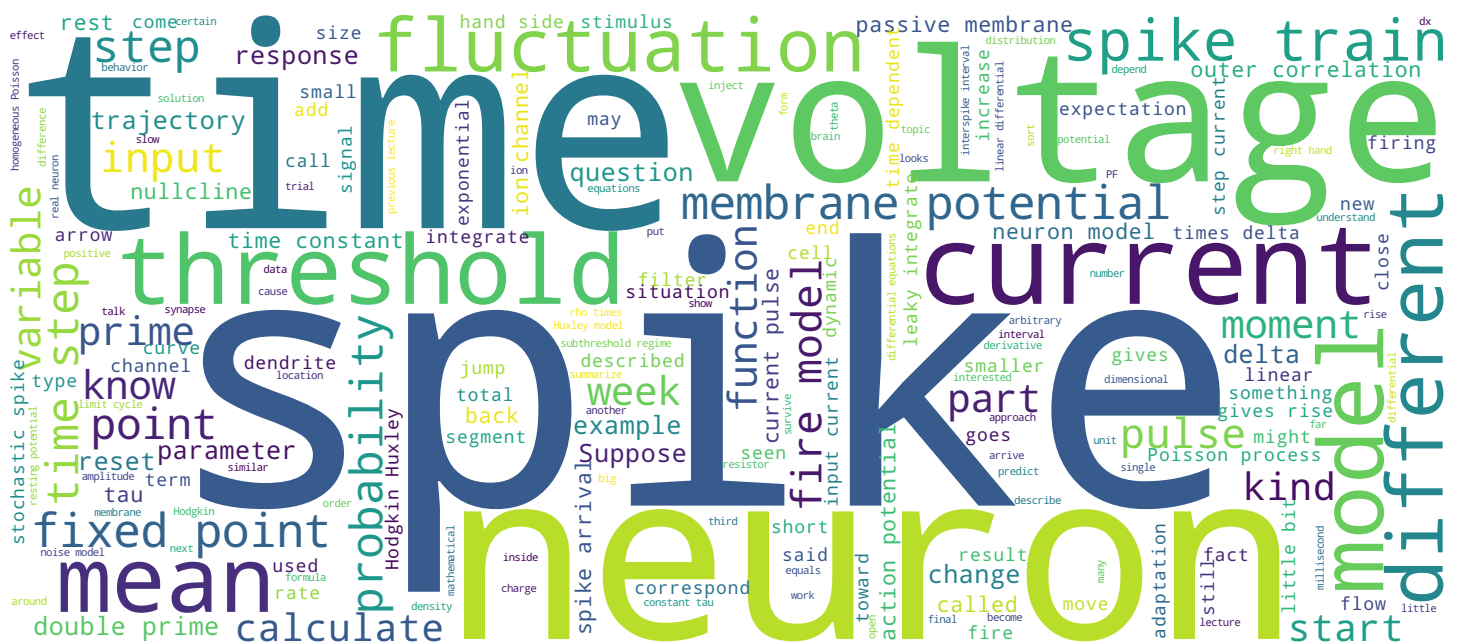


ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

EPFL, Lausanne, Switzerland

- subthreshold and superthreshold



EPFL



Week 5 – part 4b : Membrane potential fluctuations



✓ 5.1 Variability of spike trains

- experiments

✓ 5.2 Sources of Variability?

- Is variability equal to noise?

✓ 5.3 Three definitions of Rate code

- Poisson Model

5.4 Stochastic spike arrival

- Membrane potential fluctuations

5.5. Stochastic spike firing

- subthreshold and superthreshold

So welcome back to part 5.4. I promised that we would say something about fluctuations of the membrane potential caused by stochastic spike arrival. So far, we calculated the mean. I said a little bit about fluctuations. But the question arises, can we calculate the fluctuations?

