

# Computational Neuroscience: Neuronal Dynamics of Cognition



**Continuum models:**

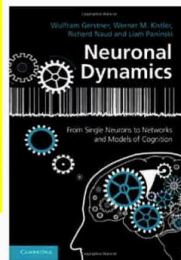
**Cortical fields and perception**

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**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)

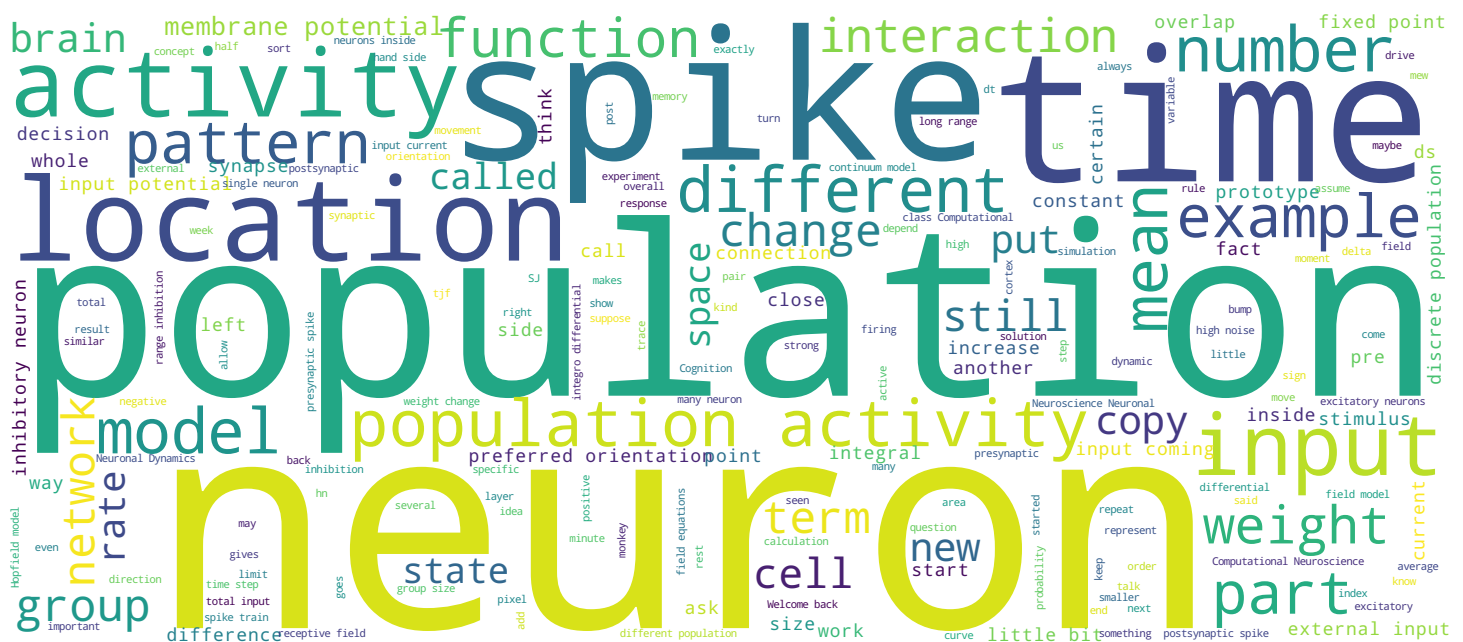
- field equations

## 5. Solution types

- uniform solution
- bump solution

## 6. Perception

## 7. Head direction cells



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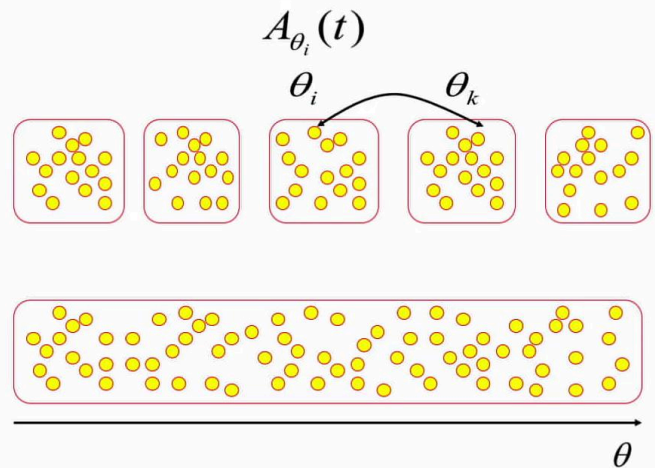
**Video**



**EPFL**



## 4. multiple populations → continuum



**Mathematical aim:  
perform continuum limit**

So welcome back to the class Computational Neuroscience: Neuronal Dynamics of Cognition. This week we work on continuum models and this part now is the hard mathematical work where I will derive the spatial continuum model, the so-called field model. Now, the way we do this is we start off with a set of discrete populations, then we take the continuum limit and it will show you the mathematical tricks that allow you to turn a discrete population into a continuous population, how to translate a set of discrete populations into a field model.

Notes

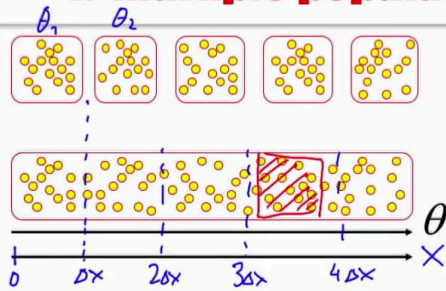
Summary



0m 19s



## 4. multiple populations → continuum



activity  
 $A_n(t)$   
 input potential  
 $h_n(t)$   
 group size  
 $N_n$

