

Week 6 – part 1 : Escape noise



Neuronal Dynamics: Computational Neuroscience of Single Neurons

Week 6 – Noise models: Escape noise

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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

- likelihood function

6.4 Comparison of noise models

- escape noise vs. diffusive noise

6.5. Rate code vs. Temporal Code

- timing codes
- stochastic resonance



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- Time-dependend ISI
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- escape noise vs. diffusive noise

6.5. Rate code vs. Temporal Code

- timing codes
- stochastic resonance

Welcome to the first part of week six of the class Neuronal Dynamics. Last week, we have seen that spike timing is variable. If you repeat the same stimulus several times while recording for one neuron, you will find different spike types between one trial and the next. This week, we'll continue our discussion of noise models. And we'll encounter the powerful, mathematical tool of stochastic point processes.

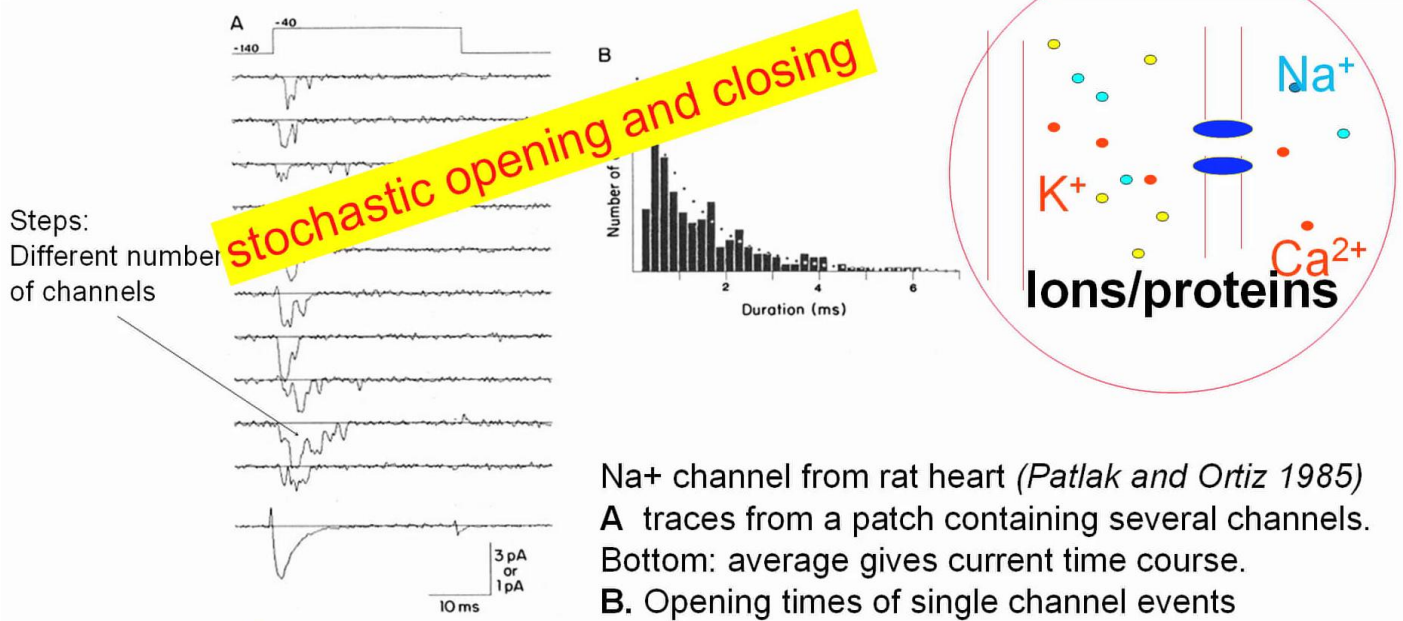
Notes

Summary



0m 04s

Review from 2.5 Ion channels



So as you have seen, there are intrinsic noise sources that contribute to the variability. Ion channels open and close stochastically. There's a finite number of ion channels working at finite temperature. This is something like an intrinsic noise source. And indeed, you can follow the stochastic opening and closing of ion channels if you do patch recordings from a piece of membrane. So there is stochasticity reflected in the spontaneous opening and closing of ion channels, and this is a first noise source.

