Three Theoretical Problems Suggested by Recent Bird Song Experiments

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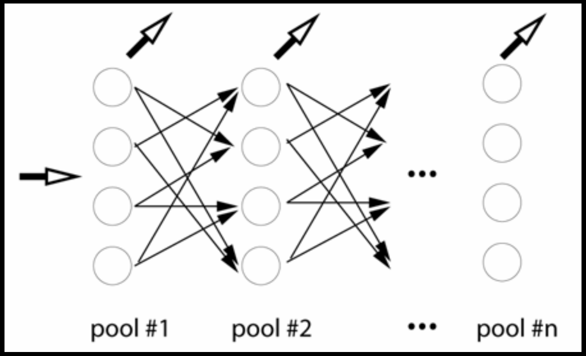
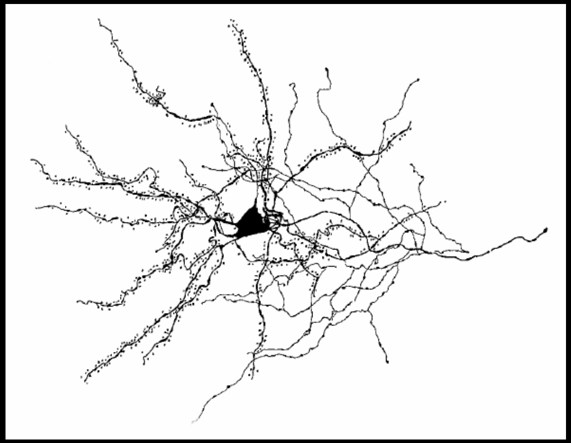
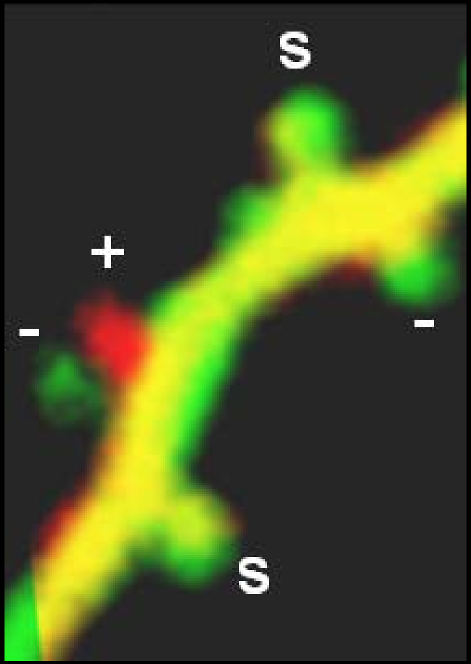






March 21, 2008

Outline

1. Mechanism of sequence generation: synfire chains?

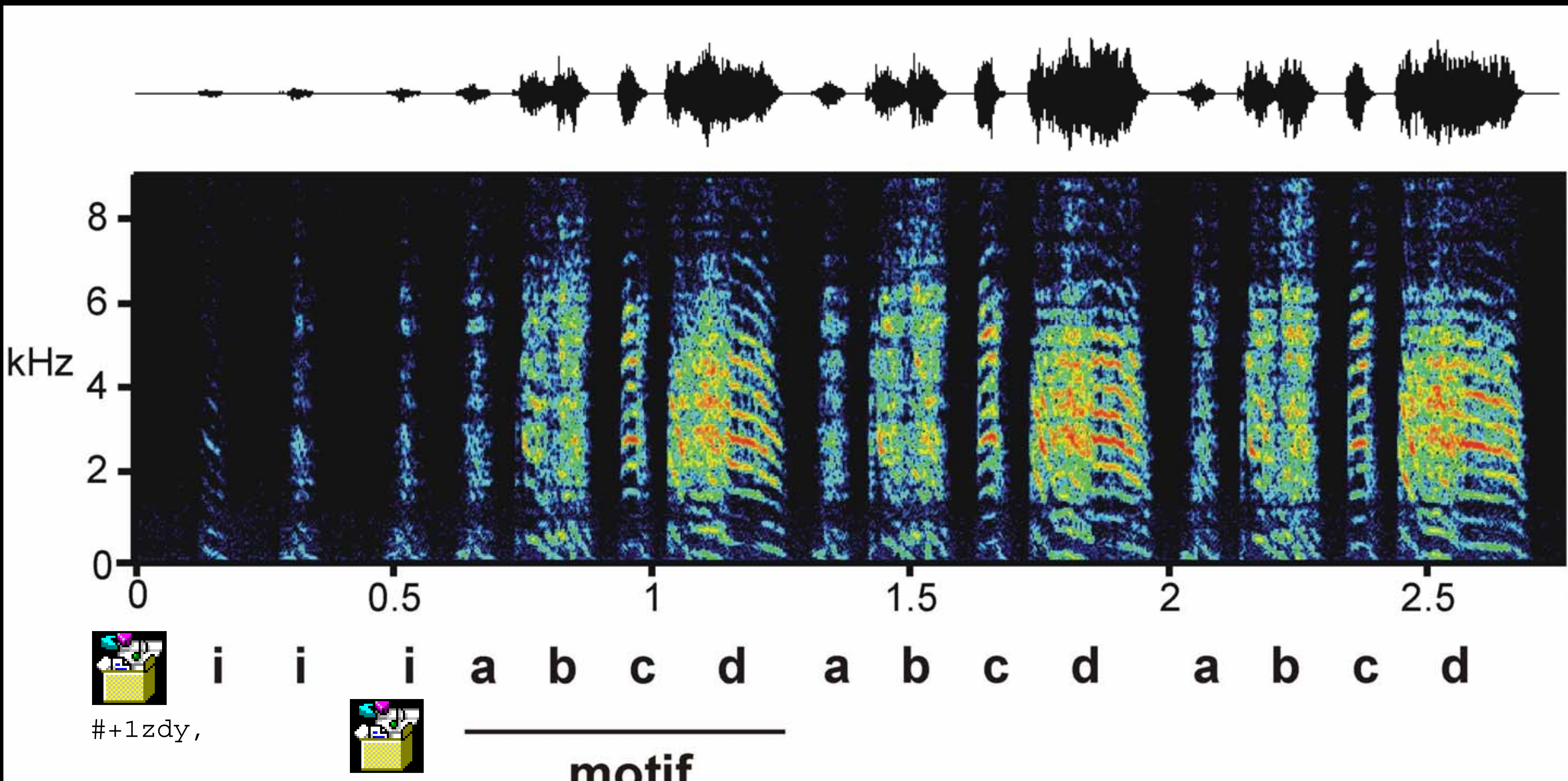
2. Quantitative connection between song learning and spine growth and decay in HVC?

3. Mechanism of LMAN variability engine?

Songbirds: Auditory-Guided Vocal Learning

1. Sequence memorization, production, motor learning.
2. Songbirds inherently motivated to learn conspecific highly stereotyped songs.
3. NIH interest: language deficits (stuttering).

Zebra Finch Temporal Structure: Notes, Syllables, and Motifs

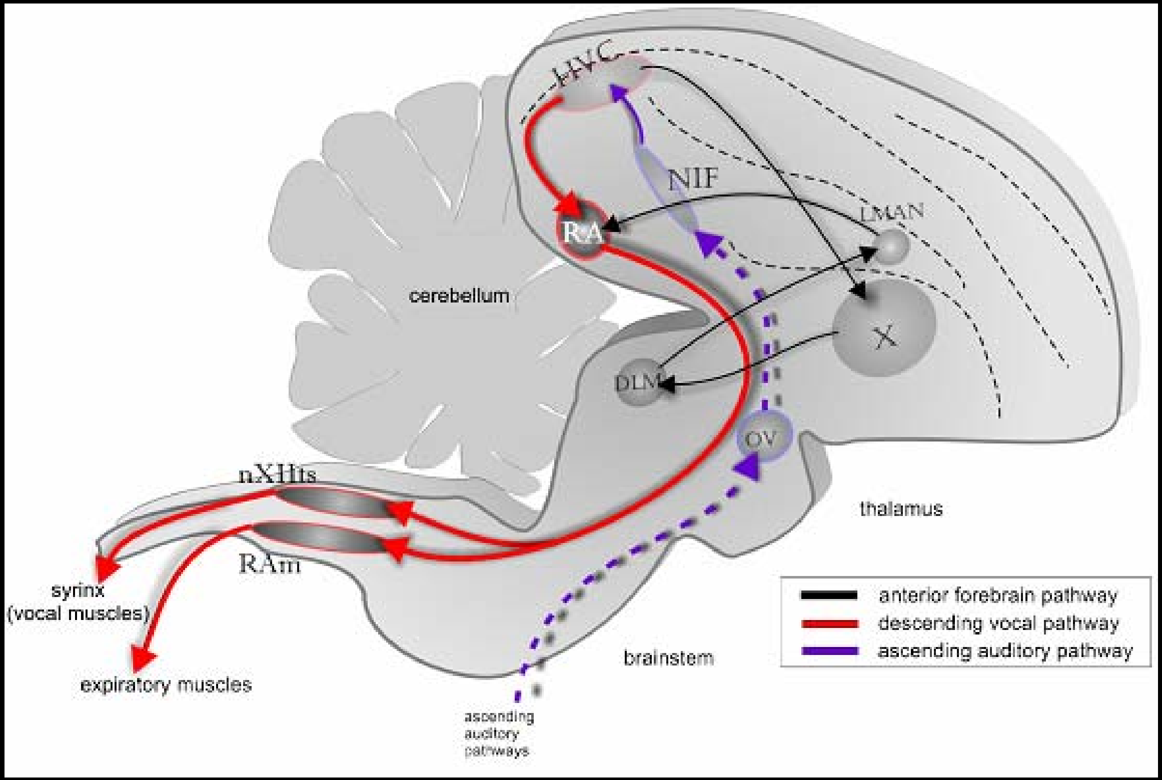


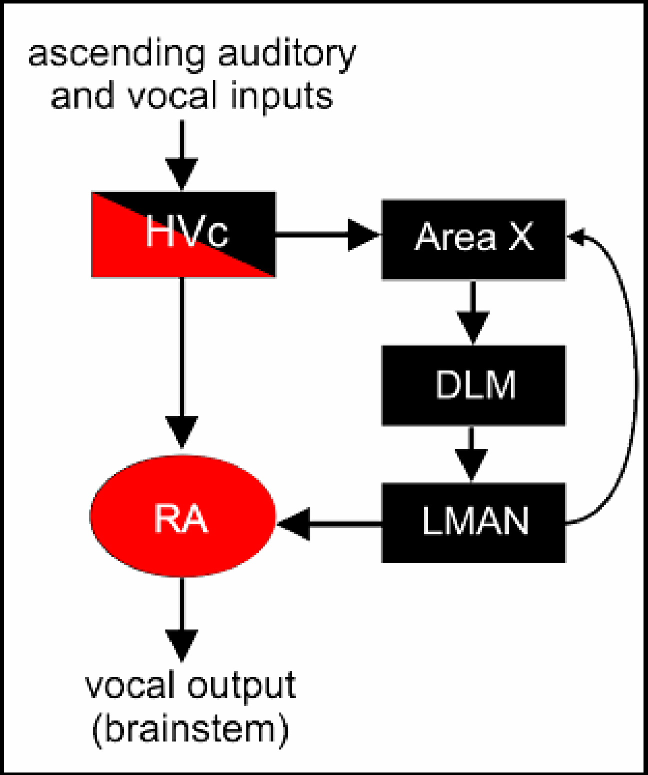
Sequence Generation Mechanisms

- Asymmetric recursive Hopfield networks (Sompolinsky, Kleinfeld, others).
- Central pattern generator plus delay lines.
- Circular feedforward chains.
- Hierarchical (inter-nuclear) dynamics.

Experimental constraints: Hopfield net not easily consistent with sparse excitatory firing, tonic inhibitory firing. Anatomy?

