

Week 5 – part 4 :Stochastic spike arrival



Neuronal Dynamics: Computational Neuroscience of Single Neurons

Week 5 – Variability and Noise: The question of the neural code

Wulfram Gerstner

EPFL, Lausanne, Switzerland

✓ 5.1 Variability of spike trains

- experiments

✓ 5.2 Sources of Variability?

- Is variability equal to noise?

✓ 5.3 Three definitions of Rate code

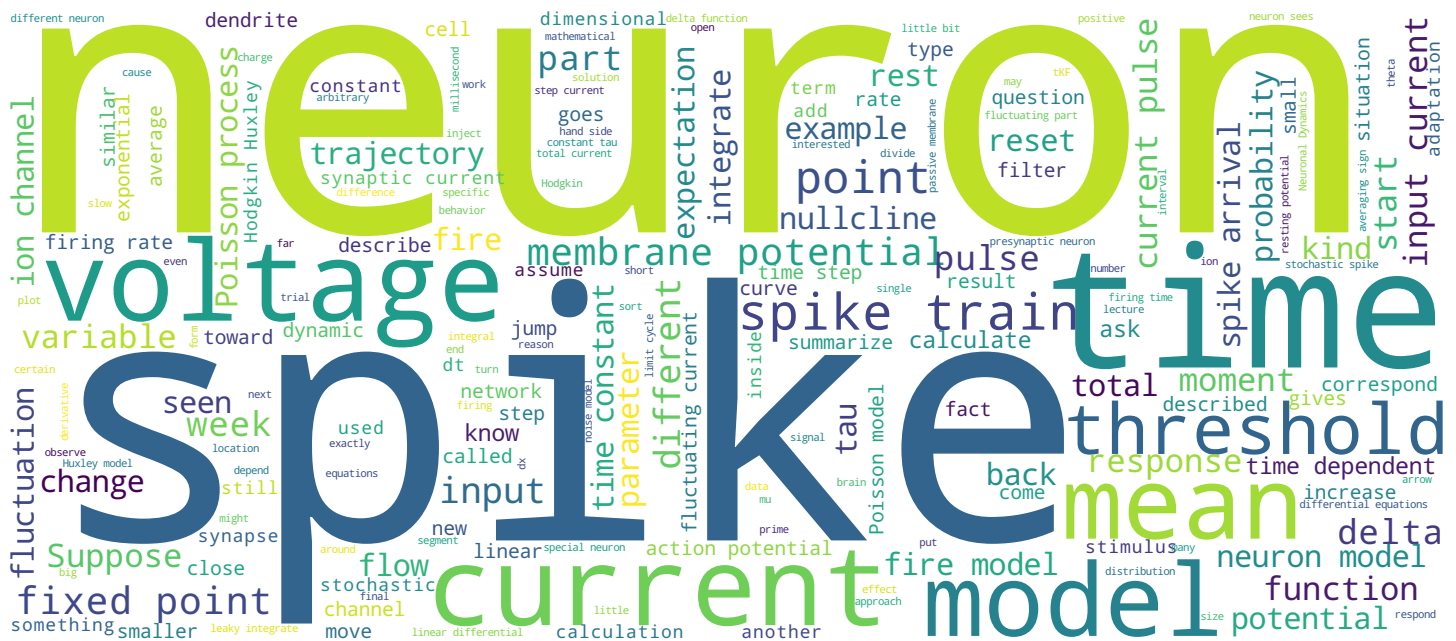
- Poisson Model

5.4 Stochastic spike arrival

- Membrane potential fluctuations

5.5. Stochastic spike firing

- subthreshold and superthreshold



EPFL

Video



Week 5 – part 4 :Stochastic spike arrival



✓ 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

Welcome to part four of week five of the class Neuronal Dynamics. In the previous lectures of this week, I focused on experimental data, showing fluctuating membrane potentials and fluctuations of spike timing.