Notes

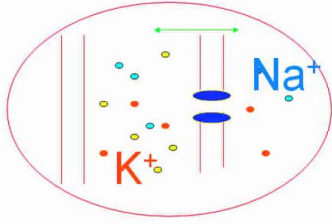
Summary



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Neuronal Dynamics – Review: Sources of Variability

- Intrinsic noise (ion channels)

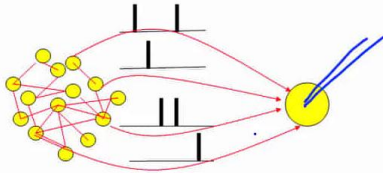


-Finite number of channels

-Finite temperature

small contribution!

-Network noise (background activity)



-Spike arrival from other neurons

-Beyond control of experimentalist

Noise models?

big contribution!

However, the importance of this noise source is limited compared to another noise source. From the point of view of the single neuron from which we record, spike timing looks stochastic. It's out of the control of the experimentalist. While the stimulus applied is always the same, spike arrivals caused by spiking from other neurons, is beyond the control. And this contributes to the variability of neuronal output. The question I will ask this week is, what kind of descriptions can be used to describe these fluctuations, to describe variability in spike timing? What are noise models?

Notes

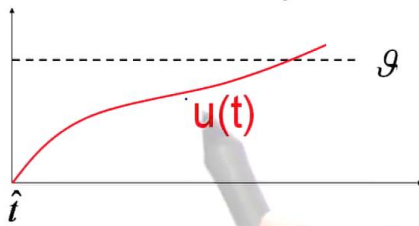
Summary



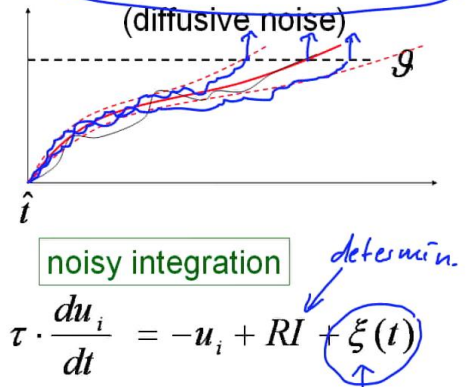
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Noise models

escape process,
stochastic intensity



stochastic spike arrival
(diffusive noise)



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

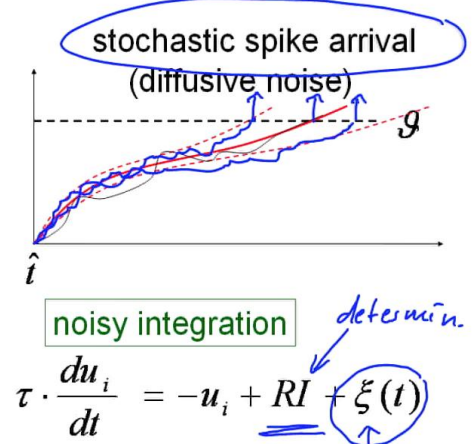
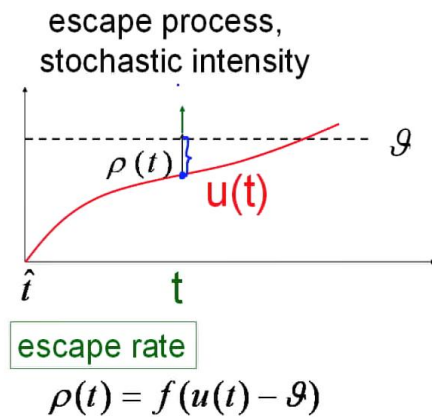
Now, last week we have seen a first noise model related to stochastic spike arrival. Suppose you have a leaky integrate-and-fire neuron. It's essentially a passive membrane. Now if you have a deterministic part of the stimulus, then integration of this equation will give a noise-free trajectory. However, since there are also stochastic contributions described here by a noise term, the actual trajectory is different from the noise-free trajectory. An actual trajectory is different between one trial and the next. It shows fluctuations, and overall, it stays fairly close to the reference trajectory, to the deterministic trajectory. It stays sort of in some tube around the reference trajectory, but the exact spike timings vary between one trial and the next. So this is the first noise model. I call this diffusive noise because this noise term here leads to sort of a diffusion off the actual trajectory away from the noise-free reference trajectory. So that's a first noise model. Now, we can take a completely different point of view. Let's just focus on our deterministic trajectory. The trajectory I would get if I just used the deterministic part of the input, the part of the input that's controlled by the experimentalist, that's repeatable between one trial and the next.

