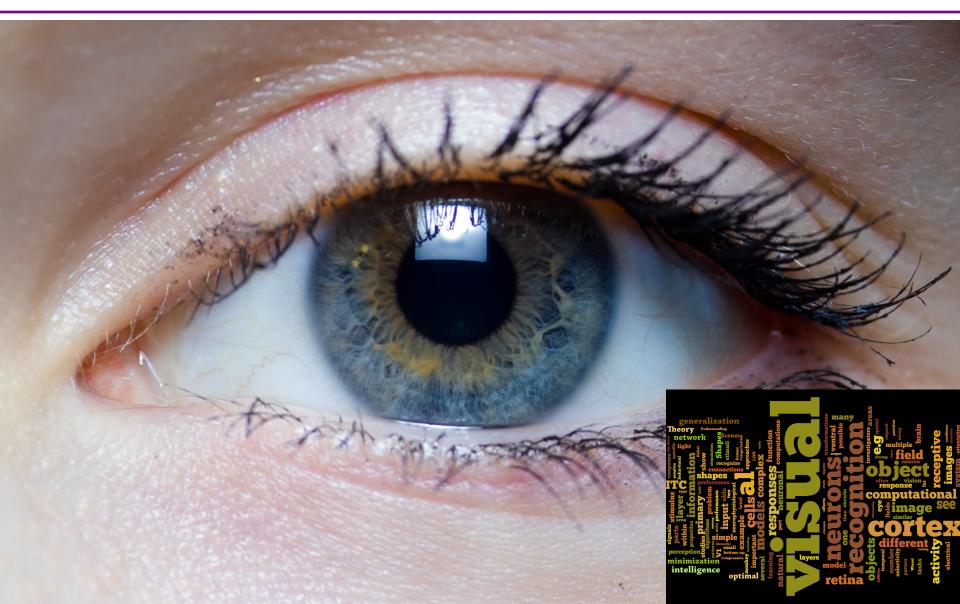
#### Visual Object Recognition Computational Models and Neurophysiological Mechanisms Neuro 130/230. Harvard College/GSAS 78454



#### Visual Object Recognition Computational Models and Neurophysiological Mechanisms Neurobiology 230. Harvard College/GSAS 78454

Class 1 [09/02/2020]. Introduction to Vision

- Class 2 [09/14/2020]. Natural image statistics and the retina
- Class 3 [09/21/2020]. The Phenomenology of Vision
- Class 4 [09/28/2020]. Learning from Lesions
- Class 5 [10/05/2020]. Primary Visual Cortex
- October 12th: University Holiday
- Class 6 [10/19/2020]. Adventures into terra incognita
- Class 7 [10/26/2020]. From the Highest Echelons of Visual Processing to Cognition

#### Class 8 [11/02/2020]. First Steps into in silico vision

- Class 9 [11/09/2020]. Teaching Computers how to see
- Class 10 [11/16/2020]. Computer Vision
- Class 11 [11/23/2020]. Connecting Vision to the rest of Cognition
- Class 12 [11/30/2020]. Visual Consciousness
- FINAL EXAM, PAPER DUE 12/14/2020. No extensions.

## OUTLINE

### 1. Why build computational models?

- 2. Single neuron models
- 3. Network models
- 4. Algorithms and methods for data analysis

## Why bother with computational models?

"Verbal models" are not real models: Vague and prone to subjective interpretation Lack of quantitative predictions Not falsifiable

-Quantitative models force us to formalize hypotheses and assumptions

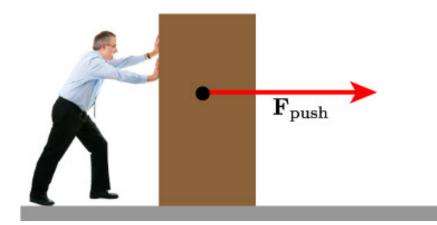
-Models can integrate observations across experiments, resolutions and laboratories

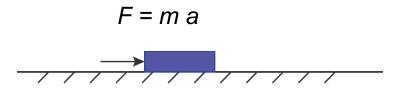
-A model can lead to (non-intuitive) experimental predictions

-A model can point to missing data, critical information and decisive experiments

-A model can be useful from an engineering viewpoint (e.g. face recognition)

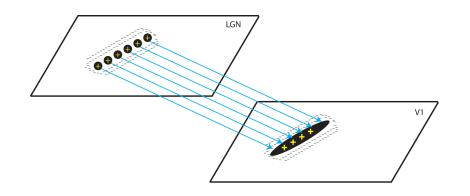
## What is a model, anyway?

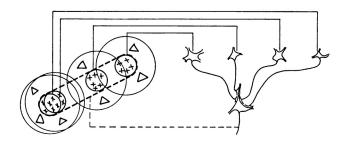




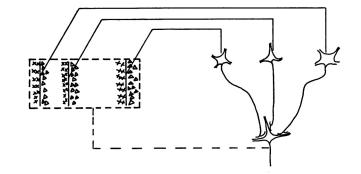
- Which hand was the person using?
- What is the shape/color/material of the object?
- What day of the week is it?
- What type of surface is it?
- What is the temperature/humidity?
- What is the force exerted by the person?
- What is the weight of the object?
- What is the force of gravity on this object?
- Where is the force exerted?
- What is the person wearing?
- How much contact is there between the object and the surface?