So let's think of neurons in the cortex responding to different preferred orientations. So for example, the neurons here would have a preferred orientation of 1, the neurons here would have a preferred orientation of 2. Now, if I walk along the cortex, I can also take this axis as a spatial axis. It's sort of equivalent, the location of the neuron is also an indication of the orientation and in the following I will use  $\theta$  in notation with this spatial variable. So the way we proceed this, we start with discrete populations. I started here, then I have here, a, I have here 2, I have here 3, and all of these populations should have roughly equal size. And then I can ask, what's the activity of one of the populations? For example, this population, this population here. The activity of this population is the population  $n$ , in this case with  $n$  equal 3, and I can define this activity as a function of time. Similarly, I can ask, what's the membrane potential or the input potential of this population? And it will be the population at location  $n$ , and it is time-dependent input potential. And then I can ask, how many neurons are inside this group? And I call this the group size, and this is  $N_n$ , the number of neurons inside the group.

Notes

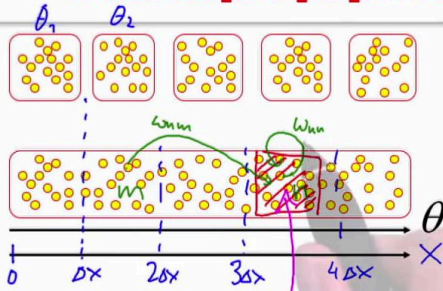
Summary



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## 4. multiple populations → continuum



activity  
 $A_n(t)$   
 input potential  
 $h_n(t)$   
 group size  
 $N_n$

$$\begin{aligned}\tau \frac{d}{dt} h_n &= -h_n + I_{\text{tot}}^{\text{tot}}(t) \\ &= -h_n + \underbrace{I_{\text{ext}}^{\text{ext}}(t)}_{\text{outside}} + I_{\text{nn}}^{\text{nn}}(t) + \sum_m I_{\text{nm}}^{\text{nm}}(t) \\ &= -h_n + I_{\text{ext}}^{\text{ext}}(t) + w_{nn} \sum_{j \in G_n^f} d(t - t_j^f)\end{aligned}$$

