Neural circuits for cognition

Neural feedback control?
&
Introduction to song learning in songbirds

MIT Course 9.49/9.490

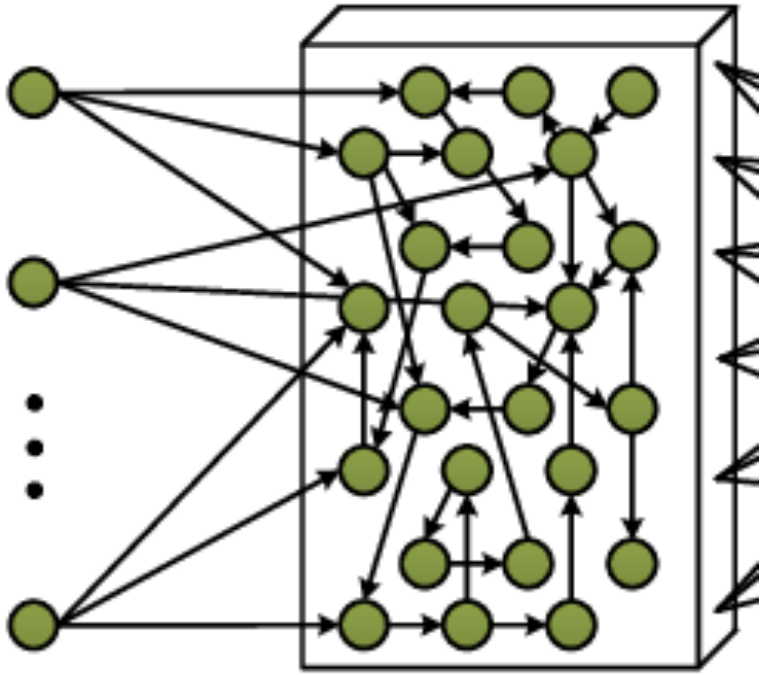
Instructor: Professor Ila Fiete

Neural models of feedback control

Liquid state machines: Jaeger and Haas, 2004; Maass et al., 2007
FORCE: Sussillo and Abbott 2009
Tightly balanced networks Boerlin, Machens, Deneve 2011
FOLLOW: Gilra and Gerstner 2018

Neural models for the generation of temporal functions

Train a full recurrent neural network

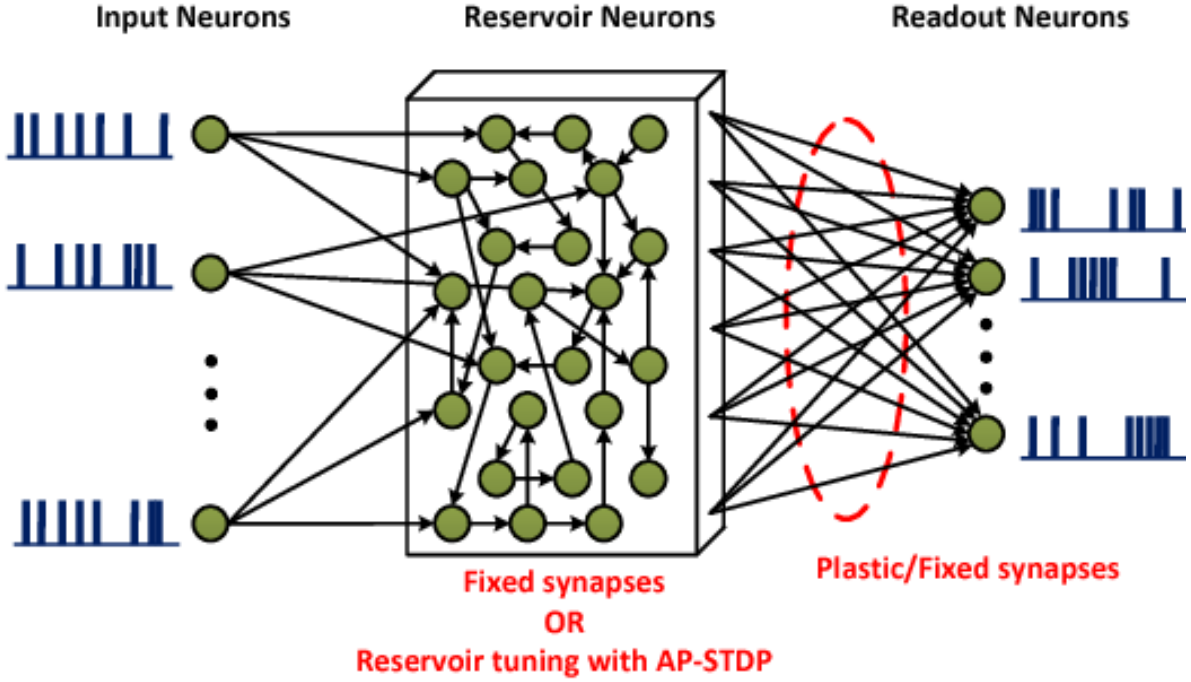


Train the recurrent weights **W** to produce the desired outcomes: problems: slow to train, difficult to control, short time-scales in general without incredible fine-tuning. Also: mixing the problem of what signal to produce at what time versus just producing some long-lived temporal dynamics.

Neural models for the generation of temporal functions

Alternative: create a general-purpose dynamical system that produces long time-scale ouptuts. Learning is in readout only.

Liquid state machine/reservoir computing/echo-state networks:

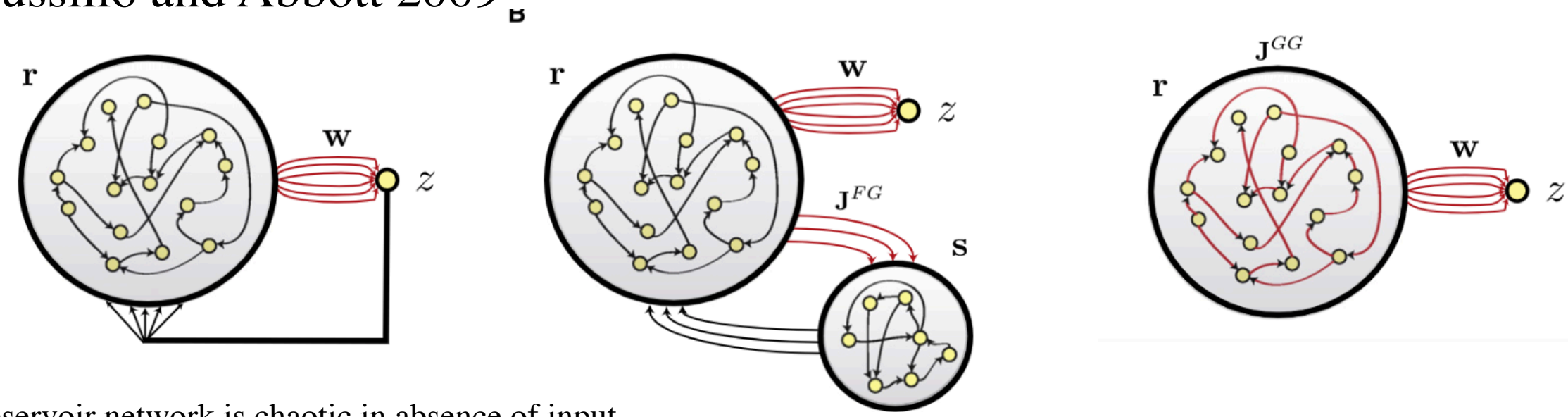


Jaeger and Haas, 2004; Maass et al., 2007

Little response in reservoir with no input; when driven with inputs, produce temporal responses that can be combined to produce desired temporal output.

