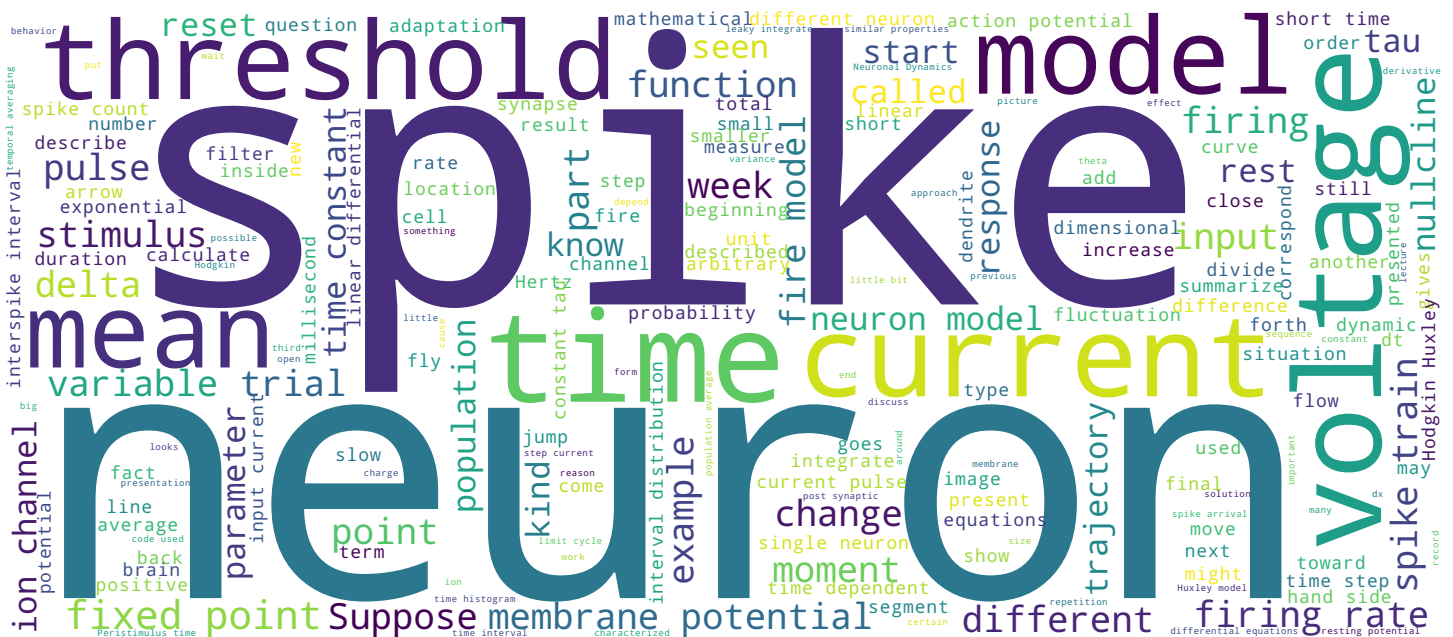


ÉCOLE POLYTECHNIQUE
FÉDÉRALE DE LAUSANNE

EPFL, Lausanne, Switzerland

- subthreshold and superthreshold



EPFL



Week 5 – part 3a :Three definitions of rate code



✓ 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 three of week five to class Neuronal Dynamics. In the previous two parts of this week, we have seen that neural signals vary, spiked trains are not regular, the membrane potential fluctuates. And then the question arises, how can we measure? How can we describe these fluctuations?

Notes

Summary



0m 04s

Neuronal Dynamics – 5.3. Three definitions of Rate Codes

3 definitions

- Temporal averaging
- Averaging across repetitions
- Population averaging ('spatial' averaging)

There are, in fact, different ways of doing this. A famous concept is the concept of rate coding, But that concept is not well-defined. There are, in fact, three different definitions for firing rate. The first one is based on temporal averaging, and let me explain this one first.