### A model for orientation tuning in simple cells





A feed-forward model for orientation selectivity in V1 (by no means the only model)



Hubel and Wiesel. J. Physiology (1962)

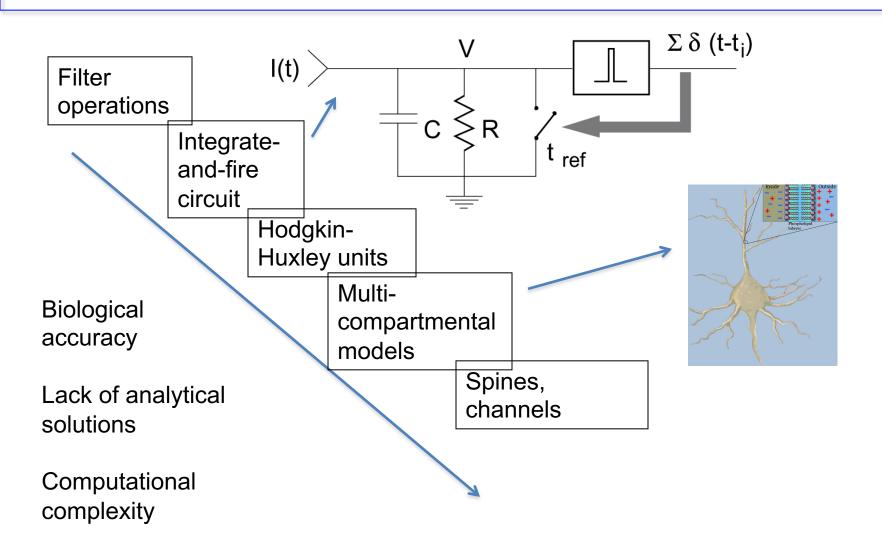
## OUTLINE

### 1. Why build computational models?

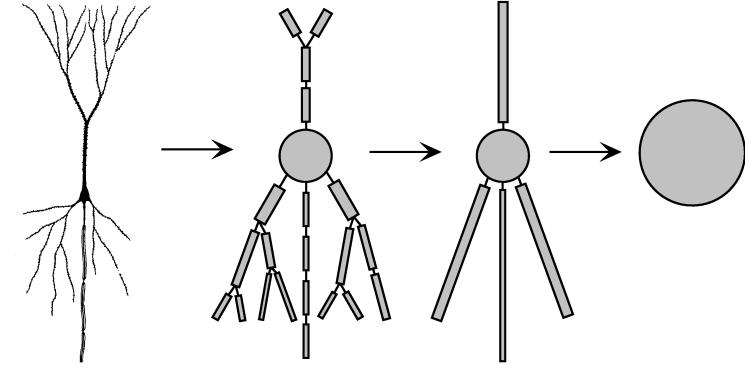
### 2. Single neuron models

- 3. Network models
- 4. Algorithms and methods for data analysis

## A nested family of single neuron models



# Geometrically accurate models vs. spherical cows with point masses



A central question in Theoretical Neuroscience: What is the "right" level of abstraction?

# The Hodgkin-Huxley Model

$$I(t) = C\frac{dV}{dt} + \overline{g}_L(V - E_L) + \overline{g}_K n^4 (V - E_K) + \overline{g}_{Na} m^3 h (V - E_{Na})$$

where:  $i_m$  = membrane current V = voltage

L = leak channel K = potassium channel Na = sodium channel

g = conductances (e.g.  $g_{Na}$ =120 mS/cm<sup>2</sup>;  $g_{K}$ =36 mS/cm<sup>2</sup>;  $g_{L}$ =0.3 mS/cm<sup>2</sup>) E = reversal potentials (e.g.  $E_{Na}$ =115mV,  $E_{K}$ =-12 mV,  $E_{L}$  = 10.6 mV) n, m, h = "gating variables", n=n(t), m=m(t), h=h(t)

Hodgkin, A. L., and Huxley, A. F. (1952). A quantitative description of membrane current and its application to conduction and excitation in nerve. Journal of Physiology *117*, 500-544.