Notes

Summary



Noise models



Relation between the two models:
later this week (lecture 6.4)

And now I add noise in a completely different way. I say, well, despite the fact that the membrane potential has not yet reached the threshold θ , there is already a probability to escape across the threshold. And this instantaneous rate of escaping across the threshold depends on the momentary difference in between the membrane potential at time t and the threshold. So this is the stochastic intensity, the instantaneous rate of firing a spike. Spikes are formal events. They are points in time. And so overall, this is the stochastic intensity of a point process. Let's call this instantaneous intensity of firing the escape rate, the probability to escape across the threshold. Now, this is the noise model we will discuss now.

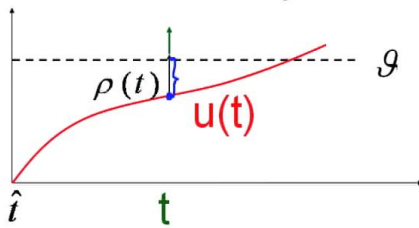
Notes

Summary



Noise models

escape process,
stochastic intensity

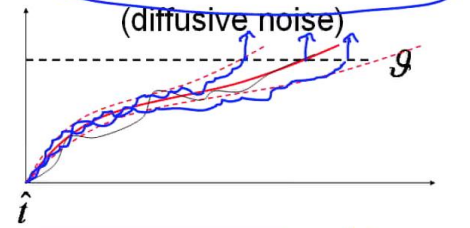


escape rate

$$\rho(t) = f(u(t) - g)$$

Now:
Escape noise!

stochastic spike arrival
(diffusive noise)



noisy integration

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

Relation between the two models:
later this week (lecture 6.4)

Later this week, I will discuss the relation between the two different noise models.

Notes

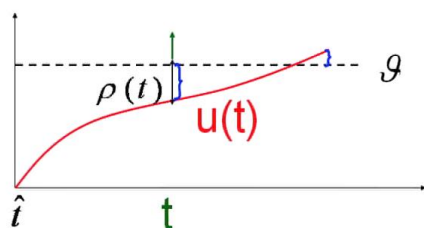
Summary



5m 33s

Neuronal Dynamics – 6.1 Escape noise

escape process

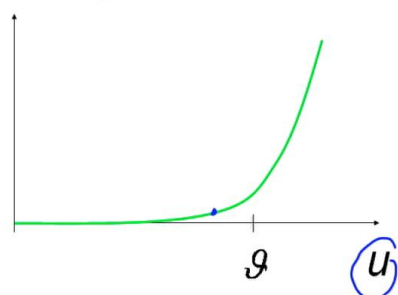


escape rate

$$\rho(t) = \frac{1}{\Delta} \exp\left(\frac{u(t) - \theta}{\Delta}\right)$$

escape rate

$$\rho(t) = f(u(t) - \theta)$$



Example: leaky integrate-and-fire model

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

$$\text{if spike at } t^f \Rightarrow u(t^f + \delta) = u_r$$

But let's focus on escape noise now. So here, again, the basic idea. I can construct a deterministic trajectory, for example, in the leaky integrate-and-fire model, by looking at the deterministic part of the input. This gives me a trajectory. And then I'll say, well, even though the trajectory hasn't reached the final threshold yet, there's already an instantaneous escape rate, the escape across the threshold leading to a rate of momentary spike fire, even though the deterministic part of the trajectory hasn't reached a threshold yet. But there could also be an instance that I continue to integrate deterministically, and I even cross the threshold. And despite the fact that the deterministic trajectory has crossed the threshold, no firing takes place. So this stochastic intensity or escape rate will depend on the difference between the momentary value of the membrane potential and the threshold. And as the membrane potential u approaches the threshold, this instantaneous escape rate increases. While it's below threshold, there's a small rate of firing. If it's above threshold, this escape rate grows rapidly. One possibility is to say, well, the escape rate is an exponential function of u minus θ .