Neural models of feedback control, learning

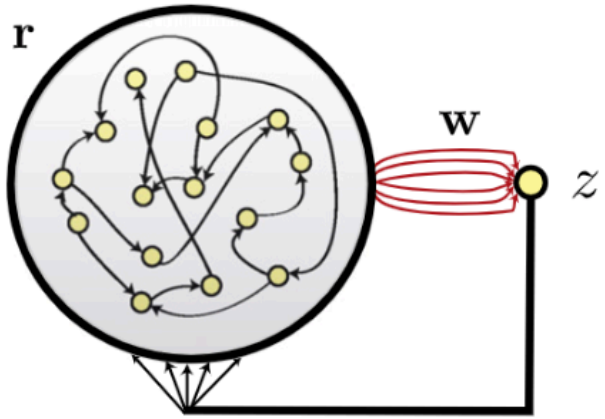
FORCE: combining random chaotic dynamics with feedback control:
Sussillo and Abbott 2009



Reservoir network is chaotic in absence of input
Network training suppresses chaos when input present
Synaptic modifications must be strong and rapid during initial learning
the initial phases of training
Error feedback for learning: strong error pushes output to nearly equal desired state
Training of weights by recursive least-squares, non-local

Neural models of feedback control, learning

FORCE: combining random chaotic dynamics with feedback control: Sussillo and Abbott 2009



$$z(t) = \mathbf{w}^T \mathbf{r}(t)$$

$$z(t) = f(t)$$ target function

$$e_-(t) = \mathbf{w}^T(t - \Delta t)\,\mathbf{r}(t) - f(t)$$ Error before wt update at t

$$e_+(t) = \mathbf{w}^T(t)\,\mathbf{r}(t) - f(t)$$ Error after wt update

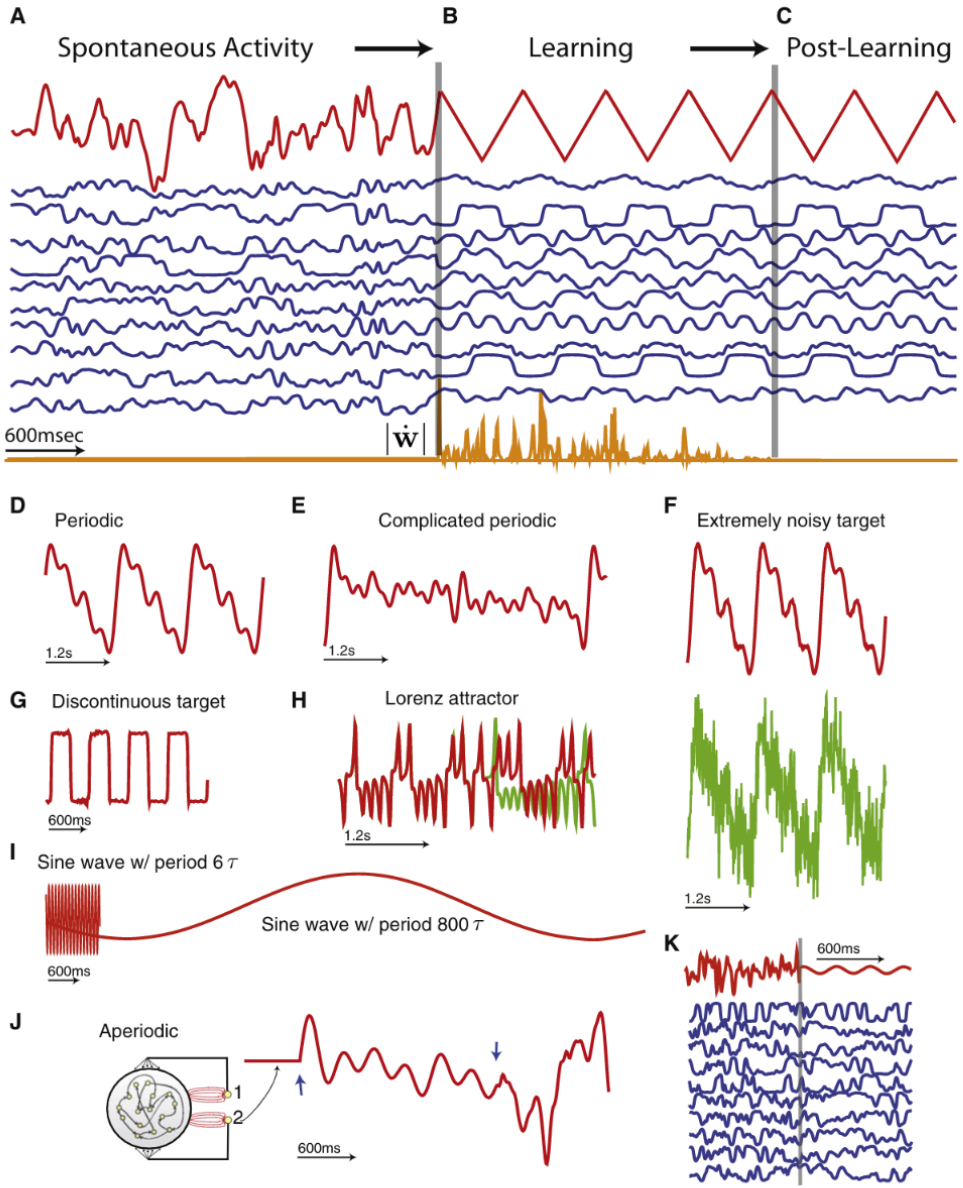
Learning rule: recursive least-squares (fully supervised, non-biological, iterative approach related to Kalman filtering)

$$\mathbf{w}(t) = \mathbf{w}(t - \Delta t) - e_-(t)\,\mathbf{P}(t)\,\mathbf{r}(t)$$

$$\mathbf{P} = \left({}_t\, \mathbf{r}(t)\,\mathbf{r}^T(t) + \alpha \mathbf{I} \right)^{-1}$$