# The Hodgkin-Huxley Model

function val = bn(v)

```
% Gabbiani & Cox, Mathematics for Neuroscientists
                                                             100 r
% clamp.m
% Simulate a voltage clamp experiment
% usage: clamp(dt,Tfin)
                                                         V (mV)
% e.g. clamp(.01,15)
                                                              50
function clamp(dt,Tfin)
vK = -6;
            % mV
GK = 36:
            % mS/(cm)^2
                                                               0
vNa = 127; % mV
                                                                                 2
                                                                                          3
                                                                                                           5
                                                                                                                            7
                                                                                                                                    8
                                                                                                                                             9
                                                                0
                                                                         1
                                                                                                   4
                                                                                                                   6
                                                                                                                                                     10
GNa = 120; % mS/(cm)^2
for vc = 8:10:90,
    j = 2;t(1) = 0;v(1) = 0;
                                                              30
    n(1) = an(0)/(an(0)+bn(0));  % 0.3177;
                                                       g_K (mS/cm<sup>2</sup>)
    m(1) = am(0)/(am(0)+bm(0));  % 0.0529;
                                                              20
    h(1) = ah(0)/(ah(0)+bh(0));  % 0.5961;
    gK(1) = GK*n(1)^{4};
    gNa(1) = GNa*m(1)^{3*h(1)};
                                                              10
    while j*dt < Tfin,
        t(j) = j*dt;
        v(j) = vc*(t(j)>2)*(t(j)<Tfin);</pre>
                                                               0
        n(j) = (n(j-1) + dt*an(v(j)))/(1 + dt*(an(v(j)))))
                                                                                 2
                                                                                          3
                                                                0
                                                                                                           5
                                                                                                                            7
                                                                                                                                    8
                                                                                                                                             9
                                                                         1
                                                                                                  4
                                                                                                                   6
                                                                                                                                                     10
);
        m(j) = (m(j-1) + dt*am(v(j)))/(1 + dt*(am(v(j))))
                                                              40<sub>1</sub>
);
       h(j) = ( h(j-1) + dt*ah(v(j)) )/(1 + dt*(ah(v(

gK(j) = GK*n(j)^4;

gNa(j) = GNa*m(j)^3*h(j);

j = j + 1;

plot(3,1,1); plot(t,v); hold on

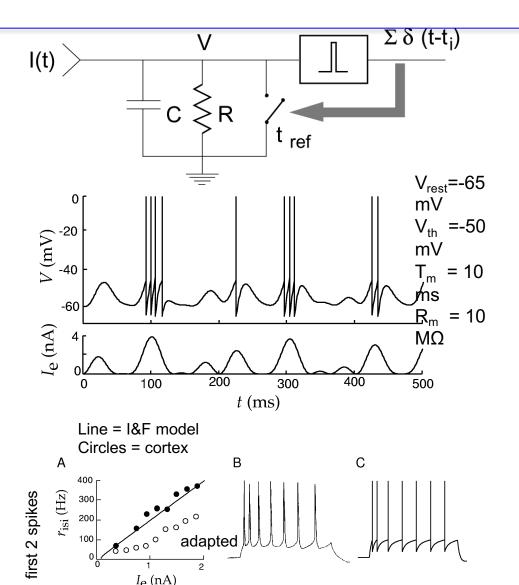
plot(3,1,2); plot(t,gK); hold on
                                                              30
);
                                                              20
    end
                                                              10
    subplot(3,1,1); plot(t,v); hold on
    subplot(3,1,2); plot(t,gK); hold on
                                                               0
    subplot(3,1,3); plot(t,qNa); hold on
                                                                Ó.
                                                                                 2
                                                                                          3
                                                                                                           5
                                                                                                  4
                                                                                                                   6
                                                                                                                            7
                                                                                                                                    8
                                                                                                                                             9
                                                                                                                                                     10
                                                                         1
end
                                                                                                       t (ms)
 subplot(3,1,1);ylabel('v','fontsize',16);hold off
subplot(3,1,2);ylabel('g K', 'fontsize',16);hold off
Huxley (1952). From Gabbiani and Cox 2010.
function val = an(v)
val = .01*(10-v)./(exp(1-v/10)-1);
```

# The leaky integrate-and-fire model

- Lapicque 1907
- Below threshold, the voltage is governed by:

$$C\frac{dV(t)}{dt} = -\frac{V(t)}{R} + I(t)$$

- A spike is fired when V(t)>V<sub>thr</sub> (and V(t) is reset)
- A refractory period t<sub>ref</sub> is imposed after a spike.
- Simple and fast.
- Does not consider spike-rate adaptation, multiple compartments, sub-ms biophysics, neuronal geometry

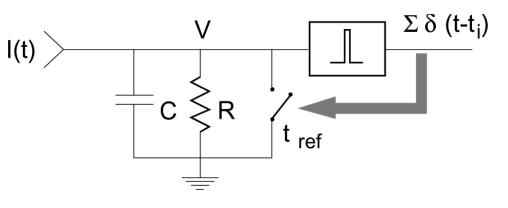


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- A refractory period  $t_{ref}$  is imposed after a spike
- Simple and fast
- Does not consider:
  - spike-rate adaptation
  - multiple compartments
  - sub-ms biophysics
  - neuronal geometry



#### function

```
[V,spk]=simpleiandf(E_L,V_res,V_th,tau_m,R_m,I_e,dt
,n)
```

 $\$  ultra-simple implementation of integrate-and-fire model

```
% inputs:
```

8 Inputs	•													
% E_L	= leak potential [e.g65 mV]													
% V_res	= reset potential [e.g. E_L]													
% V th	= threshold potential [e.g50 mV]													
% tau_m	= membrane time constant [e.g. 10 ms]													
% R_m	= membrane resistance [e.g. 10 MOhm]													
	= external input [e.g. white													
noise]														
% dt	= time step [e.g. 0.1 ms]													
	= number of time points [e.g. 1000]													
8														
% returns														
% V	= intracellular voltage [n x 1]													
% spk	= 0 or 1 indicating spikes [n x 1]													
<pre>V(1)=V_res; % initial voltage spk=zeros(n,1); for t=2:n     V(t)=V(t-1)+(dt/tau_m) * (E_L - V(t-1) + R_m * I_e(t)); % Key line computing the change in voltage at time t     if (V(t)&gt;V_th) % Emit a spike if V is above threshold         V(t)=V_res; % And reset the voltage         spk(t)=1;     end</pre>														
end														

