Three classic ideas in neural networks

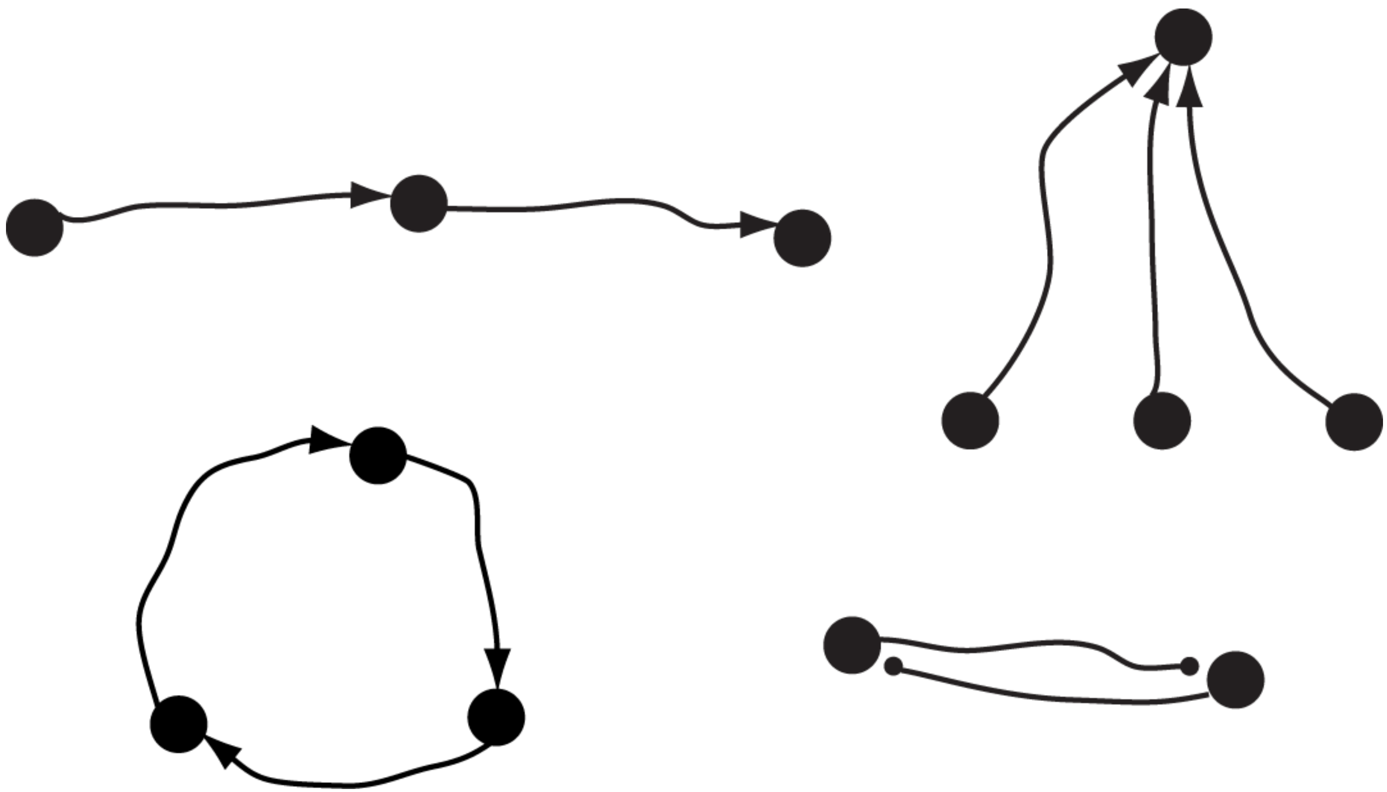
Sebastian Seung

HHMI and MIT

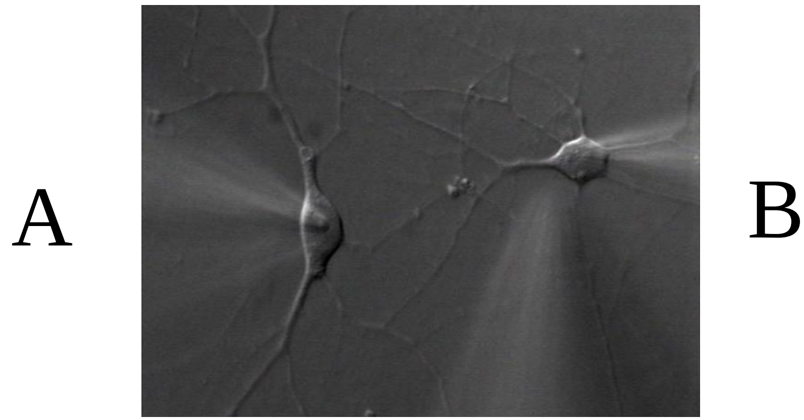
Three classic ideas

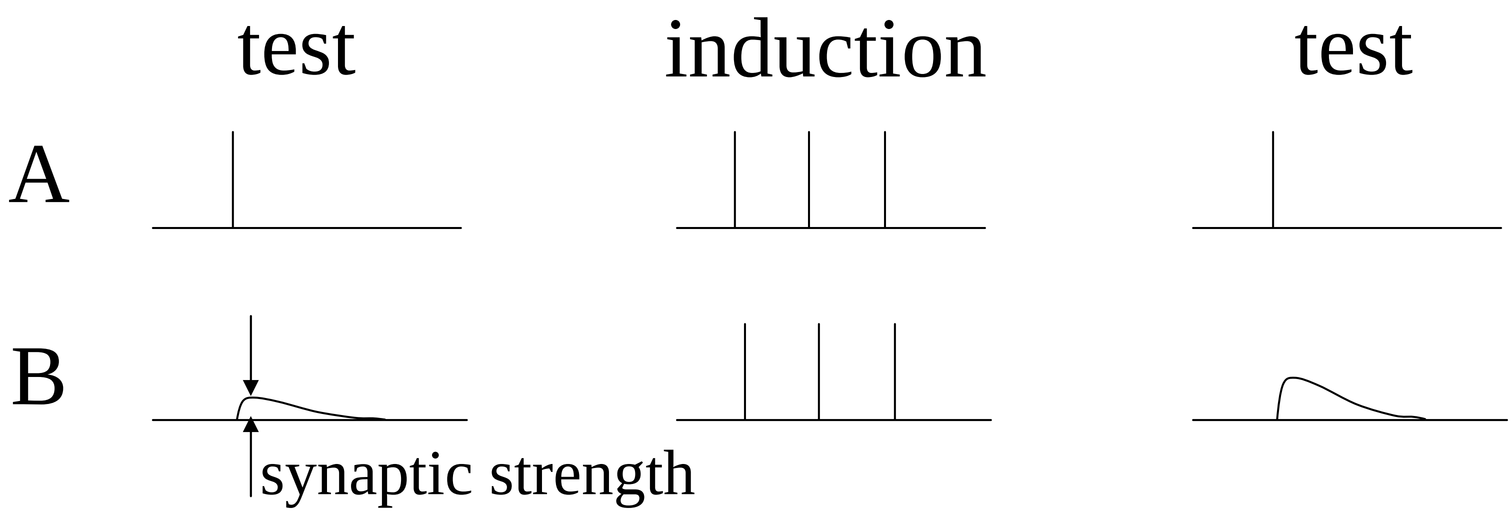
- Network structure-function relationships
- Hebbian synaptic plasticity
- Reward-dependent synaptic plasticity

Network motifs

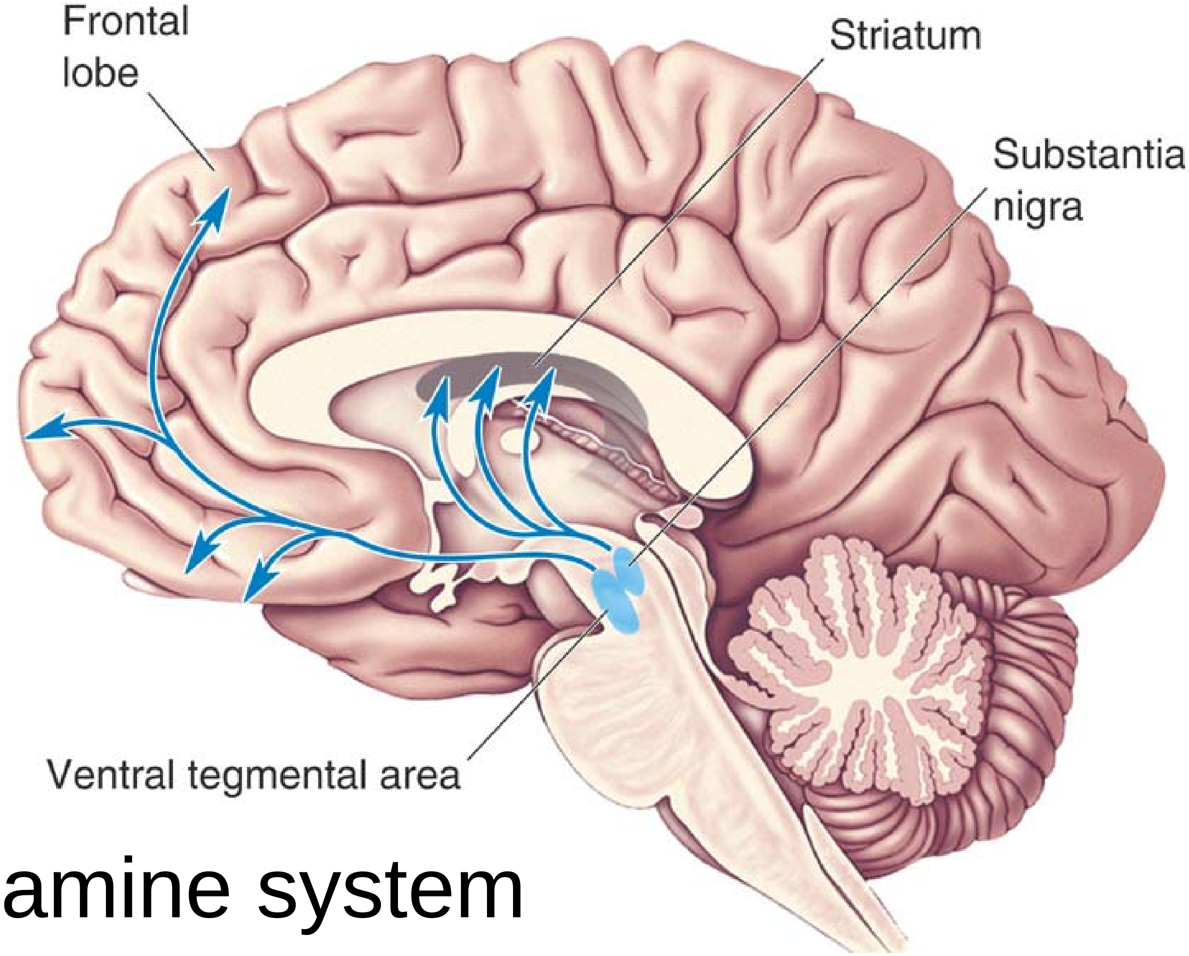


Hebbian synaptic plasticity





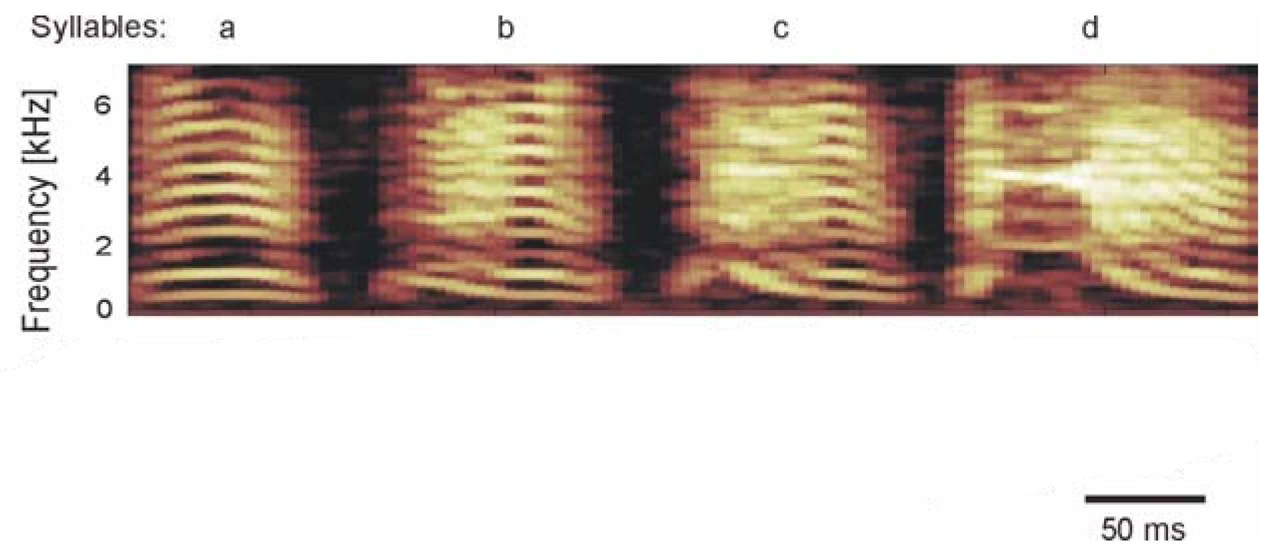
Reward-dependent synaptic plasticity



- Dopamine system

Zebra finch song

- Repetitions of a motif (0.5 to 1 sec)



- A motif is composed of 3-7 syllables.