Now, let's look at one of these populations. I look at population  $n$ , and write down the differential equation for this population,  $d/dt h_n$ , minus  $h_n$  plus the total external input. Now, the input can arise from interactions within the same population, so this neuron here talks to all other neurons with the connection weight  $w_{nn}$ , but this neuron also receives input from a neuron outside, with connection weight  $w_{nm}$  from population  $m$  to population  $n$ . Now basically I would like to redo the calculation I did at the beginning of this week's session. So let's copy here this part, and the total input is the input that's really external, really I would say the input, an input coming from the outside, which I call external of  $t$ . Then there would be input coming from inside the same population. And then there would be input coming from other populations, and that's sum of all these other populations,  $m$ . I can copy the first part, and now for the interactions, the current that's coming from inside this population with the calculation before, I can just repeat it. So this current would be the sum of all neurons that are part of this group  $n$  of this population here, and this sum of all the spikes, and then spikes contribute a synaptic current  $t$  minus  $t_j^f$ , and these interactions come with a weight  $w_{nn}$ .

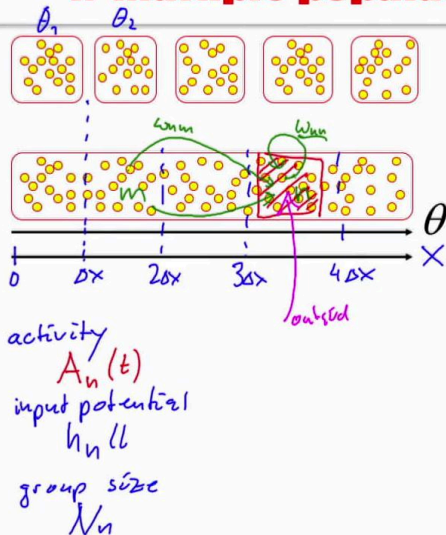
Notes

Summary





## 4. multiple populations → continuum



$$\begin{aligned}
 \tau \frac{d}{dt} h_n &= -h_n + I^{\text{tot}}(t) \\
 &= -h_n + \underbrace{I^{\text{ext}}(t)}_{\text{outside}} + I^{\text{nn}}(t) + \sum_m I^{\text{nm}}(t) \\
 &= -h_n + I^{\text{ext}}(t) + \underbrace{\sum_{j \in \text{group } n} d(t - t_j^f)}_{\text{all spikes all neurons}} + \sum_m \underbrace{\sum_{j \in \text{group } m} w_{nm} d(t - t_j^f)}_{\text{all spikes all neurons}} \\
 &= -h_n + I^{\text{ext}}(t) + \underbrace{w_{nn} N_n \int d(s) A_n(t-s) ds}_{\text{all spikes all neurons}} + \sum_m \underbrace{w_{nm} N_m \int d(s) A_m(t-s) ds}_{\text{all spikes all neurons}}
 \end{aligned}$$

$\sum_m$  including  $m=n$

This is my  $w_{nn}$ . Now, the input coming from other neurons force completely analogously. So I sum up all the other groups, and for each group, I sum up all neurons  $j$  that are part of this group, and sum of all spikes, I will have weight  $w_{nm}$ , and I will have current pulses  $t$  minus  $t_j^f$ . If you know what this is, this is the sum of all spikes of all neurons in that population. So this is just  $A_n$  of  $t$  minus  $s$  with integral of  $s$ . Now you should remember that the activity's actually the sum of all spikes all neurons divided by the number of neurons in that population. I don't -- if I don't divide by this number, I have to multiply out. So, now, this is all spikes all neurons. And then I can copy the weight in front,  $w_{nn}$ . And I can do the same thing for the other populations. Sum of  $m$ , I will use the weight and put it in front,  $w_{nm}$ , and then this gives  $A_m$  of  $t$  minus  $s$ , of  $s$  integral, that should be a  $ds$  for both, and I still have now to add this number  $N_m$ . So this is the sum of all spikes of all neurons in the other population  $m$ . I can copy the rest, minus  $h_n$  plus external of  $t$  plus. Now you see that I can really put these back into one single summation, sum of all populations including  $m$  equal  $n$  and write it down as  $w_{nm}$ .