## Interlude: MATLAB is easy

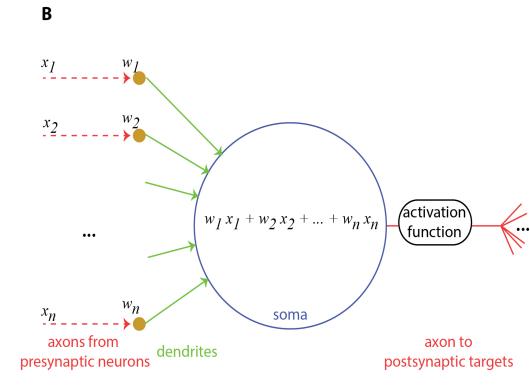
```
function [V,spk]=simpleiandf(E_L,V_res,V_th,tau_m,R_m,I_e,dt,n)
```

 $C\frac{dV(t)}{dt} = -\frac{V(t)}{R} + I(t)$ 

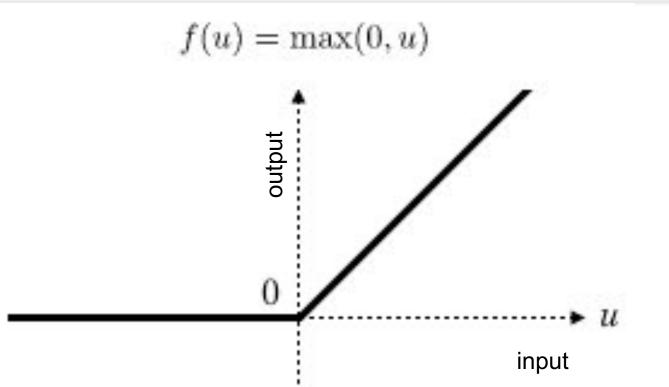
% ultra-simple implementation of integrate-and-fire model % inputs: = leak potential % E L [e.g. -65 mV] % V res = reset potential [e.g. E L] All of these lines are comments % V th = threshold potential [e.g. -50 mV] % tau m = membrane time constant [e.g. 10 ms] % R m = membrane resistance [e.g. 10 MOhm] % I e = external input [e.g. white noise] % dt = time step [e.g. 0.1 ms] % n = number of time points [e.q. 1000] 웅 % outputs: = intracellular voltage 8 V [n x 1] = 0 or 1 indicating spikes [n x 1] % spk This is the key line integrating the V(1)=V res; % initial voltage differential equation spk=zeros(n,1); for t=2:n V(t)=V(t-1)+(dt/tau m) \* (E L - V(t-1) + R m \* I e(t));% Change in voltage at time t if (V(t)>V th)% Emit a spike if V is above threshold V(t)=V res; % And reset the voltage spk(t)=1;end

# Typical units in neural networks

Α



# ReLU



## OUTLINE

- 1. Why build computational models?
- 2. Single neuron models
- 3. Network models
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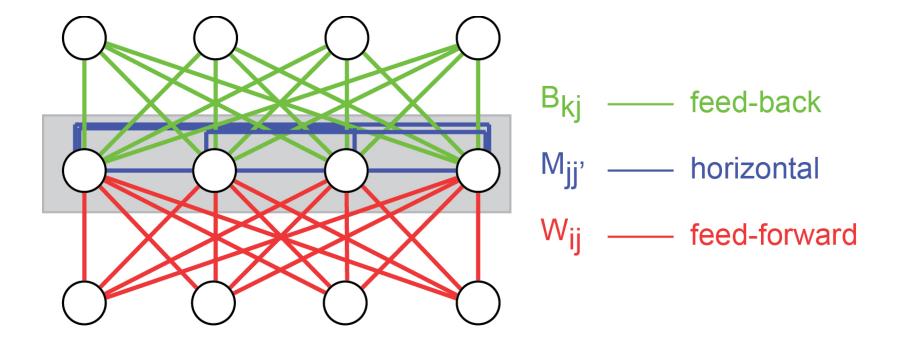
## From neurons to circuits

•Single neurons can perform many interesting computations (e.g. Gabbiani et al (2002). Multiplicative computation in a visual neuron sensitive to looming. Nature 420, 320-324)