Notes

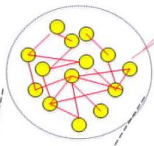
Summary



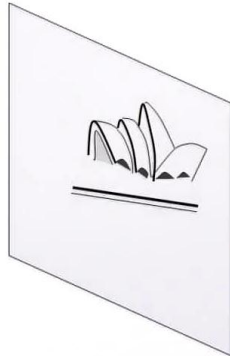
0m 26s

Neuronal Dynamics – 5.3. Rate codes: spike count

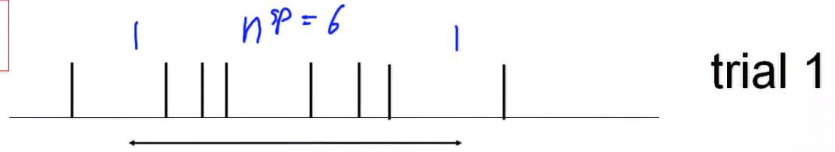
Variability of spike timing



Brain



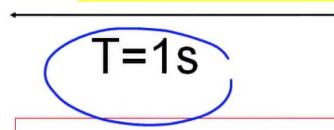
stim



rate as a (normalized) spike count:

$$v(t) = \frac{n^{sp}}{T} = \frac{6}{1s} = 6 \text{ Hz}$$

single neuron/single trial:
temporal average



Suppose you look at an image, and different neurons in various brain areas will respond to the presentation of this image. For example, neurons in the visual cortex, neurons in memory-related areas. And these neurons are often organized in groups of neurons with similar properties. Suppose now that you report for on one single neuron. At a given moment in time, you show the image. The image is presented to the eyes. The information goes on to the brain, and the neurons respond. Now you report from a single neuron, and what you see is a sequence of spikes. And there are many spikes during the presentation of the stimulus. Now one thing you can do is you count the number of spikes. So in this case here, we would have six spikes in the period during the presentation of the stimulus. Then you divide by the duration of the stimulus. Suppose the stimulation time is 1 second. So I have six spikes in 1 second, or I have a firing rate of 6 Hertz. The rate in this case is a normalized spike count normalized by the duration T after measuring interval. In order to evaluate the rate, you just have to measure a single neuron for a single trial, but we have to average over time. Your measurement interval has to be sufficiently long.

Notes

Summary

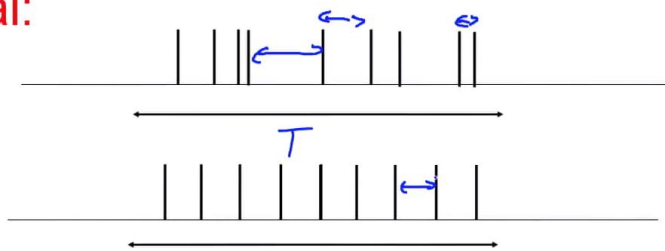


0m 47s

Neuronal Dynamics – 5.3. Rate codes: spike count

single neuron/single trial:
temporal average

$$\nu(t) = \frac{n^{sp}}{T}$$



Now in this case, we have nine spikes in our measuring interval T. Now a different neuron may also have nine spikes, but the spike train in this case is much more regular. In order to distinguish between the first case and the second one, it's important to look at the distribution of interspike intervals. In this case, there are some short intervals, there are some medium intervals, there are some long intervals. Whereas in the other case, all the intervals are nearly the same.

Notes

Summary

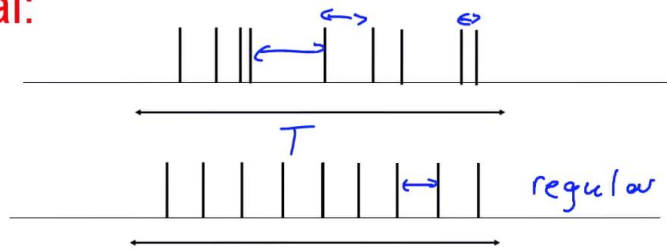


2m 35s

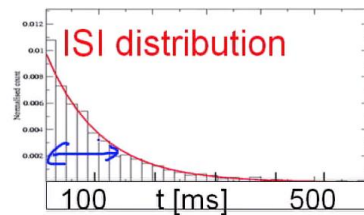
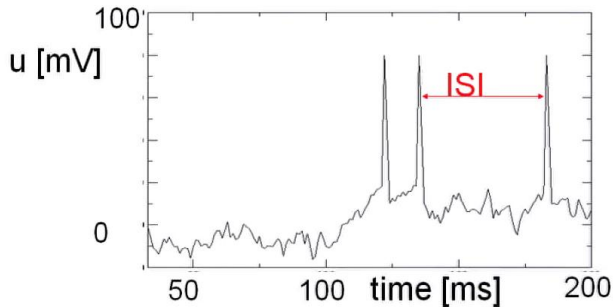
Neuronal Dynamics – 5.3. Rate codes: spike count

single neuron/single trial:
temporal average

$$\nu(t) = \frac{n^{sp}}{T}$$



Variability of interspike intervals (ISI)



So that interspike interval distribution measures the variability of the firing where it's a measure of the regularity. This would be a regularly firing neuron, a regular firing spike train. And this would be a rather irregular spike train. And an irregular spike train is characterized by a broad distribution of interspike intervals.