$$\mathbf{P}(0) = \frac{\mathbf{I}}{\alpha}$$

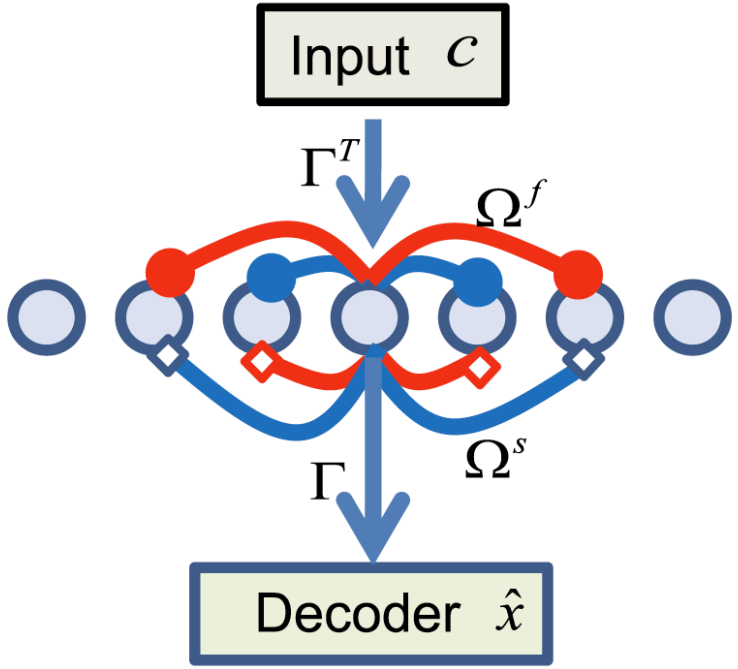
FORCE: combining random chaotic dynamics with feedback control: Sussillo and Abbott 2009



Neural models of feedback control, learning

Tightly balanced networks Boerlin, Machens, Deneve 2011

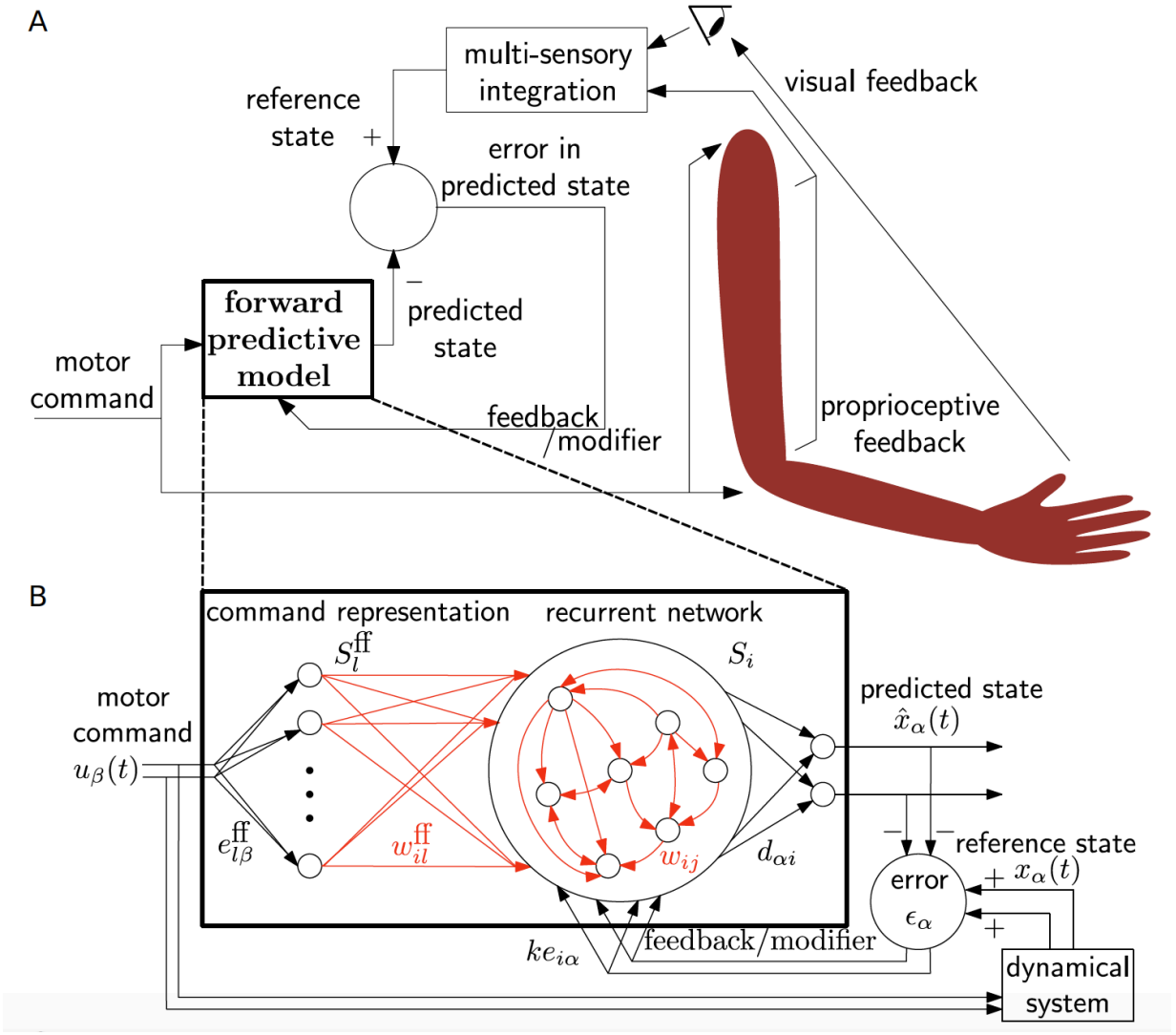
Truly spike-based
Non-local learning rule
Autoencoder: encoder, decoder pair