Notes

Summary

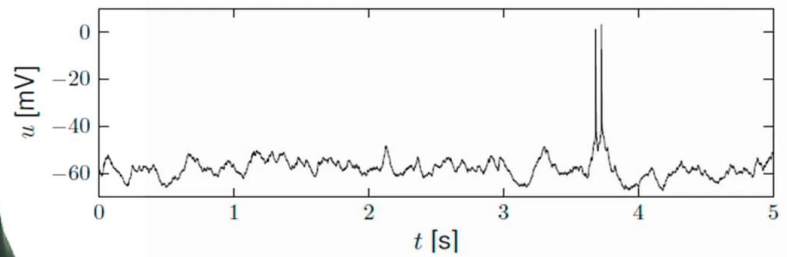


0m 04s

Neuronal Dynamics – 5.4 Variability in vivo

Spontaneous activity *in vivo*

Variability
of membrane potential?
awake mouse, freely whisking,



Crochet et al., 2011



Now, fluctuations of the membrane potential are indeed observed in vivo. So it's interesting to know a little bit how these variances to fluctuations could possibly arise. and to do so, we develop a model.

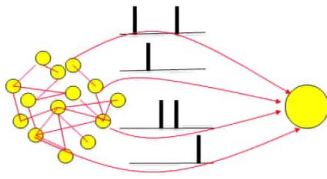
Notes

Summary



0m 30s

Neuronal Dynamics – 5.4b. Fluctuations of potential



Synaptic current pulses of shape α

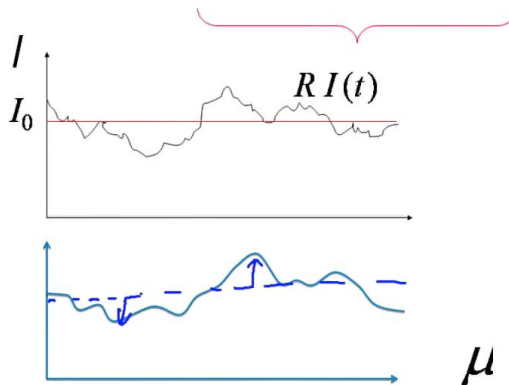
$$RI^{syn}(t) = \sum_k w_k \sum_f \alpha(t - t_k^f)$$

EPSC

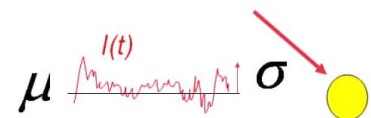
Passive membrane

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

→ Fluctuating potential



$$I^{syn}(t) = I_0 + I^{fluct}(t)$$



Fluctuating input current

⌕ / ☐ ➡

So we have already seen, in the previous part, that synaptic current pulses caused by stochastic spike arrival add up and give rise to some current, which can be described as a mean plus a fluctuating part. Now, this current is injected into the differential equation of a passive membrane and gives rise to a fluctuating potential. The question then arises, can we say something about the mean of this fluctuating potential? And we did so in the previous lecture. But moreover, can we say something about the typical size of these fluctuations? And that's the topic for now.

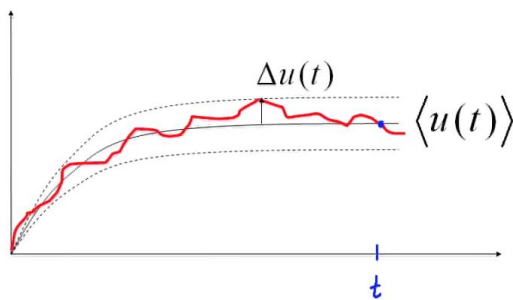
Notes

Summary



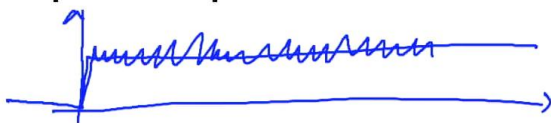
0m 46s

Neuronal Dynamics – 5.4b. Fluctuations of potential



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

Input: step + fluctuations



⏮ ⏪ ⏩ ⏭

So if the mean at a given moment in time, at time t , is something like $\bar{u}$ or expectation of u of t , then we are interested in these fluctuations of size Δu . And we look at the expectation of these fluctuations. Now, the specific situation here is that of a current. We can think of a step current like this. But the input a fluctuating version of this step current-- something like this. Now, this is low pass filtered by the differential equation and gives rise to this kind of fluctuating membrane potential trajectory. And the question is can we calculate these fluctuations?