Notes

Summary

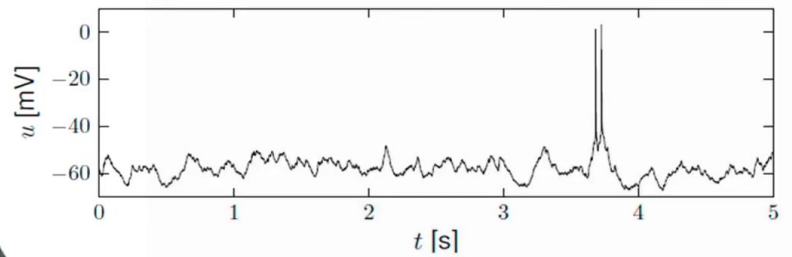


0m 03s

Neuronal Dynamics – 5.4 Variability in vivo

Spontaneous activity *in vivo*

Variability
of membrane potential?
awake mouse, freely whisking,



Crochet et al., 2011



We now turn to our first model that should allow to explain that observed fluctuations of the membrane potential.

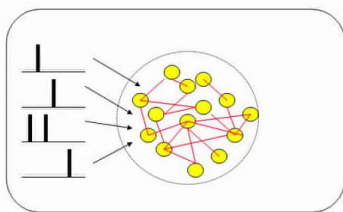
Notes

Summary



0m 22s

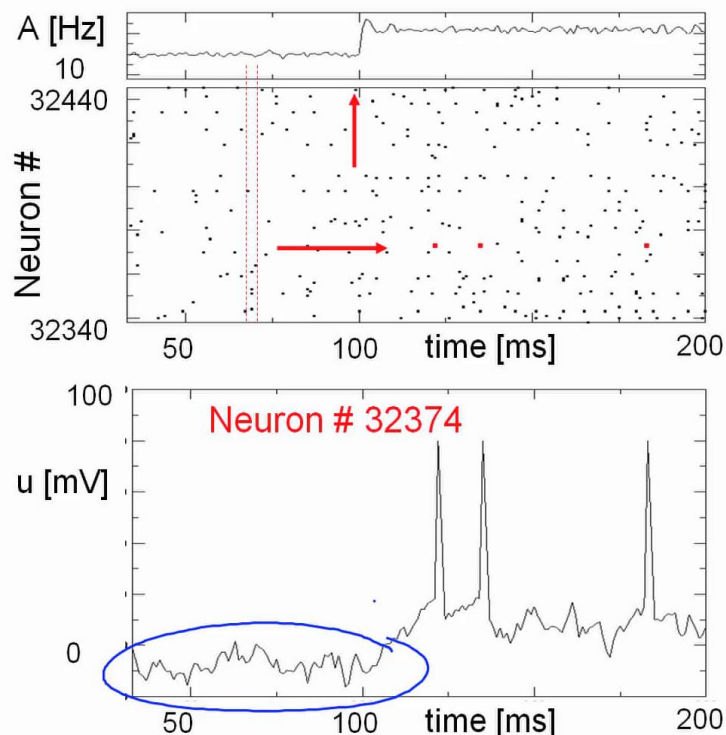
Random firing in a population of LIF neurons



input { low rate
high rate

Population

- 50 000 neurons
- 20 percent inhibitory
- **randomly connected**



We have seen that fluctuating membrane potentials can be observed randomly connected network of leaky integrate-and-fire neurons. Let's now take one of the neurons.

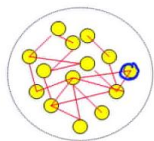
Notes

Summary



0m 35s

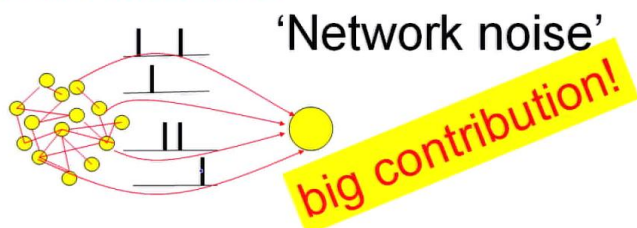
Neuronal Dynamics – 5.4 Membrane potential fluctuations



from neuron's point
of view:

stochastic spike arrival

Pull out one neuron



We have here our big network of neurons. Let's just arbitrarily pick one of the neurons-- say, this one here-- and say, this is my special neuron. I will consider the input to this neuron. Now, from the point of view of this neuron, what these neuron sees are spikes, and the spike arrival looks stochastic.

