

Computational Neuroscience: Neuronal Dynamics of Cognition



Continuum models:

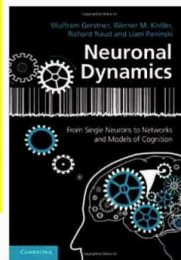
Cortical fields and perception

Wulfram Gerstner

EPFL, Lausanne, Switzerland

Reading:
NEURONAL DYNAMICS
Ch. 18 +
+Ch. 12.3.7+Ch 15.1-15.2.3

Cambridge Univ. Press



1. Aims and challenges

- review: mean-field arguments

2. Transients

- generalized integrate-and-fire model
- transients can be sharp or slow

3. Spatial continuum (cortex)

- orientation columns

4. Spatial continuum (model)

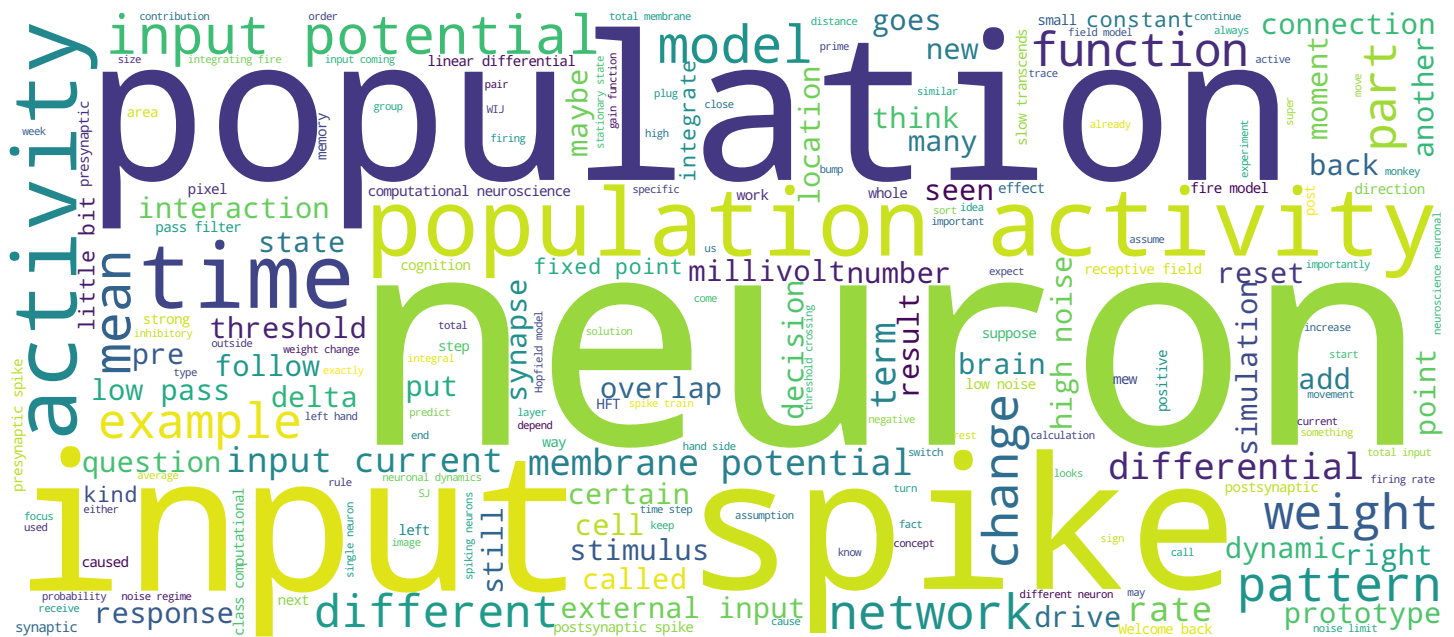
- field equations

5. Solution types

- uniform solution
- bump solution

6. Perception

7. Head direction cells



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Video



EPFL

2. Aims of this section: Transients



- beyond stationary states
→ transients?
- but then neuron model matters!
→ introduce **generalized integrate-and-fire models**:
 - Spike Response Model (SRM)
 - Generalized Linear Model (GLM)

Welcome back to the class computational neuroscience, neuronal dynamics of cognition. In order to continue with our discussion of field models, we now have to look at transient. To our first mathematical aim is to go beyond the stationary state. Focus on transient, focus on the dynamics. It turns out that in this case, the neuron model matters, and therefore I have to tell you a little bit about integrating fire neuron models.

