t / \tau)]$$

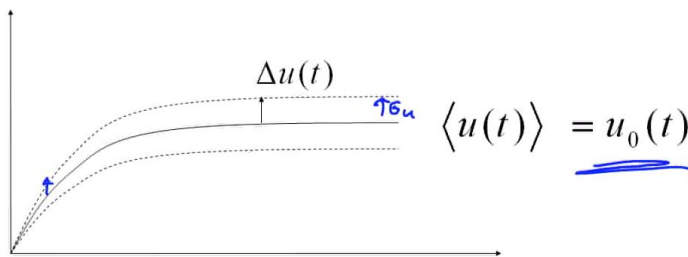
Now if you do this math argument, then what we will see is that there is this variance of the different trajectories, which I can plot here, or I can point it out here. There's the variance here. There's a variance here. There's a variance here. And this variance is small at the beginning. In fact, it's 0 at time 0 because all trajectories start at the same value. And then it blows up slightly. Now one can calculate this, and one finds that there's a final value of the voltage distribution, the variance. The standard deviation of the voltage distribution is sigma u. The variance is sigma u squared. And this final value is reached over time. And is the standard deviation at the beginning is much smaller than at the end. The standard deviation does not increase infinitely. It saturates at some final value. And this is expressed here. That's the final value, and that's the approach towards this final value. Now the mean, this value u0, at any moment t can be called calculated by considering the equation just up to this part here. We integrate the deterministic part of the input current. Let's show this in three examples. In each case, we will consider the distribution of membrane potentials.

Notes

Summary



Diffusive noise (stochastic spike arrival)



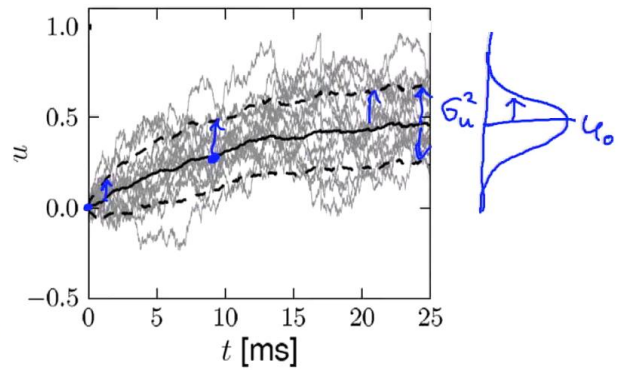
$$\langle \Delta u(t) \Delta u(t) \rangle = \langle u(t) u(t) \rangle - \langle u(t) \rangle^2 =$$

$$\langle \Delta u(t') \Delta u(t) \rangle = \langle u(t) u(t') \rangle - \langle u(t) \rangle \langle u(t') \rangle =$$

Math argument

$$p(u, t) = \frac{1}{\sqrt{2\pi \langle \Delta u^2(t) \rangle}} \exp \left\{ -\frac{[u(t) - u_0(t)]^2}{2 \langle \Delta u^2(t) \rangle} \right\}$$

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



$$\langle [\Delta u(t)]^2 \rangle = \sigma_u^2 [1 - \exp(-2t / \tau)]$$

And this distribution of membrane potentials is a Gaussian with a mean value u_0 and a certain variance. u of t is one sample trajectory. And so this is the probability density that, at time t , I would find a trajectory at the value u . The distribution is Gaussian with a center at u_0 of t .