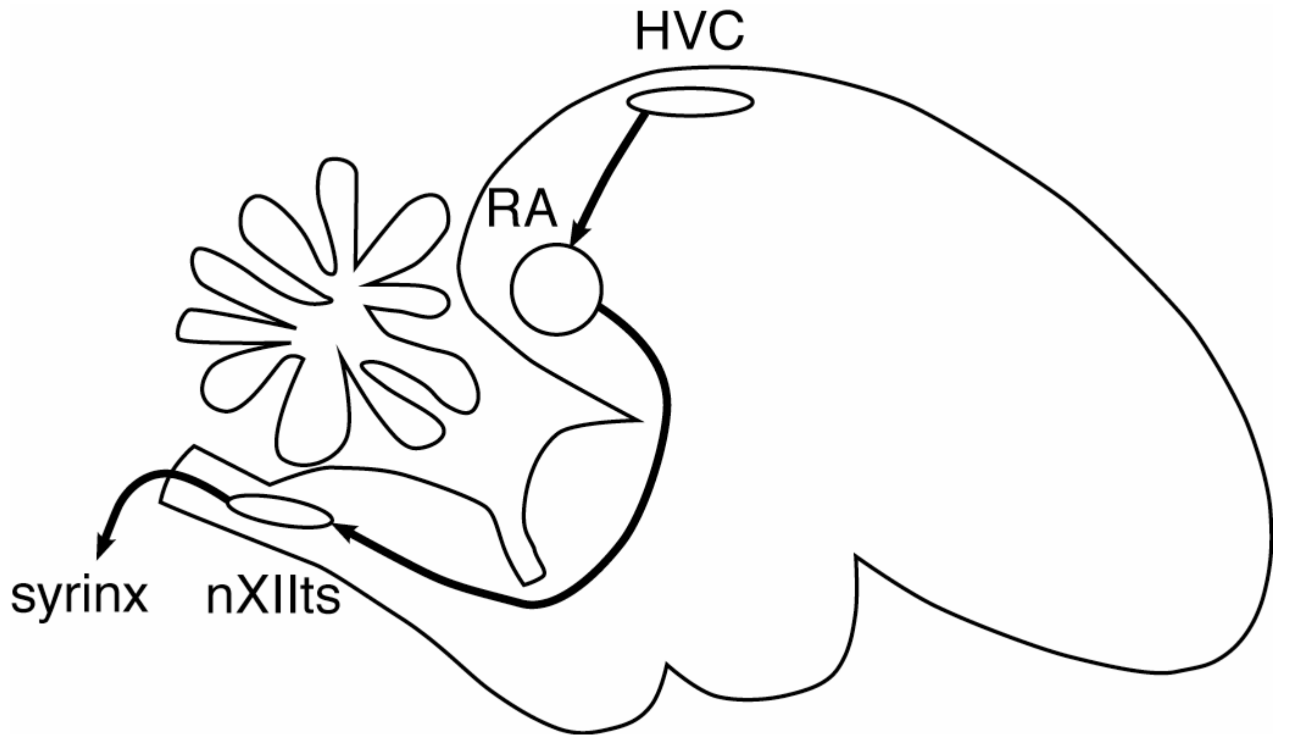
Birdsong

- Structure-function relationships
  - Synaptic chain model of sequence generation
- Hebbian synaptic plasticity
  - Learning sequences
- Reward-dependent synaptic plasticity
  - Learning motor commands

Synaptic chain model of HVC

with Dezhe Jin and Fethi Ramazanoglu

HVC is crucial for song production



- “high vocal center”

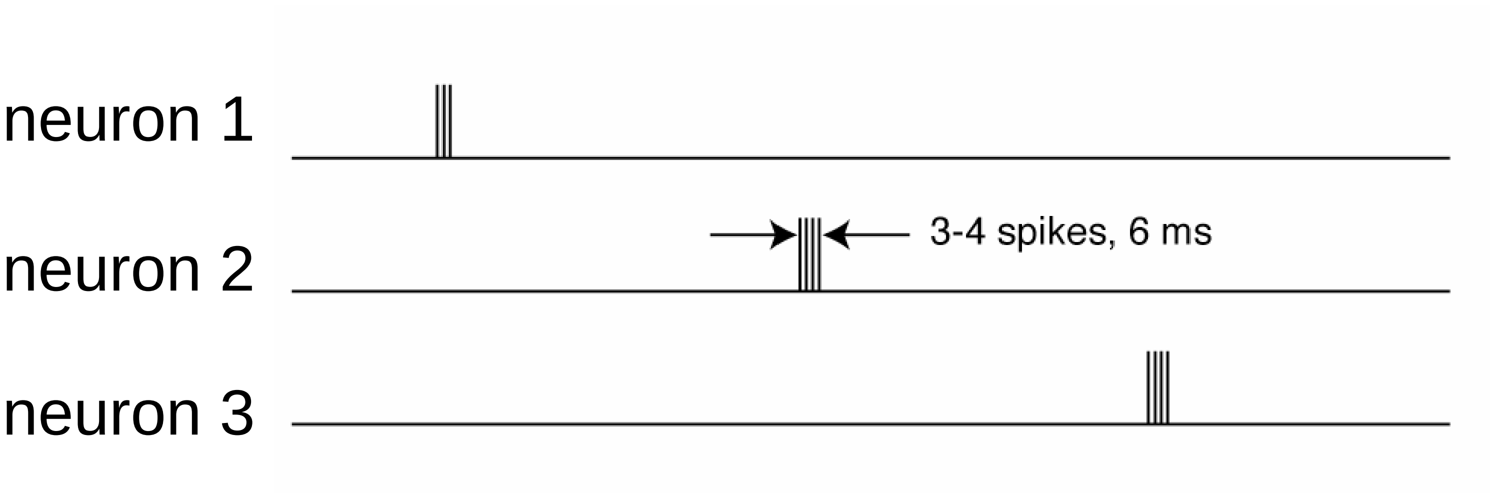
Two classes of HVC neurons

- Projection neurons (HVC_{RA})
  - Project from HVC to RA
  - Excitatory
- Interneurons (HVC_{IN})
  - Make synapses onto other HVC neurons.
  - Inhibitory

QuickTime™ and a
DV/DVCPRO - NTSC decompressor
are needed to see this picture.

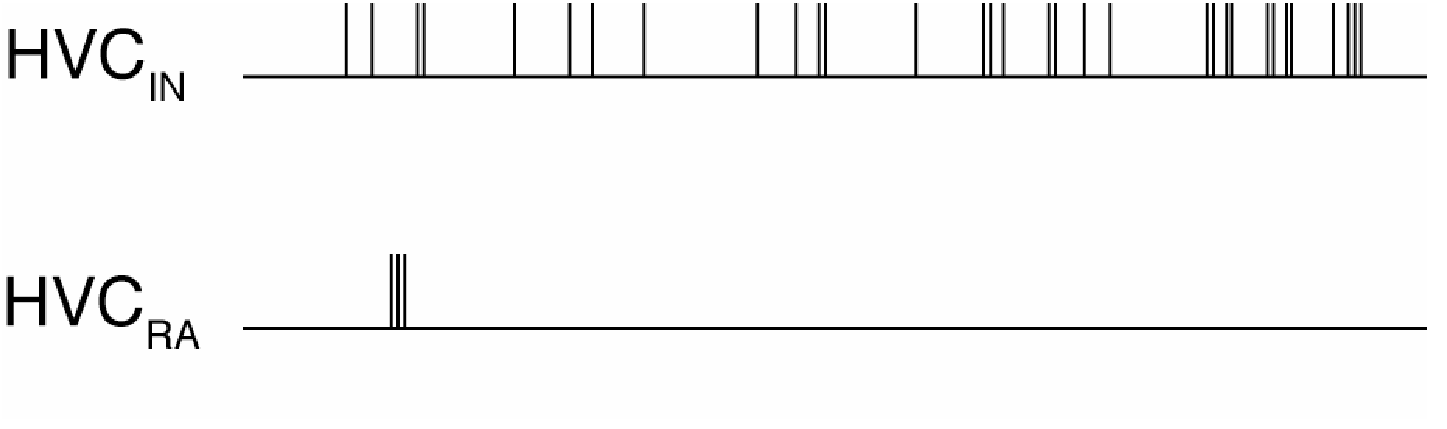
Michale Fee

Spiking of projection neurons is temporally selective



- Hahnloser et al., *Nature* (2002)

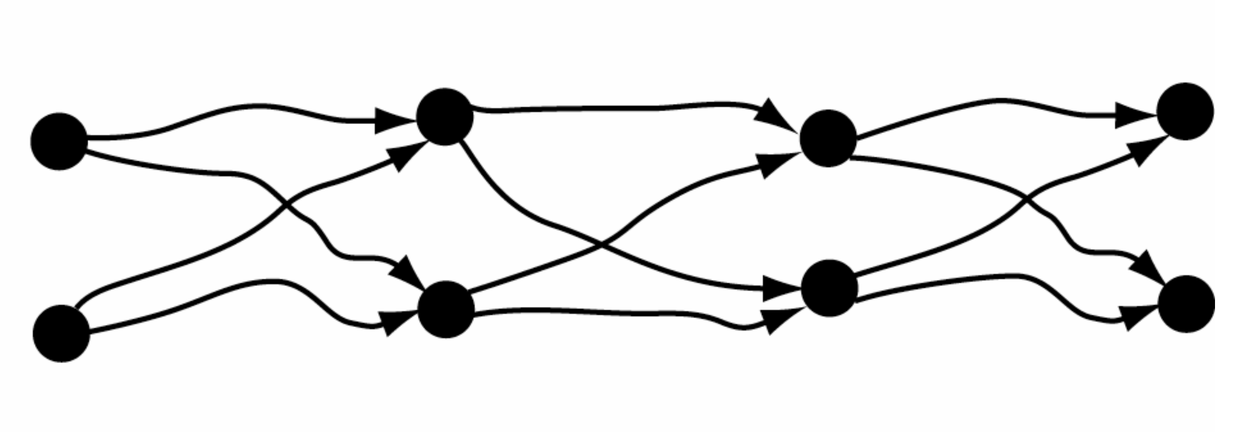
Spiking of interneurons is temporally unselective

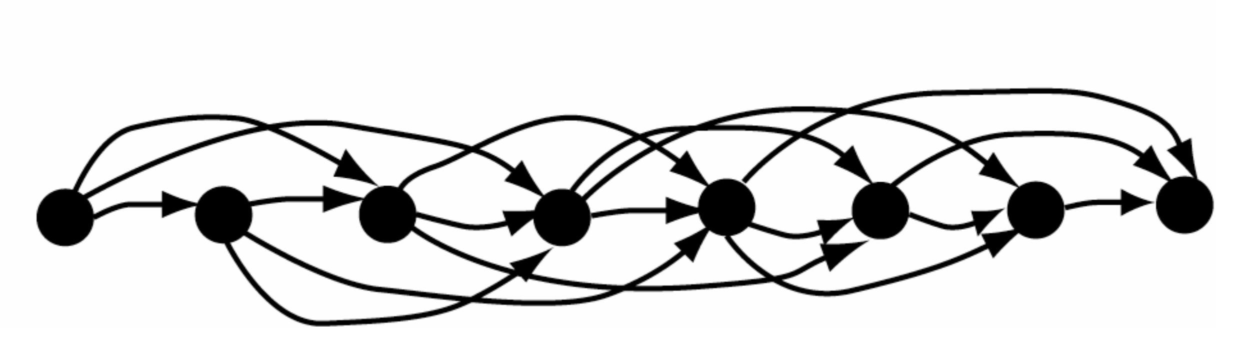


The arrow of time

- Hypothesis: There is a directionality to the network of excitatory synapses between projection neurons
- Li and Greenside (2006)
- Jin, Ramazanoglu, Seung (2007)
- Jin (unpublished)

Chain-like network structures



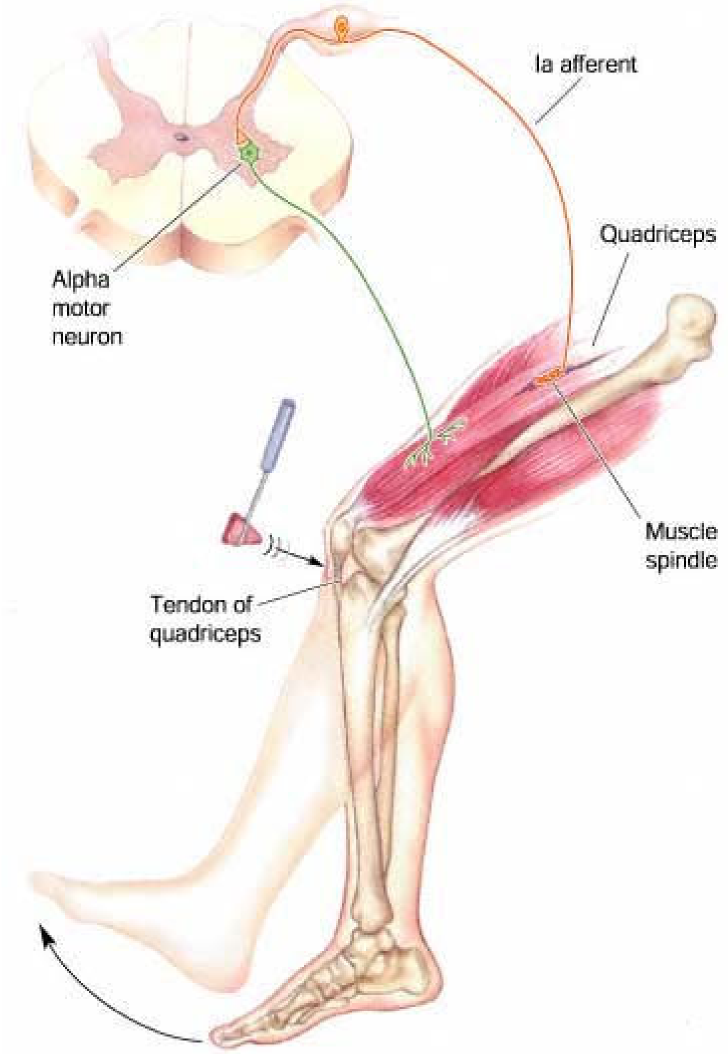


Synaptic chain models

- Amari (1972): “Type II net”
- Abeles (1982)
- Kleinfeld (1986)
- Kanter and Sompolinsky (1986)
- …

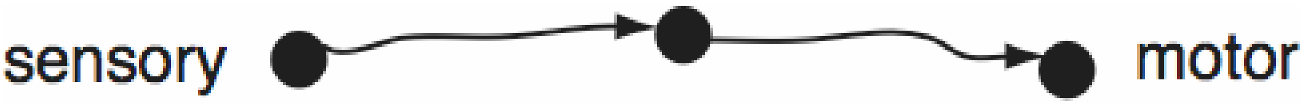
The knee-jerk reflex

- Reflex behavior:
  - Rapid, involuntary, stereotyped response to a specific stimulus.