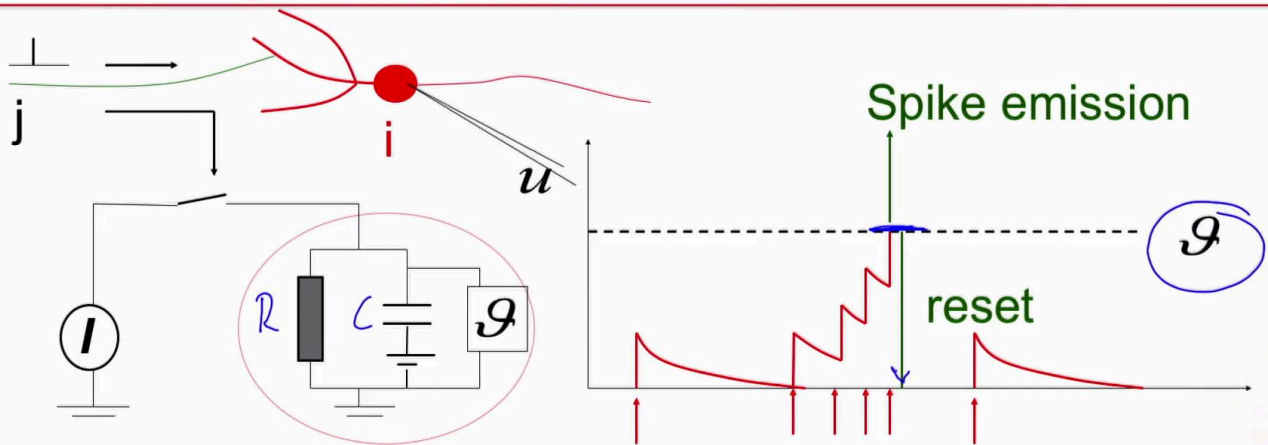
Notes

Summary



0m 12s

2. Leaky Integrate-and-Fire Model



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

linear

$$u(t) = G \Rightarrow \text{Fire+reset } u \rightarrow u_r$$

threshold

So in the integrating fire models like a linear differential equation, I can visualize this dynamics as an RC circuit and each time that a spike arrives, a little charge is put on the capacitor, and the result is that the membrane potential goes up, and then decays exponentially. So this is the response to a single pulse. If I have many input pulse, pulses, then I would simply add up these different responses, and then finally I would go to spike. Now, the spike is emitted at the moment of threshold crossing, and afterwards, be reset to a lower value and the whole process starts again.

Notes

Summary

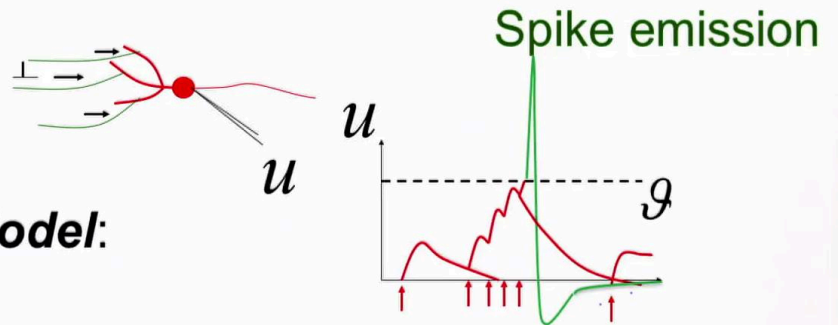


2. Generalized Integrate-and-Fire Model

Leaky Integrate-and-Fire Model:

passive membrane
+ threshold
+ reset

equivalent
description



Input spike causes an EPSP
= excitatory postsynaptic potential

-output spikes are events
-generated at threshold
-after spike: reset/refractoriness

add $\eta(s)$ (spike afterpotential)

So there's a slightly different way of looking at this and this is to say, well, each input spike causes an excitatory postsynaptic potential EPSP. If you have several input spikes you add them up until the threshold, and then instead of the reset, we say okay we paste in the spike and importantly, we paste in this spike after potential. So, we replace the reset by an equivalent formulation, which is, we add a spike after potential, we add something negative to bring the potential down again.