Notes

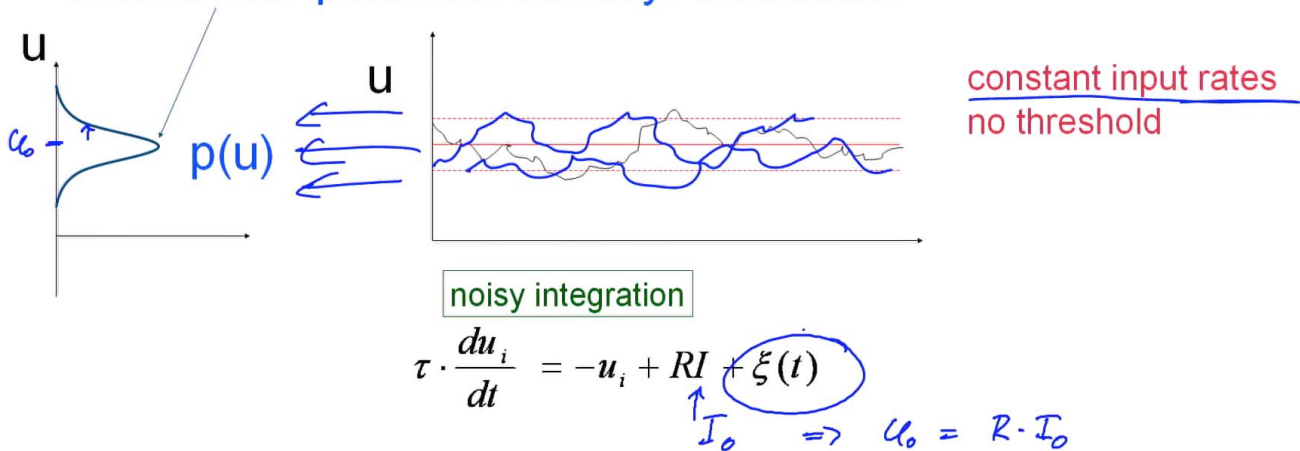
Summary



Neuronal Dynamics – 6.4. Diffusive noise/stoch. arrival

A) No threshold, stationary input

Membrane potential density: Gaussian



So here are the three examples. Suppose for the moment that the input is stationary. This could be a constant deterministic input, or you can think of constant input rates with Poisson spike arrival. And as before, there's no threshold. Then I have a distribution of membrane potentials. And in each trial, it's a slightly different trajectory. But if I project the trajectory out on to the vertical voltage axis, I find a distribution. And this mean value, u_0 , is constant because the input is stationary. So for constant input, this mean value, u_0 , would just be R times I_0 . And the width of this Gaussian distribution is controlled by the amplitude of the noise signal here.

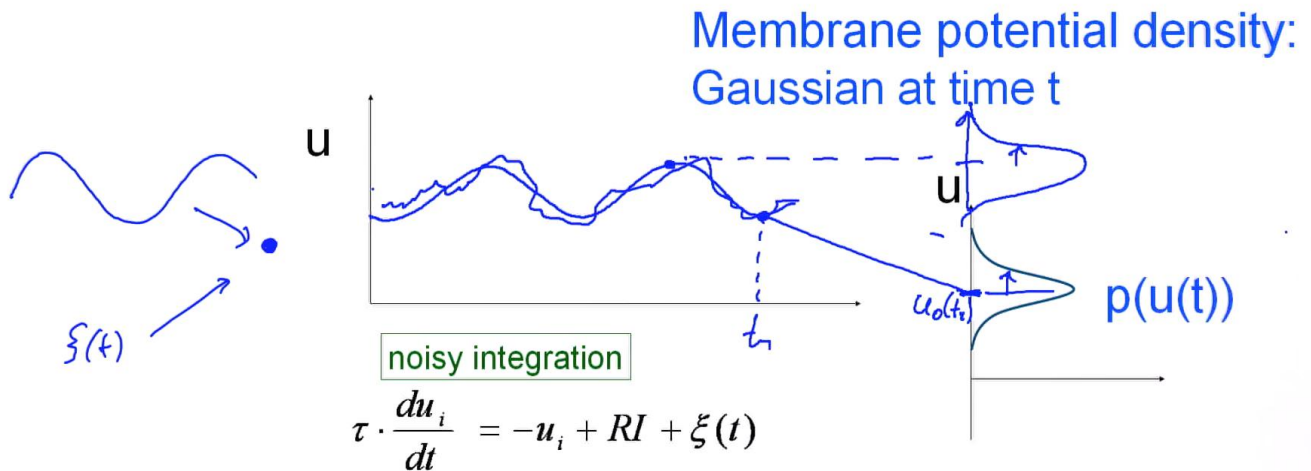
Notes

Summary



Neuronal Dynamics – 6.4. Diffusive noise/stoch. arrival

B) No threshold, oscillatory input



Second example-- as before, there's no threshold. But now we have an input at a neuron which is oscillatory. And I add to this input a noise term with 0 mean. Now integrating this oscillatory input will give rise to an oscillation of the membrane potential with the same frequency. Actual trajectories stay in the neighborhood of this reference trajectory. If I evaluate the distribution of membrane potentials at some point here, I will get some distribution. Let's call this t_1 . Then this is centered around the mean trajectory, around your deterministic trajectory, u of t_1 , and the distribution has a certain width. If I evaluate the distribution at some other point in time, I find again a Gaussian distribution of the same width but with a different mean. In other words, the distribution as a whole will periodically move up and down, up and down.