Notes

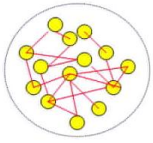
Summary



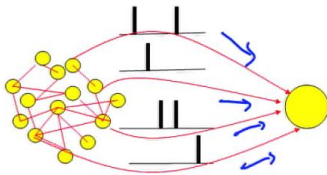
0m 53s

Neuronal Dynamics – 5.4. Stochastic Spike Arrival

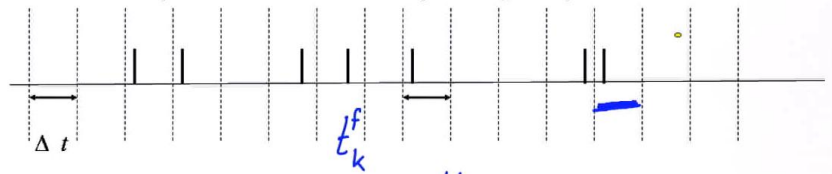
math detour
now!



Pull out one neuron



Total spike train of K presynaptic neurons



spike train

$$S(t) = \sum_{k=1}^K \sum_{f \in \text{spike times}} \delta(t - t_k^f)$$

Poisson

Probability of spike arrival:

$$P_F = K \rho_0 \Delta t$$

So we consider the input to this one neuron. It's not a special neuron. It's an arbitrary neuron of the network, but for us, it's a special neuron because we look at its input. Now, here's the spike train that these neuron may see-- the total spike train arising from k presynaptic neurons. Let's describe this spike train. Any impulse occurs at some firing time, t_k^f . Now, this might be a pulse arising from neuron number k. So I have a short pulse described by a [INAUDIBLE] pulse, S of t_k^f . Now, this neuron will send out many spikes as sum of all the different spike times. And then K is just one of the neurons. There's a total of capital K neurons that send inputs to our neuron that we observe. So far, the observed spike train-- I said previously that from the point a few of this neuron, the spike train looks stochastic. So let's take our Poisson model. Let's assume that each of the K neurons fires at a constant rate, ρ_0 . Then the total probability that one of the bins here is filled with a spike is the firing rate of each individual presynaptic neuron times k , the total number of presynaptic neurons. So we can now ask with our spike train, what would be the probability of observing a spike in this short time bin?

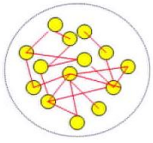
Notes

Summary

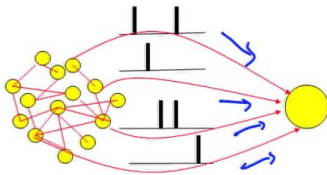


Neuronal Dynamics – 5.4. Stochastic Spike Arrival

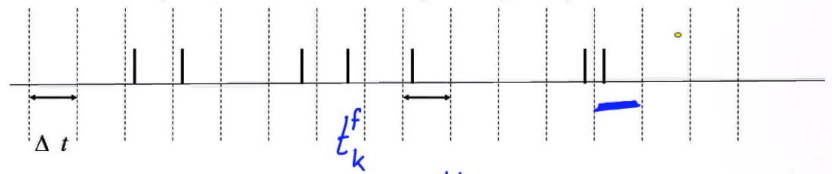
math detour
now!



Pull out one neuron



Total spike train of K presynaptic neurons



spike train $S(t) = \sum_{k=1}^K \sum_{f \text{ spike times}} \delta(t - t_k^f)$

Poisson Probability of spike arrival:

$$P_F = K \rho_0 \Delta t, \text{ divide by } \Delta t$$

Take $\Delta t \rightarrow 0$ expectation

$$\langle S(t) \rangle = \sum_{k=1}^K \sum_f \delta(t - t_k^f) = K \cdot \rho_0$$

If I have a time bin, then this is the probability that I observe a spike arrival, by definition of the Poisson model. When I take the limit delta t to 0, I can ask what would be that instantaneous find probability? Well, I take delta t to 0, and I divide by delta t. So divide by delta t, take delta t to 0, then we sort of are back to our spike train. We just have pulses. And I ask for the expectation. This is expectation sign. I ask for this expectation that I would see these spikes. Well, the expectation of having a spike at each moment of time is the rate. I have a total of k neurons. So this is k times rho 0. So the firing rate of a Poisson model can be estimated from the spike train by looking at the expectation value. And the experimental procedures of estimating a rate, be it population averaging or trial averaging are approximations to this mathematical averaging sign.