Notes

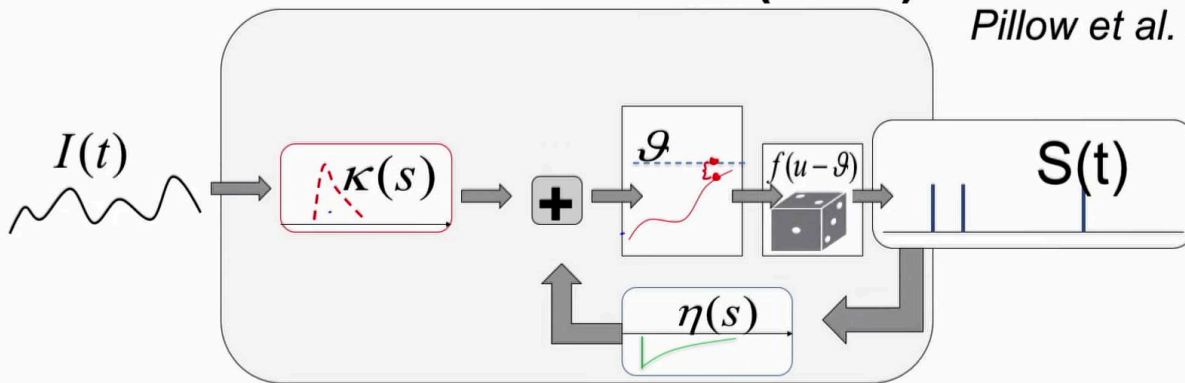
Summary



1m 13s

Spike Response Model (SRM) Generalized Linear Model (GLM)

Gerstner et al.,
1992, 2000
Truccolo et al., 2005
Pillow et al. 2008



potential $u(t) = \int \eta(s) S(t-s) ds + \underbrace{\int_0^\infty \kappa(s) I(t-s) ds}_{h(t) \text{ input potential}} + u_{rest}$

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

(escape noise) e.g. $\rho(t) = \rho_0 \exp\left[\frac{u(t) - \theta}{\Delta}\right]$

So in a schematic view, we arrive at the following picture, I have an input current. It's filtered. This gives rise to the membrane potential. If you hit the threshold out goes the spike. Then these spikes, contribute to the contribute a negative part of the membrane potential, which I have to add in back here to the total membrane potential is the effect of this negative feedback the spike after potential caused by the spikes and the effect of the input itself. So, this is what I call HFT, this is what I called the input potential. The part of the potential. That's caused by the input. Now there's one more thing I would like to say, and that is normally an integrated fire model we would have a strict threshold crossing criterion for spike. However, we can loosen this criteria. For example, we may say that you look at the momentary distance between the membrane potential, and the threshold. If this distance, U have T minus θ is small. Then there's already a certain likelihood to fire, even though the membrane for this one has not yet reached formerly the threshold. For example, if U of T is just one millivolt below threshold, so I would have...

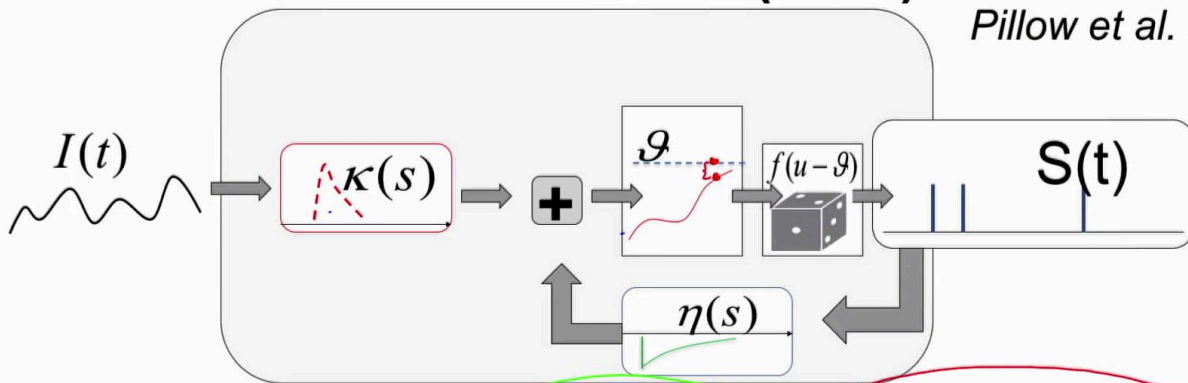
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Summary



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

(escape noise) e.g. $\rho(t) = \rho_0 \exp\left[\frac{u(t) - \theta}{\Delta}\right]$

and if delta is 1 millivolt, I would have here, E to the -1 which is already a certain fine rate a certain instantaneous rate a certain instantaneous probability of firing. So this parameter Delta describes the softness of the threshold. If delta is 0.01 millivolt, then it's basically back, we are back to a threshold crossing. If delta is 2 millivolt or 5 millivolt, it's very noisy of a high noise threshold model. So the trick for the following is to separate this total membrane potential in these two components apart, that's caused by the input and a part, that's caused by the feedback.