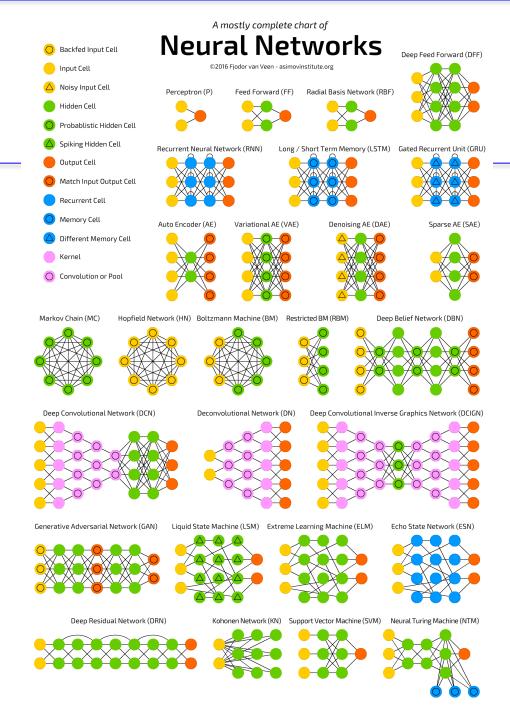
•But neurons are not isolated. They are part of circuits. A typical cortical neuron receives input from  $\sim 10^4$  other neurons.

•It is not trivial to predict circuit-level properties from single neuron properties. There can be interesting properties emerging at the network level.

#### Circuits – some basic definitions



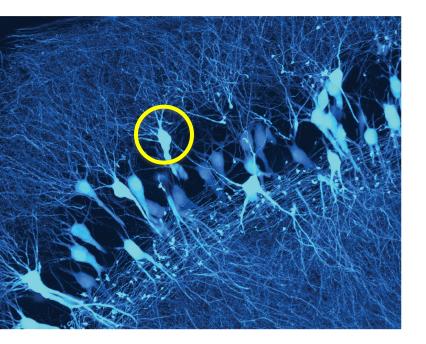
# A big happy family of neural networks



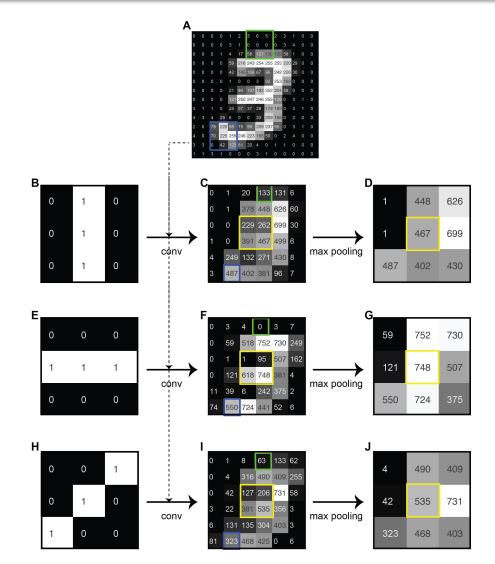
https://towardsdatascience.com/themostly-complete-chart-of-neuralnetworks-explained-3fb6f2367464

### From neural circuits to neural networks

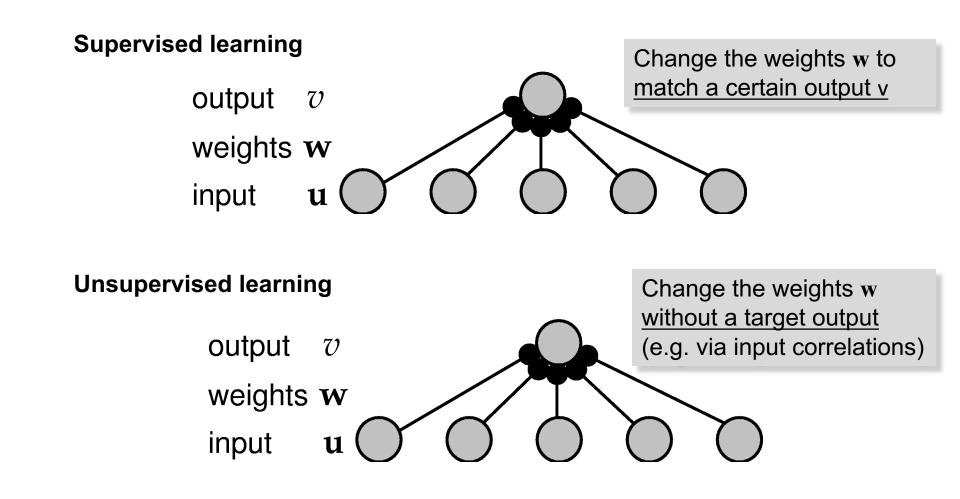
Α



### The convolution operation



### Supervised versus unsupervised learning



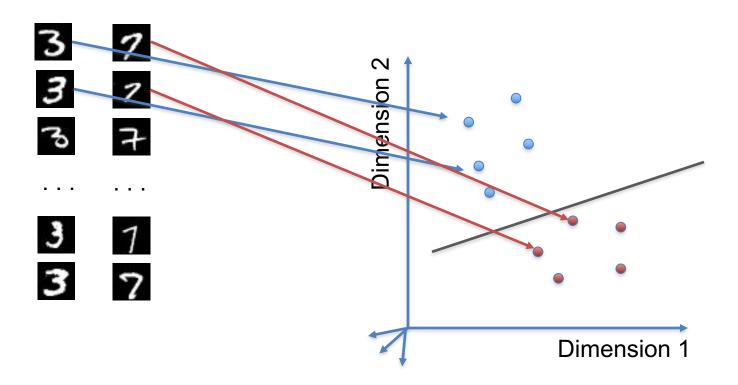
### Learning from examples – Digit classification