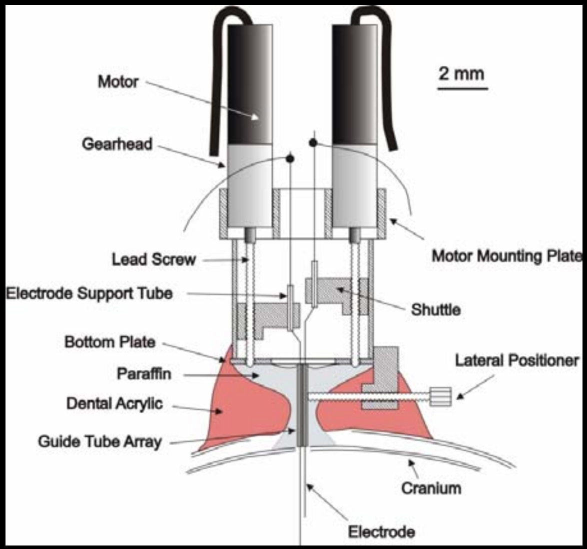
Nucleus HVc Necessary For Song Production and Learning





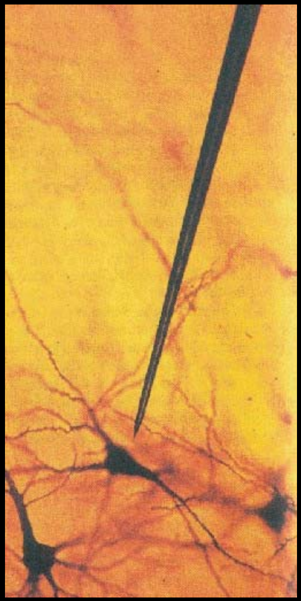
Anatomical connections are function of time…

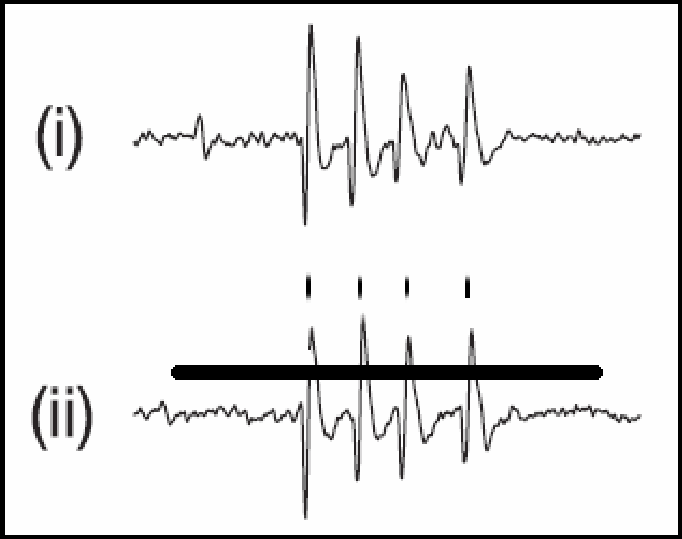
Activity of Neurons During Singing



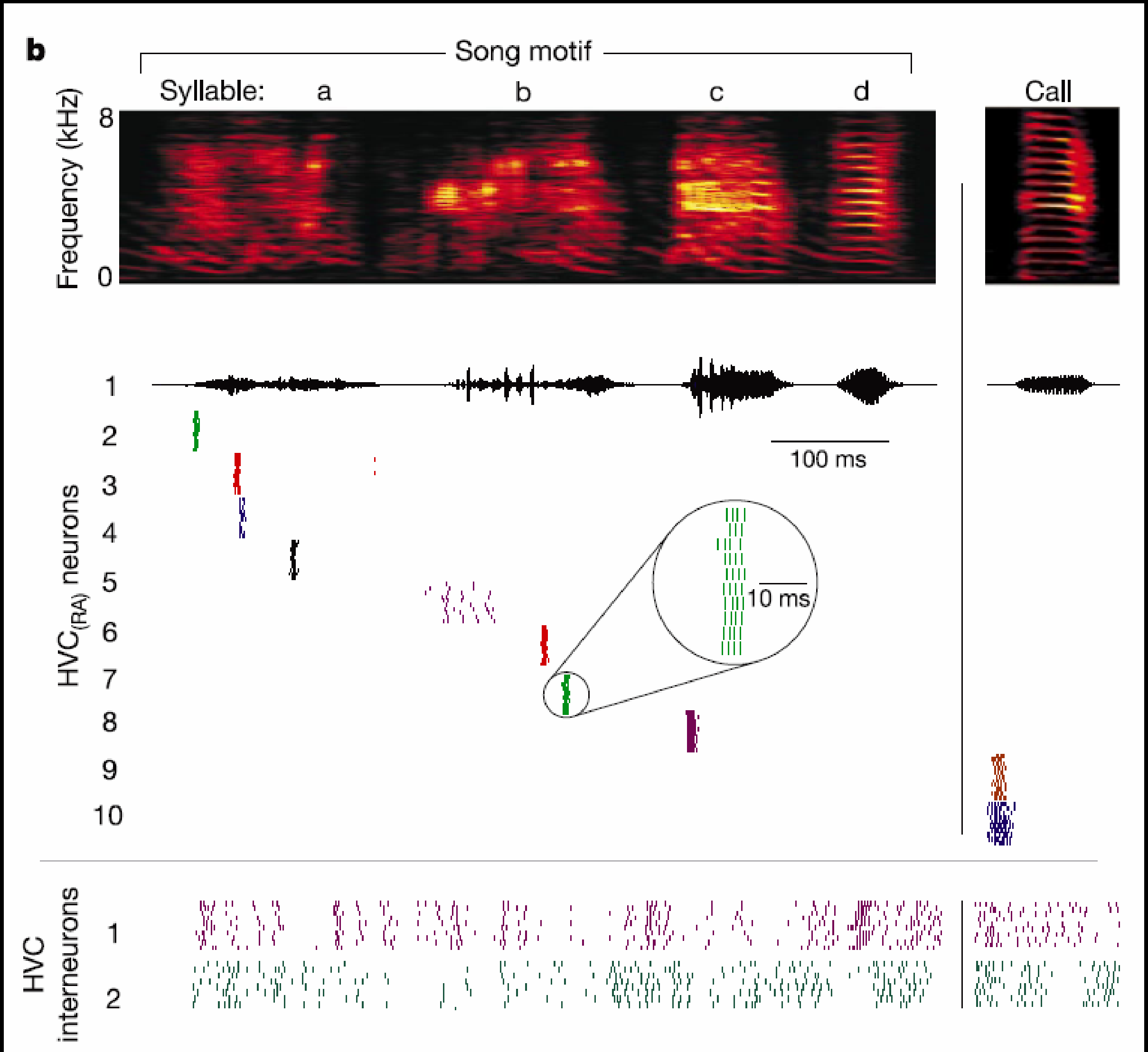
Michale Fee, MIT

Dr. Jon Prather, Mooney Lab





Ultra-sparse Bursting of HVC_{RA} Neurons During Singing



Issues:

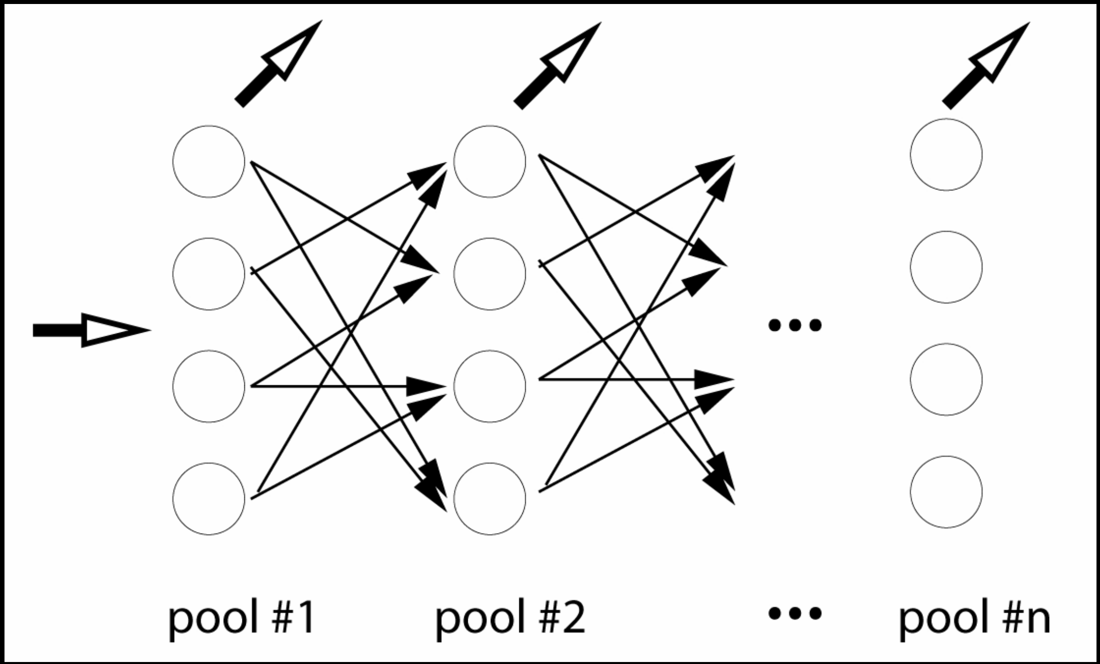
sparsity

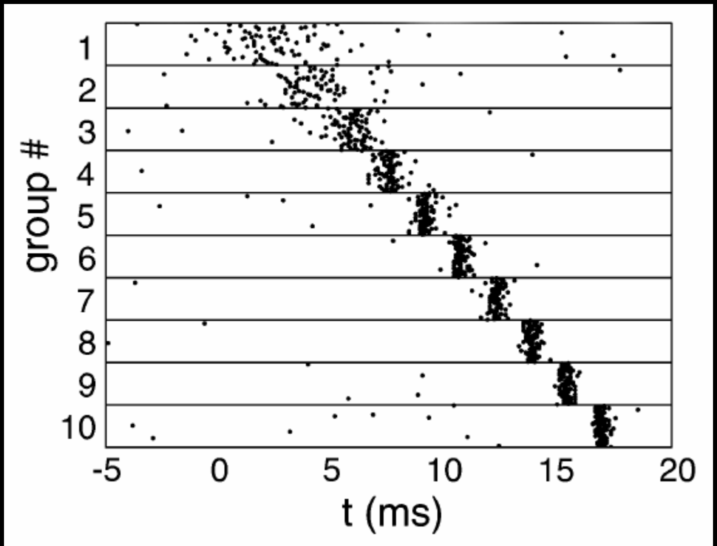
precision

robustness

R. Hahnloser, A. Kozhevnikov, M. Fee Nature **419**:65-70 (2002)

A Possible Simple Explanation: Feedforward Synfire Chain





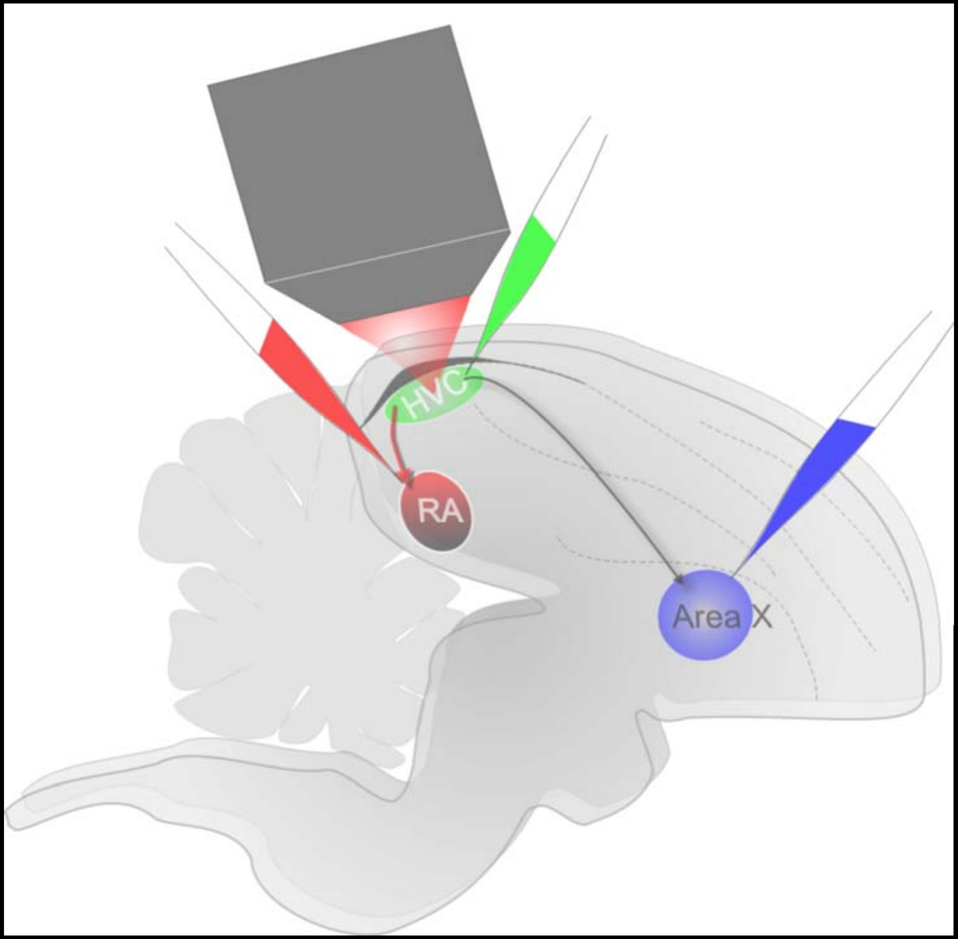
Theoretical support for burst propagation
Li and Greenside 2006,
Jin, Ramanazaglou, and Seung 2007
but further experiments are needed.