The reflex arc

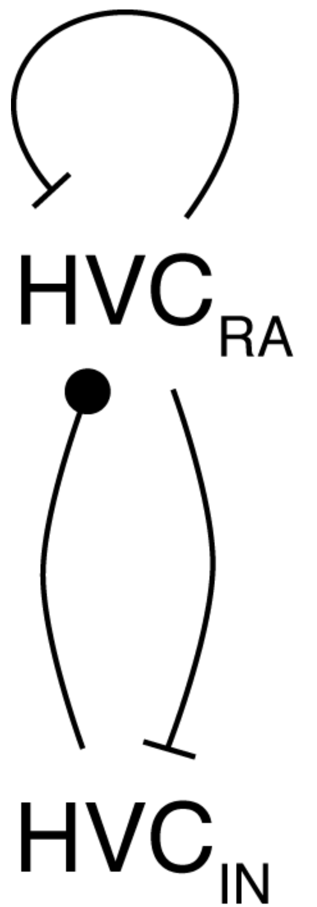
- Chain of cause and effect



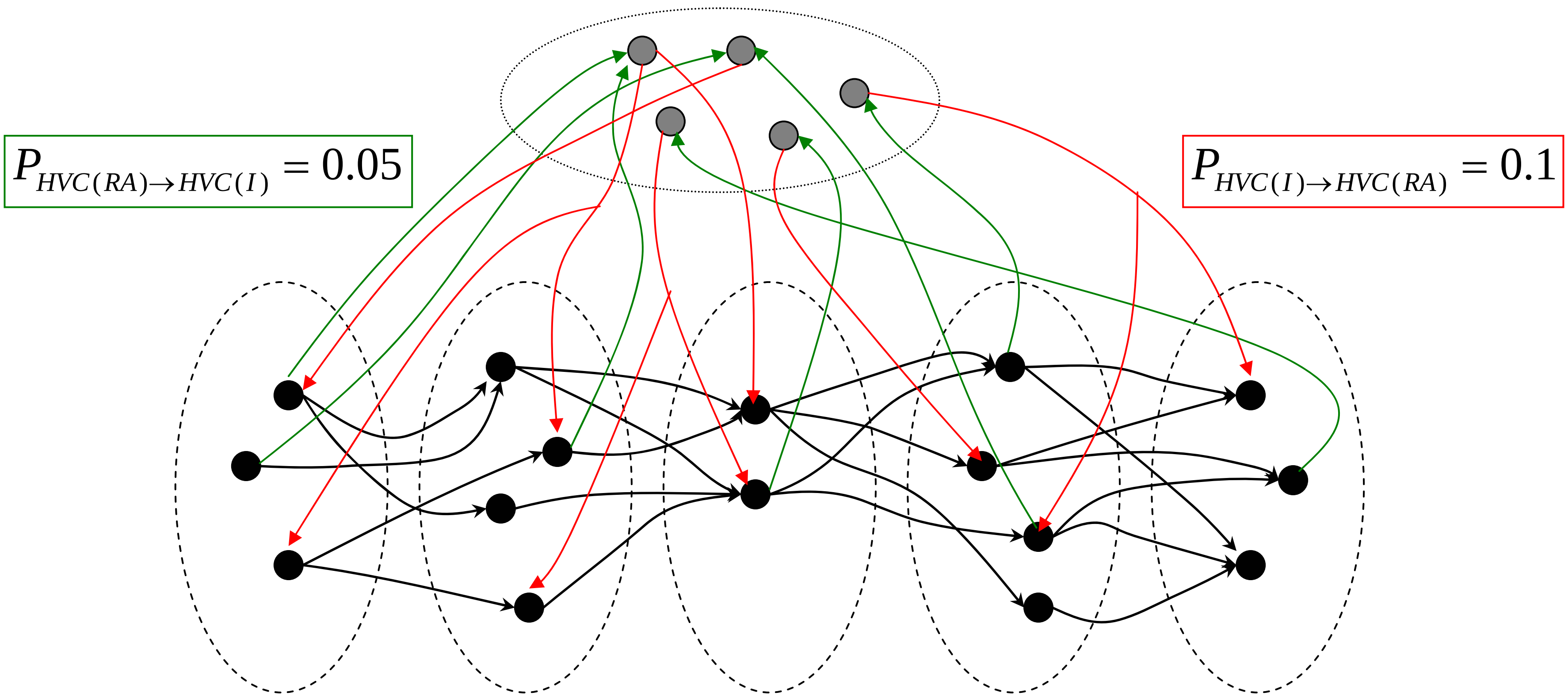
- Stimulus-response behaviors.
- Temporal sequence generation.

Excitation and inhibition

- Mooney and Prather (2005).

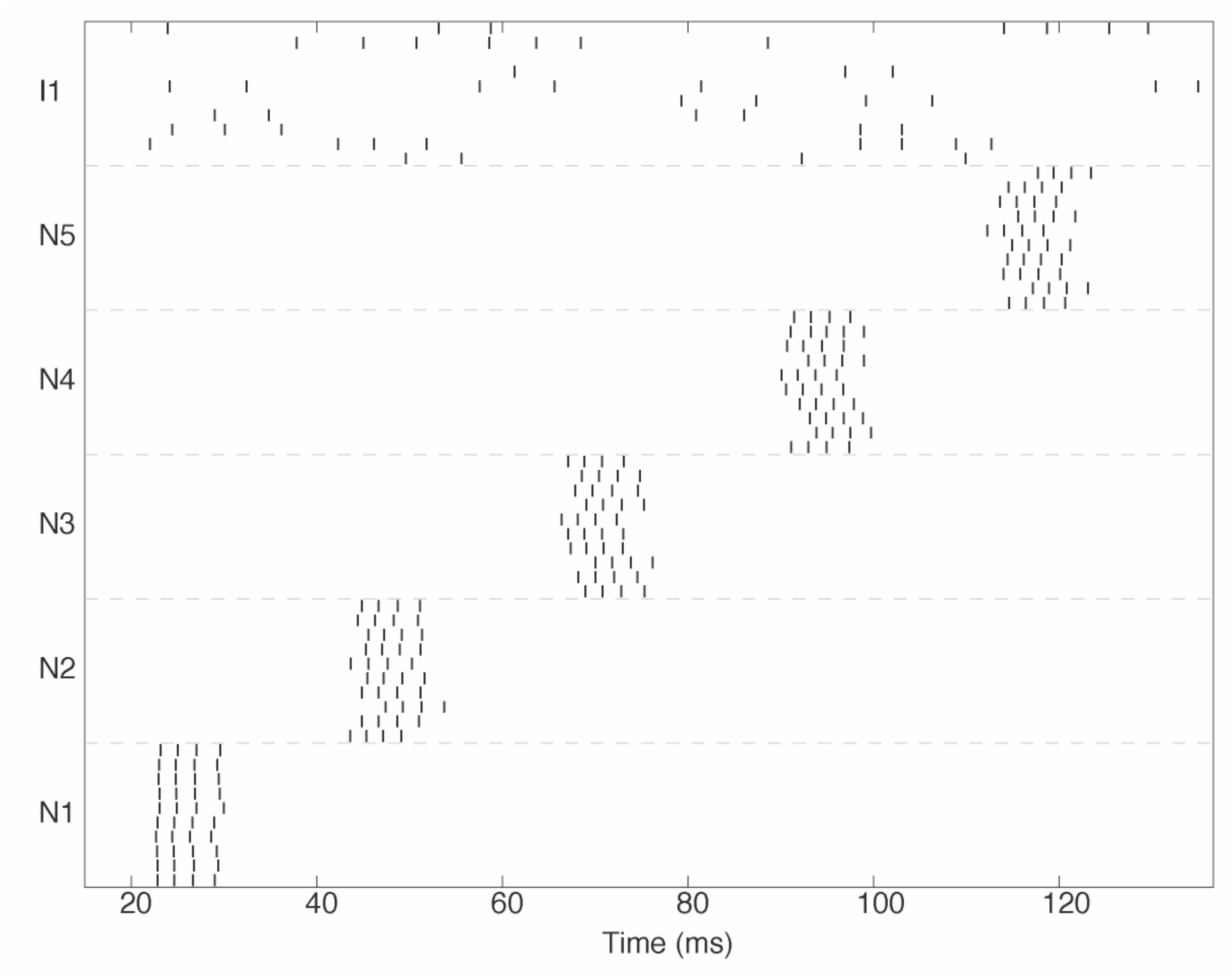


Chain with recurrent inhibition

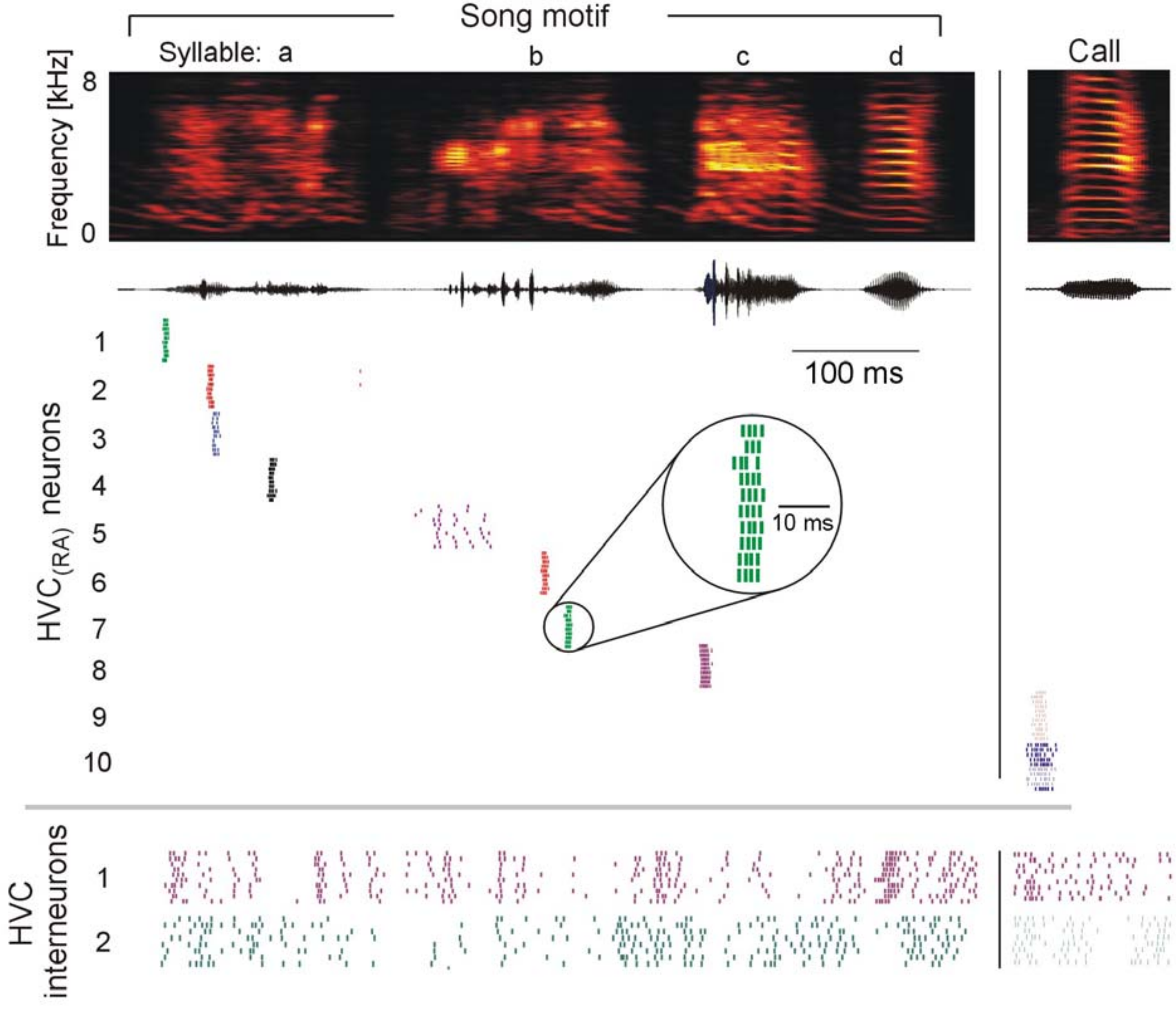


- 70 groups of 30 projection neurons
- 300 interneurons

Numerical simulation of spiking activity



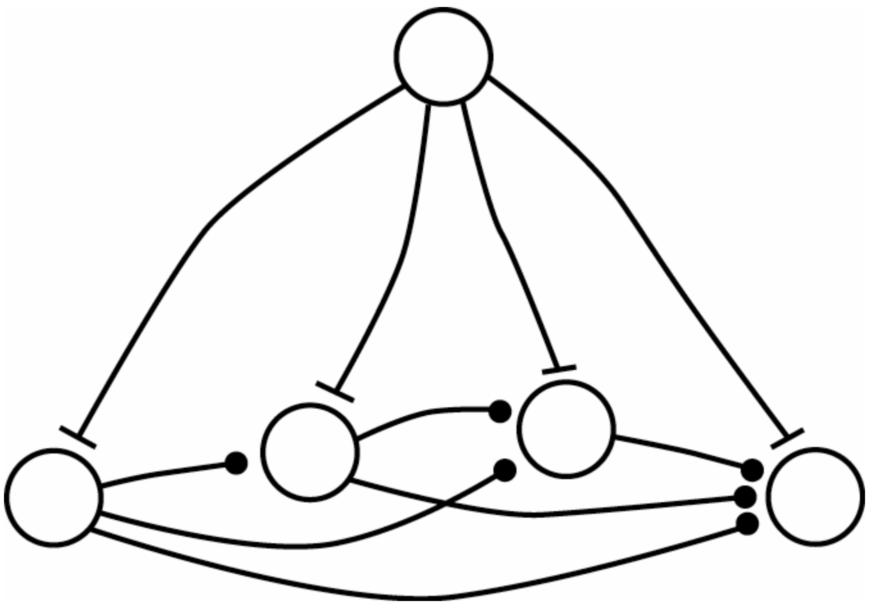
HVC spiking is temporally precise

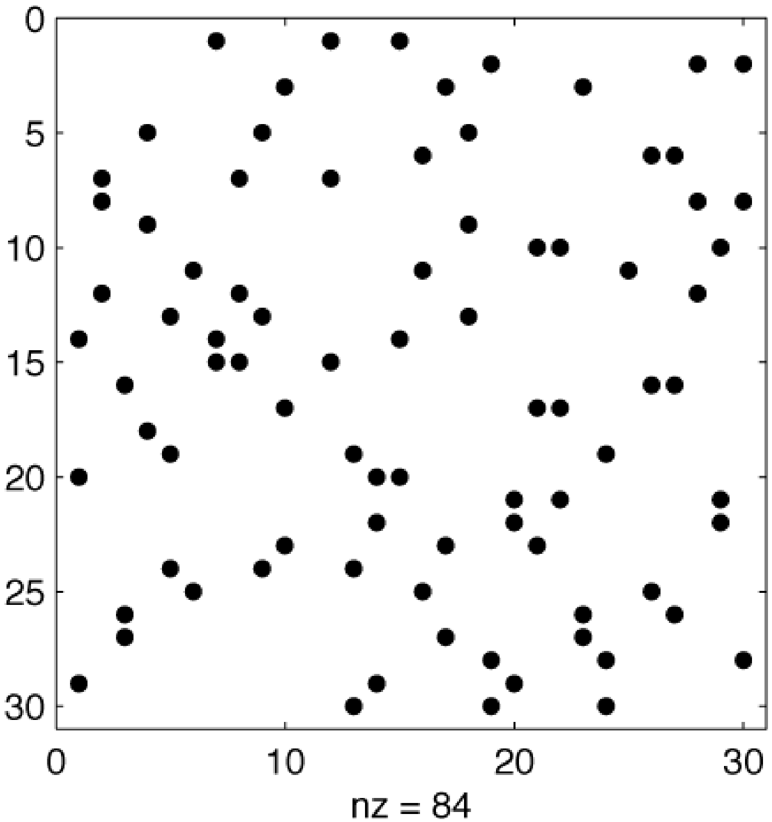


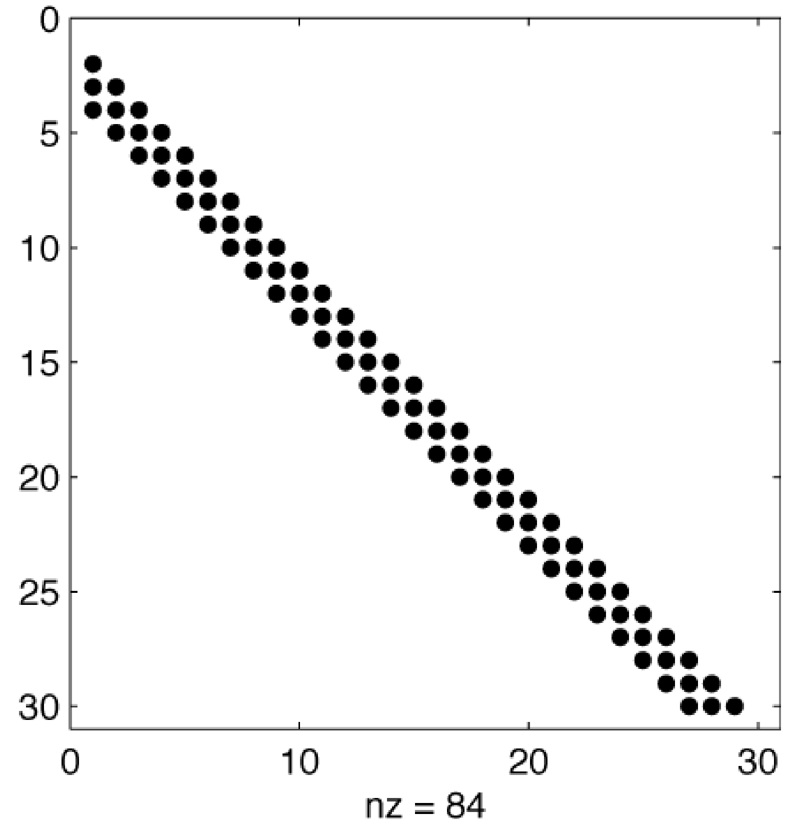
Intrinsic cellular properties

- Hypothesis: HVC_{RA} neurons are intrinsically bursting, so that burst *duration* is set by cellular properties.
- Eliminates runaway instability
- Less tuning is required to get multiple spikes per burst