Notes

Summary

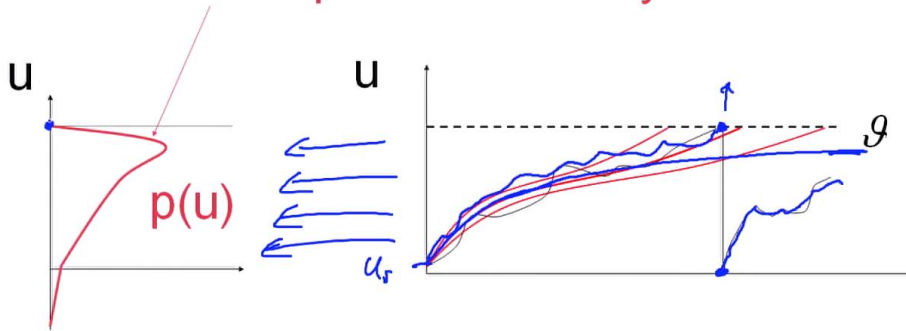


11m 38s

Neuronal Dynamics – 6.4. Diffusive noise/stoch. arrival

C) With threshold, reset/ stationary input

Membrane potential density



Third example-- now we add the threshold. We have stationary input. So the input itself is stationary. However, each time there is a spike, the membrane potential is reset to the reset value u_r . And after the spike, integration starts again. So the mean trajectory, the reference trajectory itself, is time-dependent. It will saturate at some fixed value. The actual trajectories are different, and they may reach the threshold at some moment in time before the reset occurs. And then the whole process starts again. If you go on with a simulation of such a stationary process for a long time and, again, we project out all the different voltage values, we find, again, a membrane potential density. And in this case, it's not Gaussian. It cannot be Gaussian. At the threshold, the density for white noise input is always 0.