Notes

Summary



2. Leaky Integrate-and-Fire Model: input potential

$$\tau \cdot \frac{d}{dt} u = -(u - u_{rest}) + \underbrace{RI(t)}_{I^{ext}(t) + I^{reset}(t)}$$

$$\begin{aligned} \tau \frac{dh}{dt} &= -h + R \cdot I^{ext}(t) \\ h(t) &= \frac{R}{\tau} \int_0^\infty e^{-s/\tau} I^{ext}(t-s) ds \\ &= \underbrace{\int_0^\infty k(s) \cdot I^{ext}(t-s) ds}_{\text{input potential}} \end{aligned}$$

$$u(t) = u_{rest} + \text{input potential} + \text{reset potential}$$

So if you go back to the leaky integrated fire model we have a linear differential equation. I will now use this to separate out the input potential from the recent part. To really do this is to say, well, this input current is really the current caused by the input external input, plus, it's a current that's caused by the reset. It's the internal currents, gen, and currents generated in the neuron that cause the reset. Since it's a linear differential equation, I can just integrate up the two parts separately, and I will just focus on this external input part. Since it's only one contribution. I revived the differential equation now with the new variable, H, which is the same equation, but I just focus not on this part of the input. And that can integrate this up, and they get an H of T, which is external of T - S and I integrate over S, with -(S/T), in the exponent. Now I need to have the unit correct, and the way to do this is to right here, R over tau, tau is RC so this could also be a 1 over C 1 one over the capacitance of the RC circuit. So, I can write this HFT as some filter kappa of S I of T - SES, and the Indigo runs from here over infinity, and this is the input potential.

Notes

Summary



4m 08s

2. Leaky Integrate-and-Fire Model: input potential

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

$$\underline{I^{ext}(t)} + \underline{I^{reset}(t)}$$

$$\tau \frac{d}{dt} h = -h + R \cdot I^{ext}(t)$$

$$\begin{aligned} h(t) &= \frac{R}{\tau} \int_0^\infty e^{-s/\tau} I^{ext}(t-s) ds \\ &= \underbrace{\int_0^\infty k(s) \cdot I^{ext}(t-s) ds}_{h(t)} \end{aligned}$$

$$u(t) = u_{rest} + \text{input potential} + \text{reset potential}$$

Now, I don't know the exact reset currents. But if I knew the reset currents. Then I could sort of redo the same calculation and write the reset potential, and then add the resting potential from up here, and I'm done, because it's a linear differential equation, I can add up the solutions to them total membrane potential is the input potential, which are called HFT plus the reset potential, plus, rest.

Notes

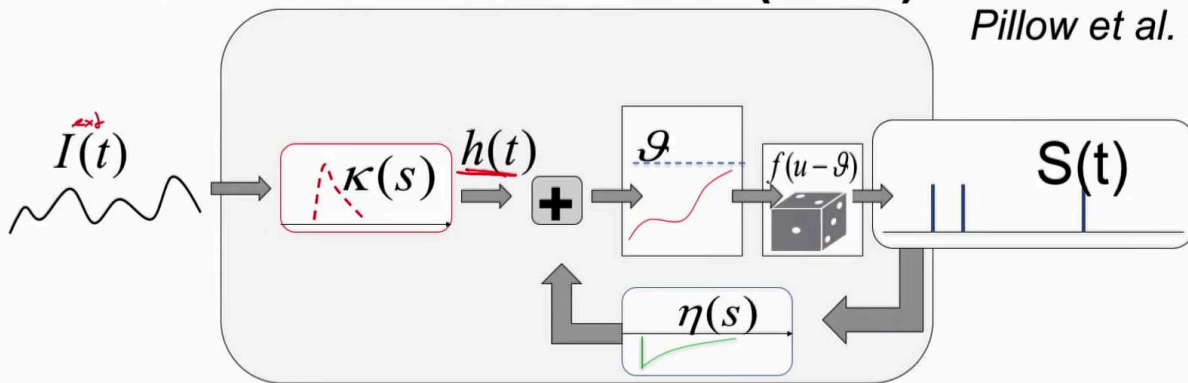
Summary



6m 01s

Spike Response Model (SRM) Generalized Linear Model (GLM)