Estes (1972)




0
5
10
15
20
25
30
0
10
20
30
nz = 84


0
5
10
15
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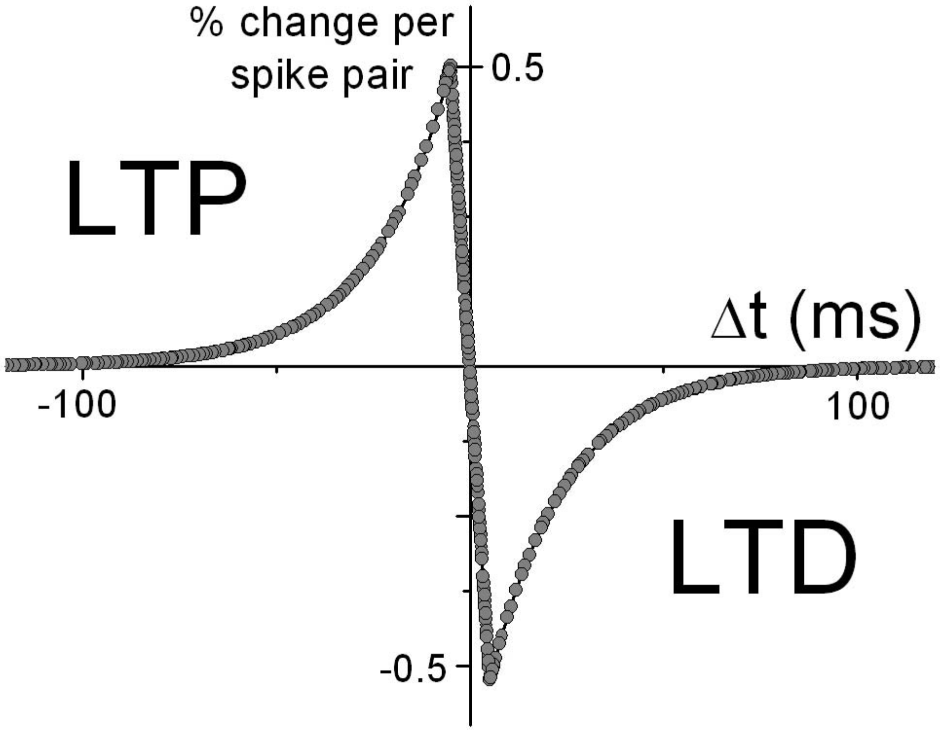
nz = 84

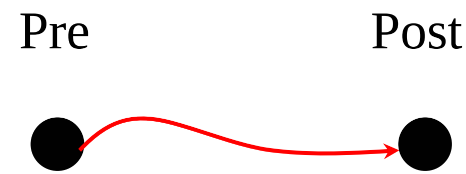
Self-organization of HVC sequences by Hebbian synaptic plasticity

Dezhe Jin and Joseph Jun

Spike-timing dependent plasticity



(Markram et al, 1997; Bi & Poo, 1998)

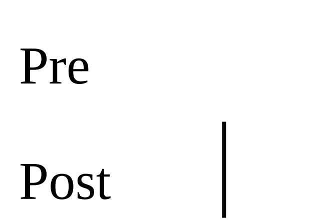


$$\Delta t = t_{spike,pre} - t_{spike,post}$$

Strengthen

$$\Delta t < 0$$

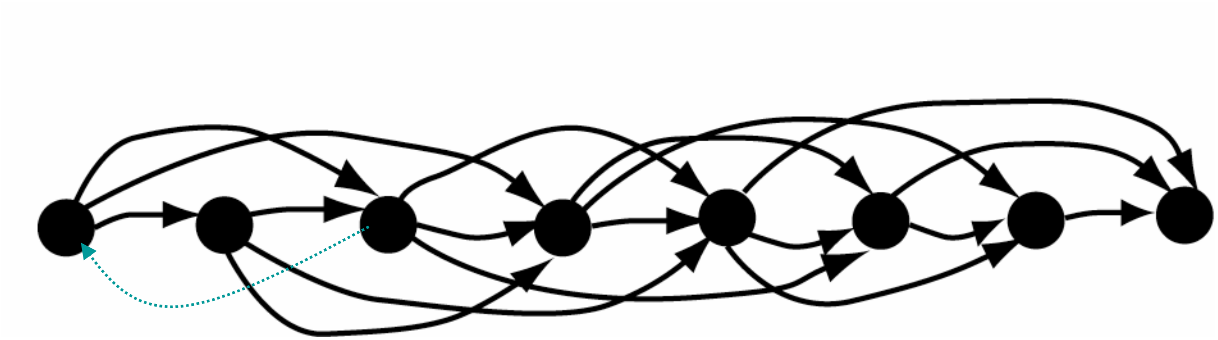
Weaken



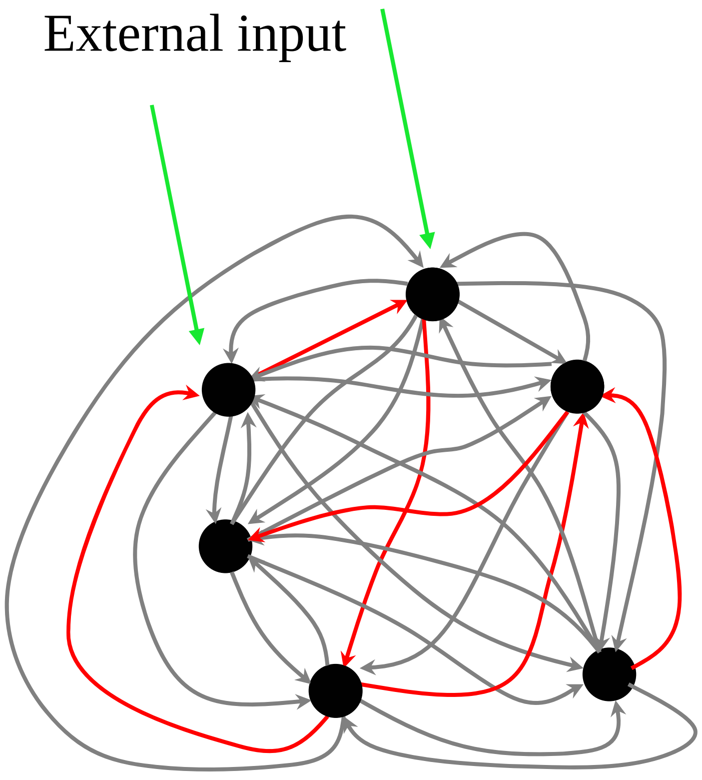
$$\Delta t > 0$$

STDP can reinforce chains

- forward connections strengthened
- backward connections weakened



Can STDP create chains?



- Low spontaneous activity
- Intermittent transient input activates a fixed set of neurons.
- A very short chain forms.

Problem: STDP fails to generate long chains.

Levy, Horn, Meilijson, Ruppin (2001)

Solution: limit the fan-out of neurons

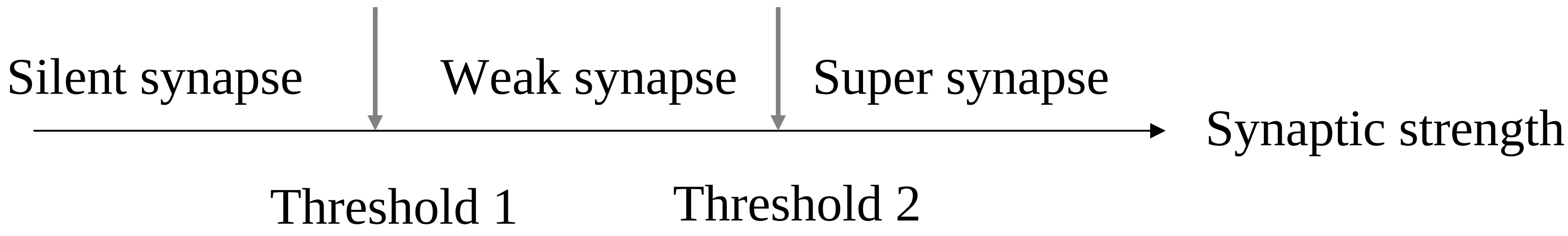
Structural vs. functional plasticity

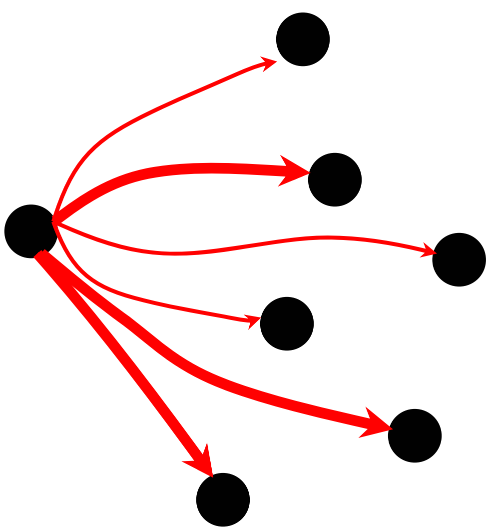
- Functional plasticity
  - Changes in the strength of existing synapses
- Structural plasticity
  - Creation and elimination of synapses.
  - Changes in dendritic and axonal arbors.

Structural and functional plasticity are intertwined

- Axonal branches with strong synapses are stabilized.
- Those with weak synapses retract.
- Meyer and Smith (2006)
- Ruthazer, Li and Cline (2006)

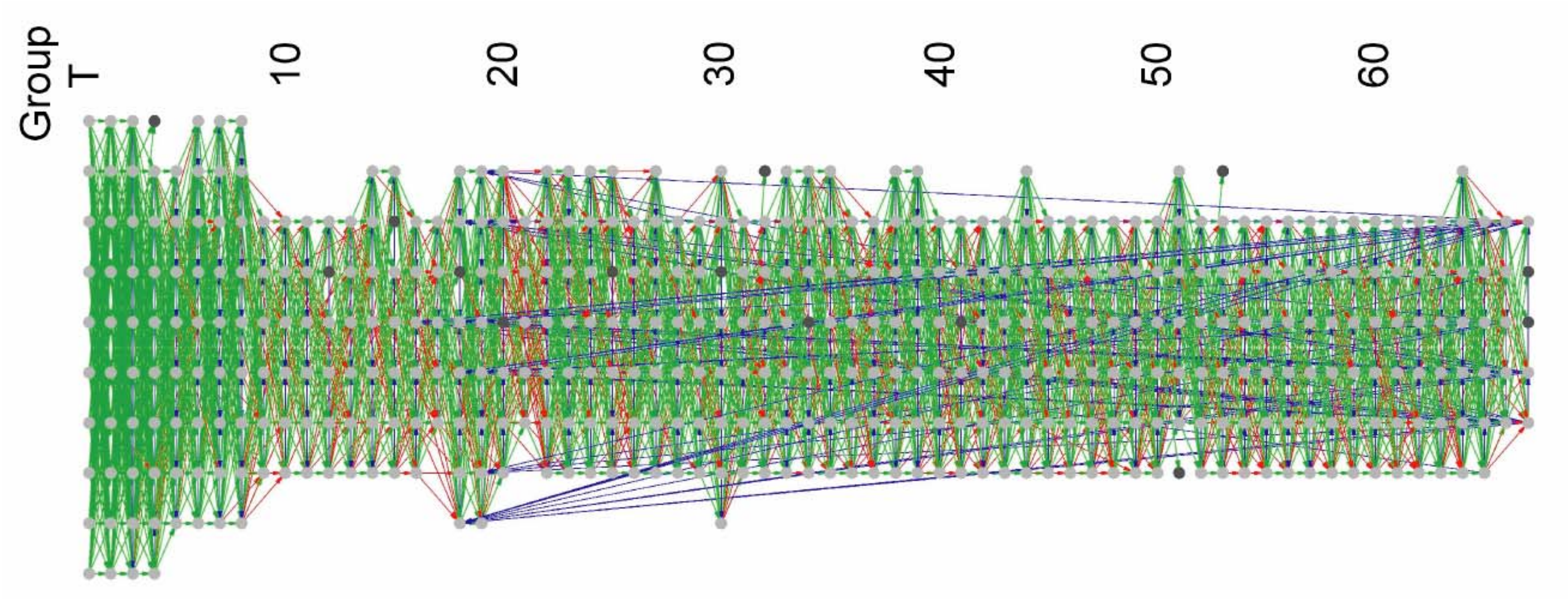
Model of axon remodeling





- If the number of supersynapses reaches N_s
- All other synapses are “withdrawn.”