Notes

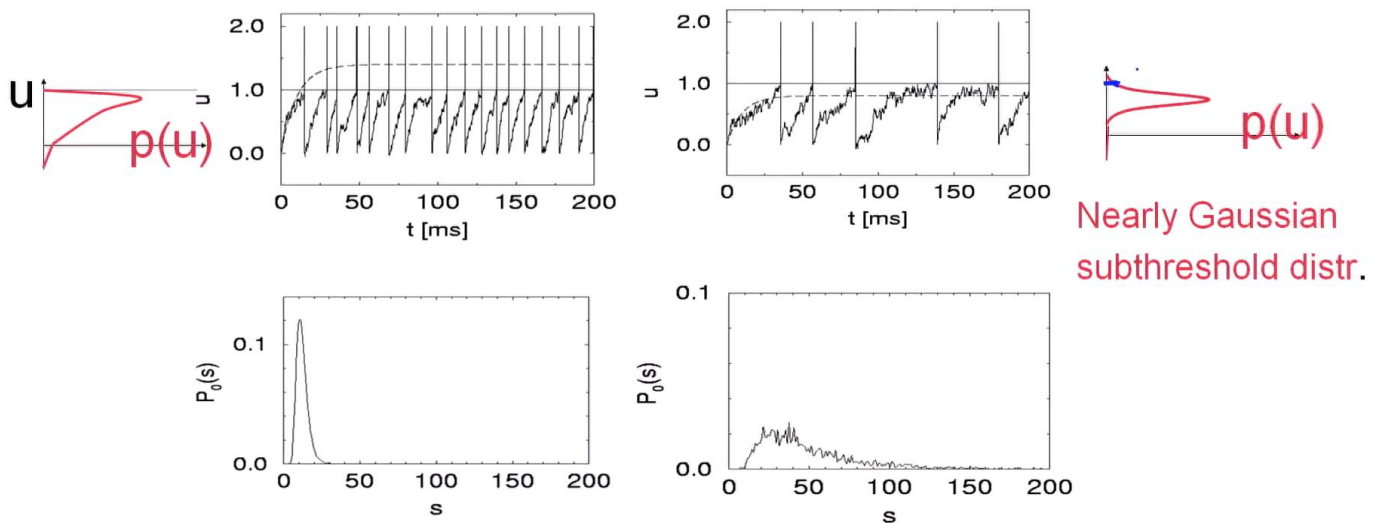
Summary



13m 11s

Neuronal Dynamics – 6.4. Diffusive noise/stoch. arrival

Superthreshold vs. Subthreshold regime



So if you go back for a moment to the superthreshold and subthreshold discussion that we did last week, then we see in the superthreshold regime, a lot of density is just below the threshold. The density at threshold is 0. The distribution is highly non-Gaussian. Whereas in the subthreshold regime, the distribution is nearly Gaussian. It's not perfectly Gaussian, because a Gaussian always has a finite width at the threshold. But if we are far enough below threshold, then the distribution is well approximated by a Gaussian.

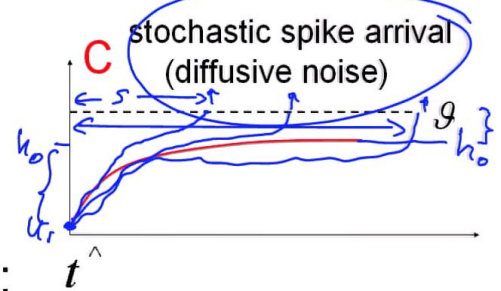
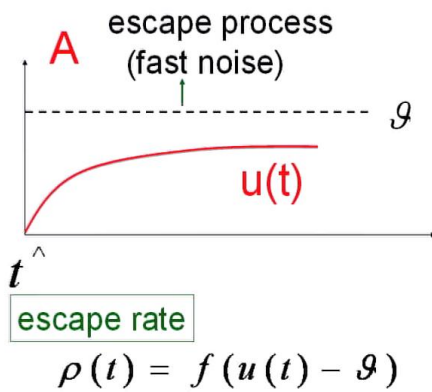
Notes

Summary



14m 21s

Neuronal Dynamics – 6.4. Comparison of Noise Models



Stationary input:
-Mean ISI

$$\langle s \rangle = \tau_m \sqrt{\pi} \int_{\frac{u_r - h_0}{\sigma}}^{\frac{g - h_0}{\sigma}} du \exp(u^2) [1 + \operatorname{erf}(u)]$$

-Mean firing rate

$$v = 1/\langle s \rangle$$

So with my model of stochastic spike rival, I can calculate distributions of membrane potential. Moreover, I can calculate something like the mean interval. One trajectory for stationary input may hit the threshold here. Another trajectory-- much, much later. A third trajectory-- over here. The last spike has occurred here. That was the moment when the reset happened. Now let's look at the interspike intervals. There are short ones, and there are long ones. The distribution of interspike intervals has some mean. And we can calculate the mean interspike interval. And this is a famous formula. What you see here is the mean value of the noise-free trajectory, h_0 . What matters is the distance of h_0 to the threshold normalized by width, σ , of the membrane potential distribution. Another important quantity is the difference between the reset potential and h_0 . Now knowing the mean interspike interval for stationary input implies that we can calculate the mean firing rate for leaky integrate-and-fire model for stationary input. And the mean firing rate is just 1 over the mean interval. Now let's look the escape process for a moment. For the escape process, we have the escape rate.