Gerstner et al.,
1992, 2000
Truccolo et al., 2005
Pillow et al. 2008



$$\text{potential } u(t) = u_{rest} + \underbrace{\int_0^\infty \kappa(s) I(t-s) ds}_{h(t)} + \underbrace{\int \eta(s) S(t-s) ds}_{\text{reset potential}}$$

$$u(t) = u_{rest} + \text{input potential} + \text{reset potential}$$

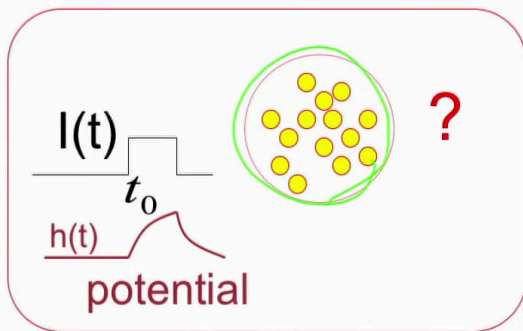
So here again, the summary slide I have my external input. I put it through a filter, the filter would be the exponential filter, but it can be something else but for the standard leak identified, just next to the exponential filter, after integration I have to input potential, it's up here. I compare with a threshold, either the noisy way or the deterministic fashion. And then I have my reset contributions, which I did not calculate for you, but that would give rise to the recent potential. You can also think of this as the drive of the neuron. This drives the neuron. And this, you can think of as recent potential as the potential shaping the gain function. If I have a neuron with strong refractoriness with a strong reset with a prolonged temporarily long spike after potential, then the gain function will have a lower firing rate at the maximum, than, if the reset is very small, and if there is no additional refractoriness.

Notes

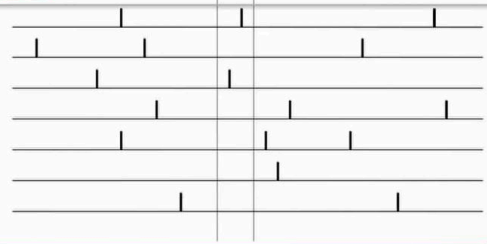
Summary



2. Transients in a population of uncoupled neurons



population activity



$$A(t) = \frac{n(t - \frac{\Delta t}{2}; t + \frac{\Delta t}{2})}{N \Delta t}$$



$$A(t) = F(h(t)) = F\left(\int \kappa(s) I(t-s) ds\right)$$

$$A(t) = g(I(t))$$

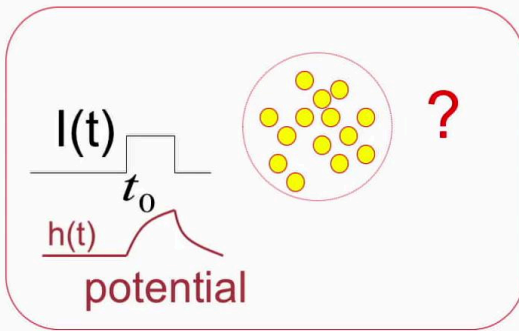
So now, we have some basic ideas about inputs and about the input potential. The question now is, suppose I have my population a year population of 500 neurons, or 1000 neurons or 5000 neurons into the big population, and all neurons are of the same type. For the moment you don't have any coupling. They are uncoupled neurons. And now, I drive these neurons, with a certain input current. This is now my external input, it would give rise to this input potential which is the low pass filter version. The question I now have for you is, do you expect this population activity, if I do my standard way of calculating the population activity, do we expect this population activity to follow the input current or do we expect this to follow the input potential, in which case it will be low pass filtered?

Notes

Summary



2. Transients in a population of **uncoupled** neurons



Which would you choose?

$$A(t) = \frac{n(t - \frac{\Delta t}{2}; t + \frac{\Delta t}{2})}{N \Delta t}$$

population activity



$$\tau \frac{d}{dt} A(t) = -A(t) + F(h(t))$$

$$A(t) = F(h(t)) = F\left(\int \kappa(s) I(t-s) ds\right)$$

$$A(t) = g(I(t))$$

$$A(t) = g(I(t), I'(t))$$

Or you could say, well, maybe it's even low pass filter twice because it will approach this new value only with an additional time constant τ or going the other direction you could say, well, maybe doesn't follow the current but it's as fast as a current step, but then it will decay down again, which case it will be a function of I of T and I prime. To the question I have for you, which model, would you choose. Here are the four models.