Self-organized synaptic chain



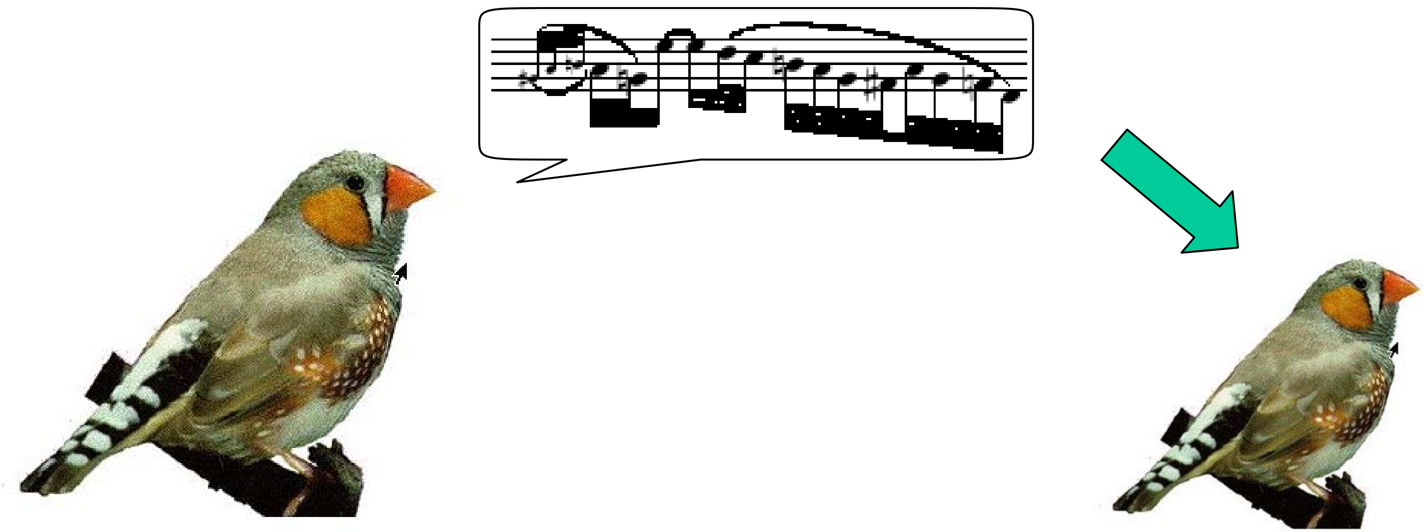
- Saturated neuron
- Unsaturated neuron
- Connection to next group
- Connection beyond next group
- Back connection

- 200000 trials (2s each)
- 443 neuron (out of 1000) organized into 67 groups

Learning motor commands

with Ila Fiete and Michale Fee

Learning phase I: sensory

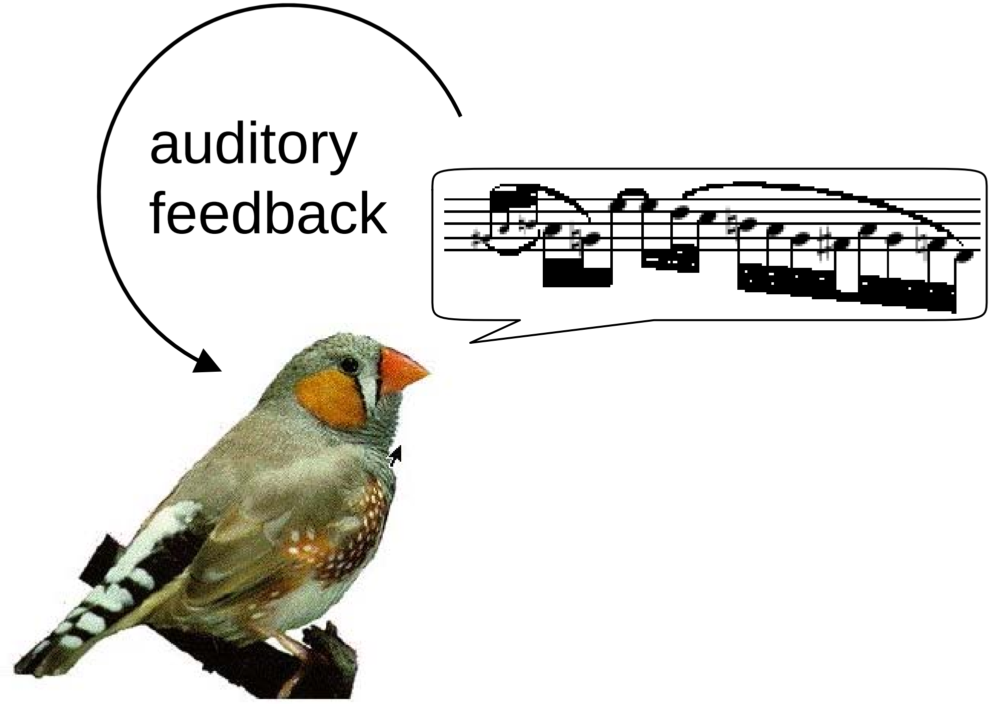


father

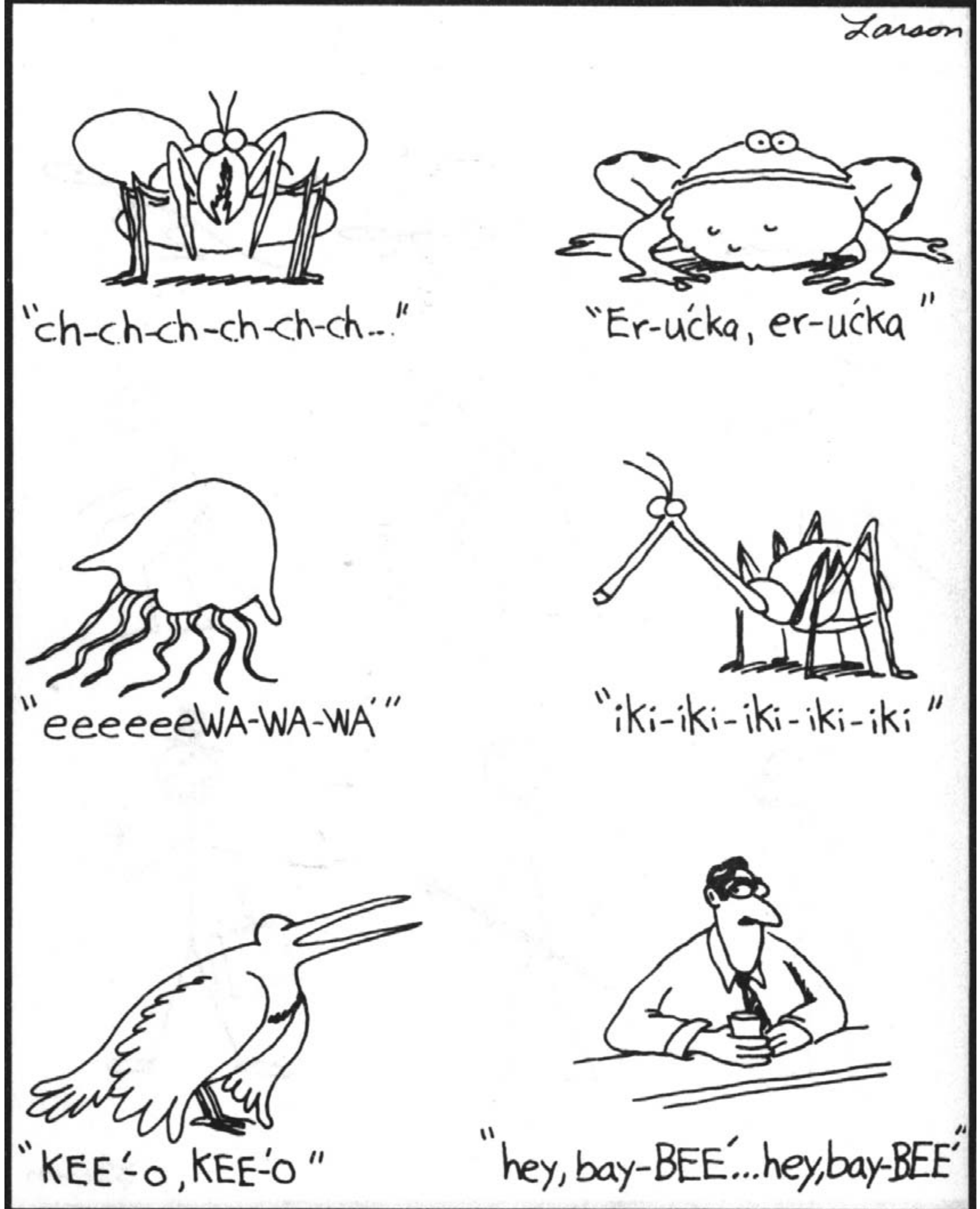
son

Template acquisition
(days 20-45)

Learning phase II: sensorimotor

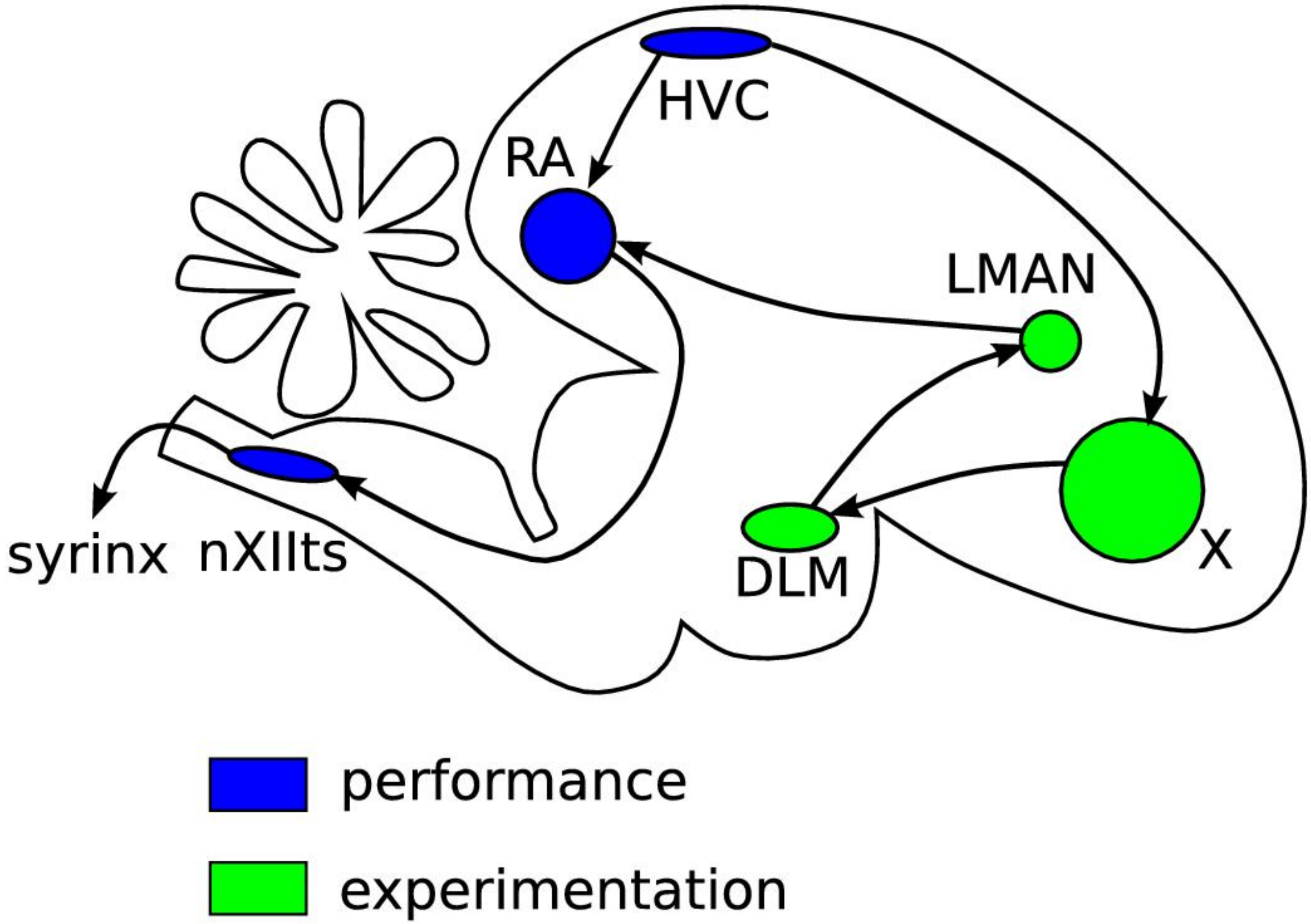


learning to reproduce the stored template (days 40-100)