Notes

Summary



1m 38s

Neuronal Dynamics – 5.4b. Calculating autocorrelations

Autocorrelation



$$\langle x(t)x(t') \rangle = \int dt' f(t-t') S(t') \int dt'' f(t-t'') S(t'')$$

$$x(t) = \sum_k \int dt' f(t-t') \delta(t'-t_k^f) = \int dt' f(t-t') S(t')$$

Mean:

$$\langle x(t) \rangle = \int dt' f(t-t') \langle S(t') \rangle$$

$$\langle x(t) \rangle = \int ds f(s) \rho_0$$

rate of homogeneous Poisson process

In the previous lecture, I've already said that any filtered spike train can be treated with a formulation. We have an arbitrary filter f . This is the spike train, including the sum over all spike times. And if you look at the mean, then this is the mean of the spike train and for the case of a homogeneous Poisson process, this would be the rate. It's the rate of this spike train. We don't consider k independent inputs anymore. Let's consider just one single input spike train, S of t . Now, what we are interested in now is the outer correlation. So my value x at time t might be related to the value at the later time t prime. Now, let's see that's whether we can use the same kind of procedure to write this down. So for x of t , I take the formal over here. I say this is integral dt prime and F of t minus t prime S of t prime. Now, for x of t prime-- now, I have a problem, because I have said this is t prime. So let's call it t hat. So for this, I take the same formula again. Let's write it down. It's another integral, dt double prime. And then what used to be t is now t hat. So it's t hat minus t double prime, S of t double prime. And at the very end, I will consider the expectation.

Notes

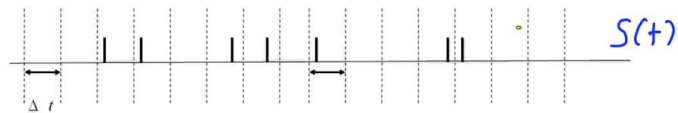
Summary



2m 36s

Neuronal Dynamics – 5.4b. Calculating autocorrelations

Autocorrelation



$$\begin{aligned} \langle x(t)x(t') \rangle &= \\ &= \left\langle \int dt' f(t-t') S(t') \int dt'' f(t-t'') S(t'') \right\rangle \\ &= \int dt' \int dt'' f(t-t') f(t-t'') \langle S(t') S(t'') \rangle \end{aligned}$$

for example $u(t)$

$$\begin{aligned} x(t) &= \sum_k \int dt' f(t-t') \delta(t'-t_k^f) \\ &= \int dt' f(t-t') S(t') \end{aligned}$$

Mean:

$$\langle x(t) \rangle = \int dt' f(t-t') \langle S(t') \rangle$$

$$\langle x(t) \rangle = \int ds f(s) \rho_0$$

rate of homogeneous
Poisson process

$$\langle x(t)x(t') \rangle = \int dt' \int dt'' f(t-t') f(t'-t'') \langle S(t') S(t'') \rangle$$

⌕ / ☐ ➡

Now, the expectation concerns only the spike trains. The spike train is stochastic. Spikes can arrive here or there or there or there. Spikes are, let's assume, generated by some Poisson process. So I would like to bring the two stochastic processes together. So let's write s of t prime, s of t double prime. Then I have the integration signs. Everything is linear. I can pull out the integrals in front-- dt prime, dt double prime. And I have f of t minus t prime coming from here. And I have the other filter, t hat minus t double prime. Now, what about the expectation signs? The expectations signs can move inside. Taking the expectation is linear procedure. I can pull it inside. And the only stochastic part are these spike trains. So this is the result. The correlation of my signal x at time t with the same signal at a later time or earlier time, t hat, expectation-- that's the outer correlation-- is given by this formula. Now, x is some arbitrary signal here. But x could be my membrane voltage. So I could take u of t . If the membrane is a passive membrane, it can be described as a linear filter. Now, there is one thing which appears here on the right hand side.