Notes

Summary

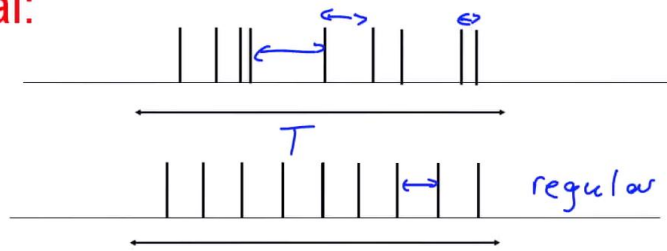


3m 09s

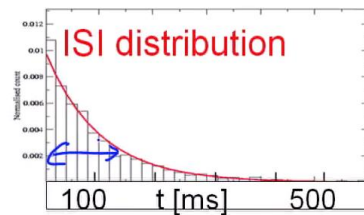
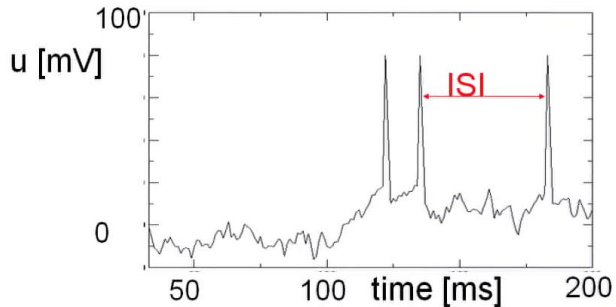
Neuronal Dynamics – 5.3. Rate codes: spike count

single neuron/single trial:
temporal average

$$r(t) = \frac{n^{sp}}{T}$$



Variability of interspike intervals (ISI) **measure regularity**



The interspike interval distribution accounts for the regularity or irregularity of a spike train.