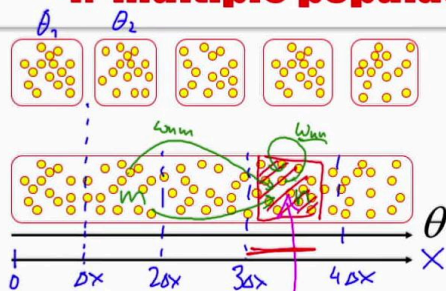
Notes

Summary





## 4. multiple populations → continuum



activity  
 $A_n(t) \rightarrow A(n \cdot \Delta x, t) = A(x, t)$   
 input potential  
 $h_n(t) \rightarrow h(n \cdot \Delta x, t)$   
 group size  
 $N_n \rightarrow$

discrete:  $\tau \frac{d}{dt} h_n$

$$\begin{aligned} \tau \frac{d}{dt} h_n &= -h_n + I_{\text{tot}}^n(t) \\ &= -h_n + \underbrace{I_{\text{ext}}^n(t)}_{\text{outside}} + I_{\text{nn}}^n(t) + \sum_m I_{\text{nm}}^n(t) \\ &= -h_n + I_{\text{ext}}^n(t) + \sum_{j \in \text{all spikes}} \sum_{f \in \text{all neurons}} w_{nj}^f \delta(t - t_j^f) + \sum_m \sum_{j \in \text{all spikes}} \sum_{f \in \text{all neurons}} w_{nm}^f \delta(t - t_j^f) \\ &= -h_n + I_{\text{ext}}^n(t) + \underbrace{w_{nn}^n N_n \int d(s) A_n(t-s) ds}_{\text{all spikes all neurons}} + \sum_m \underbrace{w_{nm}^n N_m \int d(s) A_m(t-s) ds}_{\text{all spikes all neurons}} \end{aligned}$$

I leave a little bit of space, and then I write of s,  $A_m$  of t minus s ds. I left a little bit of space because I still have to work on the group size. So let me just add this number here. And then I have to copy the rest. So what do we have now? We have a sum over different populations with different population activities and this drives the evolution of the population activity at location n. So we are still discrete. I still have my discrete populations. Now I do the actual continuum transition. Instead of talking about the population number n sitting here, I will give an index to the population for this location, and the location is s. So I will call this population here the population with seats at location, the is n times. So, this population would be the population 3. So, this is n, value, and the whole thing is still dependent on time. Similarly, for the membrane potential, I will make the transition, this is the membrane potential at location n times. That's my new value, and time t. And for the group size, well, how many neurons do I have inside? Well, this is now very important. I have chosen a value which is completely arbitrary.

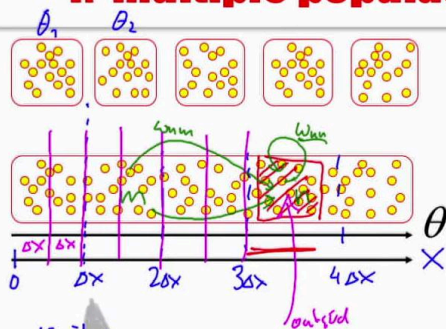
Notes

Summary





## 4. multiple populations → continuum



activity  
 $A_n(t) \rightarrow A(n \cdot \Delta x, t) = A(x, t)$   
 input potential  
 $h_n(t) \rightarrow h(n \cdot \Delta x, t)$   
 group size  
 $N_n \rightarrow d \cdot \Delta x$   
 interactions  
 $w_{nm} \rightarrow w(n \cdot \Delta x, m \cdot \Delta x) = w(x, x')$