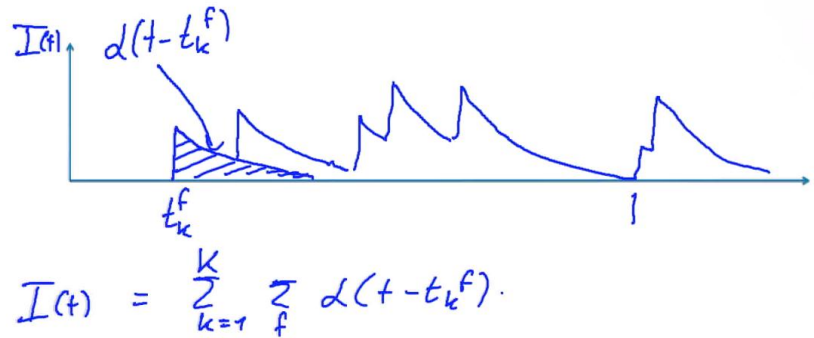
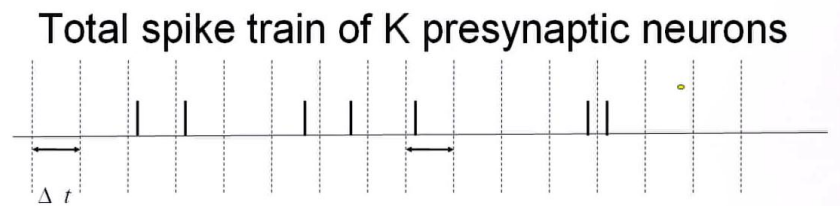
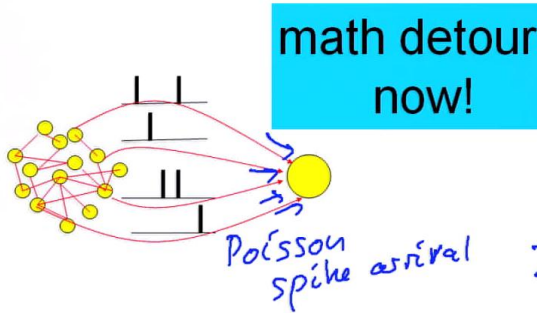
Notes

Summary



3m 33s

Neuronal Dynamics – 5.4. Fluctuation of input current



I have this spike train. And I assume that spike arrival is Poisson. I'm interested in the current that would flow into this neuron-- so the total current that this neuron sees. Well, let's assume that each of the spikes-- this spike here, for example-- causes a response. If the spike occurred at time t^f and it happened to be neuron K, then this would be the response. I describe this response as a function α of t minus t_k^f . So this function is the current injected after the spike arrival injected into the neuron. But now comes the second spike. And the second spike contributes a similar current pulse. The third spike contributes a current pulse-- the fourth one, the fifth one. And I have another two pulses. So the total current is the sum of all these current pulses. I have to sum over the different neurons. I have k presynaptic neurons. Then each neuron may send out several spikes. So this might be the first spike of neuron k . Here might be the second spike of neuron k . I have to sum over all firing times of this neuron k . I can now ask whether I can make any statement about this current. So what I see is essentially that this current fluctuates around some mean value.