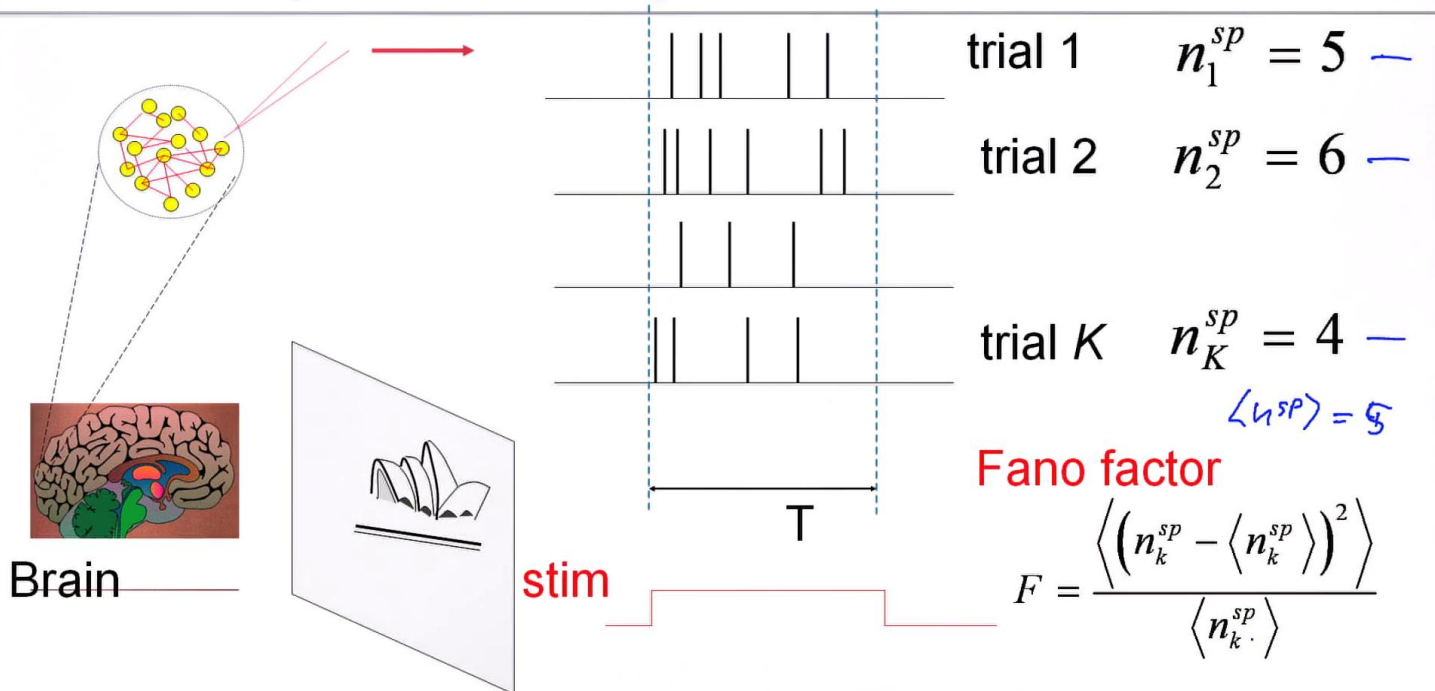
Notes

Summary



3m 33s

Neuronal Dynamics – 5.3. Spike count: FANO factor



Now let's come back to our measurement. So you have presented a stimulus. In this trial, we found 5 spikes. Now we can wait a moment so that the brain gets back to its resting state, and then we present the same stimulus again. In the second trial, we would, for example, find 6 spikes. In the next trial, three spikes. And you'd a total of, say, 200 trials, or K trials. In trial K in the last trial, we would have 4 spikes. Now you see that the spike count measure itself is variable. It changes between one trial and the next. Do you see how much this variance is, and can calculate the final factor? First, we determine the mean. So the mean spike count, in this case, would be 5. And then we look, how much does each trial vary from the mean number? So some trials, there are 6. Some trials, there are 4. There might be other files with 9 or with 1. And this variance is normalized by the mean spike count, and this is called a Fano factor.

Notes

Summary



3m 41s

Neuronal Dynamics – 5.3. Three definitions of Rate Codes

3 definitions

↓ -Temporal averaging (spike count) **Problem: slow!!!**

ISI distribution (regularity of spike train)

Fano factor (repeatability across repetitions)

- Averaging across repetitions

- Population averaging ('spatial' averaging)

That's the Fano factor-- measures repeatability across repetitions. So the spike count measure-- firing rates defined by a spike count divided by a mean firing rate-- are very useful tools to analyze experimental data recorded in real neurons. However, there's a problem. The problem is that this is a slow way off coding. While this is a good measure to analyze experimental data, it's not a code that's used by the brain. It's not the code used by the neurons.

Notes

Summary



4m 56s

Neuronal Dynamics – 5.3. Three definitions of Rate Codes

3 definitions

↓ -Temporal averaging

Problem: slow!!!

- Averaging across repetitions
- Population averaging



And to see this, let me discuss a little example. Suppose I have a little frog sitting in its pond, and it's waiting for the fly to come by. Now the fly passes close to the frog. And the total duration, when it's in the neighborhood of the frog, is less than 1 second. Now if the frog used a spike current measure, where a typical neuron fires at a few Hertz, you would have to wait at least 1 second to count enough spikes. But after 1 second, the fly has already passed. So this is definitely not the code used by the neurons. So let's look at a different definition of firing rate.