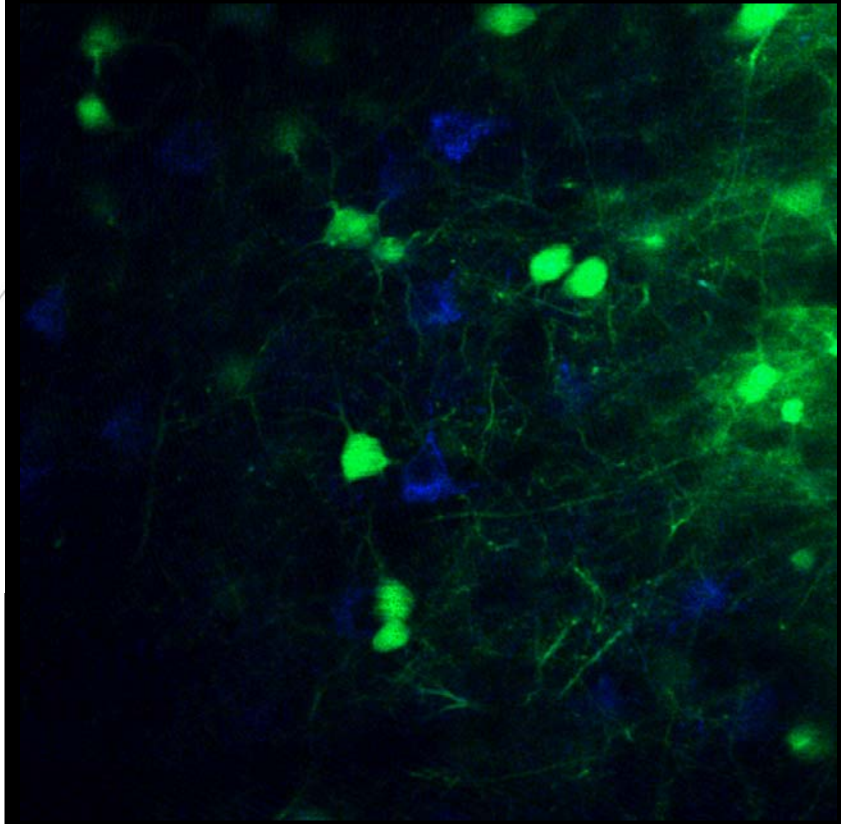
II: Anatomical Changes During Learning?

- Changes in spine volume (synaptic weight).
- Creation and deletion of spines.
- Apoptosis and neurogenesis.

A big question: can we *quantitatively* understand and so predict anatomical changes in HVC during song learning?

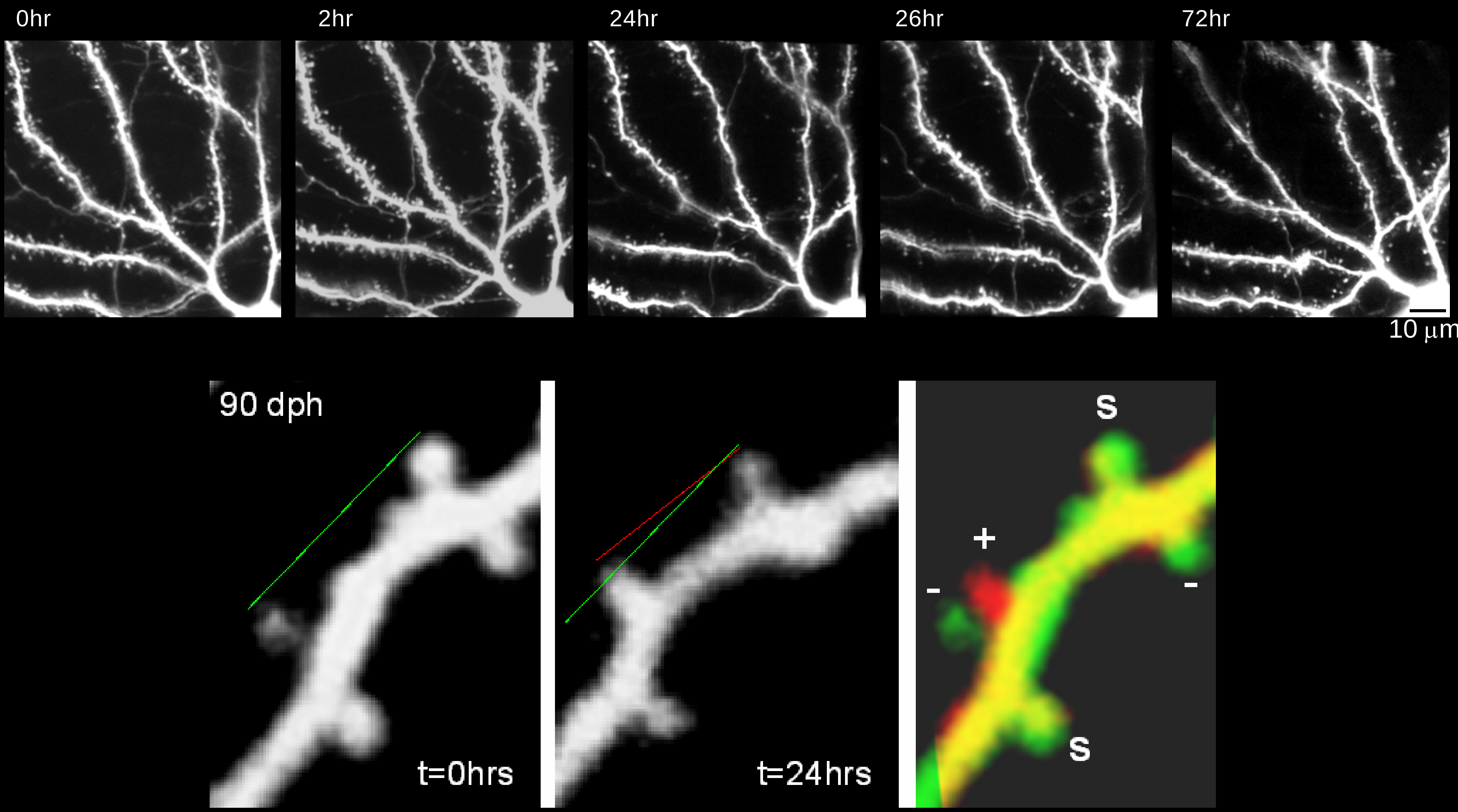
Two-Photon Imaging of HVC Neurons *In vivo*



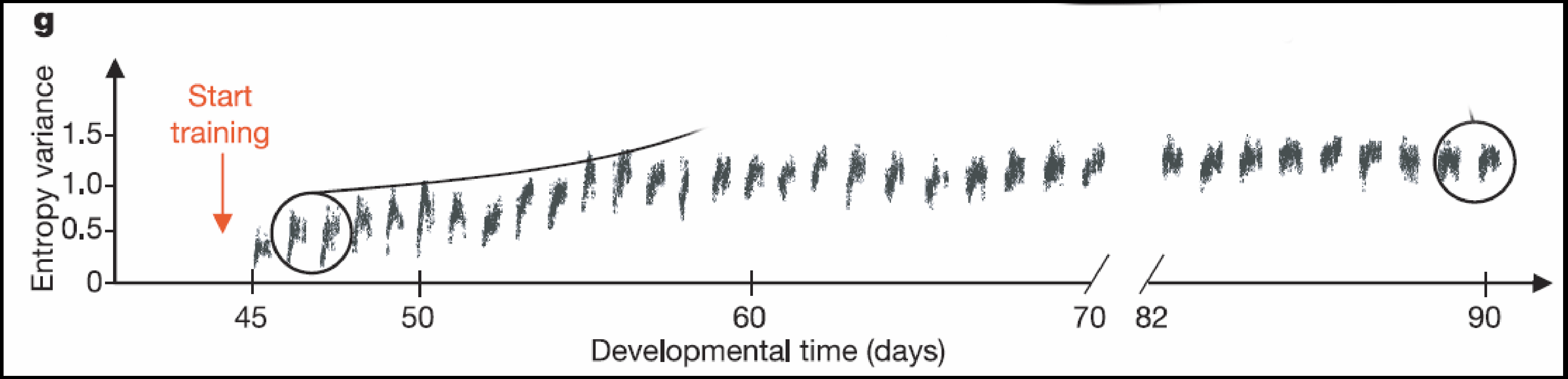


Todd Roberts, Katie Lewin, Rich Mooney
(unpublished)

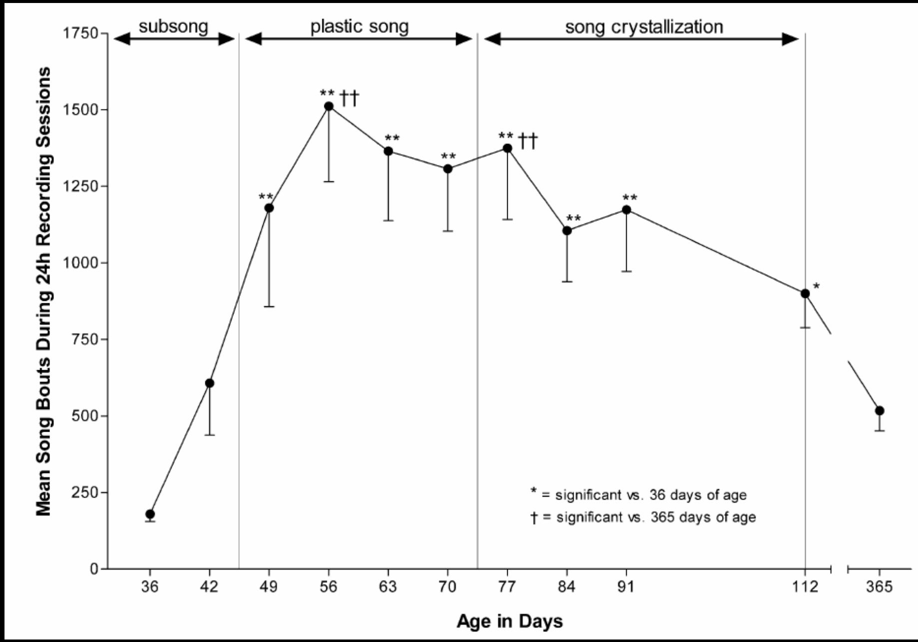
Longitudinal Two-Photon Imaging of HVC Dendritic Spines *In vivo*