Notes

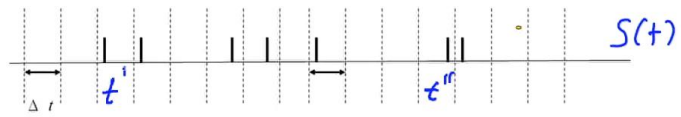
Summary



4m 49s

Neuronal Dynamics – 5.4b. Calculating autocorrelations

Autocorrelation



$$\begin{aligned} \langle x(t)x(t') \rangle &= \\ &= \left\langle \int dt' f(t-t') S(t') \int dt'' f(t-t'') S(t'') \right\rangle \\ &= \int dt' \int dt'' f(t-t') f(t-t'') \langle S(t') S(t'') \rangle \end{aligned}$$

for example $u(t)$

$$\begin{aligned} x(t) &= \sum_f \int dt' f(t-t') \delta(t-t'_f) \\ &= \int dt' f(t-t') S(t') \end{aligned}$$

Mean:

$$\langle x(t) \rangle = \int dt' f(t-t') \langle S(t') \rangle$$

$$\langle x(t) \rangle = \int ds f(s) \rho_0$$

rate of homogeneous Poisson process

$$\langle x(t)x(t') \rangle = \int dt' \int dt'' f(t-t') f(t'-t'') \langle S(t') S(t'') \rangle$$

⏮ ⏪ ⏩ ⏭

And that's the outer correlation of the spike train. This is my spike train. I have a spike here and I have a spike there. And the question is can I say anything about the probability that the spike here at time t is correlated with a later spike at time t' ?

Notes

Summary



6m 53s

Neuronal Dynamics – 5.4b. Autocorrelation of Poisson

math detour
now!

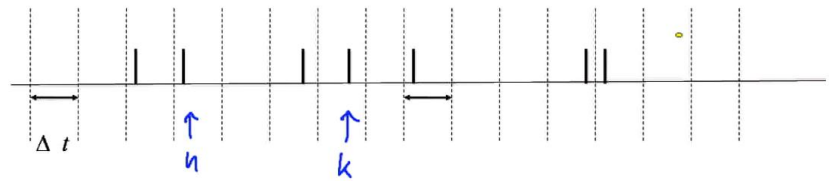
Probability of spike
in step n AND step k

for $n \neq k$

$$P(n, k) = P_F \cdot P_F \\ = \rho_0^2 \cdot (\Delta t)^2$$

for $n = k$

$$P(n, n) = P_F = \rho_0 \cdot \Delta t$$



spike train

Probability of spike in time step:

$$P_F = \underline{\rho_0 \Delta t} \quad \text{homogen. Poisson}$$

⌕ / ☰ ➡

This is my spike train. Suppose that the probability of firing in each time step is $P_F = \rho_0 \Delta t$, a constant rate, times Δt . So we are in the case of a homogeneous Poisson process. Now, Poisson process means that the firing probability in this time step-- let's call this time step n -- is completely independent from the probability of firing in some other time step k . So the probability of having a spike in step n and in step k -- now, these are different time steps. n is not equal to k . Then the joint probability of having a spike in step n and a spike in step k is just P_F times P_F or $\rho_0 \Delta t$ times $\rho_0 \Delta t$, another $\rho_0 \Delta t$ times Δt . However, nobody said here that n and k must be different. I should also consider the probability of having a spike in step n and in step n . Now, this sounds kind of stupid. Well, if I have a spike in step n , I know that I have a spike in step n . So the probability of having a spike in step n is just P_F . The probability of a spike in some time step is $\rho_0 \Delta t$. So what we learn from this simple argument is that we have to distinguish the two cases-- the case where we talk about spikes in the same time step-- And if I have a spike in that time step, I know that I have a spike in that time step-- and the normal case, that the time steps are different.

Notes

Summary



7m 15s

Neuronal Dynamics – 5.4b. Autocorrelation of Poisson

math detour
now!

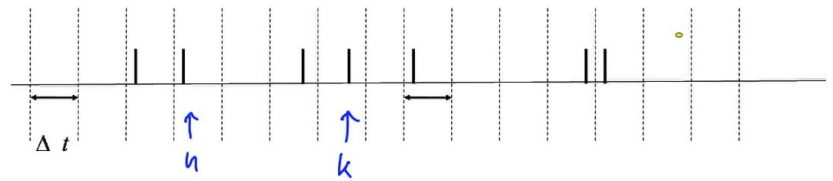
Probability of spike
in step n AND step k