Notes

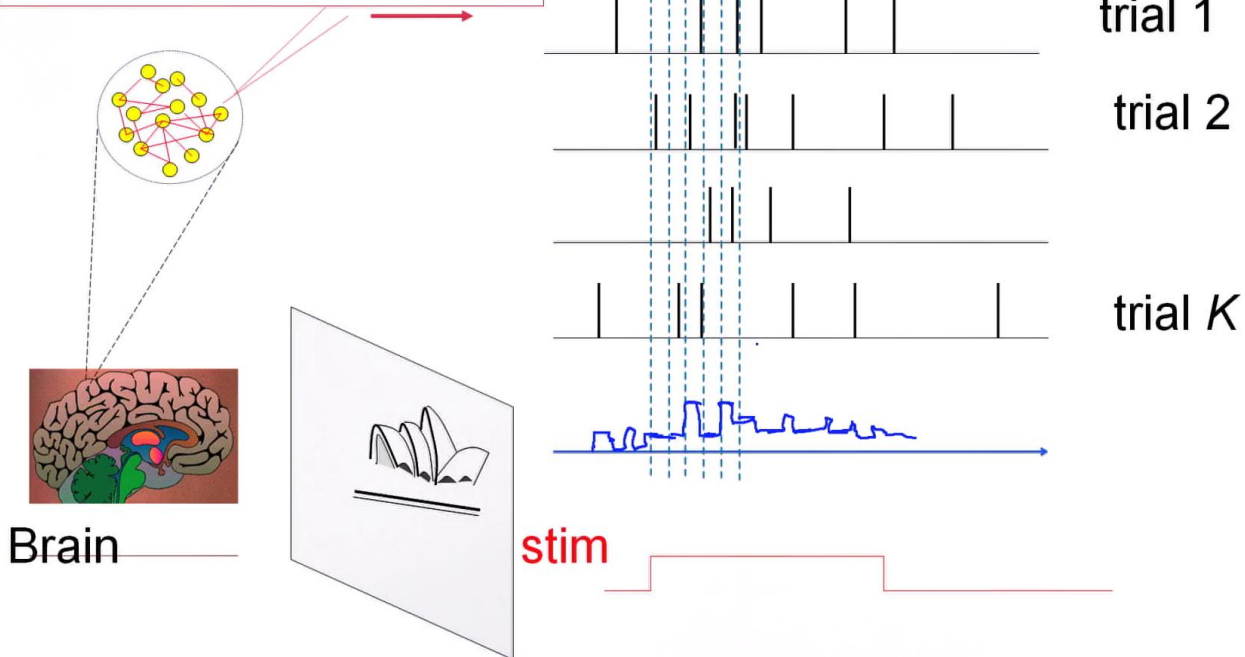
Summary



5m 40s

Neuronal Dynamics – 5.3. Rate codes: PSTH

Variability of spike timing



So let's again present our stimulus-- say, the Sydney Opera House-- and we record in a first trial a certain number of spikes. And then, we take a pause. We wait so that the brain comes back to the resting state, and we present the stimulus again, and we find it again, and again. But now, instead of just counting the total number of spikes, we define short time windows. For example, in this first interval, we could count across all repetitions, we would find 1 spike. In the next time interval, we would find 1 spike, then we find 3 spikes, then we find 1 spike and we find 3 spikes again, and so forth. And so, you can imagine that overall, this gives a time-dependent response. This is the PSTF-- the peristimulus time histogram. Peristimulus time histogram. The histogram can start slightly before the stimulus, so we would have a few spikes before the stimulus starts. Peristimulus time histogram.

Notes

Summary

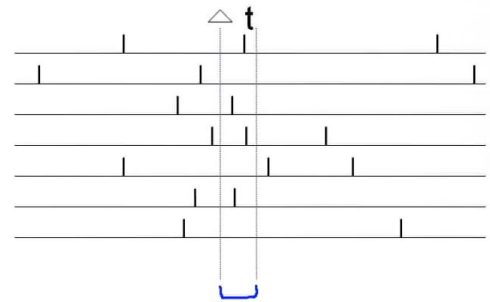


Neuronal Dynamics – 5.3. Rate codes: PSTH

Averaging across repetitions

$$PSTH(t) = \frac{n(t; t + \Delta t)}{K \Delta t}$$

K repetitions

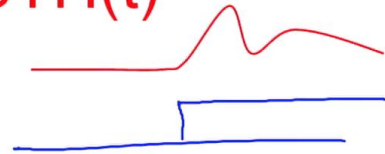


Stim(t)



K=50 trials

PSTH(t)



Now formally, this means we count the number of spikes in a short time in the delta T across K repetitions. We divide by K. We divide by the duration of our counting interval. And then this gives a the rate measure. It's 1 over time, units are Hertz. It's a rate measure, but now with a temporal resolution defined by delta T. For example, if you picked delta T equals 1 millisecond, you have a very nice temporal response pattern. Suppose the stimulus is presented here. And you see, for example, at the beginning, we have quite a few spikes, then we have a dip, then comes the second wave of spikes, and so forth. So now we have a temporal resolution of our definition of a firing rate.