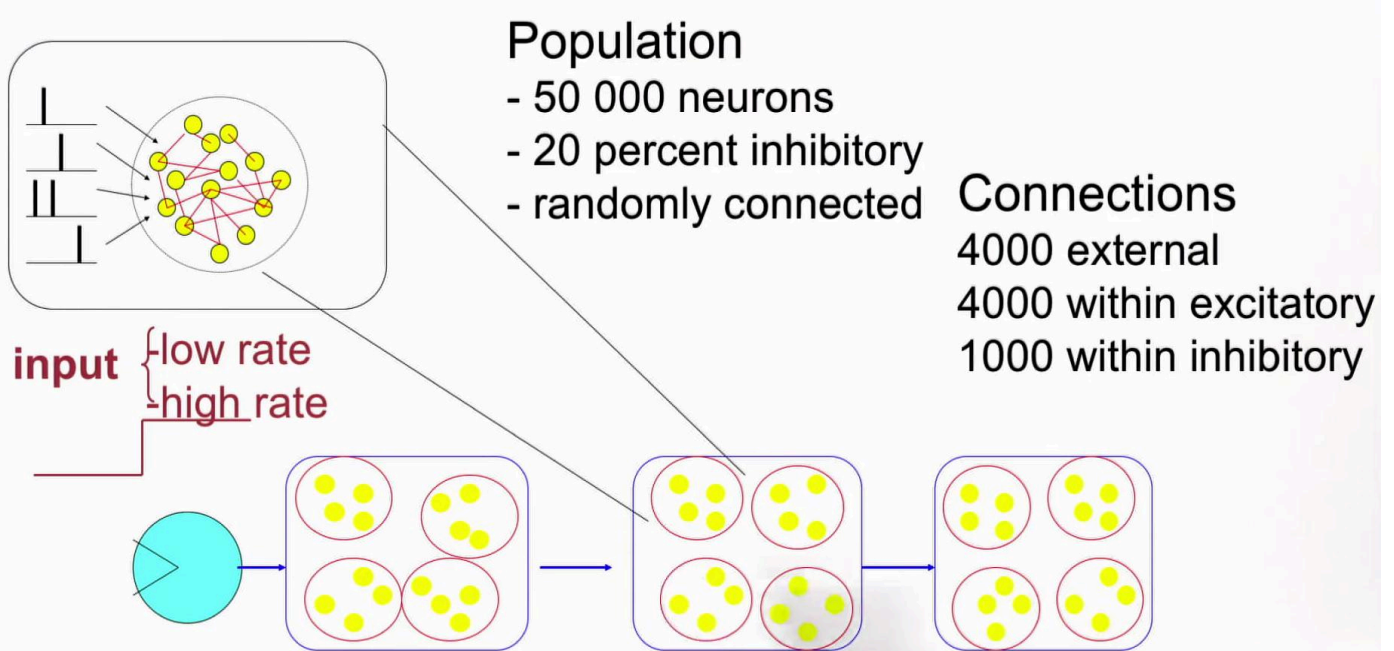
Notes

Summary



8m 40s

2. Transients in a population of neurons: simulations



Well, let's look at simulations. So the idea is that the model interacting populations, through the retina, there are some input, while the person is watching a video. So the images will change, two or three times per second, and information is transmitted through different populations. I will focus on one of these populations. And I will simulate this population of 50,000 neurons and 40,000 excited the neurons 10,000 inhibitor neurons Now because the input switches from time to time, at some point, the input rate to this population will change.

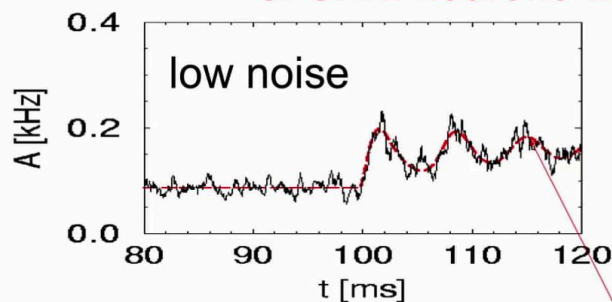
Notes

Summary



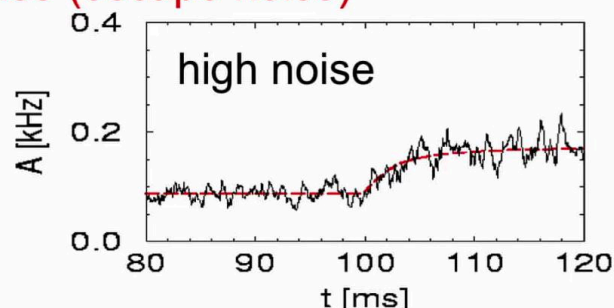
2. Transients for populations of noisy neurons