Notes

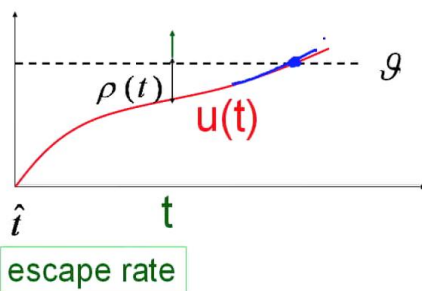
Summary



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Neuronal Dynamics – 6.1 stochastic intensity

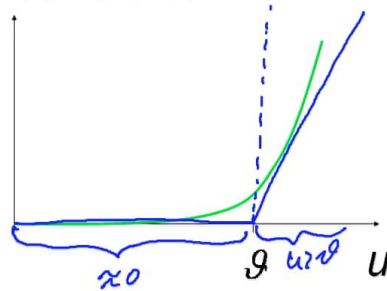
escape process



Escape rate = stochastic intensity
of point process

$$\rho(t) = f(u(t))$$

$$\rho(t) = f(u(t) - \vartheta)$$



examples

$$\rho(t) = \frac{1}{\Delta} \exp\left(\frac{u(t) - \vartheta}{\Delta}\right)$$

$$\rho(t) = \begin{cases} \varphi_0 \left[\frac{u}{\vartheta} - 1 \right] & \text{for } u > \vartheta \\ 0 & \text{for } u \leq \vartheta \end{cases}$$

And this parameter delta here would control the steepness. If I decrease delta, then it becomes steeper and steeper. So here is our first example of a stochastic intensity. It could have an exponential dependence upon u minus theta. A slightly different, simpler version would be to say, this is escape rate is proportional to u over theta whenever u is larger than theta. So at u equals theta, I have 1 minus 1. I have 0. If u is larger than theta, I have a positive contribution. And it's 0 for u smaller than theta. And this row 0 is a constant parameter. So this function is piecewise linear. It would look something like this. Now, if I change the row 0, if I increase row 0, then I change the steepness of this increase. And if as row 0 gets bigger and bigger, I get a sharper and sharper increase so that basically the escape rate is close to 0 as long as we stay below the threshold. And then it's very, very big if we are above threshold, if the membrane potential is larger than theta. And this very big escape rate essentially means that as soon as the membrane potential crosses the threshold, a spike is initiated. So the rapid increase corresponds to a rapid response as soon as the membrane potential crosses the threshold.

Notes

Summary

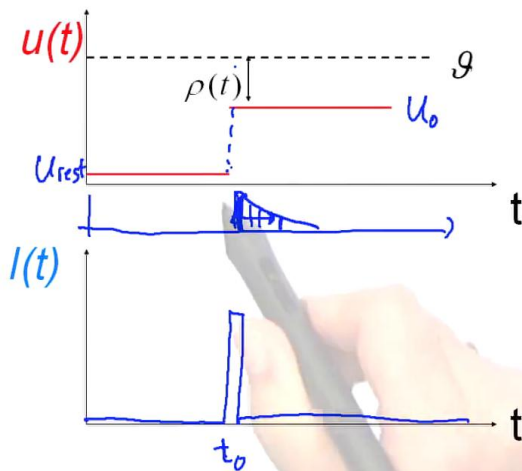


Neuronal Dynamics – 6.1 mean waiting time

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

escape rate

$$\rho(t) = f(u(t) - \vartheta)$$



mean waiting time, after switch

$$\langle T \rangle =$$

Let me explain this with this additional example. Suppose I have my leaky integrate-and-fire model with a leaky integrator for the subthreshold part, and I apply a current, which is 0 except at this moment in time where I give a short current pulse. So if I integrate this, then essentially, I have a constant value of the membrane potential. The membrane potential sits at u_{rest} , and then it jumps up to a new value which I call u_0 . Now, this momentary escape rate is then a constant. So if this is u_0 , then this would be row of u_0 . And that's a constant. So this means 1 after the switch, the neuron has a constant rate of firing. So this is just like in the homogeneous Poisson process. You know ask, what's the probability to have a first spike here? Well, what's the probability to have a first spike there? It's another probability. This probability of finding a spike, a first spike, will decrease over time just because if the neuron has fired here in the first pin, you can no longer fire its first spike a little bit later. And the mean waiting time would be the mean of this waiting time distribution. So the mean waiting time, for this exponential [? explosion, ?] will be just 1 over row of u_0 .