Notes

Summary



7m 50s

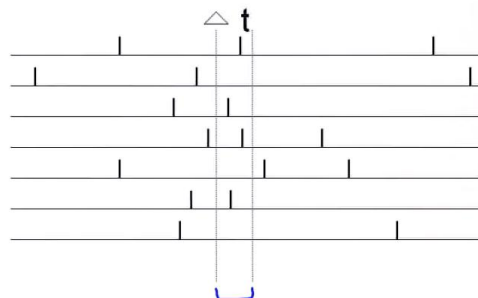
Neuronal Dynamics – 5.3. Rate codes: PSTH

Averaging across repetitions

single neuron/many trials:
average across trials

$$PSTH(t) = \frac{n(t; t + \Delta t)}{K \Delta t}$$

K repetitions

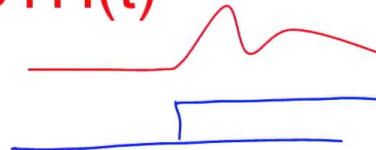


Stim(t)



$K=50$ trials

PSTH(t)



This is possible because we have averaged across trials. So this is a very powerful experimental tool.

Notes

Summary



8m 45s

Neuronal Dynamics – 5.3. Three definitions of Rate Codes

3 definitions

↓ -Temporal averaging

↓ - Averaging across repetitions

Problem: not useful
for animal!!!

- Population averaging

⌂ / ☰ ➡

However, again, it cannot be the measure used by the fly. The reason is it's way too slow. Let's again consider our fly sitting here. And now, the fly comes by, and the frog says to the fly, well, please fly again another 50 time so that I can average so that I can finally catch you. So that's not going to happen.

Notes

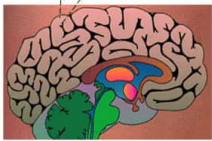
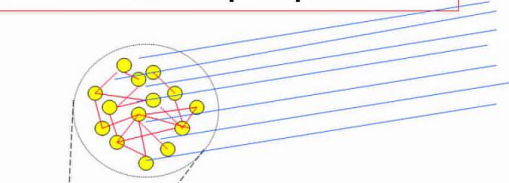
Summary



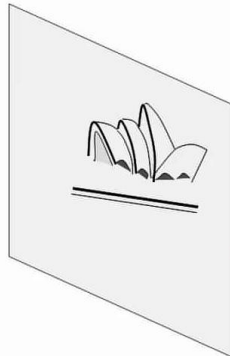
8m 54s

Neuronal Dynamics – 5.3. Rate codes: population activity

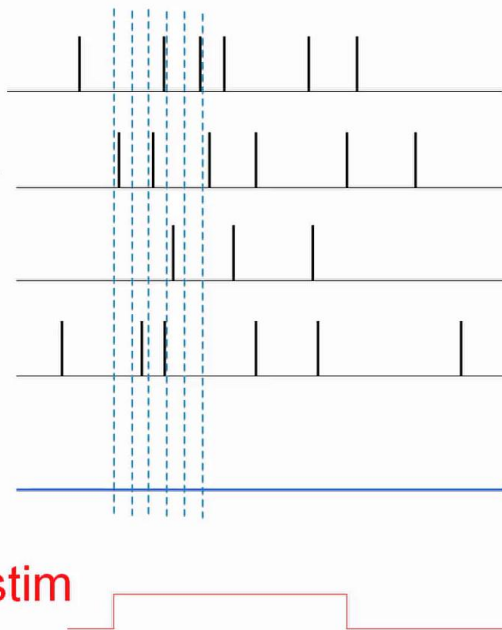
population of neurons
with similar properties



Brain



stim



neuron 1

neuron 2

Neuron K

Fortunately, there's yet another definition of firing rates. I mentioned in the beginning that neurons are often organized in pools of neurons, or populations of neurons, with similar properties. Suppose we have a population of 500 neurons, and with a multi-electrode recording array, you are able to record from all 500 neurons simultaneously while you present the stimulus. So the picture is the same as before. The difference now is that this is a single trial, and it's different neurons. The first line is neuron 1, the second line is neuron 2, that last line is neuron K .