for $n \neq k$

$$P(n, k) = P_F \cdot P_F = \rho_0^2 \cdot (\Delta t)^2$$

for $n = k$

$$P(n, n) = P_F = \rho_0 \cdot \Delta t$$



spike train

Probability of spike in time step:

$$P_F = \rho_0 \Delta t \quad \text{homogen. Poisson}$$

Autocorrelation (continuous time)

$$\langle S(t)S(t') \rangle = \rho_0 \delta(t-t') + [\rho_0]^2$$

Now, let's now take the limit, delta t to 0. And if we do that, we get the outer correlation function of the homogeneous Poisson process. So if the time-- t and t prime-- if the two times are not the same, then I just get the rho 0 squared. However, if t and t prime are identical, then I just get rho 0. So the outer correlation is a density. It's sort of a double density. I have to integrate twice to get back something similar to a probability.

Notes

Summary



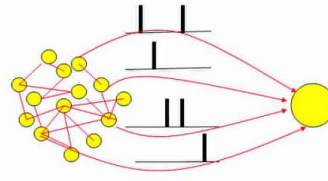
9m 51s

Neuronal Dynamics – 5.4b. Fluctuation of potential

Stochastic spike arrival:

for a passive membrane, we can analytically predict the amplitude of membrane potential fluctuations

Leaky integrate-and-fire in subthreshold regime



Passive membrane

$$u(t) = \sum_k w_k \sum_f \varepsilon(t - t_k^f)$$

$$= \sum_k w_k \int dt' \varepsilon(t - t') S_k(t')$$

fluctuating potential

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

✎ ✎ ✎ ✎

Now, let's put things together. We said for some arbitrary signal, if there's a filtering process, we can calculate the mean and the fluctuations. We can calculate the mean and the outer correlation. The fluctuations-- if I evaluate this at the same time, then this gives the size of the fluctuations. It's the outer correlation at 0 delay. In order to calculate that, we will need our S of t prime, S of t double prime, which we can calculate for Poisson processes. Now, a passive membrane is what you would find, for example, in the leaky integrate-and-fire model in the subthreshold regime. In other words, for stochastic spike arrival, in the case of a passive membrane, we can predict the amplitude of the membrane potential fluctuations. We can do calculation and predict analytically what we should see. And this is in particular true for the leaky integrate-and-fire model in the subthreshold regime.

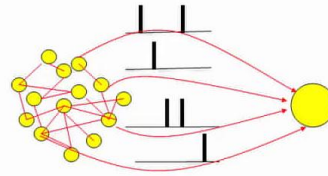
Notes

Summary



10m 44s

Neuronal Dynamics – 5.4b. Fluctuation of potential



Passive membrane

$$u(t) = \sum_k w_k \sum_f \varepsilon(t - t_k^f)$$
$$= \sum_k w_k \int dt' \varepsilon(t - t') S_k(t')$$

Fluctuations of potential

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

So if I have a leaky membrane, or generally, if I have some passive membrane-- if I have a passive dendrite-- then I can calculate the fluctuations of the membrane potential in the presence of stochastic spike arrival. Now, real neurons have a threshold. And the simplest model of a neuron with threshold would be a leaky integrate-and-fire model. In a subthreshold regime, we can use the results of the passive membrane. And we simply have to add a threshold. And that's what's going to be the topic of the final lecture of this week.

Notes

Summary

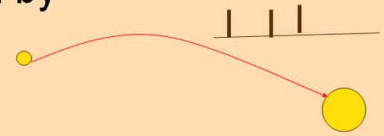


12m 09s

Neuronal Dynamics – Quiz 5.4

A linear (=passive) membrane has a potential given by

$$u(t) = \sum_f \int dt' f(t-t') \delta(t'-t_k^f) + a$$



Suppose the neuronal dynamics are given by

$$\tau \frac{d}{dt} u = -(u - u_{rest}) + q \sum_f \delta(t - t_k^f)$$

- ☐ the filter f is exponential with time constant τ
- ☐ the constant a is equal to the time constant τ
- ☐ the constant a is equal to u_{rest}
- ☐ the amplitude of the filter f is q
- ☐ the amplitude of the filter f is u_{rest}

⏮ ⏪ ⏩ ⏭

Please take a moment to look at the quiz before you continue.

Notes

Summary



12m 51s