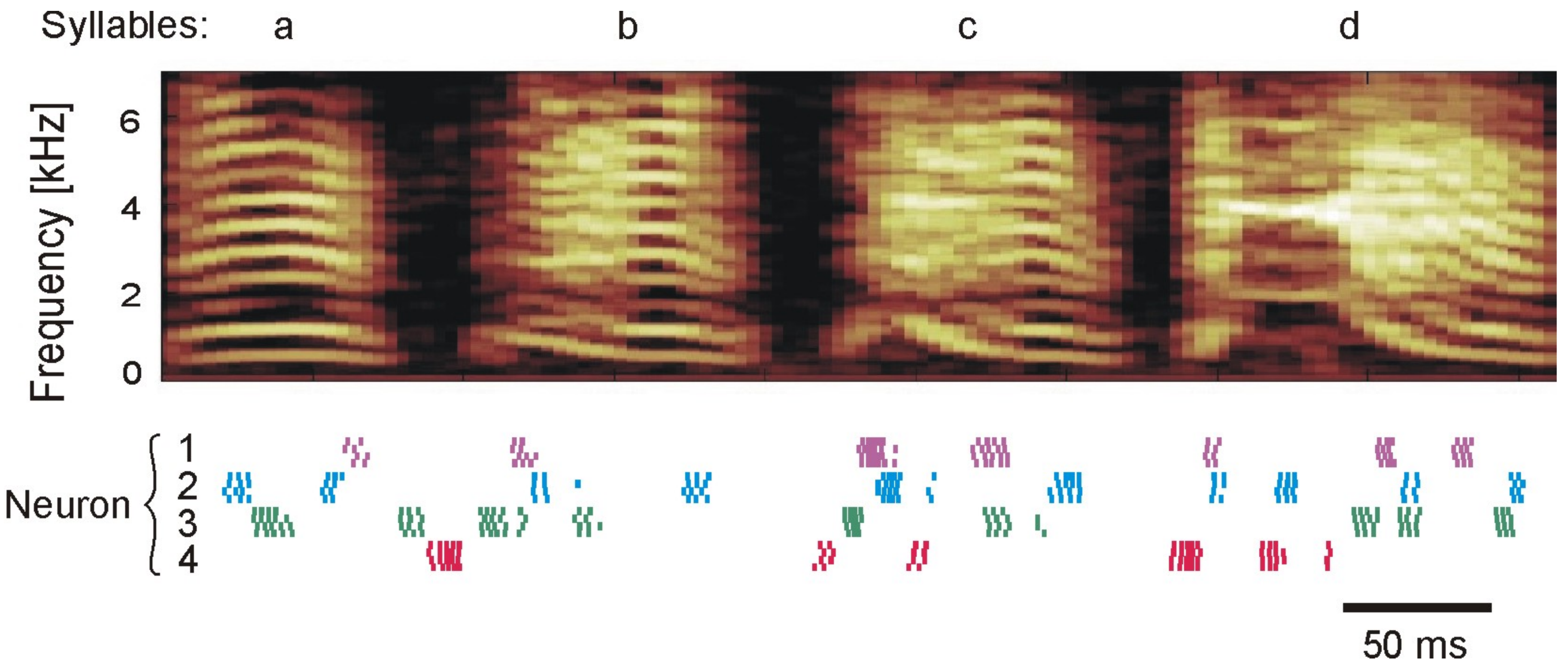


Animals and their mating songs

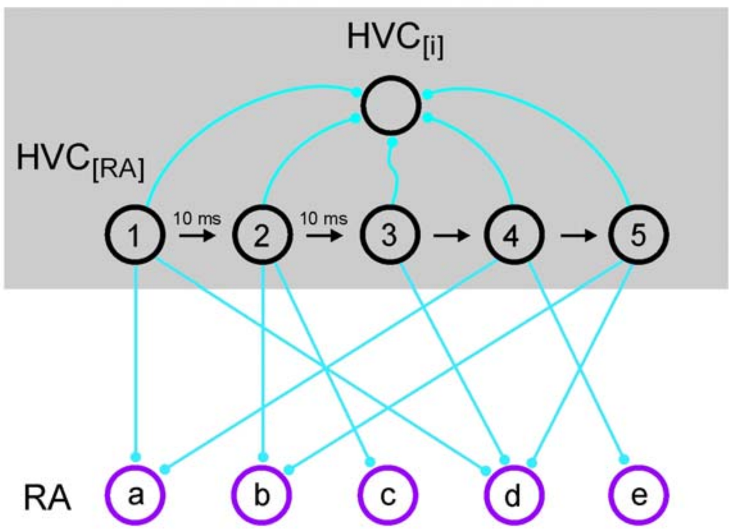
Song areas in the avian brain

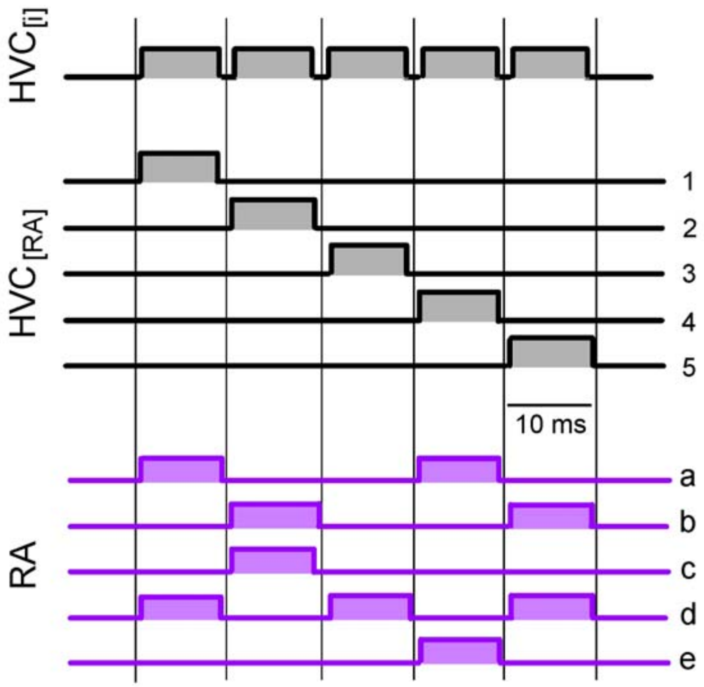


RA activity



Sparse representation

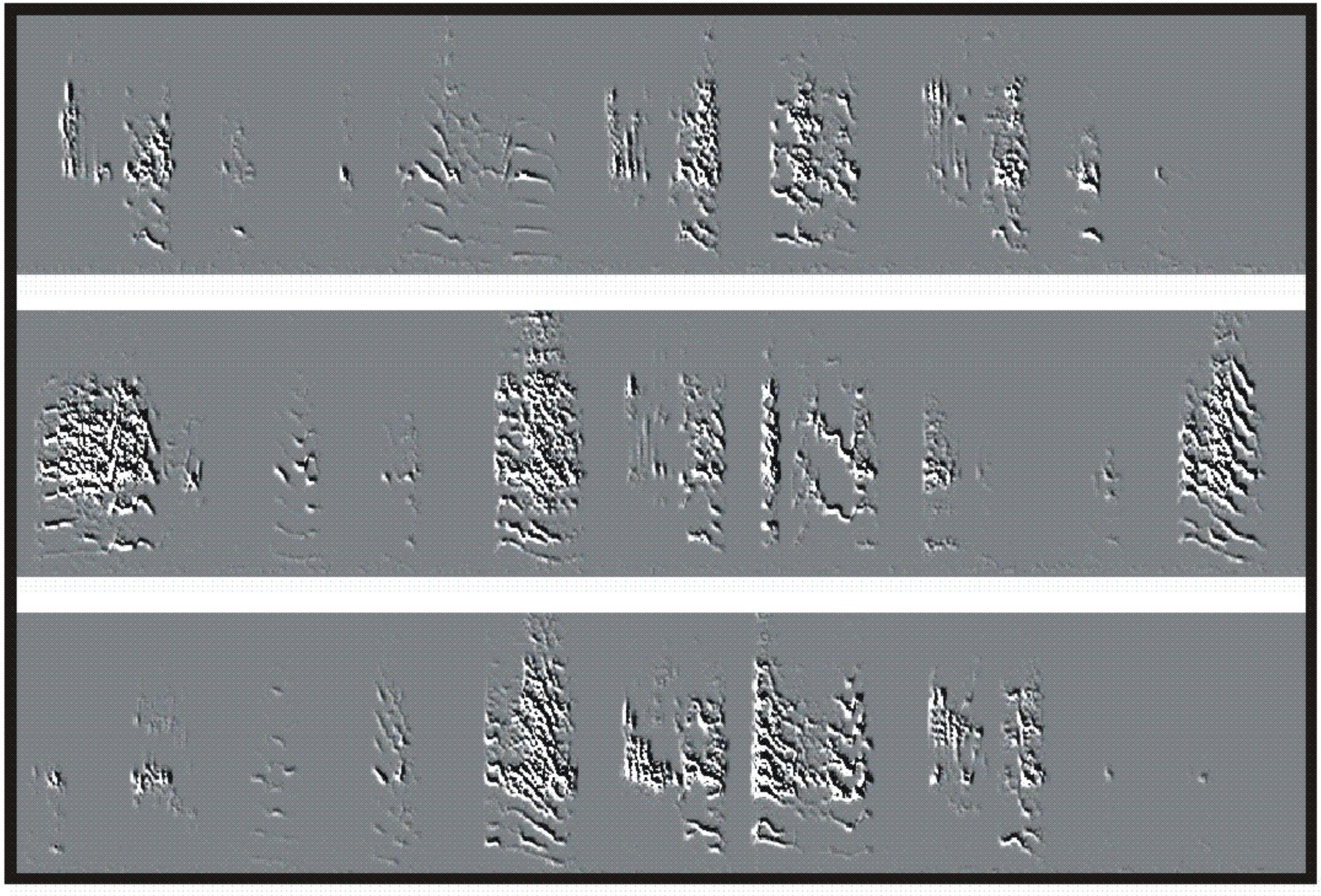




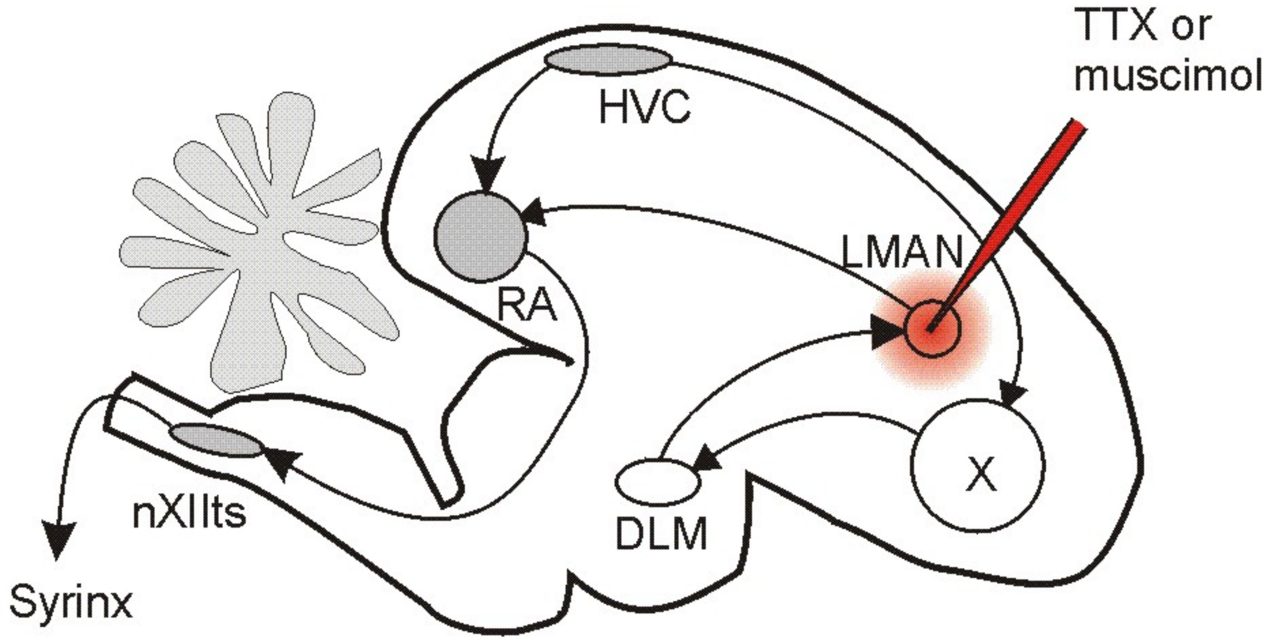
HVC generates the sequence
later stages perform the motor map
similarity to hidden Markov model

Juvenile song is variable

Before LMAN inactivation

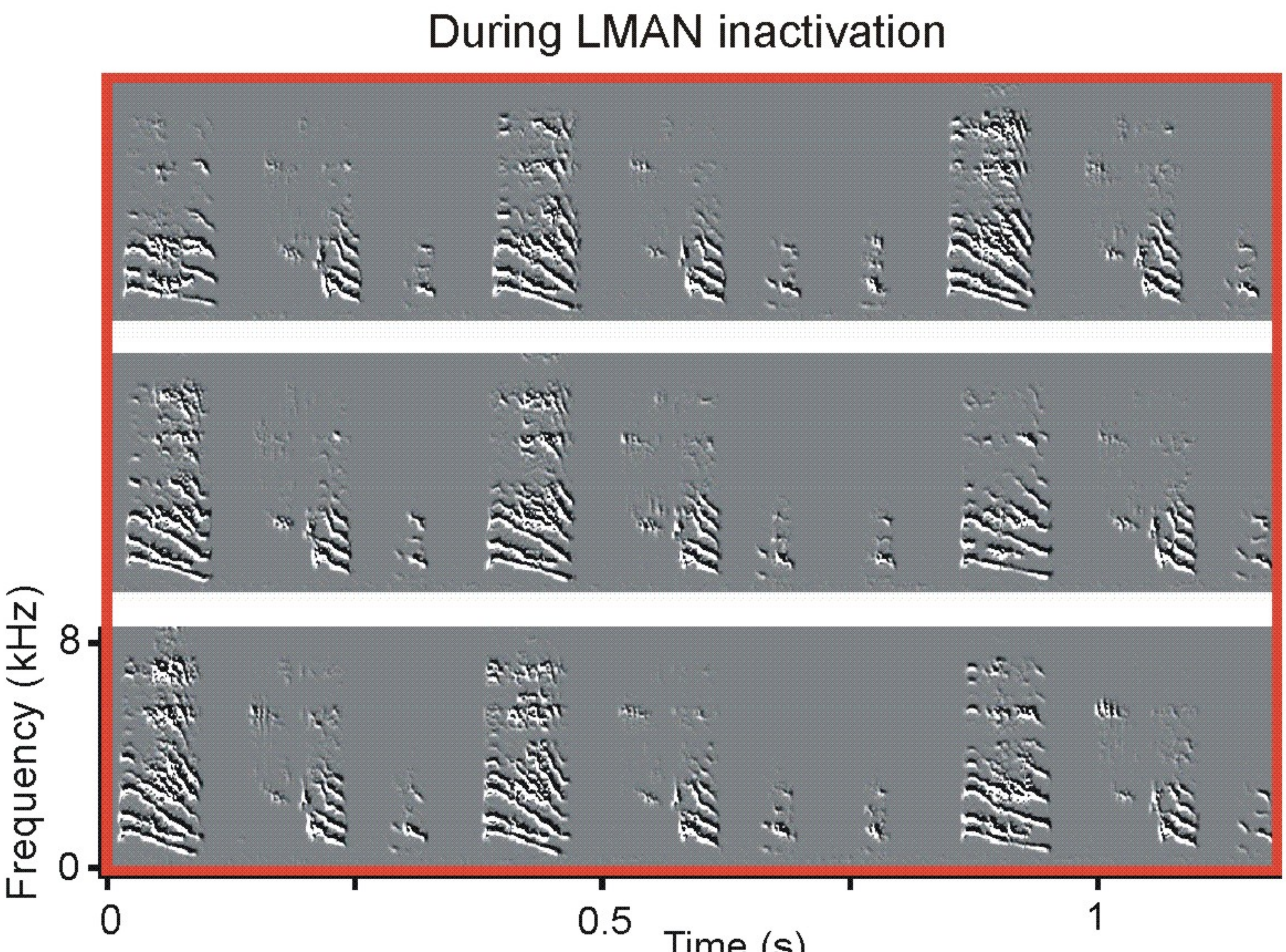


LMAN inactivation



Olveczky, Andalman, Fee (in review)

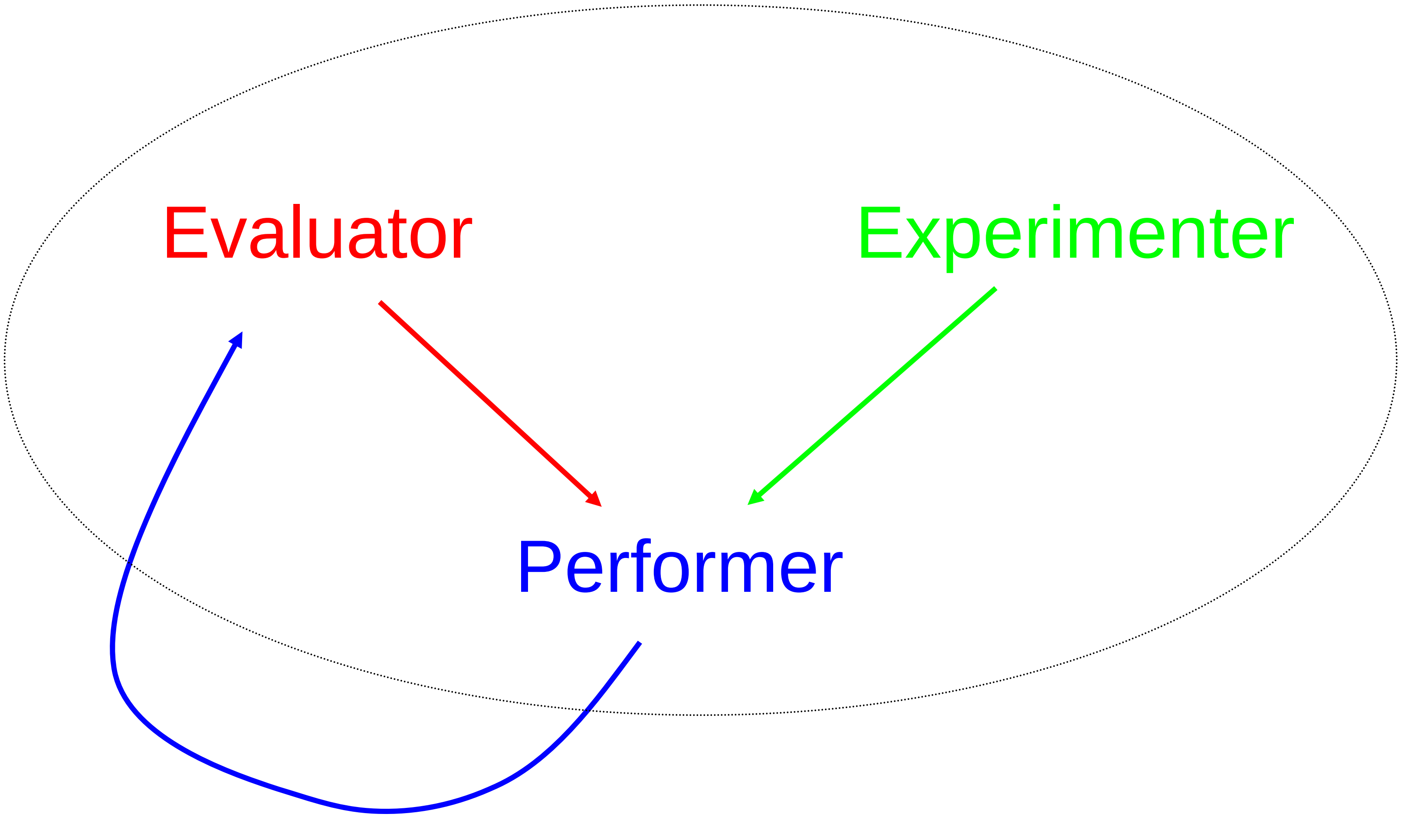
Stereotyped song



Hypothesis: LMAN is an experimenter

Doya and Sejnowski (2000)

A triune brain?