Notes

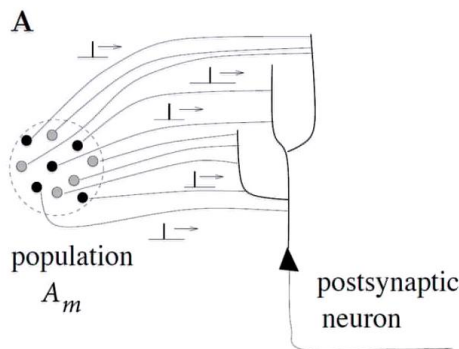
Summary



9m 22s

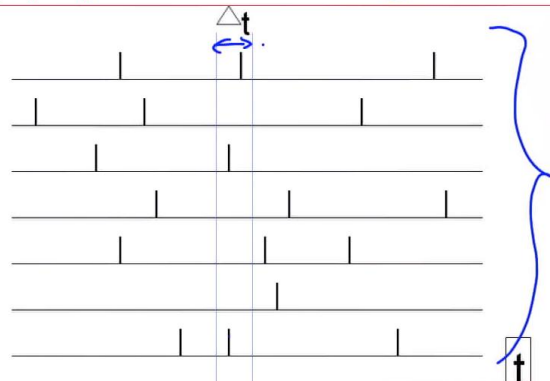
Neuronal Dynamics – 5.3. Rate codes: population activity

population activity - rate defined by population average



'natural'

population activity



$$A(t) = \frac{n(t; t + \Delta t)}{N \Delta t}$$

N Neurons

So in this case, the rate can be defined by a population average. I count in a short time interval Δt , I count all the spikes across the different neurons in a population. I divide by Δt , I divide by N , the number of neurons. There are n neurons. And because I divide by Δt , it has, again, units of rate. The units are 1 over time, the units are Hertz. Now I would claim that this is a rather natural situation for neurons. Consider a post-synaptic neuron. A post-synaptic neuron receives hundreds of inputs from other neurons. Suppose some of the inputs come from the same population of 500 neurons. So effectively, this neuron would be driven by the population activity, by the population of spikes arriving in each short time interval Δt . So in that sense, this definition of a firing rate-- firing rate defined as a population average-- is natural.

Notes

Summary



Neuronal Dynamics – 5.3. Three definitions of Rate codes



Three averaging methods

-over time

Too slow
for animal!!!

- over repetitions

Not possible
for animal!!!

- over population (space)

'natural'

So let me summarize. They are at least three different definitions of a firing rate. All three are useful experimental tools for data analysis. The first one is based on temporal averaging. Temporal averaging cannot be the code used by neurons, because it's too slow. The second one is repetition across different trials, and then averaging. Again, in an actual situation, an animal is not going to average all the different trials before it can react. And the final definition is that of a population average. Let's assume that there are groups of neurons with similar properties. Then, you can define a population activity-- a firing rate averaged across the population. So your reputation experiment-- measuring a single neuron, and then averaging over K repetitions of same experiment-- can be seen as an approximation of the population coding used by the brain.

Notes

Summary



11m 28s

Neuronal Dynamics – Quiz 5.2.

Rate codes. Suppose that in some brain area we have a group of 500 neurons. All neurons have identical parameters and they all receive the same input. Input is given by sensory stimulation and passes through 2 preliminary neuronal processing steps before it arrives at our group of 500 neurons. Within the group, neurons are not connected to each other. Imagine the brain as a model network containing 100 000 nonlinear integrate-and-fire neurons, so that we know exactly how each neuron functions.

Experimentalist A makes a measurement in a single trial on all 500 neurons using a multi-electrode array, during a period of sensory stimulation.

Experimentalist B picks an arbitrary single neuron and repeats the same sensory stimulation 500 times (with long pauses in between, say one per day).

Experimentalist C repeats the same sensory stimulation 500 times (1 per day), but every day he picks a random neuron (amongst the 500 neurons).

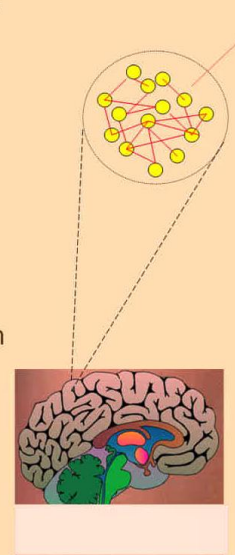
All three determine the time-dependent firing rate.

☐ A and B and C are expected to find the same result.

☐ A and B are expected to find the same result, but that of C is expected to be different.

☐ B and C are expected to find the same result, but that of A is expected to be different.

☐ None of the above three options is correct.



Before we continue, please have a look at the quiz.

Notes

Summary



12m 43s