0	0	0	0	0	0	0	0	0	) (	) (	) (	) (	) (	) (	) (	) (	) (	0 0	) (	0	0	0	0	0	0	0	(
0	0	0	0	0	0	0	0	C	) (	) (	) (	) (	) (	) (	) (	) (	) (	) (	) (	0	0	0	0	0	0	0	(
)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	C
)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	(
)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	(
כ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	(
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	(
0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-			253		-	0	0	0	0	0	0	(
0	0	0	0	0	0	0	0	0	0	0	0									250		0	0	0	0	0	(
0	0	0	0	0	0	0	0	-												252		0	0	0	0	0	1
0	0	0	0	0	0	0		-	-	-	-	252	-		19	39			-	252		0	0	0	0	0	
0	0	0	0	0	0	-	186						53	0	0	-		252			20	0	0	0	0	0	
0	0	0	0	0	0	-	242				59	0	0	0	0		-	252			0	0	0	0	0	0	
0	0	0	0	0		185				67	0	0	0	0	17 121			252		•.	0	0	0	0	0	0	
0 0	0 0	0	0	0 0	0	83 0	205 0	0	24 0	0	0	0	0	-	247				24 0	0	0	0	0 0	0	0	0	
0	0	0	0	0	0	0	0	0	0	0	0	0	-	253				0	0	0	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	0	0	0	0	-	-	255			39	0	0	0	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	0	0	0	0	-		253			2	0	0	0	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	0	0	0	-	102					0	0	0	0	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	0	0	-		252			2	0	0	0	0	0	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	0	0	41	252	252	217	0	0	0	0	0	0	0	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	0	40	155	252	214	31	0	0	0	0	0	0	0	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	0	165	252	252	106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	43	179	252	150	39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	137	252	221	39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	67	252	79	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

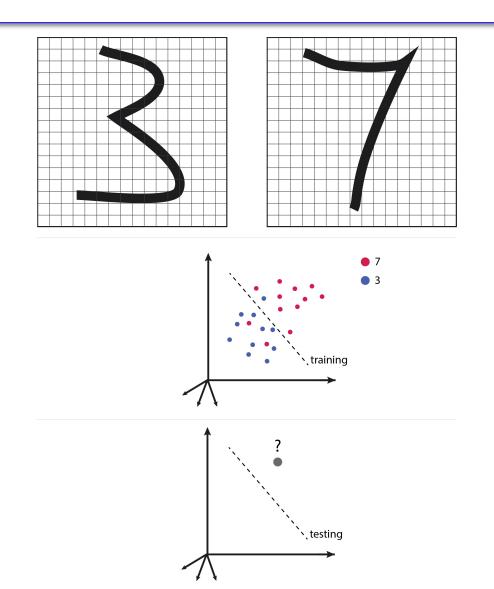




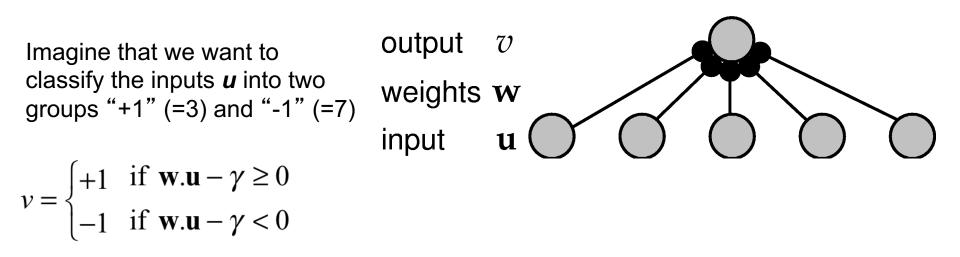
### Learning from examples – Classifiers



### Learning from examples – Classifiers and cross-validation



### Learning from examples – The perceptron



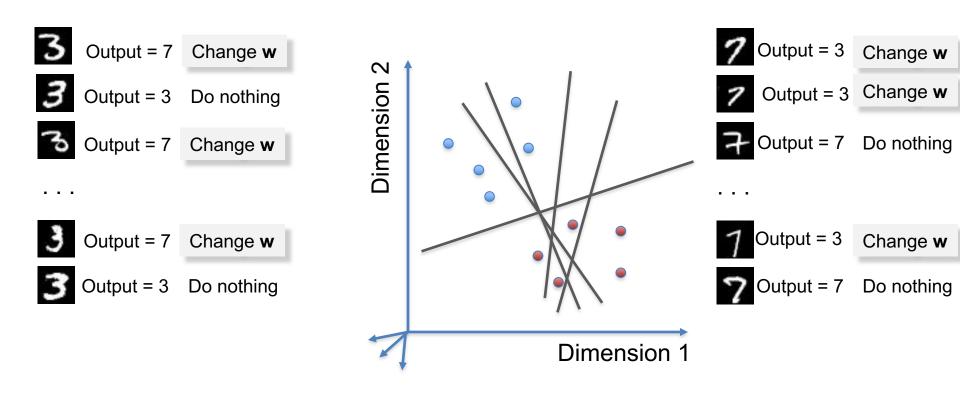
Training examples: {**u**<sub>m</sub>,*v*<sub>m</sub>}