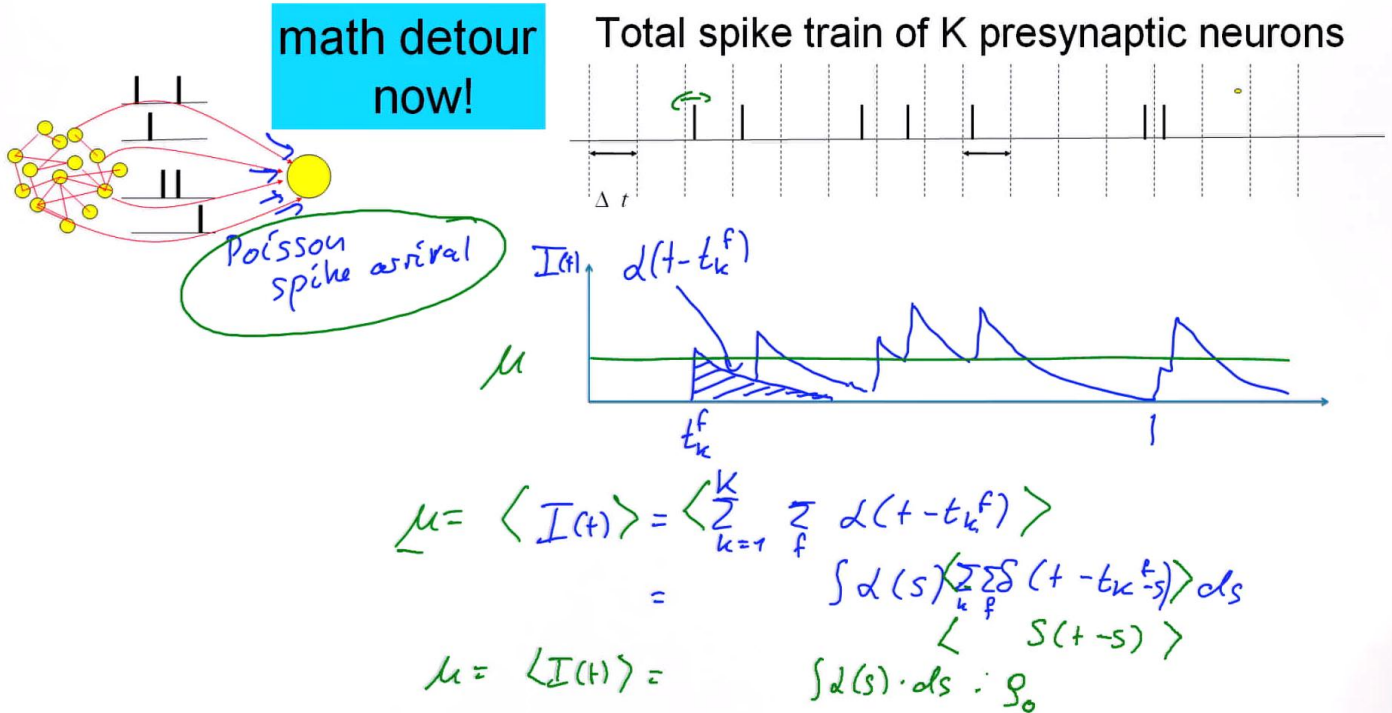
Notes

Summary



5m 08s

Neuronal Dynamics – 5.4. Fluctuation of input current



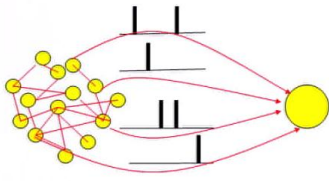
So the mean would be something like the expectation around this current. So I have to calculate this expectation. How would I do that? Well, sometimes, things will become simpler if you first make it look more complicated. So let's write this in a slightly more complicated fashion. I say this is the same as-- but I introduce an integral, alpha of S. And then I say delta of t minus tKF minus S dS. So if I integrate this delta function, I am back to the situation here. All the summation signs can go inside. So I have here sum over K sum over F. Now, let's add the averaging signs. I'm interested in the mean current, mu. The averaging signs-- well, what is stochastic here? Stochastic are the spike times. They may have a jitter. This spike may occur in this bin in that bin. This spike may occur everywhere. So this stochasticity over which we average is just in the spike train. It's in here. I can pull in the averaging side inside the integral. Now, this is my spike train, S of t minus S. The definition of the spike train was a sum over all these different spikes-- sum over the delta functions. But the expectation of the spike train under a Poisson model is just rho. Suppose I have homogeneous Poisson process. So this gives rho 0. And I have a result, mu. It's the average of my current. It's constant in time. And the result is alpha of S dS times rho 0.