III: Song Learning Complicated Process



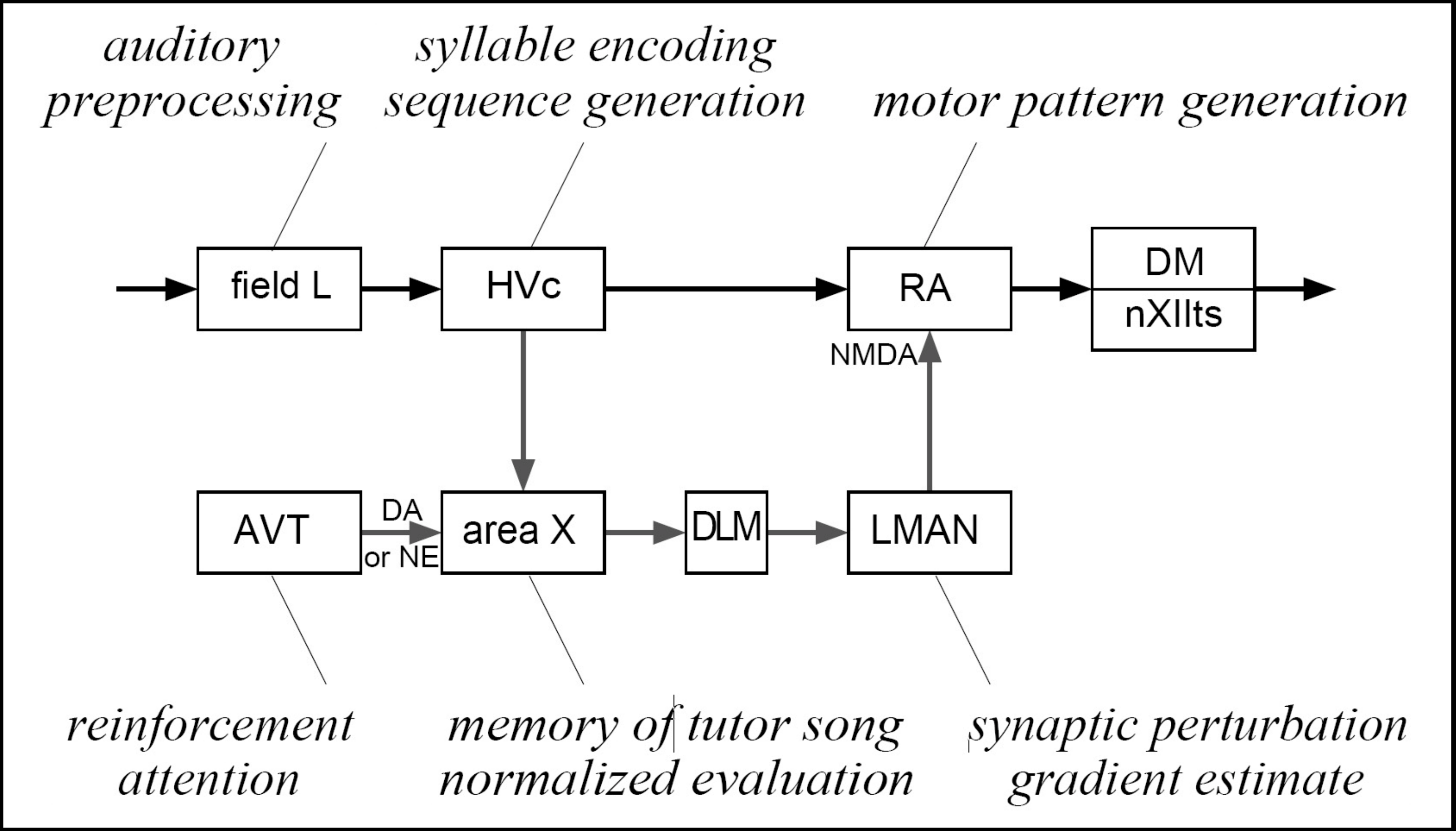
S. Deregnaucourt et al, Nature **433**:710-716 (2005)



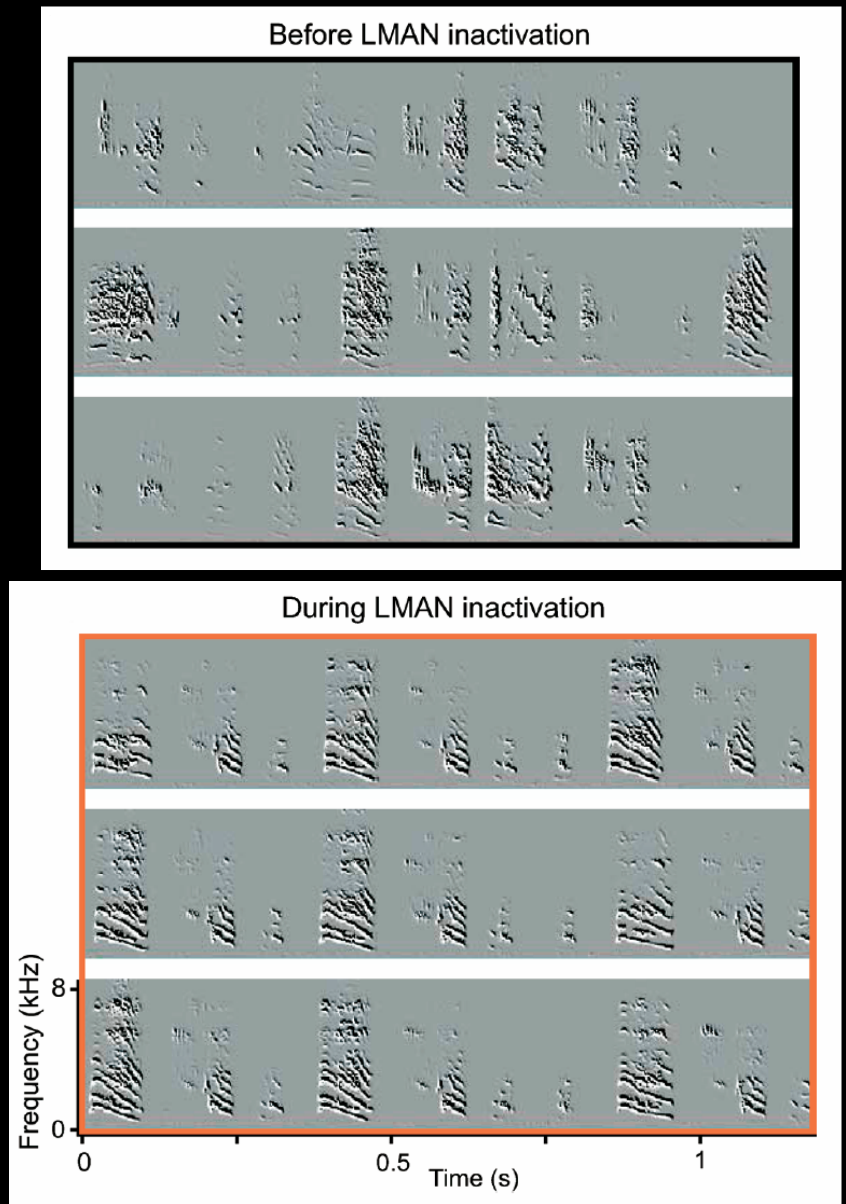
> 50,000 songs to converge

Johnson et al, Behavioral Brain Research **131**:57-65 (2002)

Doya and Sejnowski 1998: Reinforcement Learning Algorithm Plausible

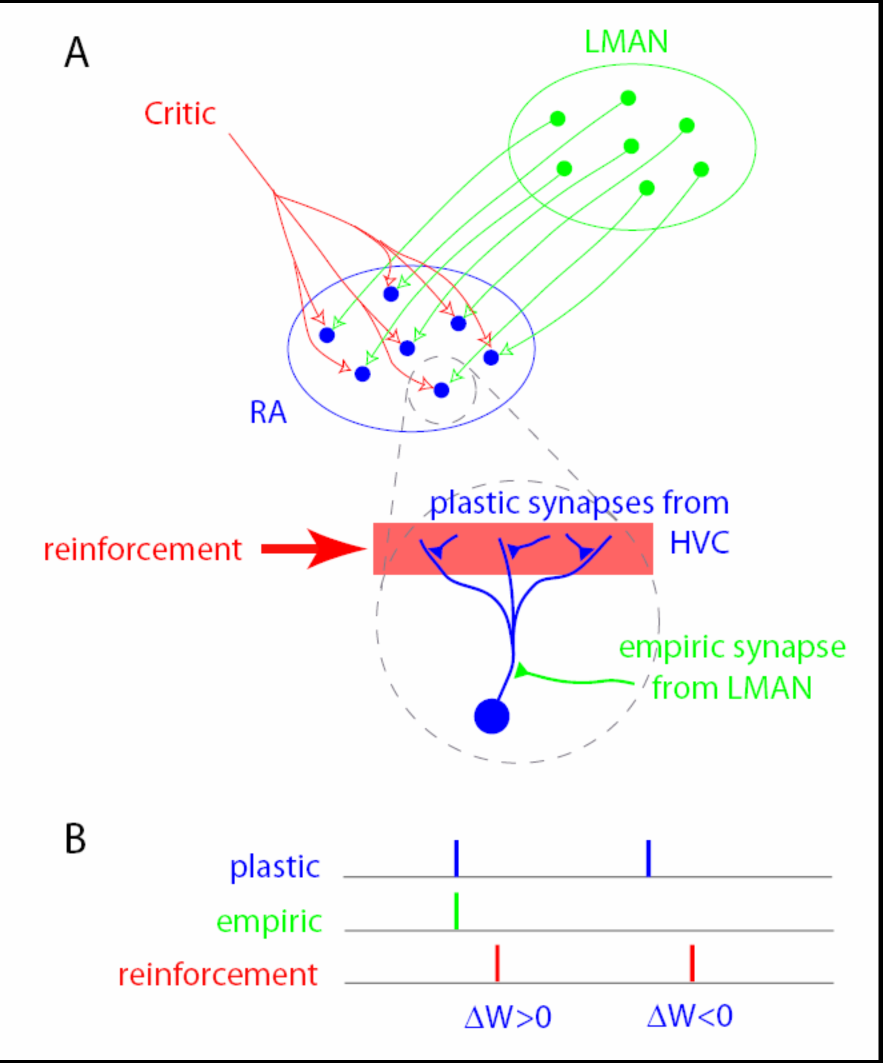


Inactivating LMAN with TTX Reduces Variability in a Juvenile (57 phd) Zebra Finch



Olveczky et al, PLoS Bio 2005.

Reinforcement Learning at Cellular Level



20:1 HVC to LMAN synapses

LMAN: NMDA
HVC: AMPA

LMAN to RA occur before HVC to RA.

"Model of Birdsong Learning Based on Gradient Estimation by Dynamic Perturbation of Neural Conductances", Fiete, Fee, Seung J. Neurophys. **98**:2038 (2007).

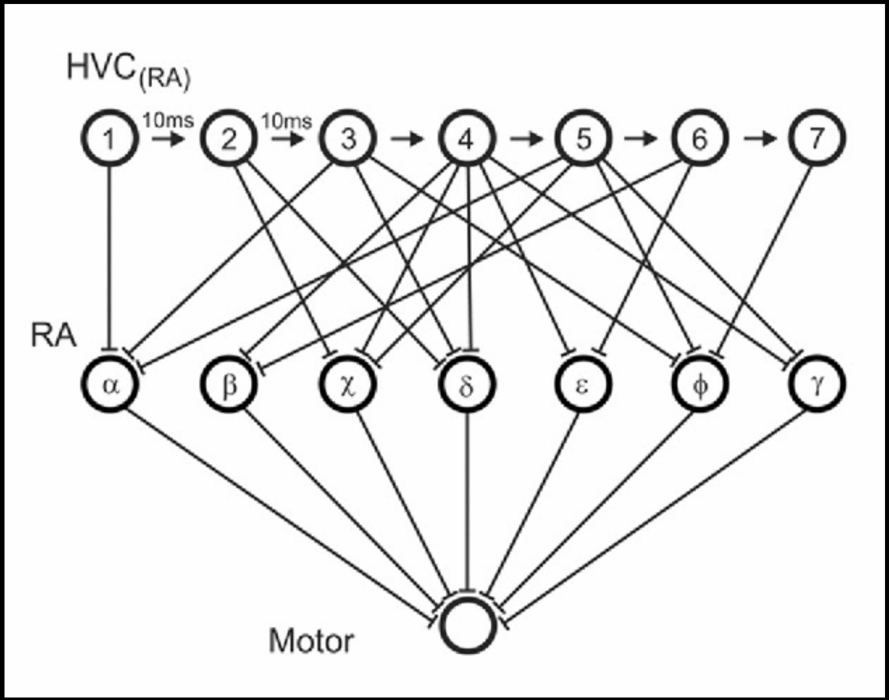
How Does LMAN Work?

- Can one confirm that birds actually use reinforcement learning? Many hard experimental questions: where is error calculated, what is the reinforcement agent?
- A theoretical step: try to understand how LMAN and HVC synapses interact on dendritic tree of single RA neuron: what are their geometric and physiological relations?