discrete:  $\tau \cdot \frac{d}{dt} h_n = -h_n + I_n^{\text{ext}} + \sum_m w_{nm} A_m(t-s)$

$$\tau \cdot \frac{d}{dt} h(x, t) = -h(x, t) + I(x, t) + \sum_m \Delta x \cdot w(x, x') \int d(s) \cdot A(x', t-s) ds$$

$$\begin{aligned} \tau \frac{d}{dt} h_n &= -h_n + I_n^{\text{tot}}(t) \\ &= -h_n + I_n^{\text{ext}}(t) + I_n^{\text{nn}}(t) + \sum_m I_n^{nm}(t) \\ &= -h_n + I_n^{\text{ext}}(t) + \sum_{j \in \text{all spikes}} d(t - t_j^f) + \sum_m \sum_{j \in \text{all neurons}} w_{nm} \cdot d(t - t_j^f) \\ &= -h_n + I_n^{\text{ext}}(t) + \underbrace{\sum_m w_{nm} N_m \int d(s) A_m(t-s) ds}_{\text{all spikes all neurons}} + \sum_m \underbrace{w_{nm} N_m \int d(s) A_m(t-s) ds}_{\text{including } m=n} \end{aligned}$$

I could have chosen a smaller, say, half the size, this is my new, in which case, well I have only as many neurons inside as I had before, so I can introduce a density of neurons, and then write times. All the populations have the same size, if the density is constant, then the number of neurons is just the density times the. There's one more thing, I have these interactions. The interactions are  $w_{nm}$ , which is the interaction from  $m$  to  $n$ , and I will write this now as interaction between  $n$  times and  $m$  times. Or, if I call this, its interaction from location  $'$  to location. And so now let's take our discrete differential equation and rewrite it in terms of these new variables. So now I have  $d/dt h$ , but  $h_n$  is  $h$  at location. At location. It's the external input which could be different at different locations, so let me just add this, this is the external input at location  $n$ , at location  $n$ , at location  $n$ , which makes it at location, and now I sum over  $m$ , including  $m$  equal  $n$ , my  $w$  is  $w$  of and  $'$  using this expression here, my  $N_m$  is times  $d$ , and this curve I copy, of  $s$ , but I replace the  $m$  by  $'$  at location  $' t$  minus  $s$ ,  $ds$ . This is still a discrete equation.

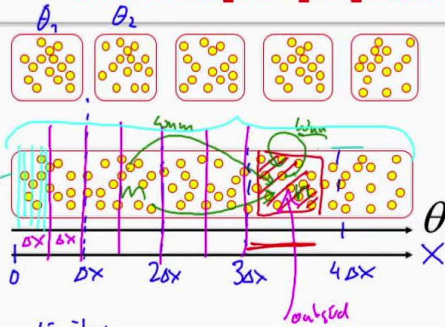
Notes

Summary





## 4. multiple populations → continuum



activity  
 $A_n(t) \rightarrow A(n \cdot \Delta x, t) = A(x, t)$   
 input potential  
 $h_n(t) \rightarrow h(n \cdot \Delta x, t)$   
 group size  
 $N_n \rightarrow d \cdot \Delta x$

interactions  
 $\omega_{nm} \rightarrow \omega(n \cdot \Delta x, m \cdot \Delta x)$   
 $= \omega(x, x')$

discrete:  $\tau \cdot \frac{d}{dt} h_n = -h_n + I_n^{\text{ext}} + \sum_m \omega_{nm} N_m \int d(s) A_m(t-s) ds$