Notes

Summary



Neuronal Dynamics – 5.4. Fluctuation of current/potential



Synaptic current pulses of shape α

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

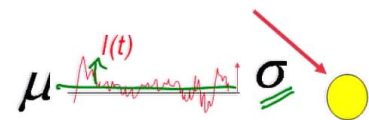
EPSC

Passive membrane

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



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



Fluctuating input current

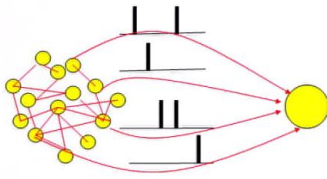
So what we did is we pulled out an arbitrary neuron. We looked at the input current into this neuron. I have these pulses, alpha. Each pulse describes an excitatory post synaptic current-- excitatory in our case. It could be an inhibitory current. Then it would be IPSC. So let's stick to the EPSC. The result of this is some fluctuating current. And I'm able to calculate the expectation value of this fluctuating current. And this gives a mean value, which I summarize as I_0 , plus a fluctuating part. So what this neuron sees here is a total input current that's just a fluctuating current fluctuating around some mean value μ . And so in that sense, a neuron embedded in the network is very similar to an isolated neuron driven by a fluctuating current with a certain mean, μ , and a certain variance of the fluctuations, called σ . So this is the input current. Now, suppose that our neuron stays in the subthreshold regime. So the neuron can be described as a passive membrane. I have a leak term, and I have an input. The input comes from the synapses. The input is exactly this guy here, the synaptic current, which I can write like this. This synaptic current has a mean part and it has a fluctuating part.

Notes

Summary



Neuronal Dynamics – 5.4. Fluctuation of current/potential



Synaptic current pulses of shape α

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

EPSC

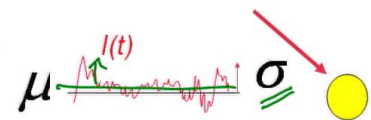
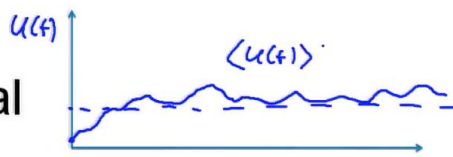
Passive membrane

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



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

→ Fluctuating potential



Fluctuating input current

This fluctuating current is injected into the neuron and will cause a response of the membrane. I inject this current into a neuron. Suppose I start here. It's a fluctuating current. It will go up and down. And the membrane acts like a low pass filter on this fluctuating input current. So if I plot here the membrane potential u of t , then I can ask again, what is the mean of this membrane potential?

Notes

Summary



Neuronal Dynamics – 5.4. Calculating the mean

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



$$I^{syn}(t) = \frac{1}{R} \sum_k w_k \sum_f \int_{-\infty}^t dt' \alpha(t - t') \delta(t' - t_k^f)$$

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

mean: assume Poisson process

$$I_0 = \langle I^{syn}(t) \rangle = \frac{1}{R} \sum_k w_k \int dt' \alpha(t - t') \left\langle \sum_f \delta(t' - t_k^f) \right\rangle$$

$$\langle x(t) \rangle = \int dt' f(t - t') \left\langle \sum_f \delta(t' - t_k^f) \right\rangle$$

$$\langle I(t) \rangle = I_0 = \frac{1}{R} \sum_k w_k \int_{-\infty}^t dt' \alpha(t - t') \nu_k(t')$$

Let me sum up a little bit. So we did this calculation of estimating a mean under the assumption of a Poisson process by rewriting it with delta functions, which essentially means I put in a spike train and integrate over the spike train. The reason is I can now perform the averaging. Averaging over the spike train just give the rate. Now, I said Poisson process. It could be a homogeneous Poisson process liking the calculation we did before. Or it could even be an inhomogeneous Poisson process. And the calculation would be just the same. In that case, it's a time dependent estimate. For a Poisson process, it's a constant. And this dependence can go away. Note that there are two different ways of writing the integral, as we have seen in the first week. I can also integrate with t minus t prime and start from minus infinity up to t . Now, this mathematical procedure is independent of the details. Suppose I have some arbitrary variable x of t , which can be described as a filtering process, and some point-like events-- pulses, for example, a spike train. Then the average is just the average of the pulses integrated with that filter.