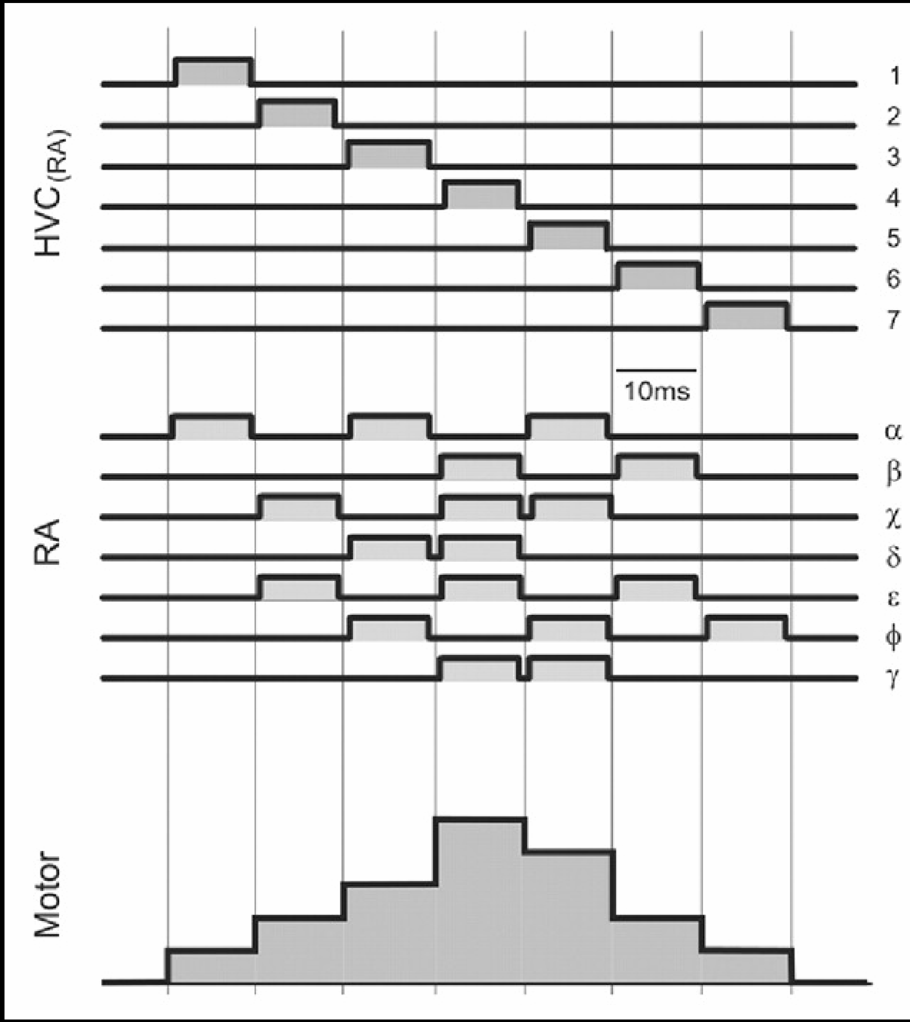
End of Talk

Questions, Discussion?

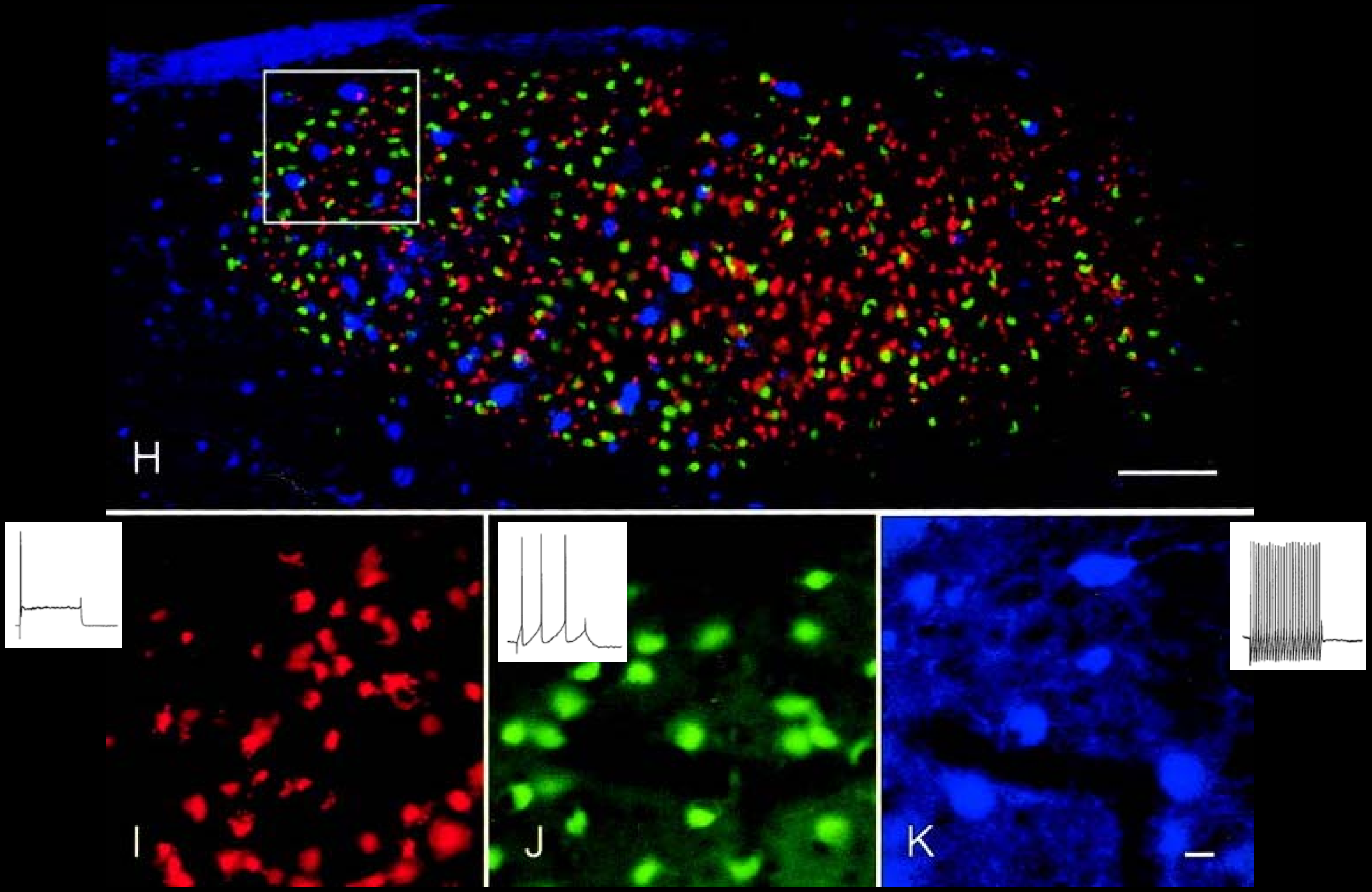
Hypothesis for Sparseness: HVC_{RA} Neurons Form a Feedforward Network



M. Fee, A. Kozhevnikov, R. Hahnloser
Annals of the New York
Academy of Science
1016: 153–170 (2004).



Anatomical Characterization of Neurons in Songbird Nucleus HVC



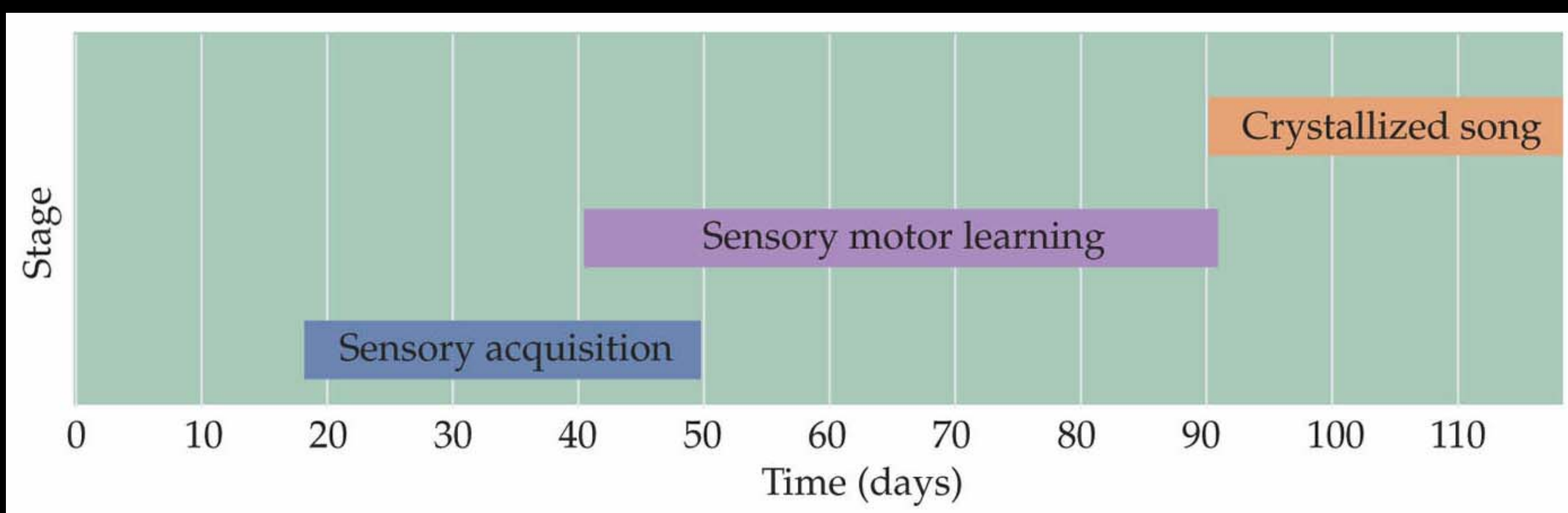
red = RA-proj   green = X-proj   blue = interneuron