Neural models of feedback control, learning

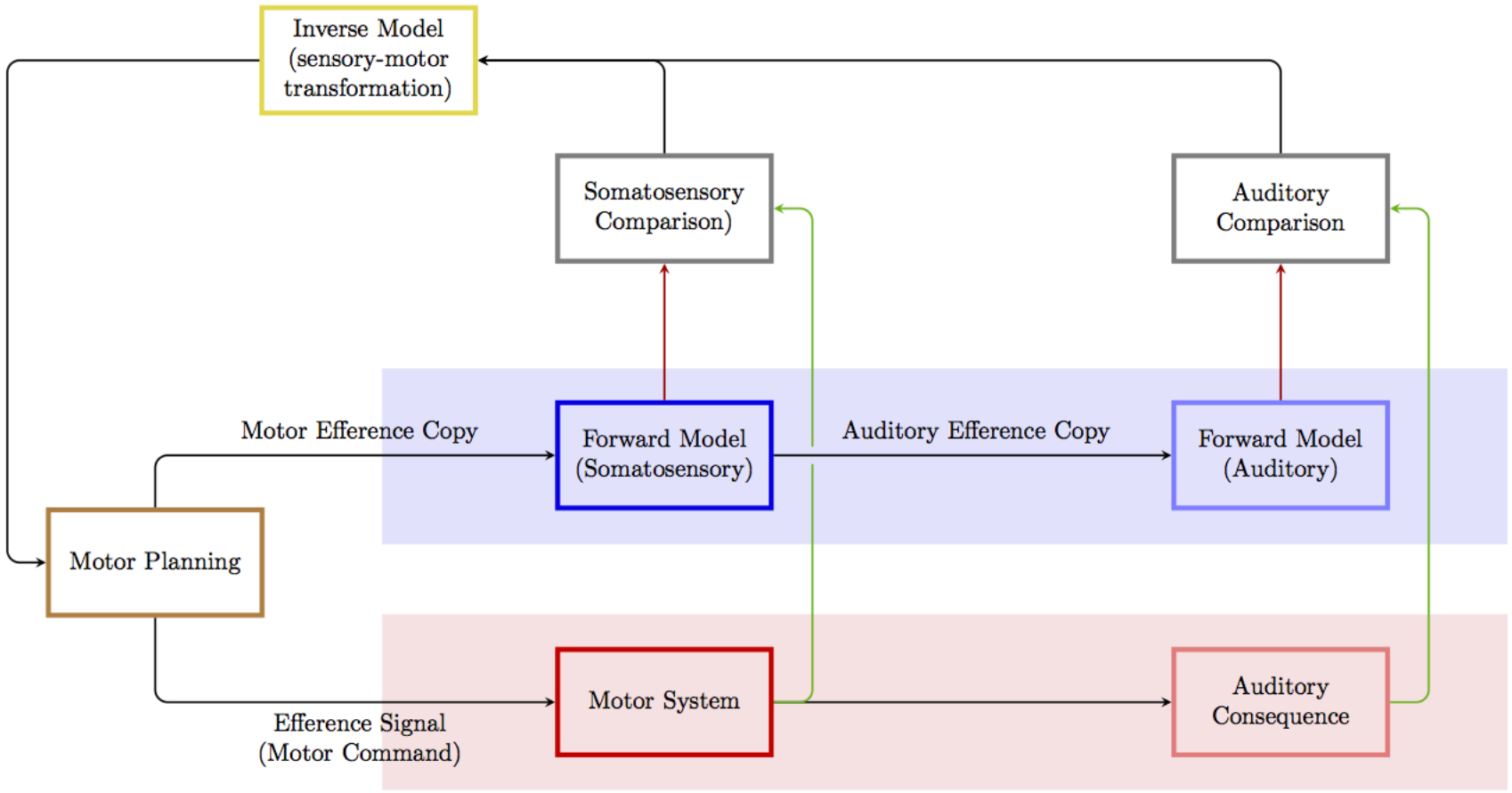
FOLLOW: Gilra and Gerstner 2018

Autoencoder: encoder, decoder pair
Local learning rule
Effectively rate-based



What about inverse models?

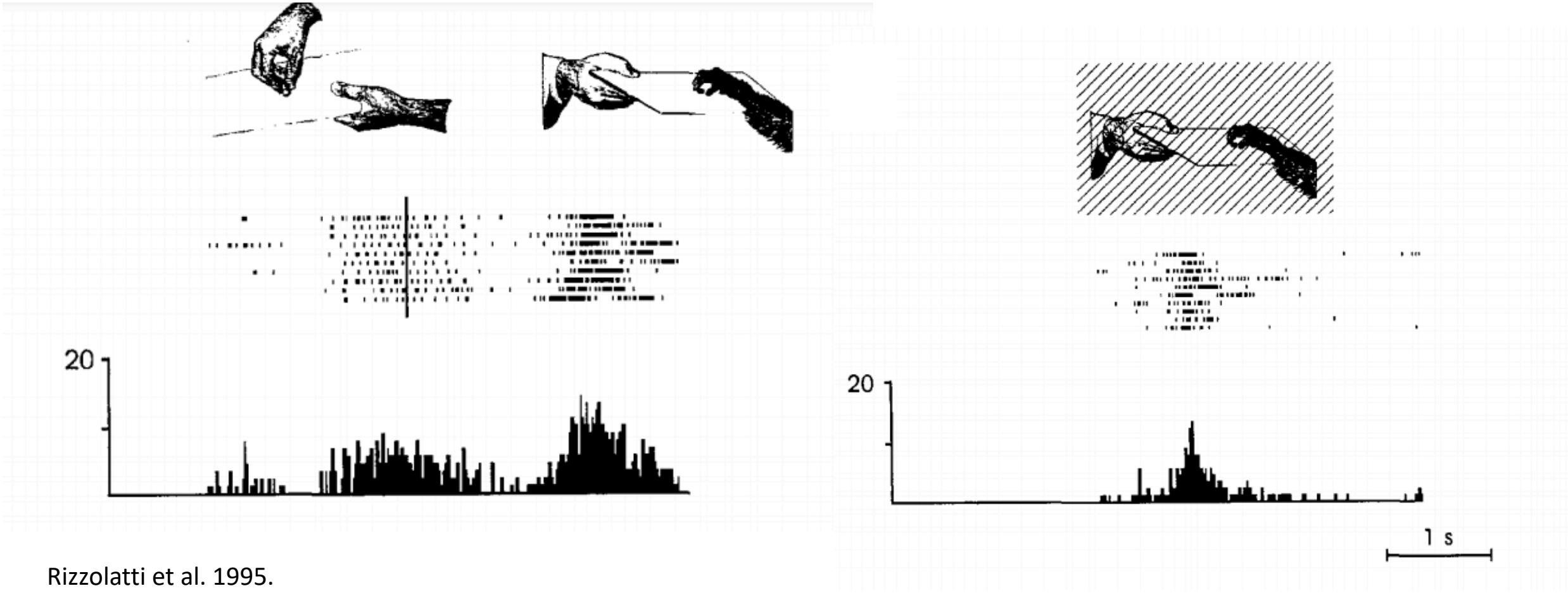
Internal models and speech



Mirror neurons

Premotor cortex, primary somatosensory (S1), supplementary motor area, inferior parietal cortex

experimenter grasps food monkey grasps food monkey grasps food in dark



Rizzolatti et al. 1995.

Mirror neurons and inverse models

Premotor cortex, primary somatosensory (S1), supplementary motor area, inferior parietal cortex

- Transform seen actions (external sensory) into internal high-level premotor representations consistent with taking/commanding those actions (sensory → command).
- More than an inverse model because it's not "desired sensory state of self", rather observed sensory state of others.
- However, presumably requires an inverse model.

imitation by infant monkey

Internal models summary

- The brain clearly constructs forward models, and in some behaviors and species also inverse models.
- Forward models should be highly context-dependent, and behavioral evidence of ”modules” (prism glass experiments).
- The cerebellum appears to play a central role in forward modeling, and its tiling/repeating motif structure is suggestive of a massive number of modules.
- Despite its clear anatomical micro-organization, a precise computational model of cerebellum that also accords with the data is still lacking.
- Not all species appear to construct inverse models for all behaviors, including crucially important behaviors (song learning in songbirds).

A biological example of temporal function learning, motor learning

The zebra finch and vocal motor learning

Zebra finches and song learning

- A special version of reservoir computing.
- Some biological motor systems optimized for learning may not use inverse models (or forward models?).