$$\begin{aligned} \tau \frac{d}{dt} h_n &= -h_n + I_n^{\text{tot}}(t) \\ &= -h_n + I_n^{\text{ext}}(t) + I_n^{\text{nn}}(t) + \sum_m I_n^{nm}(t) \\ &= -h_n + I_n^{\text{ext}}(t) + \sum_{j \in \text{sf}} d(t-t_j^f) + \sum_m \sum_{j \in \text{sf}} \omega_{nm} \cdot d(t-t_j^f) \\ &= -h_n + I_n^{\text{ext}}(t) + \underbrace{\sum_m \omega_{nm} N_m \int d(s) A_m(t-s) ds}_{\text{all species all neurons}} + \sum_m \underbrace{\omega_{nm} N_m \int d(s) A_m(t-s) ds}_{\text{including } m=n} \end{aligned}$$

$$\tau \cdot \frac{d}{dt} h(x, t) = -h(x, t) + I_n^{\text{ext}}(x, t) + \sum_m \Delta x \omega(x, x') \int d(s) \cdot A(x', t-s) ds$$

$$\tau \cdot \frac{d}{dt} h(x, t) = -h(x, t) + I_n^{\text{ext}}(x, t) + \int dx \omega(x, x') \int d(s) A(x', t-s) ds$$

integro - differential equ = field equation

We started with a certain, the blue one, now I change it to the pink one, which is smaller. I could change again and make it even smaller, and each time, the number of neurons inside one of the populations will decrease. So it's this fact of which is very important. The same time, the number of populations will increase because in the end I always have the same -- I have to cover the same total spread of population material. So we will see that this allows me to transform this sum into a Riemann integral  $d$ , and this is then the final equation.  $d/dt$  of  $h$  of  $t$ , equals minus  $h$  of  $t$ , plus  $I$  external  $t$ , plus integral  $d' w'$ , of  $s$ ,  $A$  of  $'$ ,  $t$  minus  $s$ ,  $ds$ . Okay, this is the status of the slide at minute 12:58. So now I have one equation for the whole spatially extended population, and this is an equation which has an integral on this side and a differential on this side, so it's an integro-differential equation, and this equation is also called the field equation, or it's the continuum equation for my population activity.

Notes

Summary





## 4. Field equation (continuum model)

Wilson and Cowan, 1973

Population activity

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

Membrane potential caused by input

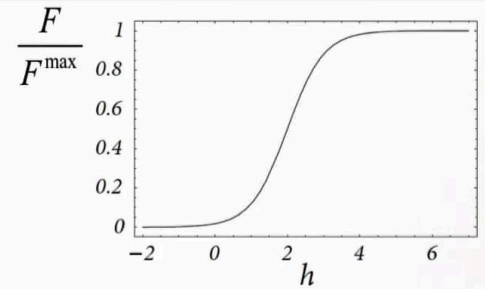
$$\tau \frac{d}{dt} h(x, t) = -h(x, t) + R I(x, t)$$

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

$$I^{netw}(x, t) = d \int w(|x - x'|) A(x', t) dx'$$

$$\tau \frac{d}{dt} h(x, t) = -h(x, t) + R I^{ext}(x, t) + d \int w(|x - x'|) F(h(x', t)) dx'$$

1 field = 1 integro-differential equation



$$w(x, x') = w(|x - x'|)$$

There's one more step we need to take. We still have the population activity on the right-hand side of this integro-differential equation. But the population activity is in this limit of high noise and slow transients, it's just a function of the membrane potential. Therefore, I can close the argument and put here my function of the membrane potential for the activity. I did one more thing, and that is, I replaced the  $w$  of and  $'$  by  $w$  of minus  $'$  and the idea is that it only depends on the difference between the two locations. So sometimes people even write, explicitly, difference between and  $'$  with absolute values, which I can also put in here. So one field is one integro-differential equation. The whole thing is a field equation or a continuum model, the first one or amongst the first ones where Wilson and Cowan in 1973. These models have been very popular. These are essentially population activity models as a function of space, but the variable can be space or something else, could also be an abstract quantity such as the preferred orientation of the cells at location.