J. Martin Wild et al, Journal of Comparative Neurology 483:79-90 (2005)

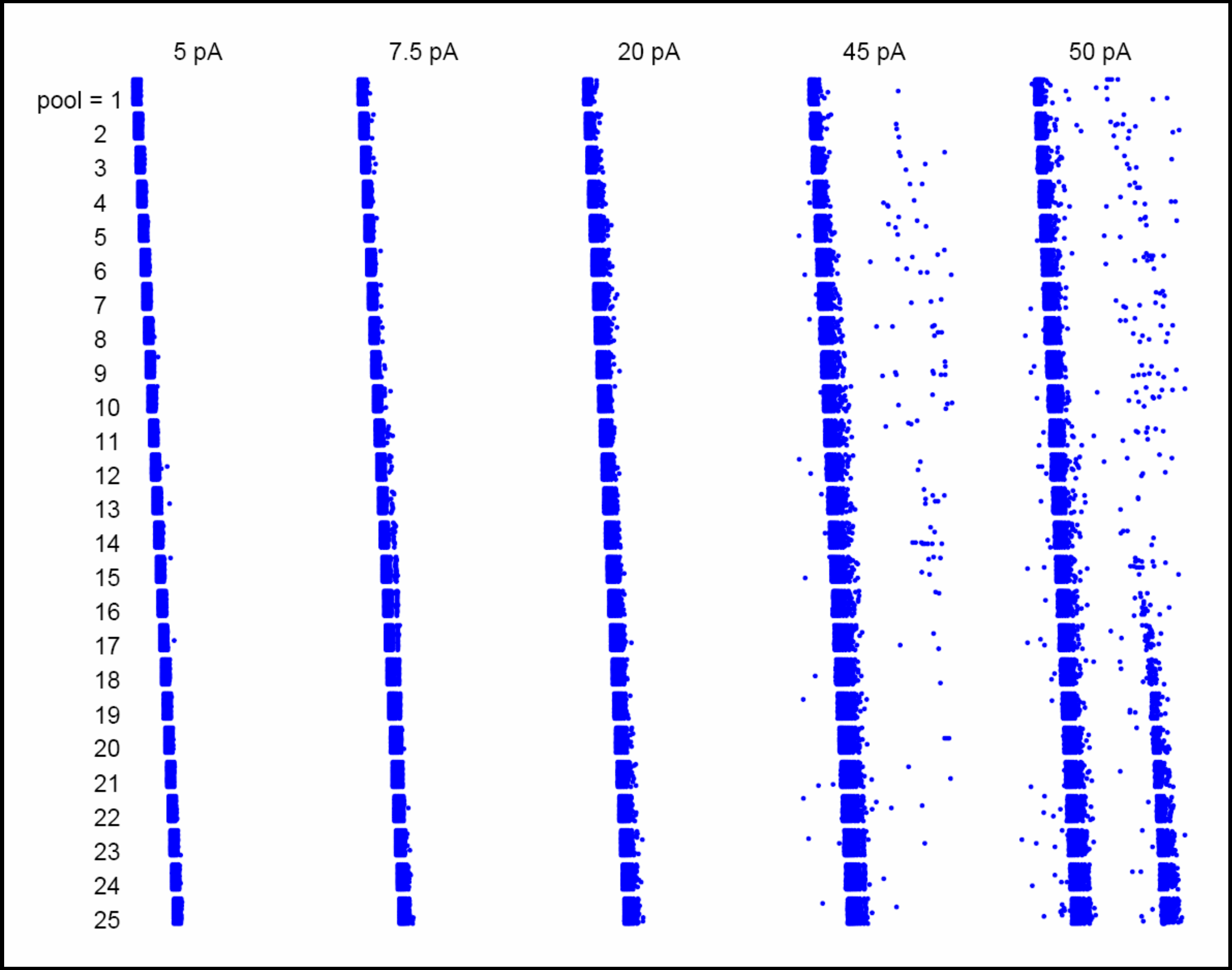
Three Stages of Song Learning

father

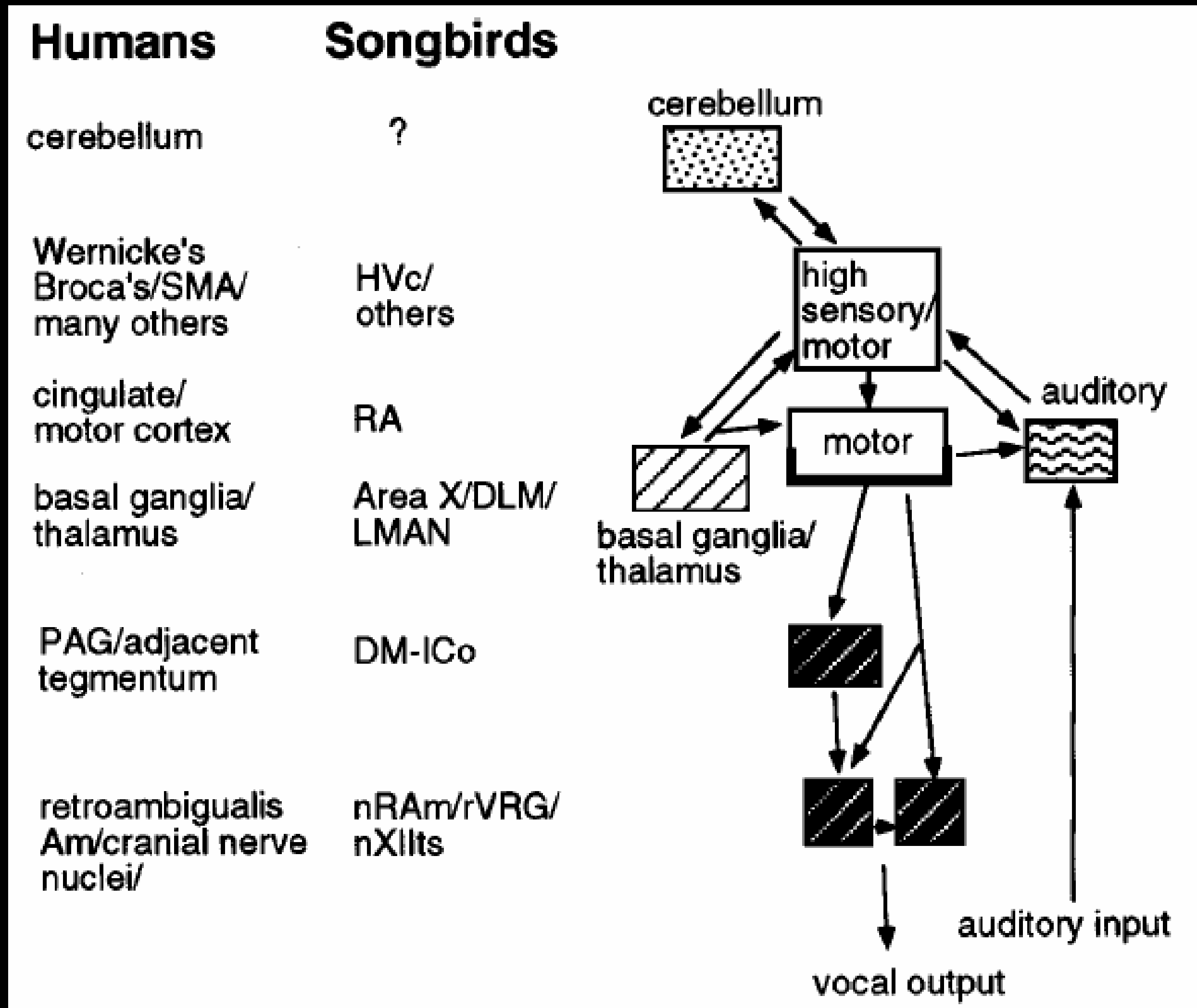
son



Bursts Survive High Levels of Noise and Network Heterogeneities

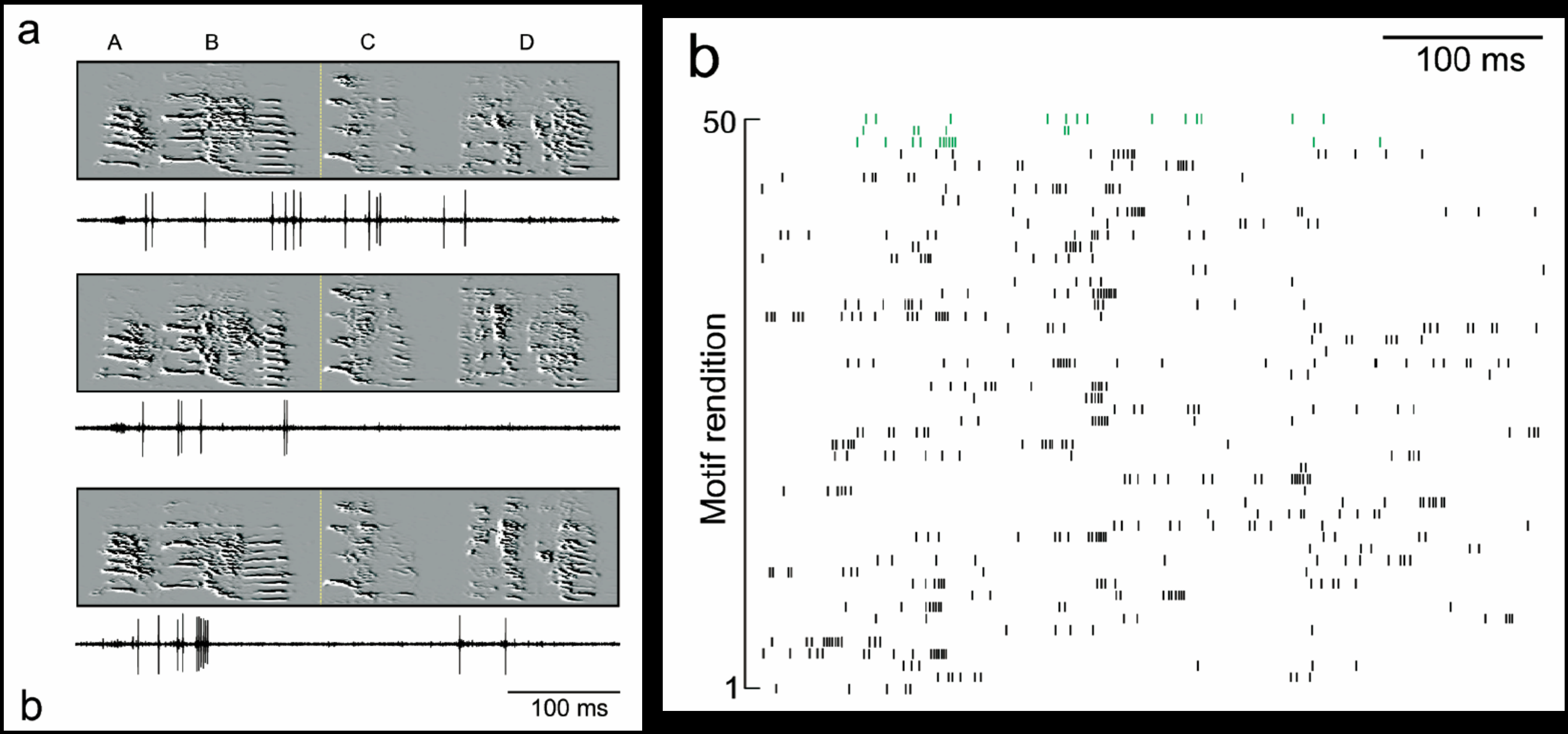


Human Versus Songbird Anatomy



A. Doupe and P. Kuhl, Ann. Rev. Neurosci 22:567-632 (1999)

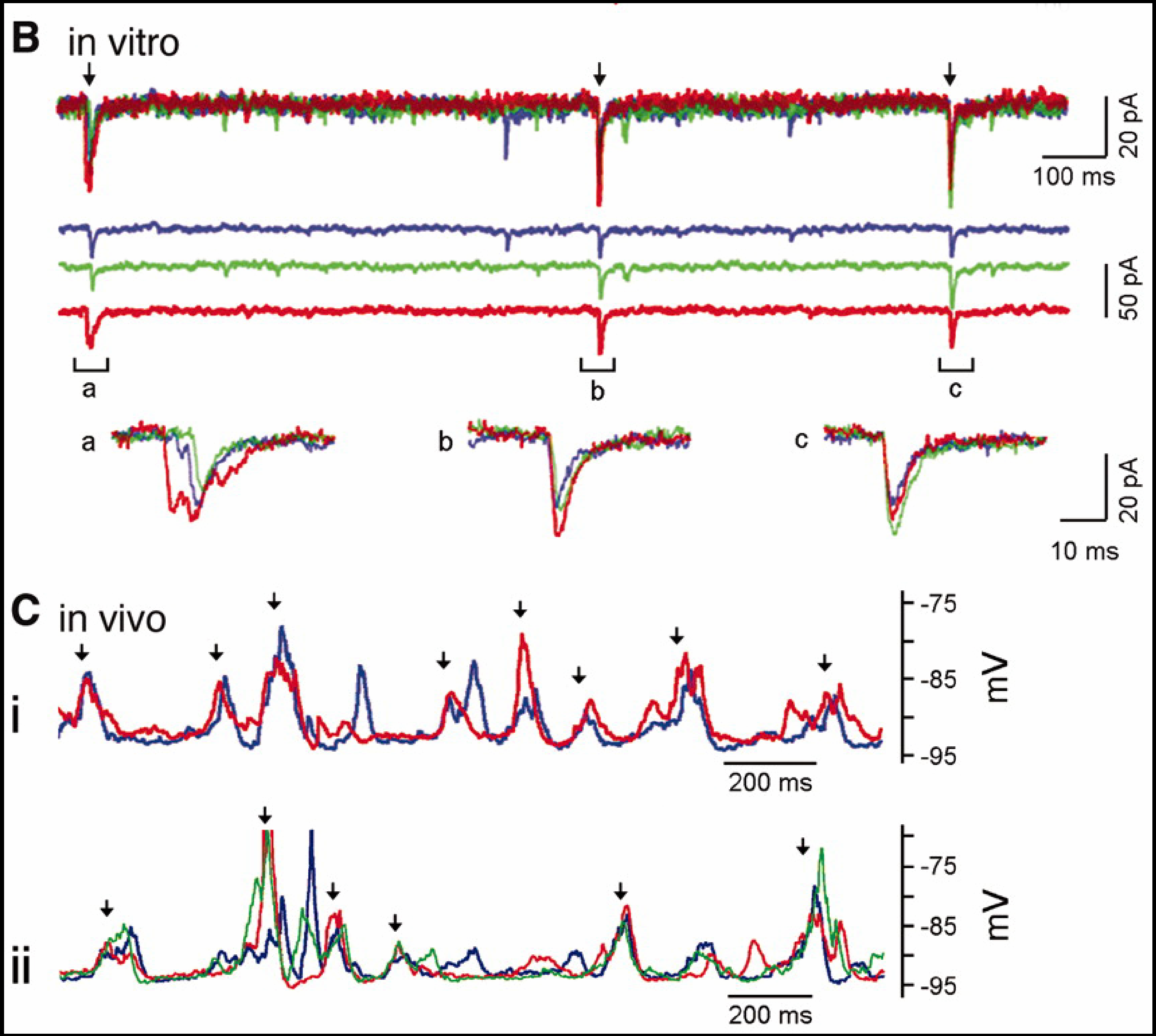
$LMAN_{RA}$ Neuronal Firing During Singing Is Highly Variable in Juveniles