Listening, memorizing, and doing

Sensory phase (days 20-45):

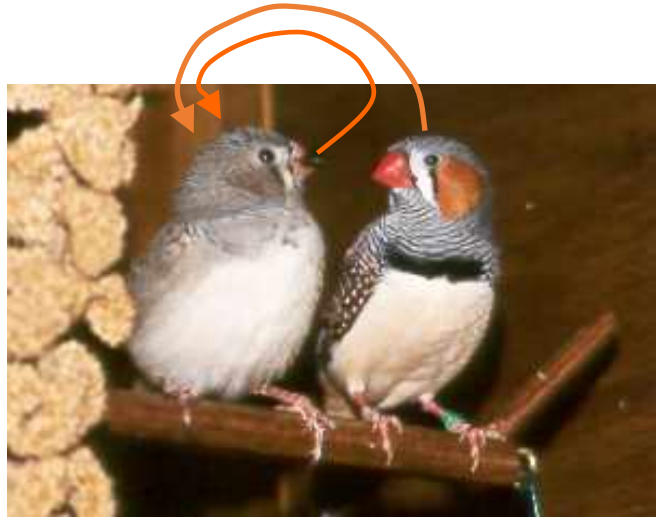
Exposure to father's song ('template') in critical period.

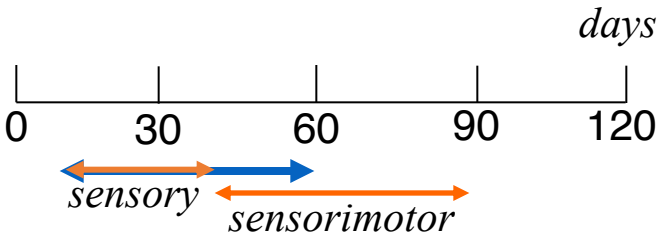
Sensorimotor phase (days 40-100):

Attempted vocalization and template matching.
Possible without tutor song.
Finch deafened now will not successfully reproduce song.
Removal of father before sensorimotor period: bird will still learn to sing father's song well.

Slow reproduction/learning of father's song suggests that the zebra finch does not possess an inverse model.

Behavior

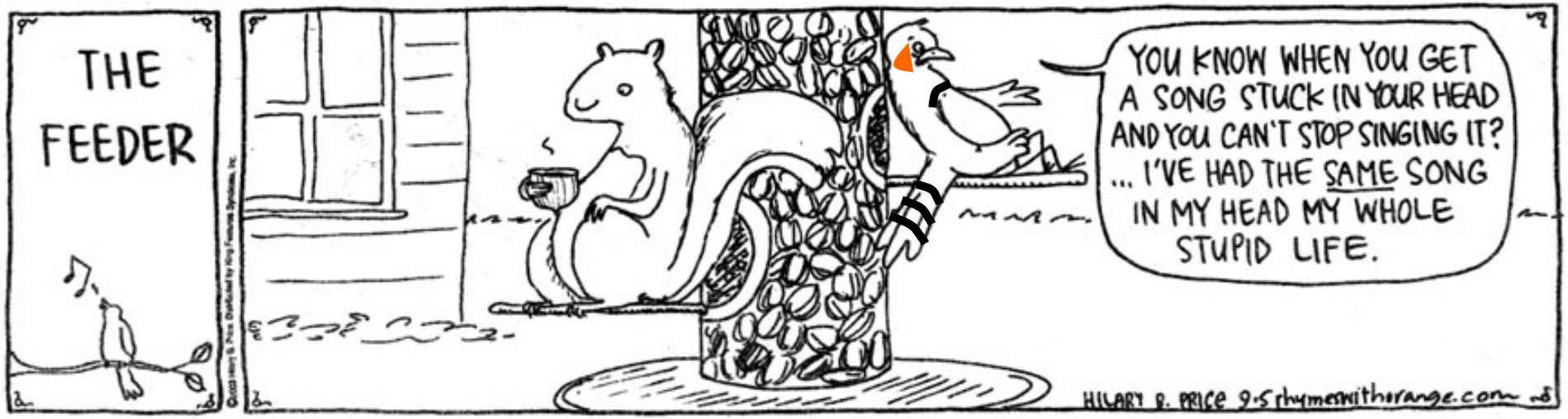




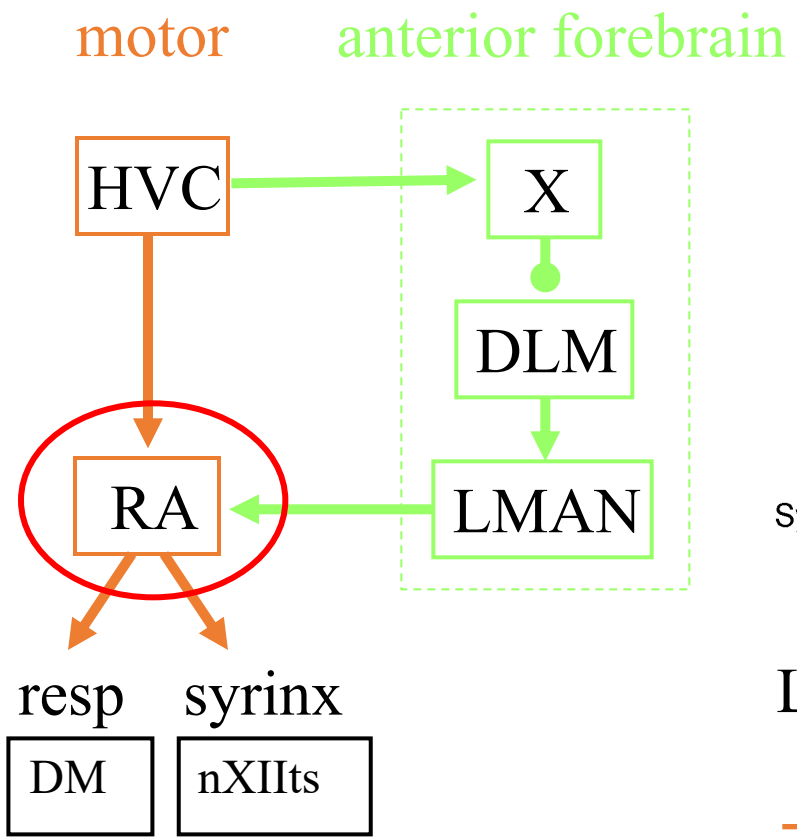
Social feedback and tutor song not needed.