 $\mathbf{w} \rightarrow \mathbf{w} + \frac{\epsilon}{2} (v_m - v(\mathbf{u}_m)) \mathbf{u}_m$ 

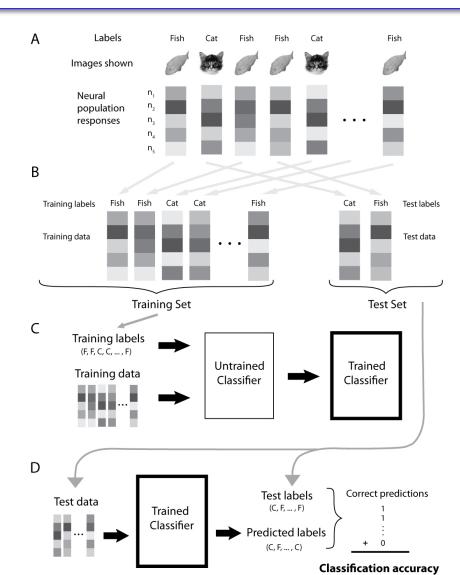
Perceptron learning rule

Linear separability: can attain zero error Cross-validation: use separate training and test data There are several more sophisticated learning algorithms

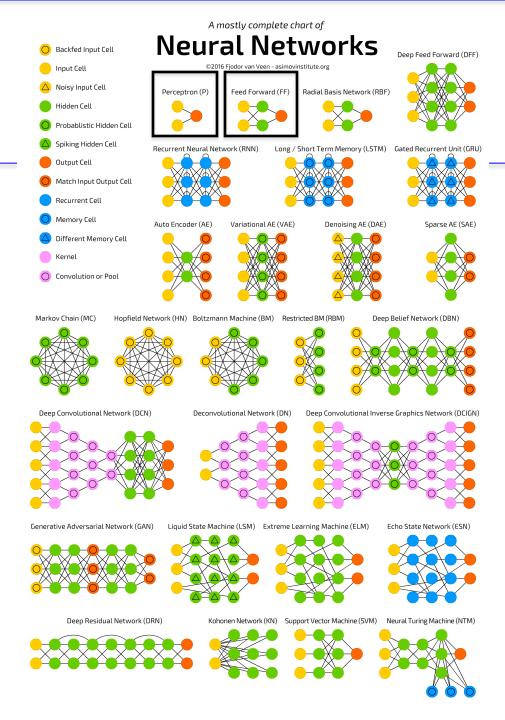
### Learning from examples – Training



### Learning from examples – Classifiers and cross-validation



# A big happy family of neural networks



https://towardsdatascience.com/themostly-complete-chart-of-neuralnetworks-explained-3fb6f2367464

### Learning from examples – Gradient descent

Now imagine that *v* is a real value (as opposed to binary)

 $\mathbf{u} = \mathbf{f}(s)$ 

 $v(s) = \mathbf{w}.\mathbf{u}$ 

We want to choose the weights so that the output approximates some function h(s)

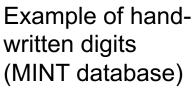
output 
$$v$$
  
weights w  
input u

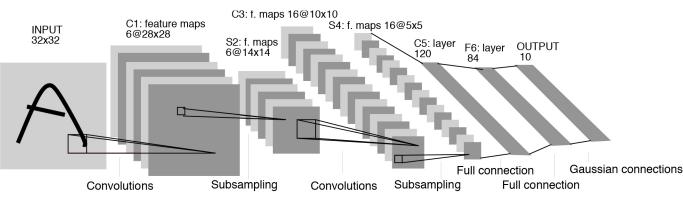
$$E = \frac{1}{2} \sum_{m=1}^{N_s} (h(s^m) - v(s^m))^2$$

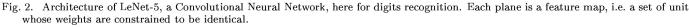
$$\mathbf{w} \to \mathbf{w} + \epsilon \nabla_{w} E \qquad \nabla_{w} E = \left\lfloor \frac{\partial E}{\partial w_{b}} \right\rfloor$$

# Example: digit recognition in a feed-forward network trained by gradient descent



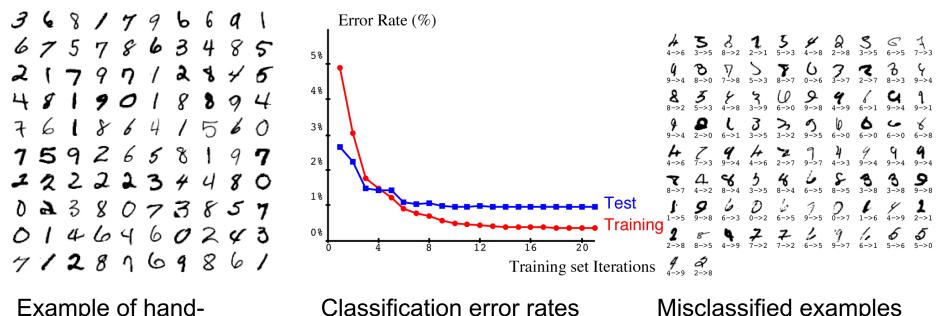






LeCun, Y., L. Bottou, Y. Bengio, and P. Haffner. 1998. Gradient-based learning applied to document recognition. Proc of the IEEE 86:2278-2324.