Notes

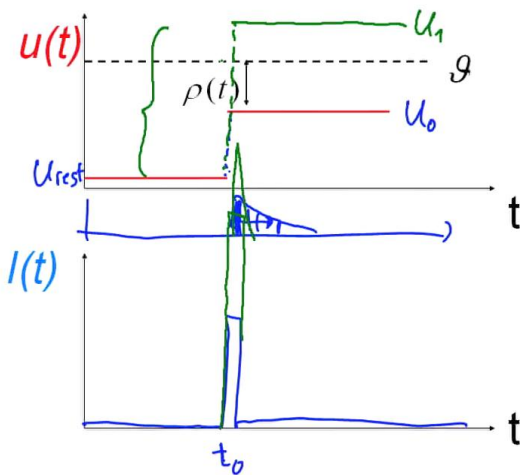
Summary



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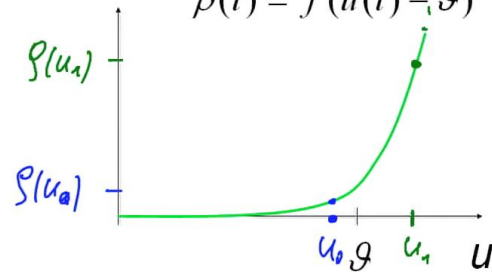
Neuronal Dynamics – 6.1 mean waiting time

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



escape rate

$$\rho(t) = f(u(t) - g)$$



mean waiting time, after switch

$$\langle \tau_0 \rangle = 1/\rho(u_0)$$

$$\langle \tau_1 \rangle = 1/\rho(u_1) \ll \langle \tau_0 \rangle$$

$$\text{if } f(u - g) \gg \infty \Rightarrow \langle \tau \rangle \rightarrow 0 \text{ for } u \gg g$$

Now let's look at a different input. Again, it's a short current pulse. But I make the current pulse twice as big so the jump is now twice as large. The jump size is twice as large, and I have a new value, u_1 . So now I'm up here, u_1 . And I have a very large instantaneous rate of high stochastic intensity. In this second case, well, the rate is so high that nearly all the spikes will occur here. So the new τ , the mean waiting time, is 1 over u_1 . Let's call this τ_1 , and τ_1 is much shorter than the earlier τ_0 , if I call this τ_0 . So the fact that this escape rate increases rapidly, it's not going to saturate. It really increases rapidly. This rapid increase guarantees that the waiting time until spike firing is really short if you are way above threshold. So the mean waiting time goes to 0 for u much larger than θ if this function f of u minus θ goes to infinity. If this function here explodes, then the mean waiting time is very short. Now this means that, as it should be, if I'm way above threshold, I push the membrane potential up above threshold, then spike firing is reliable. And it recurs immediately after the threshold crossing.

Notes

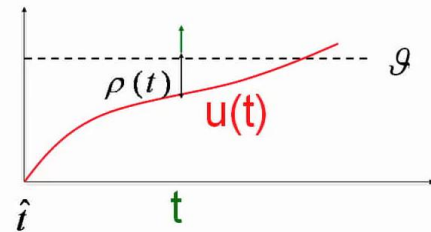
Summary



Neuronal Dynamics – 6.1 escape noise/stochastic intensity

Escape rate = stochastic intensity
of point process

$$\rho(t) = f(u(t))$$



Let me summarize. So I've introduced a notion of the escape rate. The escape rate is a way to describe the stochastic intensity of a point process beyond a framework of stochastic point processes. Spikes are events. They are points in time. They are created stochastically with a momentary intensity, which depends on the difference between the momentary value of the membrane potential and the threshold. Now, this is a useful tool to describe stochastic spike firing. It will be used throughout this week and next week. And in order for you to get used to this notion, please have a look at the quiz.

Notes

Summary



14m 33s

Neuronal Dynamics – Quiz 6.1.

Escape rate/stochastic intensity in neuron models

- ☐ The escape rate of a neuron model has units one over time
- ☐ The stochastic intensity of a point process has units one over time
- ☐ For large voltages, the escape rate of a neuron model always saturates at some finite value
- ☐ After a step in the membrane potential, the mean waiting time until a spike is fired is proportional to the escape rate
- ☐ After a step in the membrane potential, the mean waiting time until a spike is fired is equal to the inverse of the escape rate
- ☐ The stochastic intensity of a leaky integrate-and-fire model with reset only depends on the external input current but not on the time of the last reset
- ☐ The stochastic intensity of a leaky integrate-and-fire model with reset depends on the external input current AND on the time of the last reset

Notes

Summary



15m 28s