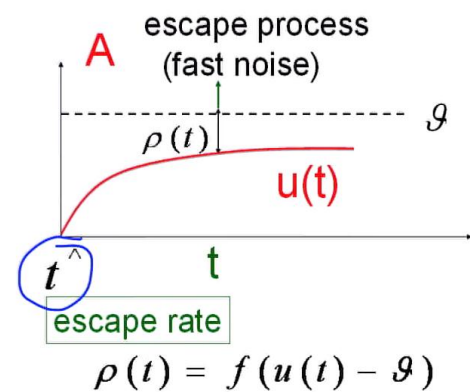
Notes

Summary



15m 01s

Neuronal Dynamics – 6.4. Comparison of Noise Models



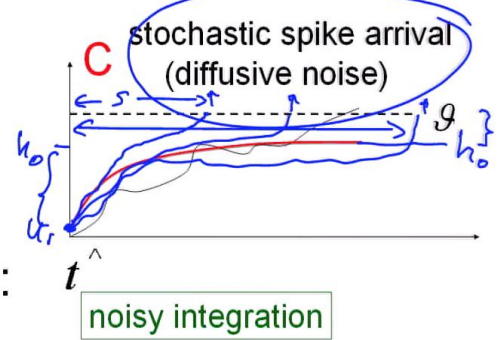
Interval distribution

$$P_I(t | t^{\wedge}) = \underbrace{\rho(t)}_{\text{escape rate}} \cdot \underbrace{\exp\left(-\int_{t^{\wedge}}^t \rho(t') dt'\right)}_{\text{Survivor function}}$$

Stationary input:
-Mean ISI

$$\langle s \rangle = \tau_m \sqrt{\pi} \int_{\frac{u_r - h_0}{\sigma}}^{\frac{u - h_0}{\sigma}} du \exp(u^2) [1 + \text{erf}(u)]$$

-Mean firing rate



$$\tau \cdot \frac{du_i}{dt} = -u_i + RI + \xi(t)$$

noise

$P_I(t | t^{\wedge})$: first passage time problem

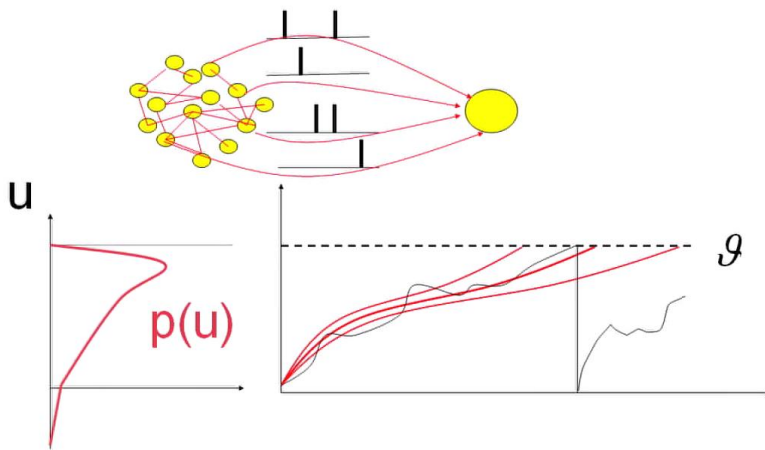
And we can calculate the interval distribution. Given the last spike occurred at $t^{\wedge}$, what's the probability density the next spike occurs at t knowing the input? And the formalized one, we discussed this week. Now importantly, this can be evaluated for constant input or for time-dependent input. For constant input, we can evaluate the integral distribution. Therefore we can calculate the mean interspike interval. Therefore we know the mean firing rate for stationary input. But moreover, in this case, we can also calculate the time-dependent interval distribution, and that's something that's rather hard to do in the other case. In fact, calculating this quantity, time-dependent interval distribution, for the case of a diffusive noise model is classified as the first passage time problem. And if a mathematical problem gets a name, that means it's difficult.

Notes

Summary



Neuronal Dynamics – 6.4. Comparison of Noise Models



Diffusive noise

- distribution of potential
- mean interspike interval
FOR CONSTANT INPUT
- time dependent-case difficult

Escape noise

- time-dependent interval
distribution

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Let me summarize the first part of lecture 6.4. For diffusive noise, we are able to calculate the distribution of membrane potential. We are able to calculate the mean interspike interval for constant input, but the time-dependent case is difficult. The advantage of an escape noise formulation is that we have access to the time-dependent interval distribution. Now the question arises whether the diffusive noise model can be approximated by an escape noise model. And that's the topic for the continuation of this lecture 6.4.

Notes

Summary



18m 21s