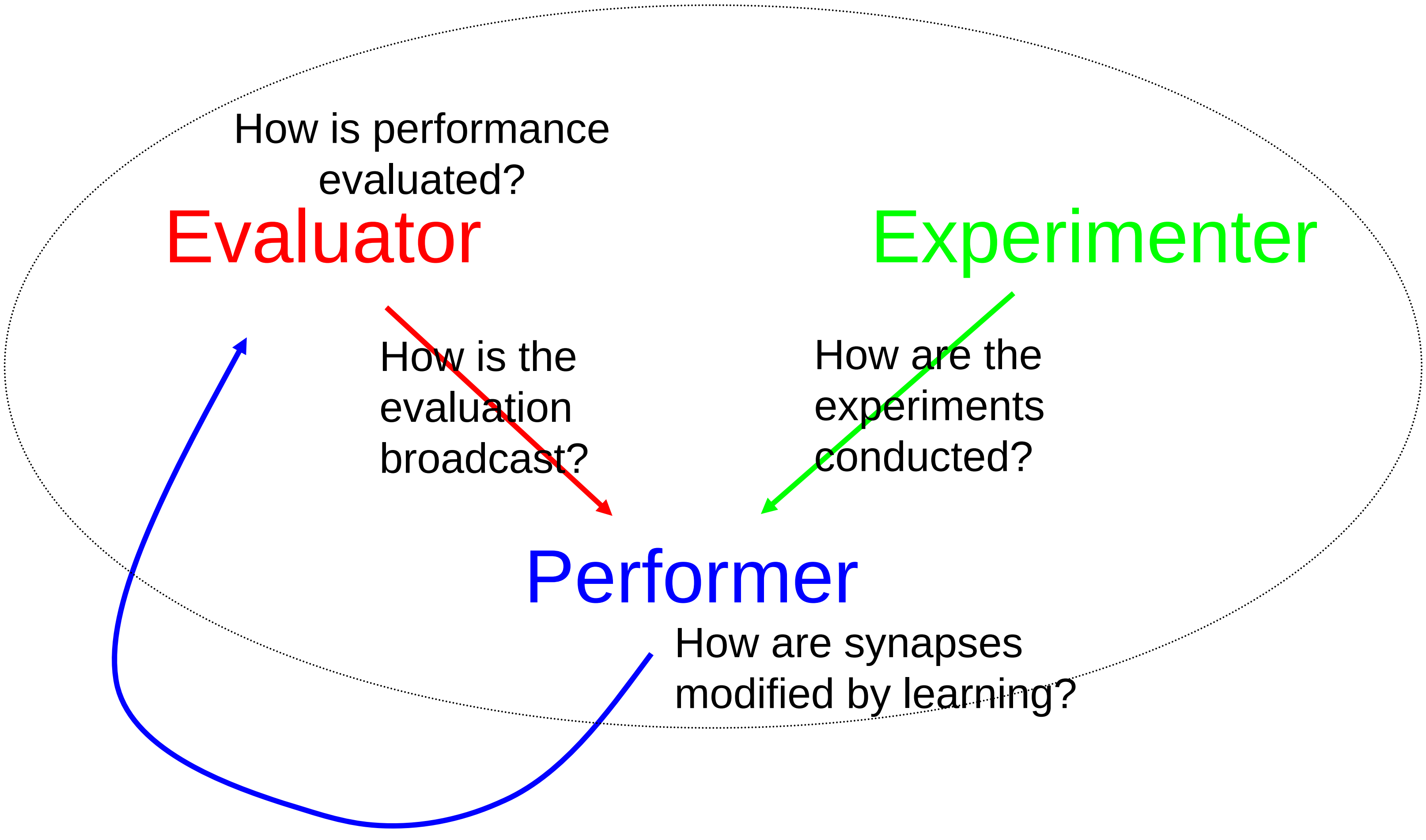
Evaluator?

- A juvenile bird learns by comparing its own song to its memory of tutor song.
- The brain area that performs this comparison is unknown.
- The output of the comparison might be a scalar evaluation signal.

Trial and error learning

- Success and failure can be evaluated.
- Little insight into how to improve.
- Slow climb up a gradient

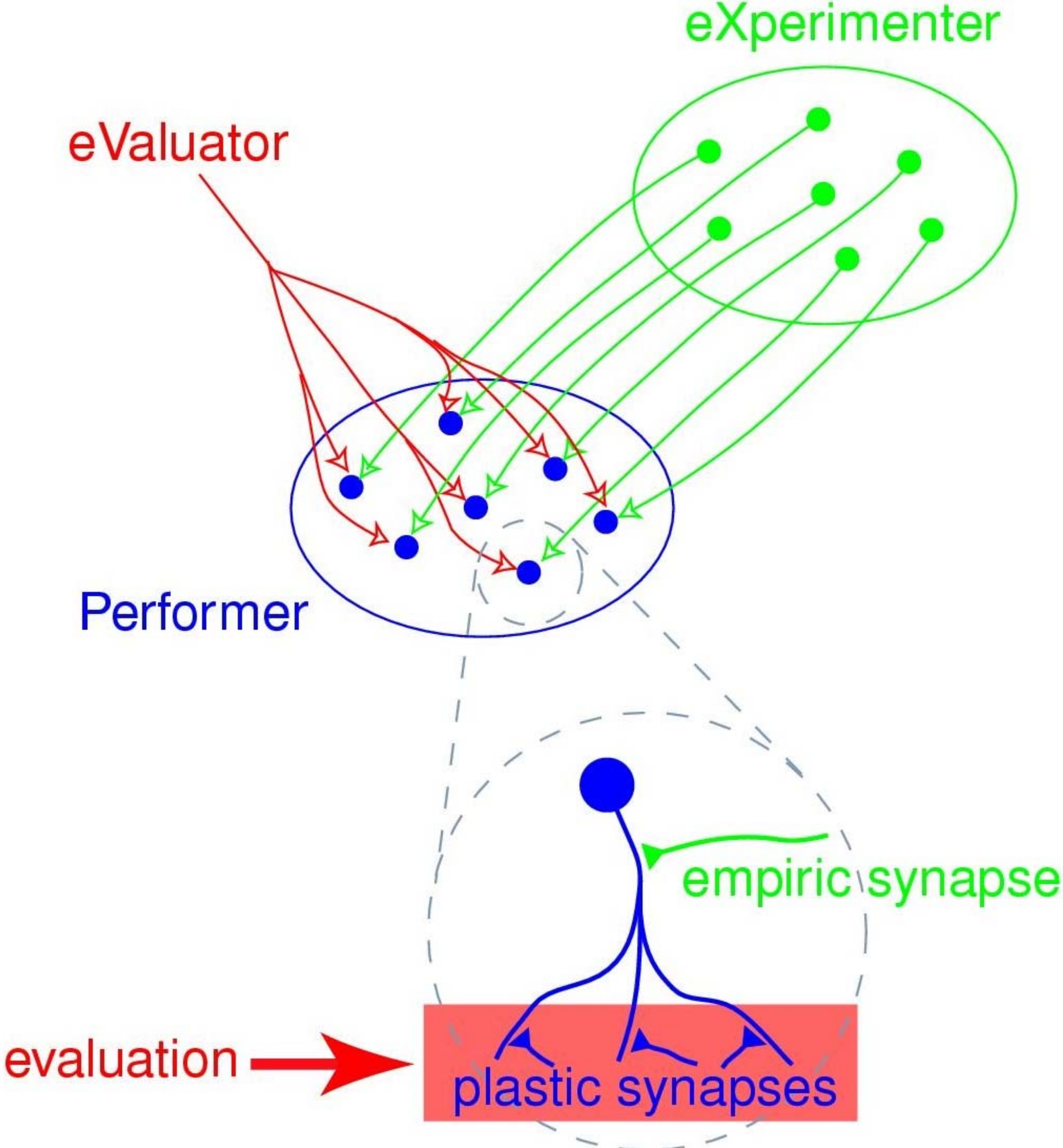
Questions


How is performance evaluated?
Evaluator
Experimenter
How is the evaluation broadcast?
How are the experiments conducted?
Performer
How are synapses modified by learning?

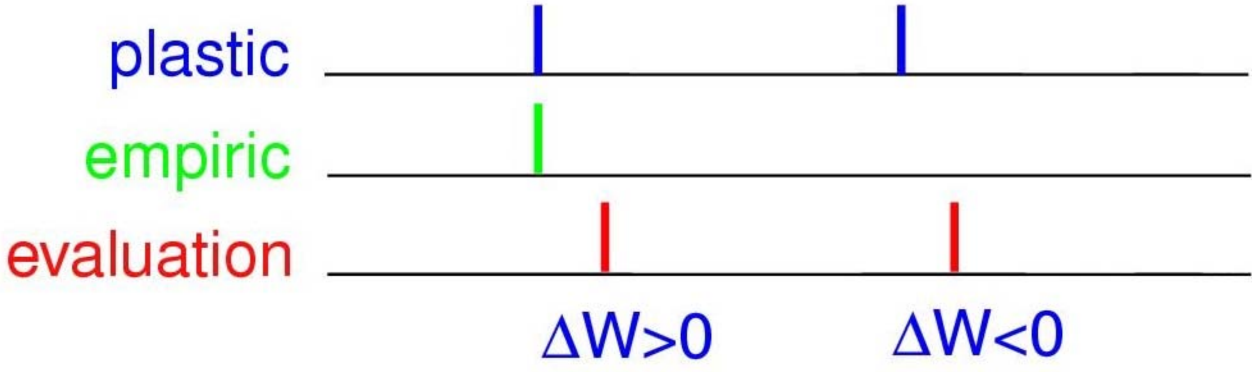
Theory of empiric synapses

- Synapses specialized for experimentation
  - Dynamic perturbation of conductances
- Results of experiments are used to modify plastic synapses.

Practice makes perfect

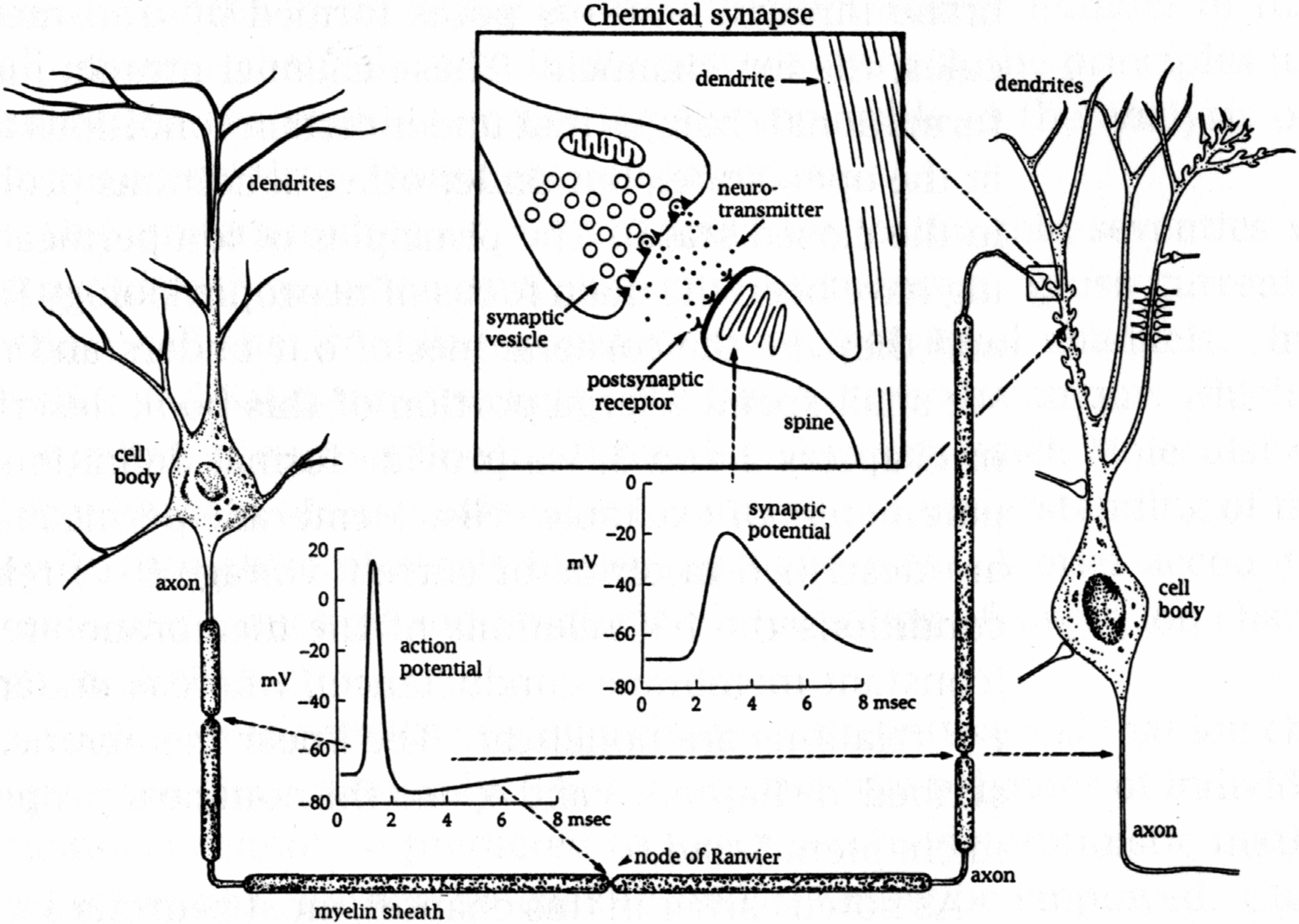

eXperimenter
eValuator
Performer
empiric synapse
evaluation
plastic synapses

Rules for synaptic modification



Stochastic gradient ascent

Fiete and Seung



Chemical synapse
dendrite
neuro-
transmitter
synaptic
vesicle
postsynaptic
receptor
spine
dendrites
dendrites
cell
body
axon
cell
body
axon
axon
synaptic
potential
mV
0
-20
-40
-60
-80
0
2
4
6
8 msec
action
potential
mV
20
0
-20
-40
-60
-80
0
2
4
6
8 msec
node of Ranvier
myelin sheath