uncoupled population
of SRM neurons with noise (escape noise)



fast transient

$$A(t) \approx g(I(t))$$



slow transient

$$A(t) = F(h(t))$$

but transient oscillations

Here's how it looks like. Here are my population of 50,000 neurons for average over all neurons, I see the population activity, which is flat here. This is the moment when I switch the input. And then the population activity is higher. Now, importantly, this switch is super-fast. It's super-fast. I don't have this low pass filter of the input potential. If you look at one of the neurons, this neuron here, you see the red spikes here that's this neuron. If you look at this membrane potential it fluctuates here. And then once I do to switch it integrates up here you see the low pass filter. However, the population as a whole is much faster than this specific neuron. Now the reason is that, in a population of spiking neurons, there's some new ones are always active. There are some neurons that have a membrane puzzle just below threshold. And when I switched input, these new interval fire immediately. So, this simulation shows the population activity can react, super rapidly to a change in the input. Transients can be fast. Here's an additional simulation, the red line gives the exact theory that we can predict that I don't want to discuss the black line is the simulation.

Notes

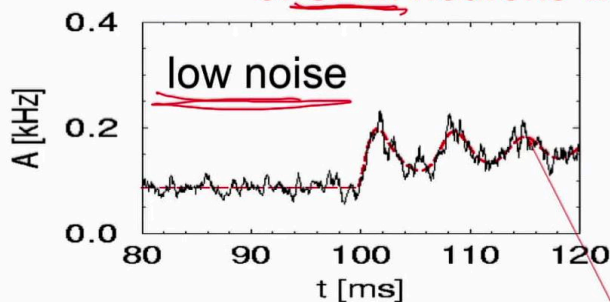
Summary



9m 56s

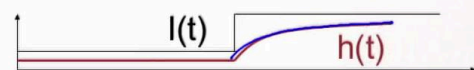
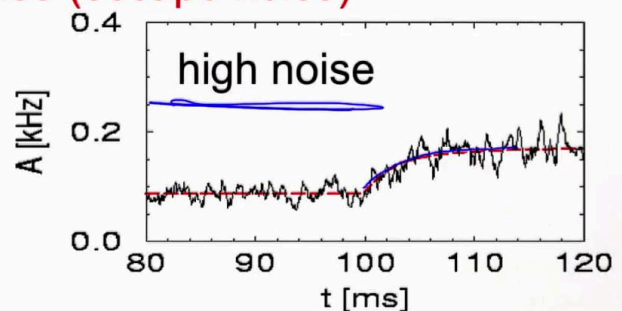
2. Transients for populations of noisy neurons

uncoupled population
of SRM neurons with noise (escape noise)



fast transient

$$A(t) \approx g(I(t))$$



slow transient

$$A(t) = F(h(t))$$

but transient oscillations

You see that for these generalized indignant fire models, also called spike response model neurons with escape noise. If I have a low noise value, then the response is super-fast. So it's a little bit like this response to the input current, except that we have these additional transient oscillations. This is for low noise. Now, if I am the high noise limit, then the response of the population is slow, it follows more or less, this input potential HFT. So, in this high noise limit. We have slow transients, and if I have slow transients, I mean I can describe the population activity as a function of the momentary value of HFT. So HFT increases slowly, after the change the input and the population activity, also follows slowly.

Notes

Summary

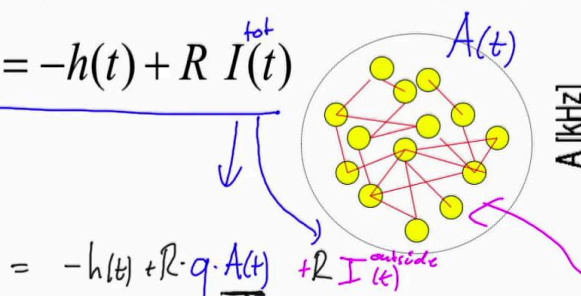


11m 20s

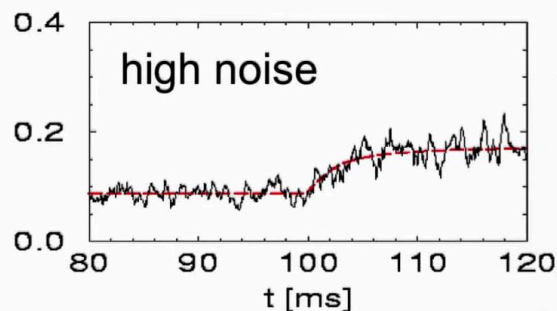
2. High-noise activity equation

Membrane potential caused by input

$$\tau \frac{d}{dt} h(t) = -h(t) + R I^{\text{tot}}(t)$$



(escape noise)