Notes

Summary



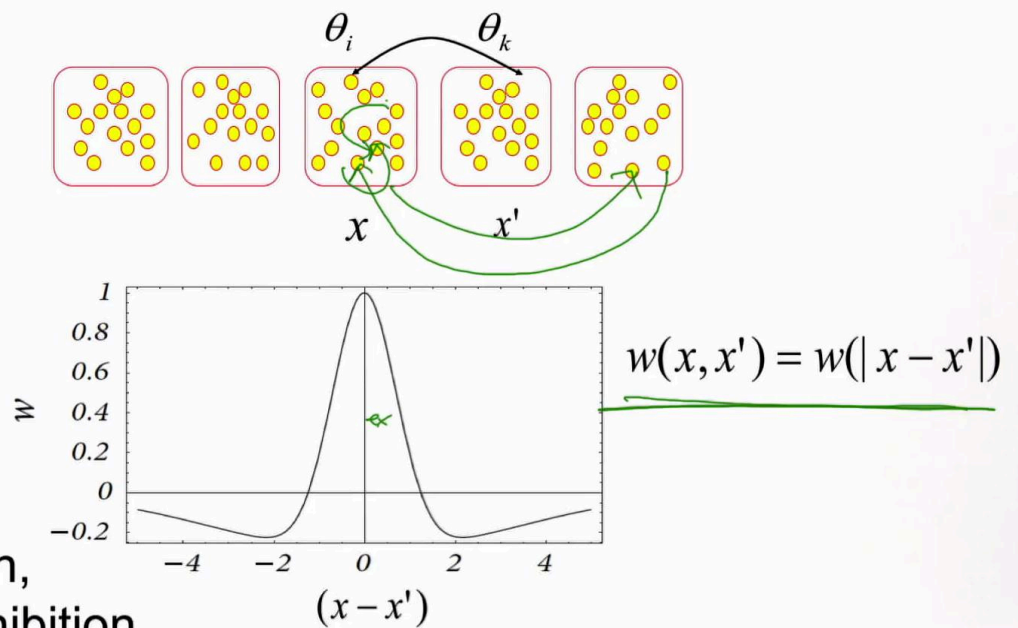
13m 44s



## 4. coupling across continuum: Mexican hat

### Mexican hat

local excitation,  
long-range inhibition



So I haven't really talked about the interactions, I said we can take it as a difference, and often this difference is such that, locally, you have excitation, so within a group, if you think in the discrete way, within a group, you have excitation, but over longer distances, you have inhibition. And this is by directional, so neurons here would inhibit neurons there, while this neuron here would excite the neuron there. It's also called a Mexican hat, for obvious reasons, and it means local excitation combined with long-range inhibition.

Notes

Summary



15m 17s







## 4. Summary: Field equations and coupling



$$\tau \frac{d}{dt} h(x, t) = -h(x, t) + RI^{ext}(x, t) + d \int w(x - x') F(h(x', t)) dx'$$

- field equations = population activity models in the spatial continuum
- coupling often distance-dependent
$$w(x, x') = w(|x - x'|)$$
- activity  $A = F(h(t))$
- effective long-range inhibition instead of local inhibitory neurons
- variable  $x$  can represent space or abstract quantity (e.g., orientation)

So let me summarise this part. This was the hard mathematical part. I've derived field equations, and with our field equations, well, these are population activity models in the spatial continuum. The coupling is thickness, distance-dependent, and importantly, these models work best if you say the activity is just a function of the input potential, which essentially means that we work in the limit of high noise. We have slow transients. Now in the model, we have this distance-dependent kernel,  $w$  of and  $'$  which assumes long-range inhibition, but that's a summary of effective interaction between excitatory and inhibitory neurons. The variable can represent the space itself, or an abstract variable, like the of the preferred orientation. And in the following sections, we are going to use this field equation repeatedly.

Notes

Summary



16m 38s