Perturbative gradient estimation

eligibility $$e(t) = \left(\xi(t) - \langle \xi \rangle \right) s(t)$$

eligibility trace $$\bar{e}(t) = \int_0^\infty dt' K(t') e(t - t')$$

$$\frac{dW}{dt} = \eta h(t) \bar{e}(t)$$

$$K(t) \sim t^n e^{-t/\tau_e}$$

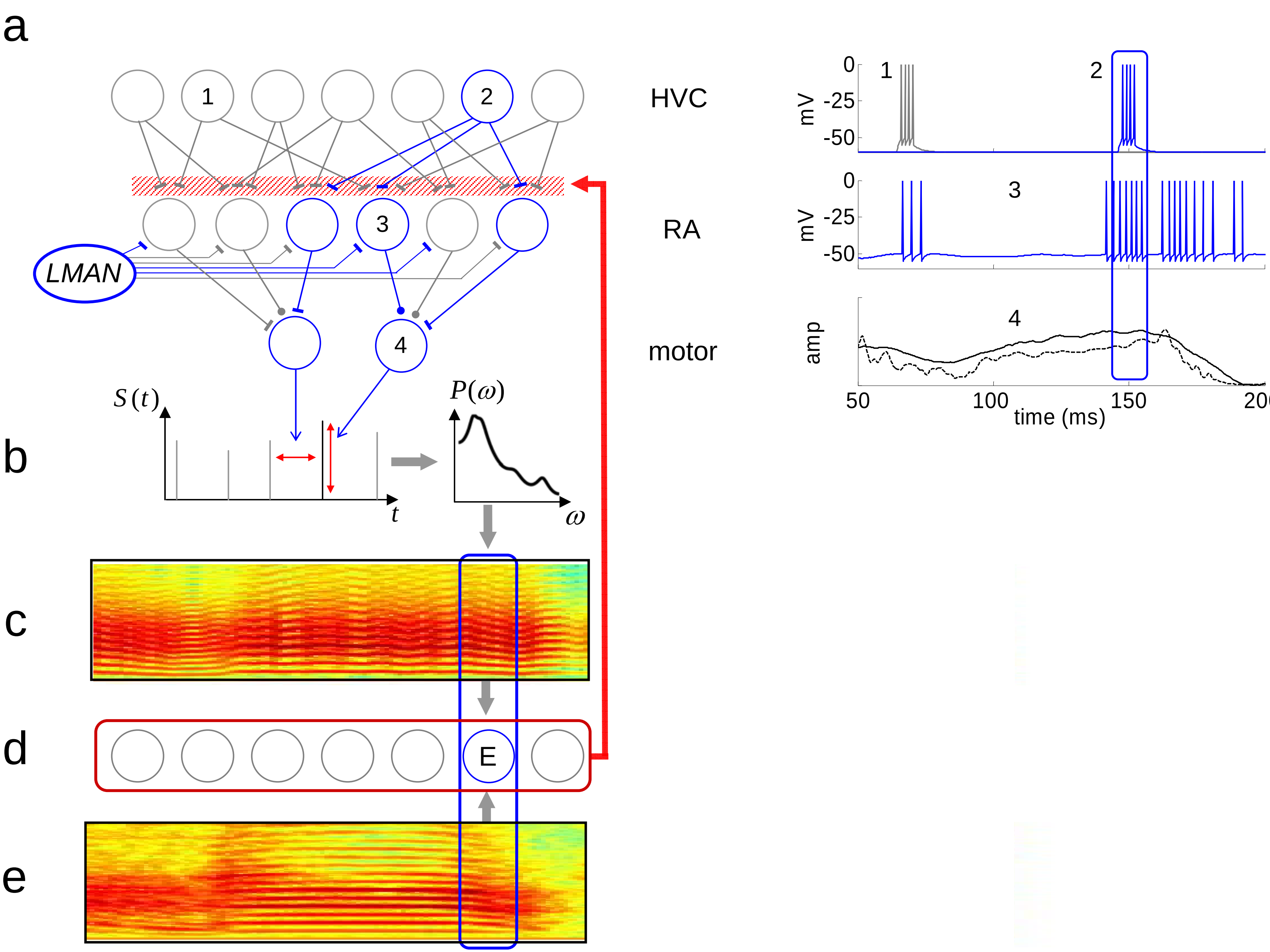
Stochastic gradient learning

$$\Delta W_{ij} = \eta \frac{\partial R}{\partial W_{ij}}$$

- In the direction of the gradient, on average.

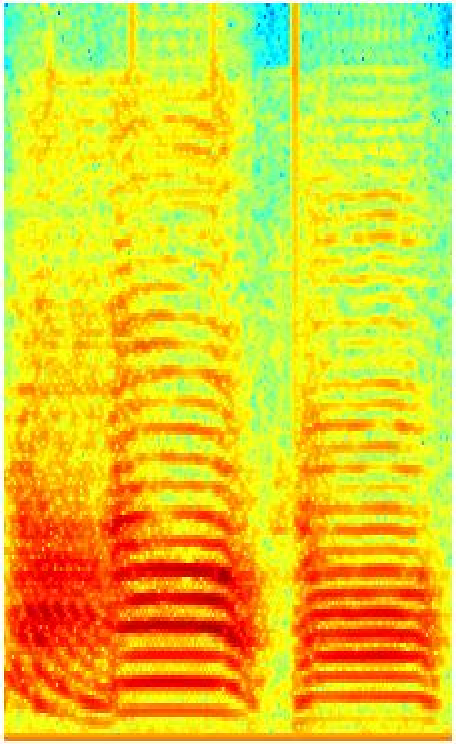
Stochastic gradient ascent

- Instructions are in the correct direction only on average
- Weak correlations require long times to detect
- Learning in large networks is potentially slow.

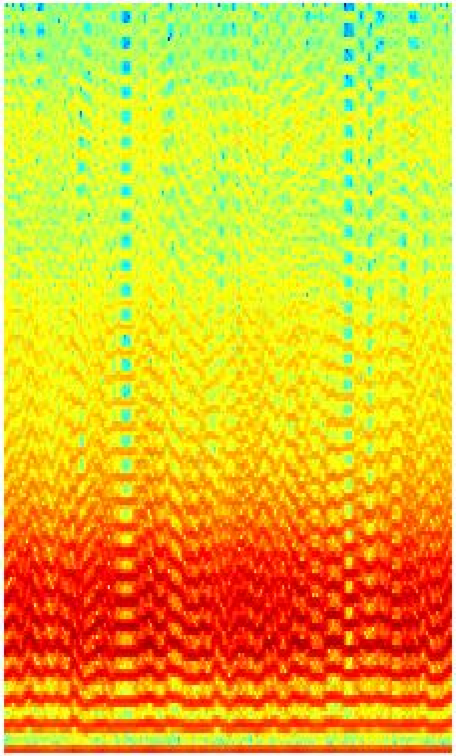

a
b
c
d
e
HVC
RA
motor
LMAN
1
2
3
4
E
S(t)
t
P(ω)
ω
mV
0
-25
-50
amp
50
100
150
200
time (ms)

Simulated song learning

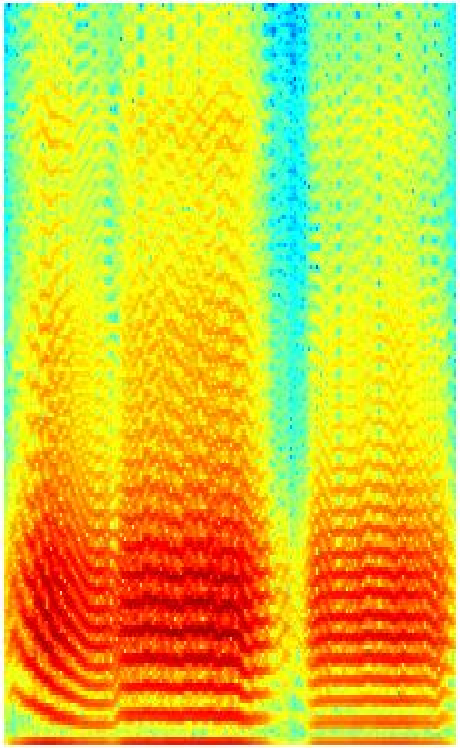
tutor

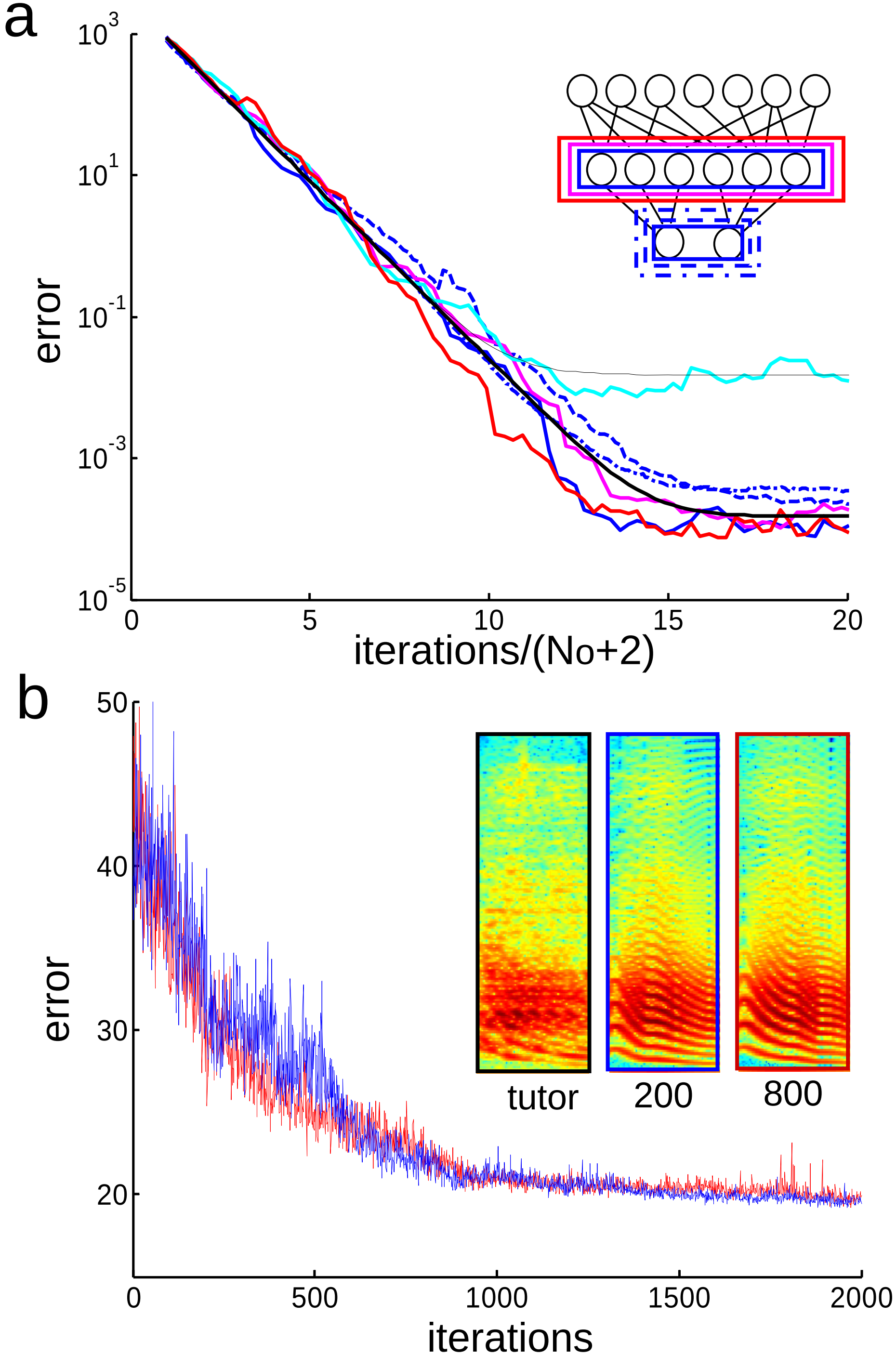


before learning



after learning

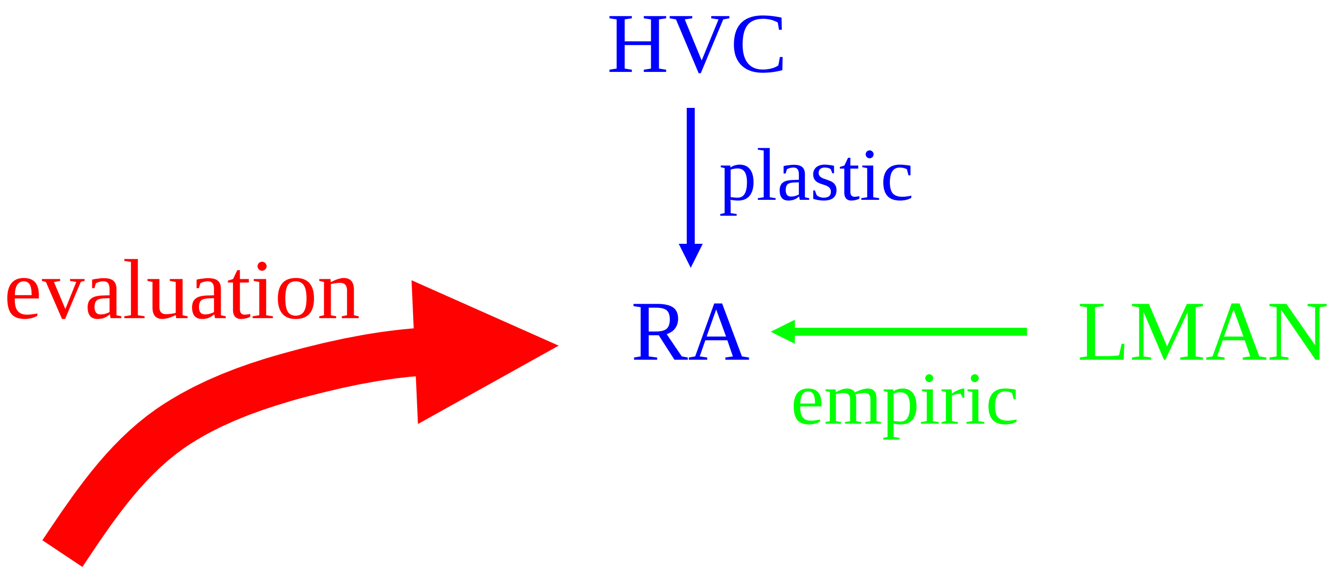




Learning time

- independent of hidden layer size
- linear in number of outputs

A proposed experiment



Theories of gradient learning

- Extrinsic experimentation
  - Empiric synapses
- Intrinsic experimentation
  - Hedonistic synapses
    - Unreliable synaptic transmission
  - Hedonistic neurons (A_{R-I})
    - Irregular spiking