### Example: digit recognition in a feed-forward network trained by gradient descent



Example of handwritten digits (MINT database)

**Classification error rates** 

Misclassified examples

LeCun, Y., L. Bottou, Y. Bengio, and P. Haffner. 1998. Gradient-based learning applied to document recognition. Proc of the IEEE 86:2278-2324.

### The "blue brain" modeling project

-http://bluebrain.epfl.ch

- IBM's Blue gene supercomputer
- "Reverse engineer" the brain in a "biologically accurate" way

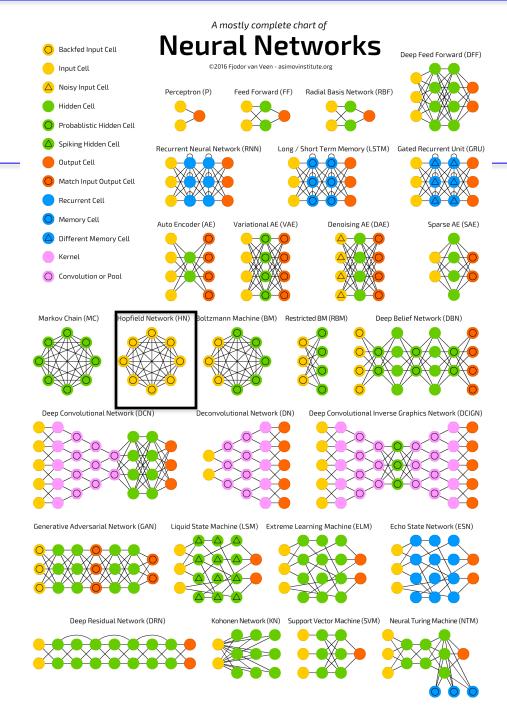
- November 2007 milestone: 30 million synapses in "precise" locations to model a neocortical column

- Compartmental simulations for neurons

- Needs another supercomputer for visualization (10,000 neurons, high quality mesh, 1 billion triangles, 100 Gb)

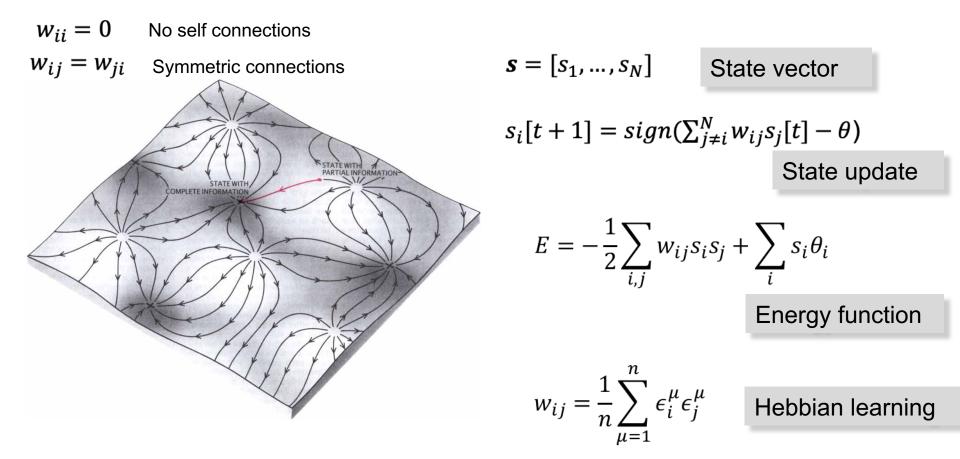
## QUESTION: What is the "right" level of abstraction needed to understand the function of cortical circuitry?

# A big happy family of neural networks



https://towardsdatascience.com/themostly-complete-chart-of-neuralnetworks-explained-3fb6f2367464

# Hopfield networks: A case study in collective computation



Hopfield, J. J. 1982. Neural networks and physical systems with emergent collective computational abilities. **PNAS** 79:2554-2558.

Tank, D., and J. Hopfield. 1987. Collective computation in neuron-like circuits. Scientific American 257:104-114

## Summary

- To understand vision, it is essential to build computational models
- We use abstract models where biological properties are simplified
- The integrate-and-fire neuron captures essential input-output properties
- The convolution operation allows extracting the same visual features throughout the entire visual field
- Basic elementary computations: filtering, normalization, pooling, thresholding
- Neural networks show emergent computational properties
- Neural networks include feedforward, horizontal and top-down connections
- Attractor-based recurrent neural networks show dynamic properties that save energy, provide flexible computations, and robustness to perturbations

## **Further reading**

- •Abbott and Dayan. Theoretical Neuroscience Computational and Mathematical Modeling of Neural Systems [2001] (ISBN 0-262-04199-5). MIT Press.
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