Notes

Summary



12m 29s

Neuronal Dynamics – 5.4. Calculating the mean

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



$$I^{syn}(t) = \frac{1}{R} \sum_k w_k \sum_f \int_{-\infty}^t dt' \alpha(t - t') \delta(t' - t_k^f)$$

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

mean: assume Poisson process

$$I_0 = \langle I^{syn}(t) \rangle = \frac{1}{R} \sum_k w_k \int dt' \alpha(t - t') \left\langle \sum_f \delta(t' - t_k^f) \right\rangle$$

$$\langle I(t) \rangle = I_0 = \frac{1}{R} \sum_k w_k \int_{-\infty}^t dt' \alpha(t - t') \nu_k(t')$$

$$\langle x(t) \rangle = \int dt' f(t - t') \left\langle \sum_f \delta(t' - t_k^f) \right\rangle$$

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

rate of inhomogeneous Poisson process

And this average, now, for the time dependent model, inhomogeneous Poisson process, is the time dependent firing rate. In the specific case at hand here, I allowed here that different neurons have different weights. So some neurons might cause a large current pulse. Other neurons might cause a smaller current pulse. Different synapses have different weights.

Notes

Summary



14m 09s

Neuronal Dynamics – 5.4. Calculating the mean

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



$$I^{syn}(t) = \frac{1}{R} \sum_k w_k \sum_f \int_{-\infty}^t dt' \alpha(t - t') \delta(t' - t_k^f)$$

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

mean: assume Poisson process

$$I_0 = \langle I^{syn}(t) \rangle = \frac{1}{R} \sum_k w_k \int dt' \alpha(t - t') \langle \sum_f \delta(t' - t_k^f) \rangle$$

use for assignment/
homework!

$$\langle x(t) \rangle = \int dt' f(t - t') \langle \sum_f \delta(t' - t_k^f) \rangle$$

$$\langle x(t) \rangle = I_0 = \frac{1}{R} \sum_k w_k \int_{-\infty}^t dt' \alpha(t - t') v_k(t')$$

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

rate of inhomogeneous
Poisson process

Now, this kind of formula can be used not just for calculating the mean synaptic current, but also for calculating the mean potential.

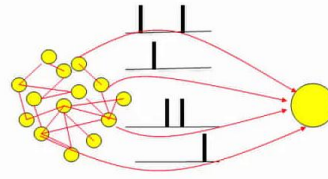
Notes

Summary

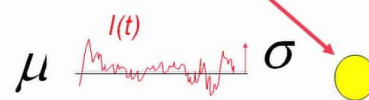


14m 41s

Neuronal Dynamics – 5.4. Fluctuation of current/potential



fluctuating input current



fluctuating potential

Let me summarize. A neuron embedded in a network will see a barrage of spike arrivals. And spike arrivals look stochastic from the point of view of that neuron. Under the assumption of Poisson-like stochastic spike arrival, we can calculate the mean input current, the fluctuating part of the input current, and also the mean potential and the fluctuations of the potential.

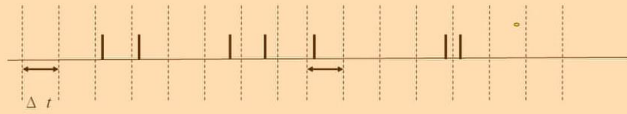
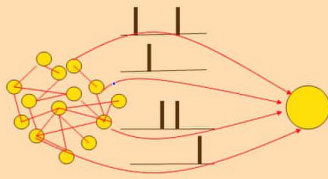
Notes

Summary



14m 51s

Neuronal Dynamics – Assignment/homework



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

A leaky integrate-and-fire neuron receives stochastic spike arrival, described as a homogeneous Poisson process.

Calculate the mean membrane potential. To do so, use the above formula.

The first step of this calculation for the potential is part of the homework assignment.

Notes

Summary