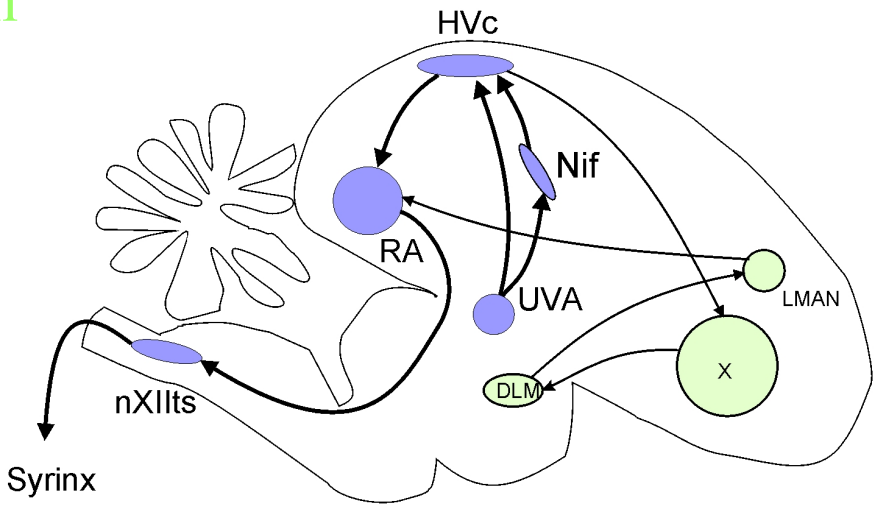
Auditory feedback of own song crucial.

RHYMES WITH ORANGE by Hilary Price



Song circuit

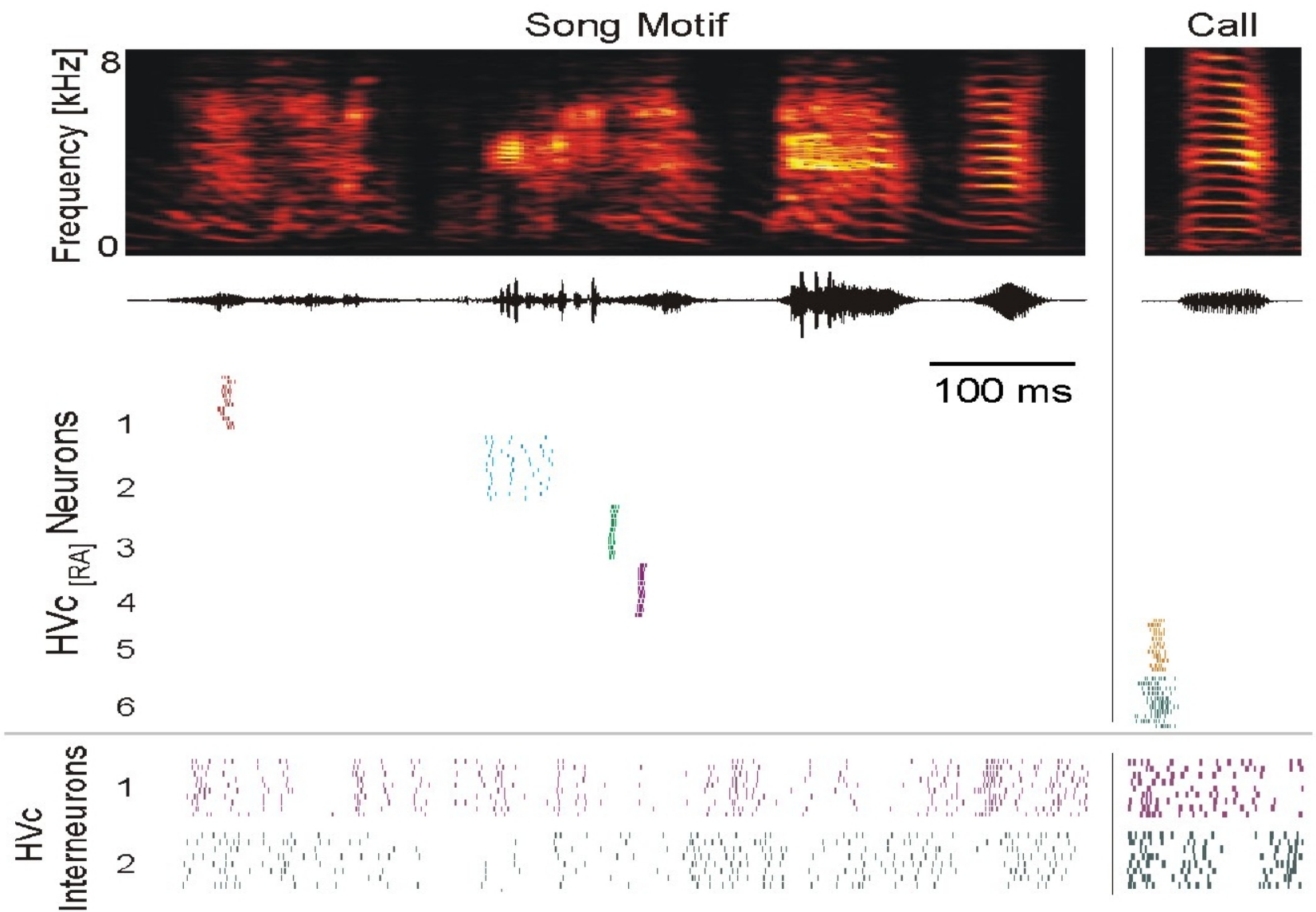




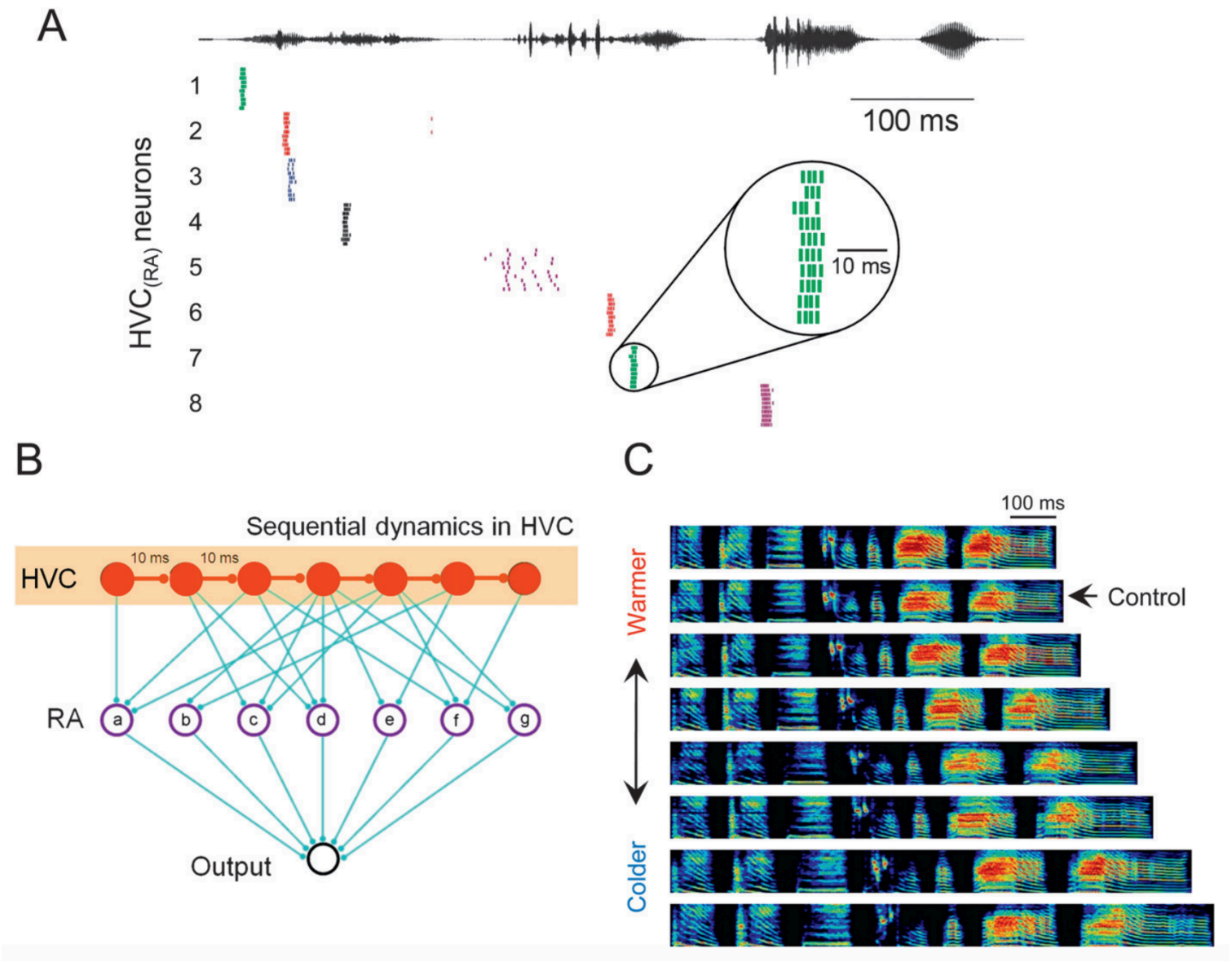
Lesion:

no song

song unaffected


Song Motif
Call
Frequency [kHz]
8
0
100 ms
HVc [RA] Neurons
1
2
3
4
5
6
HVc Interneurons
1
2

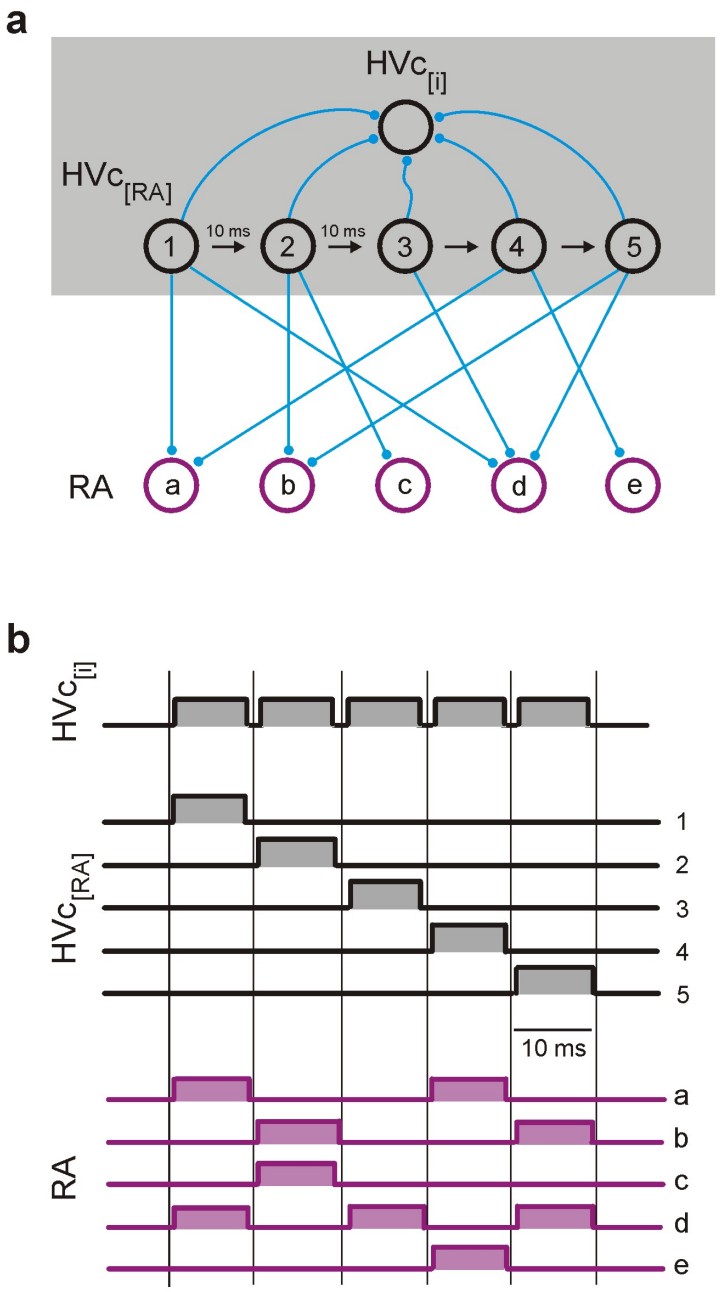
Mechanism/locus of sequence production



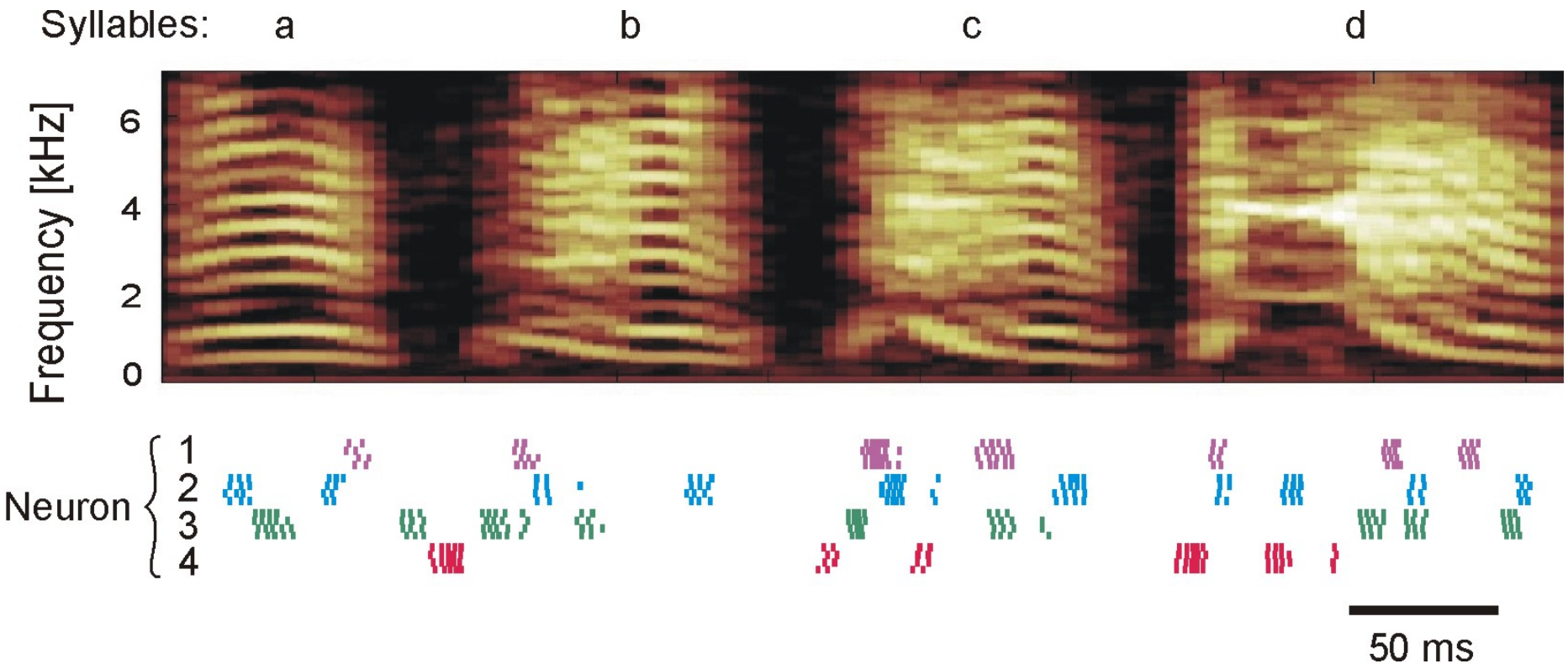
HVc activity: overview

- ~10000 HVc[RA] neurons
- Strongly adapting neurons
- Active once per song motif, for ~ 10 ms
- Burst frequency during the 10 ms: 500-600 Hz
- Several HVc neurons on at each time
- HVc interneurons sum HVc[RA] activity
- HVc activity fills time
- ~ 70 - 80% of RA activity driven by HVc