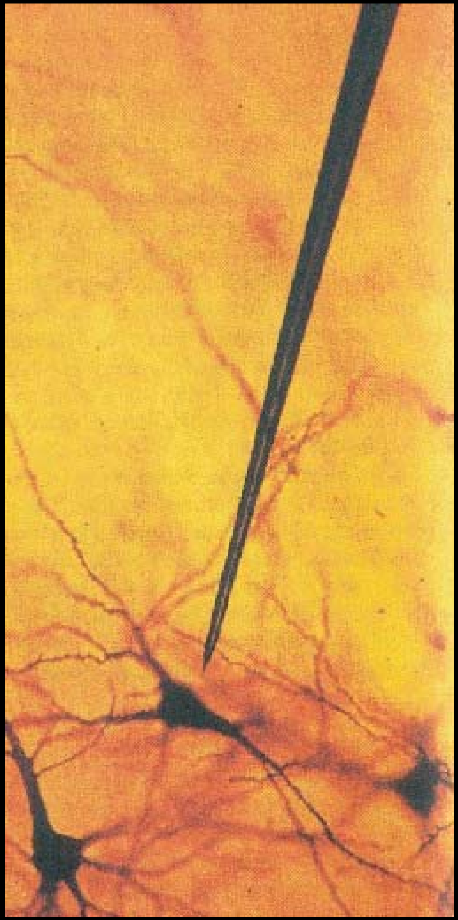
67 days post hatch

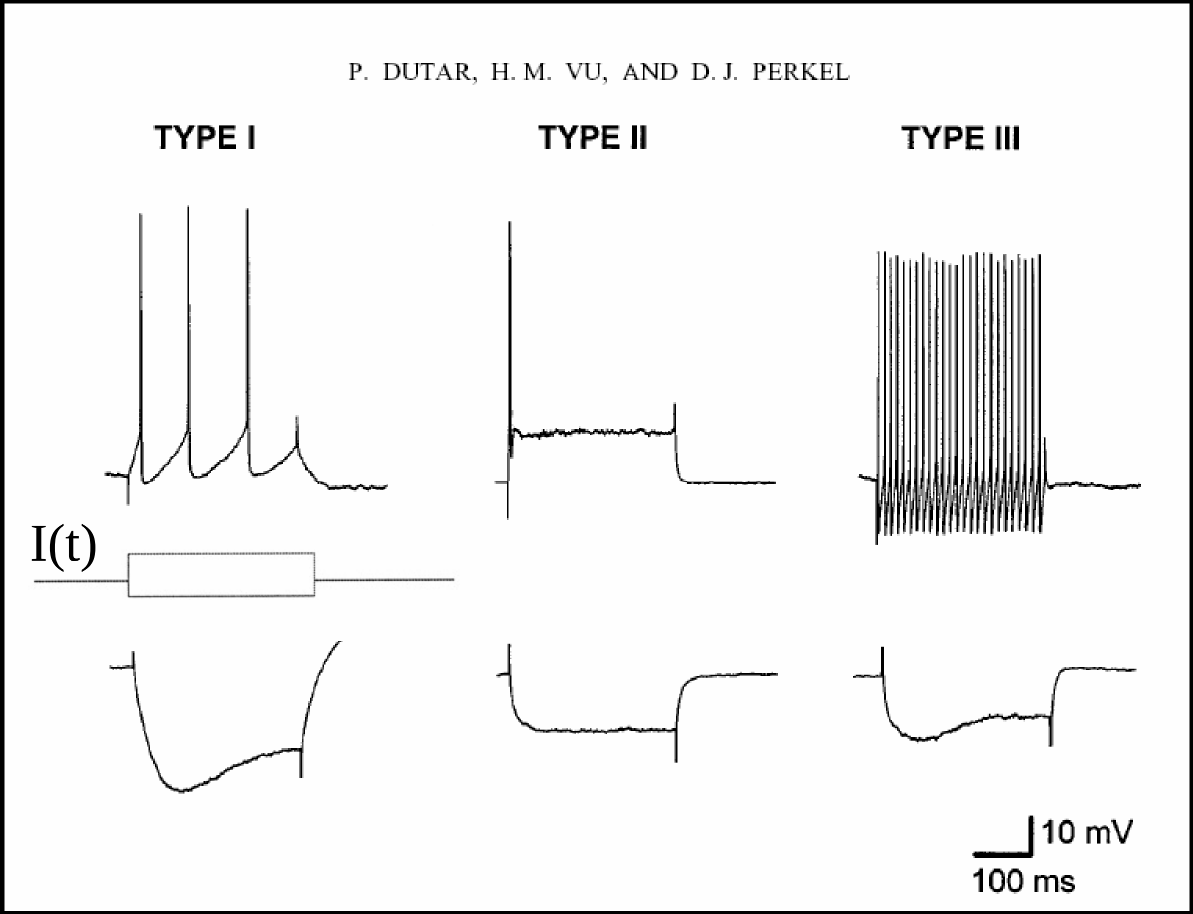
Bence P. Olveczky, Aaron S. Andalman, and Michale S. Fee, PLoS Biology 3(5):1-8 (2005)
“Vocal Experimentation in the Juvenile Songbird Requires a Basal Ganglia Circuit”

Precise Reproducible Cortical Dynamics?
Ikegaya et al, Nature **304**:559 (2004)



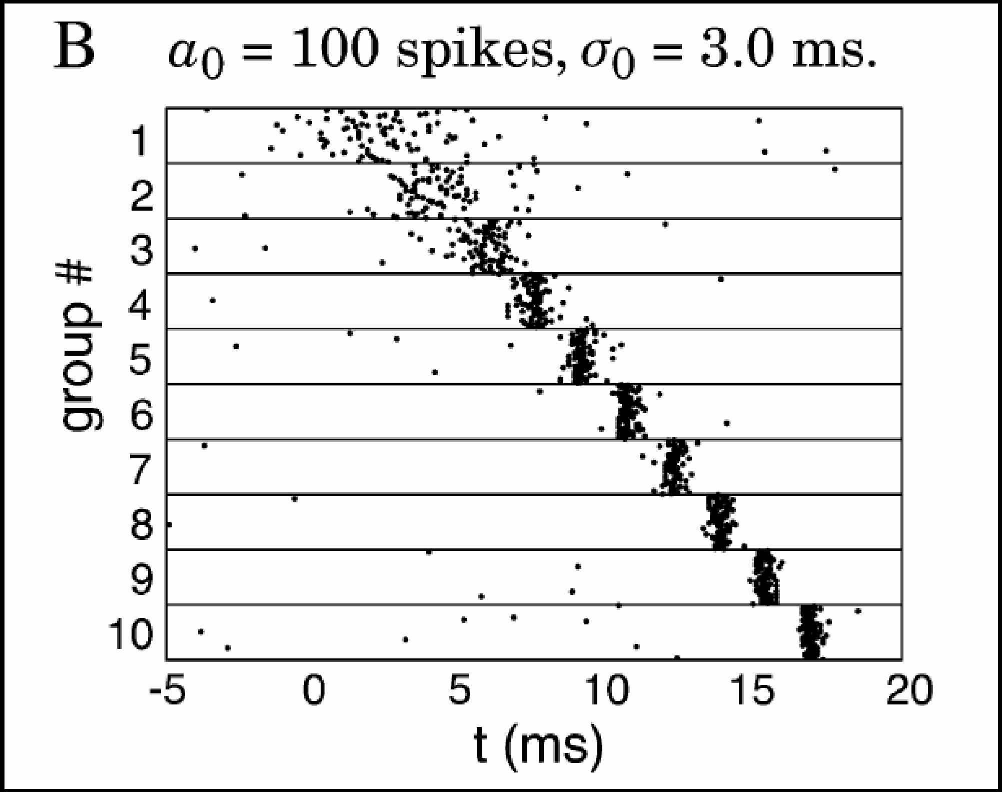
Characterization of HVC Neurons *in vitro*: Response to Constant Current Injections





P. Dutar et al, Journal of Neurophysiology **80**:1828-1383 (1998)
Note: Data obtained from brain slices in immersion chamber.

Stable Synfire Propagation



"Propagation of cortical synfire activity: survival probability in single trials and stability in the mean"
Marc-Oliver Gewaltig and Markus Diesmann and Ad Aertsen
Neural Networks **14**:657-673 (2001)

What About Bursts in Synfire Chains?
Li and Greenside, Jin et al

PHYSICAL REVIEW E **74**, 011918 (2006)

Stable propagation of a burst through a one-dimensional homogeneous excitatory chain model of songbird nucleus HVC

MengRu Li and Henry Greenside

10 parameters per neuron for leaky-integrate-and-fire model with simplest synapses.

30 parameters for Hodgkin-Huxley single-compartment neuron with simple synapses.

Extremely difficult to pin down parameters from existing data.

Equations

$$C_m \frac{dv_i^k}{dt} = \sum_{m=1}^{N} g_m(t, v_i^k)\left[V_m - v_i^k\right] + I^k_{i,e}(t) + I^k_{i,S}(t) + \xi_i^k(t)$$

$$I^k_{i,S}(t) = \sum_{j=1}^{W} M^k_{ij} \sum_{u(j)} I_S(t - t^{k-1}_{j,u(j)}, v_i^k).$$

$$I_S(t, v) = g_S C (t/\tau_S) e^{-t/\tau_S} (V_S - v)$$

$$g_m(t, v) = \bar{g}_m x_1^u(t) x_2^v(t)$$

$$\tau(v) \frac{dx}{dt} = x_\infty(v) - x$$

$$\tau(v) = t_2 + t_1 \left(1 + e^{-((v - v_2)/v_3)}\right)^{-1}$$

$$x_\infty(v) = \left(1 + e^{-(v - v_0)/v_1}\right)^{-1}$$

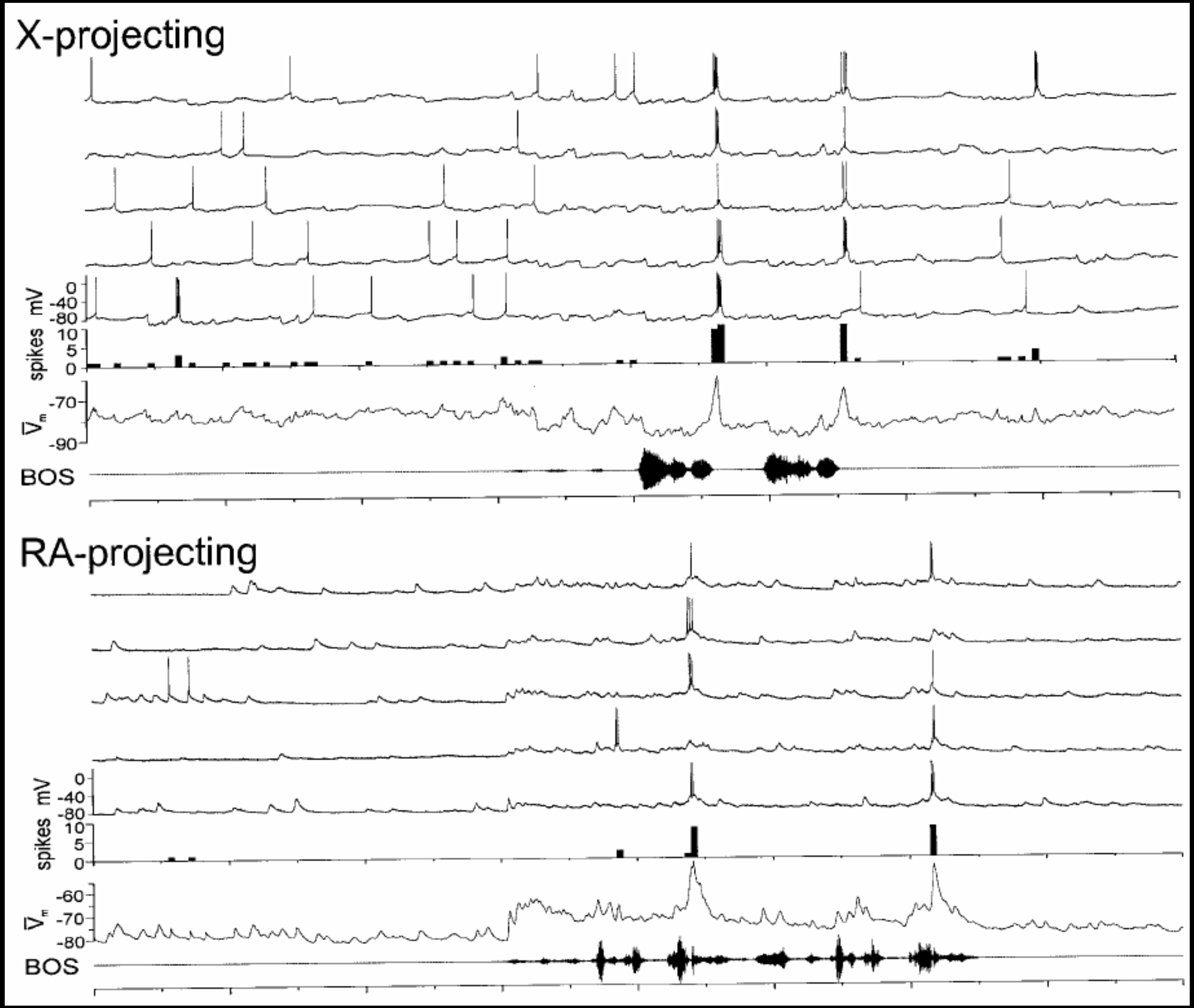
Puzzles

- Embedded synfire chain calculations: much harder to achieve stable propagation.