(*) **slow transient**
 $A(t) = F(h(t))$

In the limit of high noise,

If you have the slow transients, I can use to the population activity follows the membrane potential. Now we have seen that the input potentially itself is described for integrating fire neurons by these kind of differential equation. Now we can exploit that if I have a network of connected neurons that this input current will have a part that's really coming from the activity inside the network. This activity of the dis network activity will be A of T . To these external input is totally input will be input, coming into the neurons from neurons in the same population, and we have seen that this kind of input would be proportional to Q times A of T , and then there will be sort of true external input, coming from other populations, and I described this as, I , outside coming from, outside this specific population. So, a neuron in this network, would follow this differential equation with $R \times q \times A$ of T . So, the neuron is driven by the population activity, and the input potential represents a low pass filtered of this population activity, plus, the input from other sources outside this population. Now let me do one more step. I will use this equation here, and plug it into this A of T .

Notes

Summary



12m 21s

2. High-noise activity equation

Population activity

$$A(t) = F(h(t))$$

Membrane potential caused by input

$$\tau \frac{d}{dt} h(t) = -h(t) + R I(t)$$

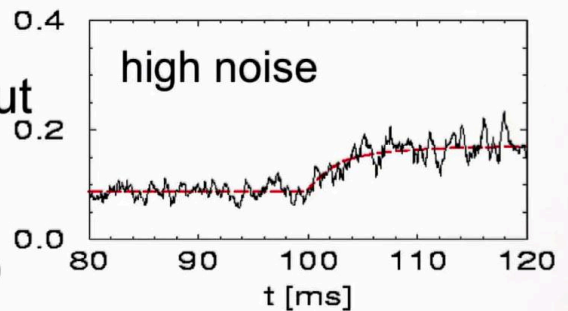
$$I(t) = I^{ext}(t) + I^{netw}(t)$$

$$I(t) = I^{ext}(t) + J_0 q A(t)$$

$$I(t) = I^{ext}(t) + J_0 q F(h(t))$$

$$\tau \frac{d}{dt} h(t) = -h(t) + R I^{ext}(t) + \gamma F(h(t))$$

(escape noise)



slow transient

$$A(t) = F(h(t))$$

1 population = 1 differential equation

A of T itself is A function of HFT. Let's call this gamma. I copied the rest, minus HFT last gamma times F of H of T plus R times I outside input coming from other sides, and I copied the left hand side HFT. So now I have a differential equation. Where I have H of T on the left hand side, DDH of T. I have H of T here and there. So we have one differential equation for one population. At the moment I have one single population for either this closed form it's just one differential equation, it was important that we used our assumption of slow transcends, which means we assumed that we are in the high noise regime. So here's again, the summary. In the high noise regime, I can always describe the population activity, as a function of the input potential for the input potential life a differential equation I plug in my input current, and in the end, I have one differential equation, for one, population.

Notes

Summary



2. Summary: Transients and population equations



$$\tau \frac{d}{dt} h(t) = -h(t) + R I^{ext}(t) + \gamma F(h(t))$$

- population activity equation
- smooth transient
- input potential determines activity

$$A = F(h(t))$$

- valid in high-noise regime
- misses sharp transients
- misses transient oscillations

So let me summarize what you have seen. I have derived a population activity equation. And we see that this population activity equation has smooth transitions. It has smooth transitions because the population activity reflects the input potential or differently, the input potential determines the activity. But this is valid only in the high noise limit. It misses the sharp transients that we would see at low noise, and it misses the transient oscillations, that we would see in spiking neurons, working in the low noise regime. Before we continue, please have a look at the quiz.

Notes

Summary



15m 29s

Population equations

A single homogeneous population of neurons is driven by a step current causing a transient response of the population activity.

- ☐ A single cortical model population can exhibit transient oscillations
- ☐ Transients are always sharp
- ☐ Transients are always slow
- ☐ in a certain limit transients can be slow
- ☐ An escape noise model in the high-noise limit has transients which are always slow
- ☐ A single population described by a single first-order differential equation (no integrals/no delays) can exhibit transient oscillations

Notes

Summary