- Songbirds like Bengalese finches have complex “finite state” grammars, hard to reconcile with synfire chains.

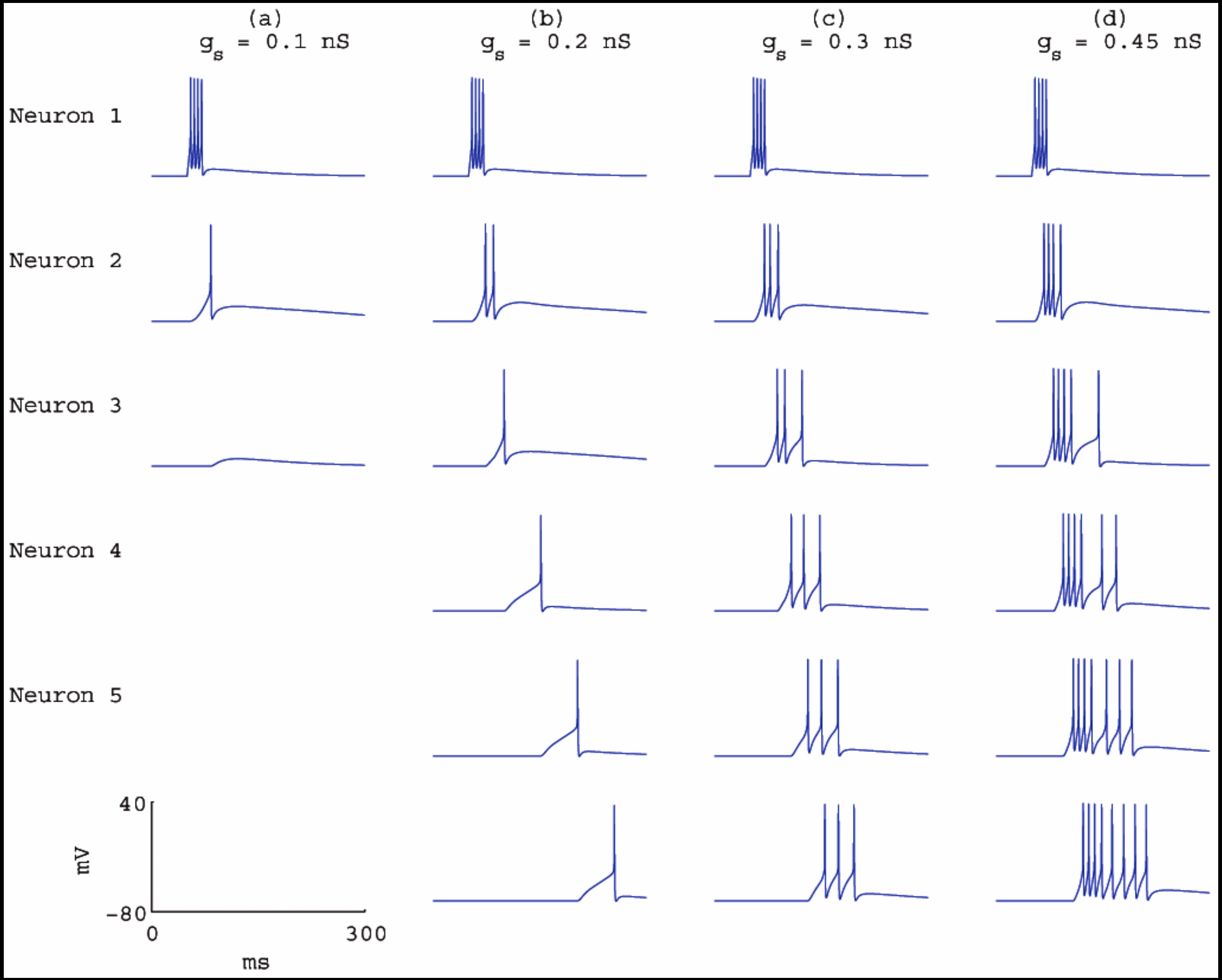
- Human speech and recursive Chomskian grammars?

Sparse Bursting Occurs During Audition In Anesthetized Zebra Finch



Richard Mooney, Journal of Neuroscience 20(14):5420-5436 (2000)

Stability and Instability of a Burst



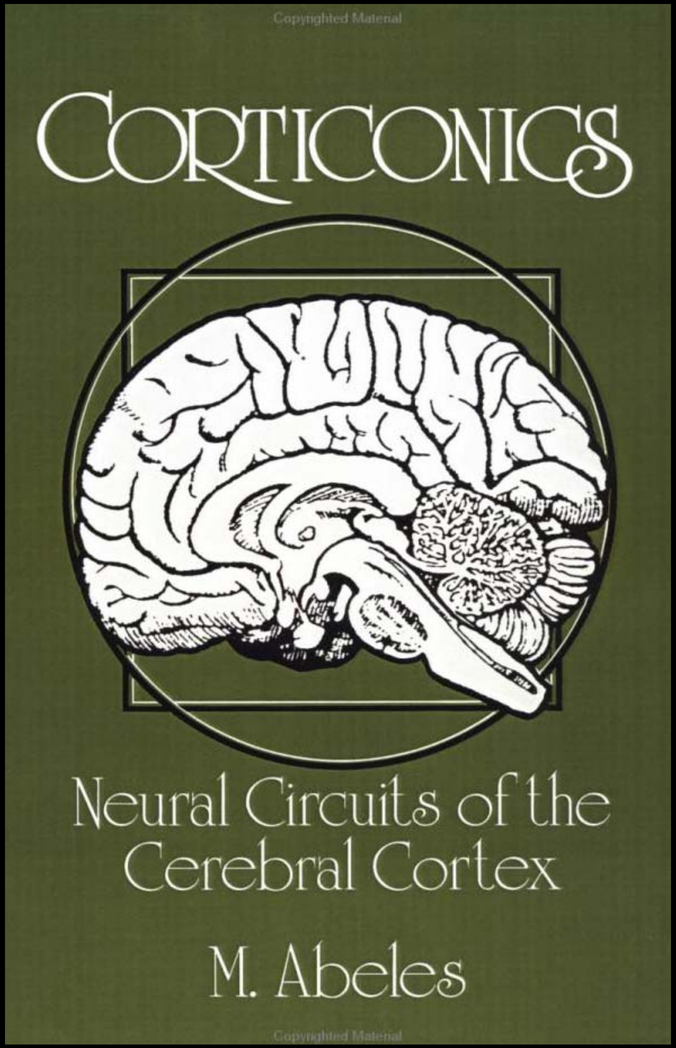
Questions

- *Sparse* firing: why do the HVC_{RA} fire just once over such a long time interval? Intrinsic and causal or externally driven?

- *Precise* firing: how do the HVC_{RA} fire with a reproducible precision of better than 1 ms?

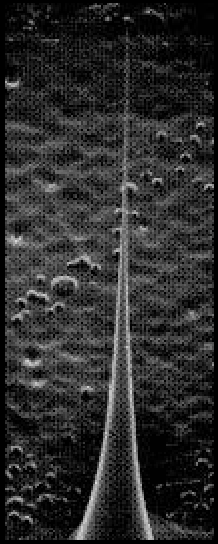
- Robustness: how does precise firing survive neurogenesis in adult HVC?

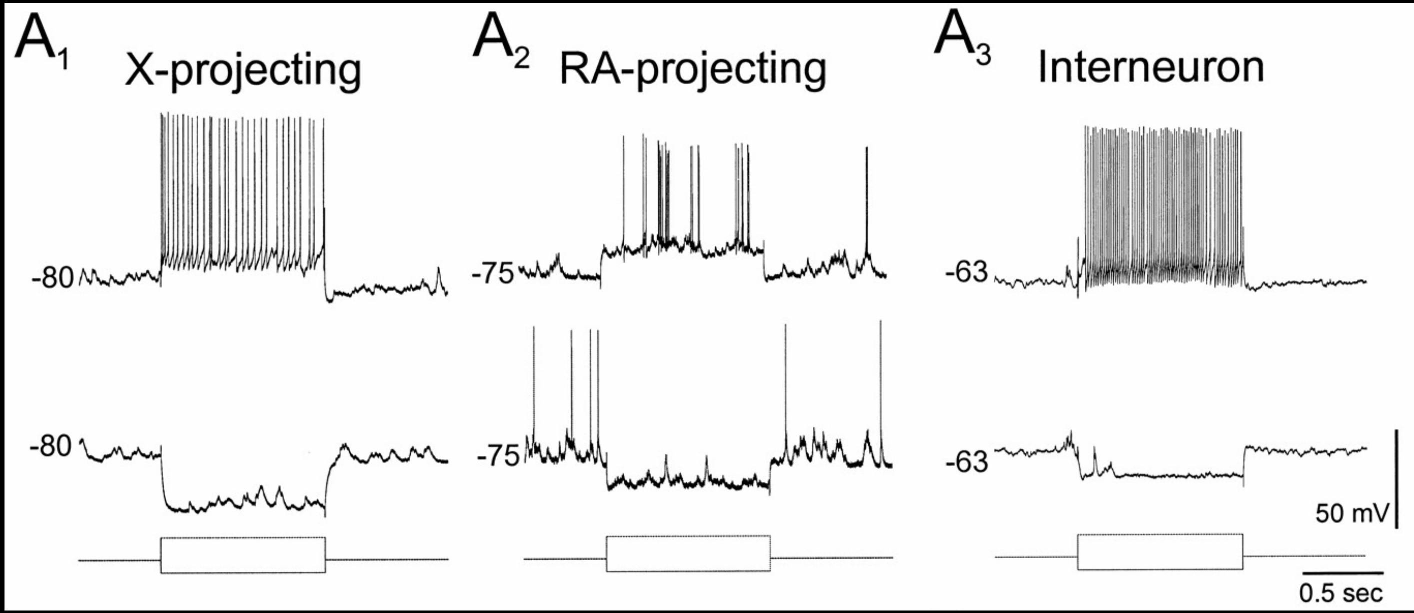
Synfire Chains, 1991

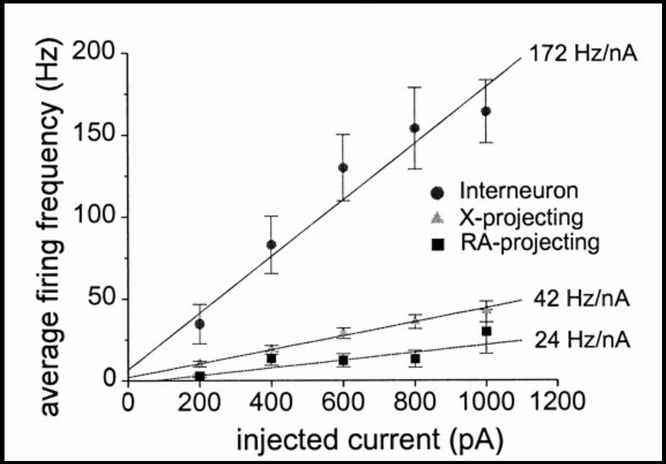


- Robust transmission
- Precise transmission
- Solution to binding…

In Vivo Intracellular Characterization of HVC Neurons in Anesthetized Bird







Richard Mooney, Journal of Neuroscience 20(14):5420-5436 (2000)