Heuristic model:
HVC as a special reservoir



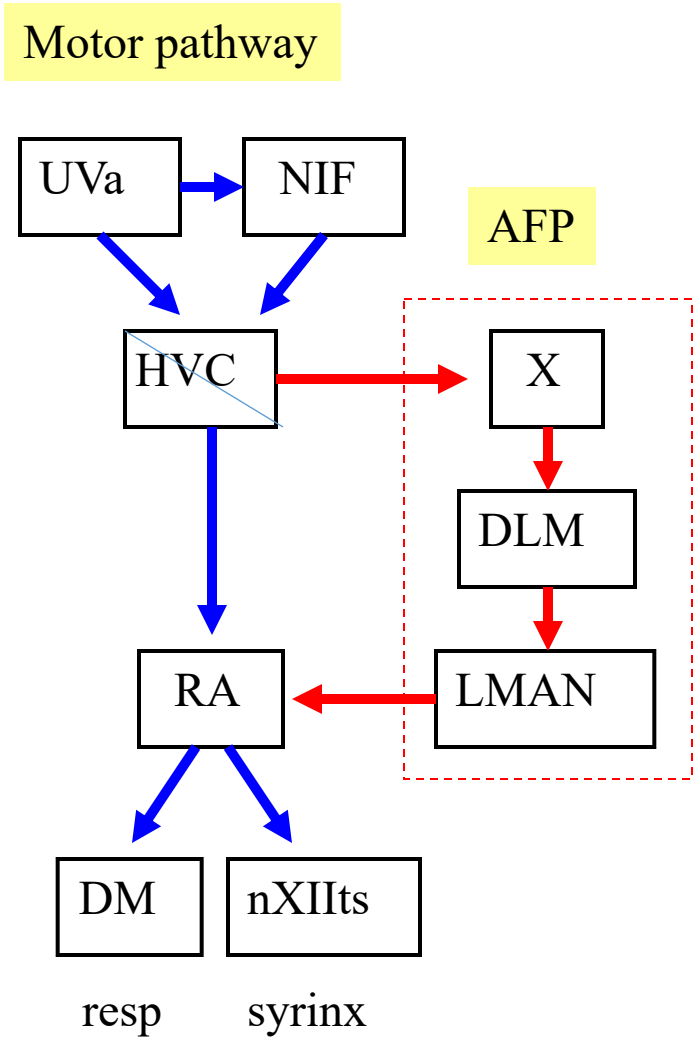
RA activity



RA activity: overview

- ~ 10000 RA neurons
- f-I curve roughly linear
- Each neuron active during 10% of song motif
- Burst duration variable
- Frequency of spiking ~ 500-600 Hz

What about the non-motor pathway?

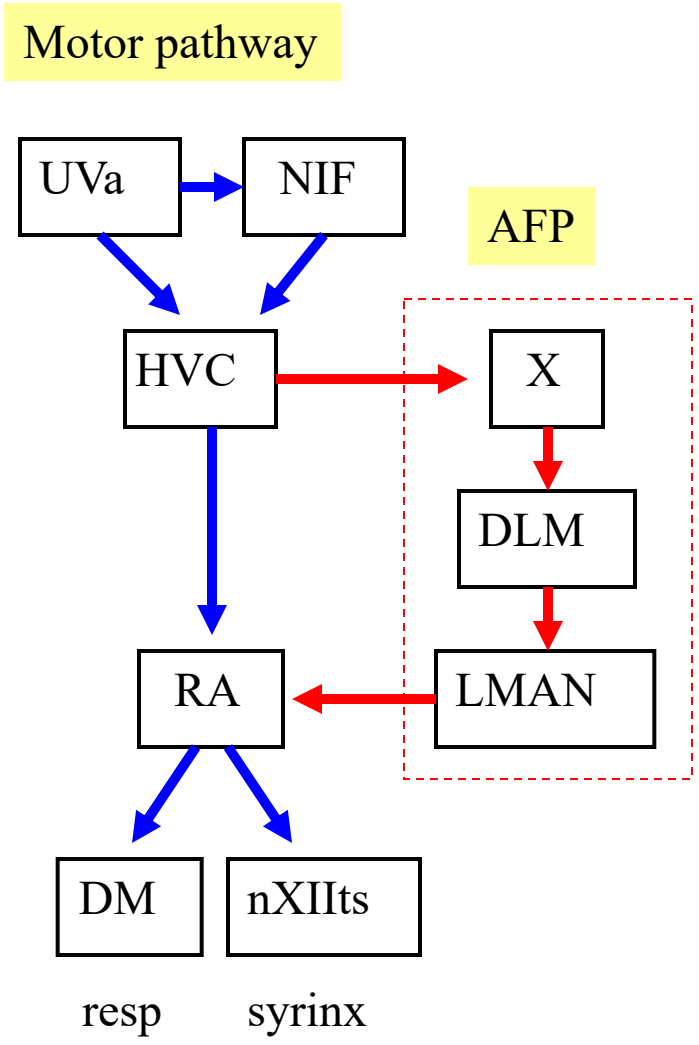


Lesion AFP in *mature* bird
→ no immediate song deterioration

Lesion AFP in *young* bird
→ learning compromised

AFP important for learning.

Distorted auditory feedback

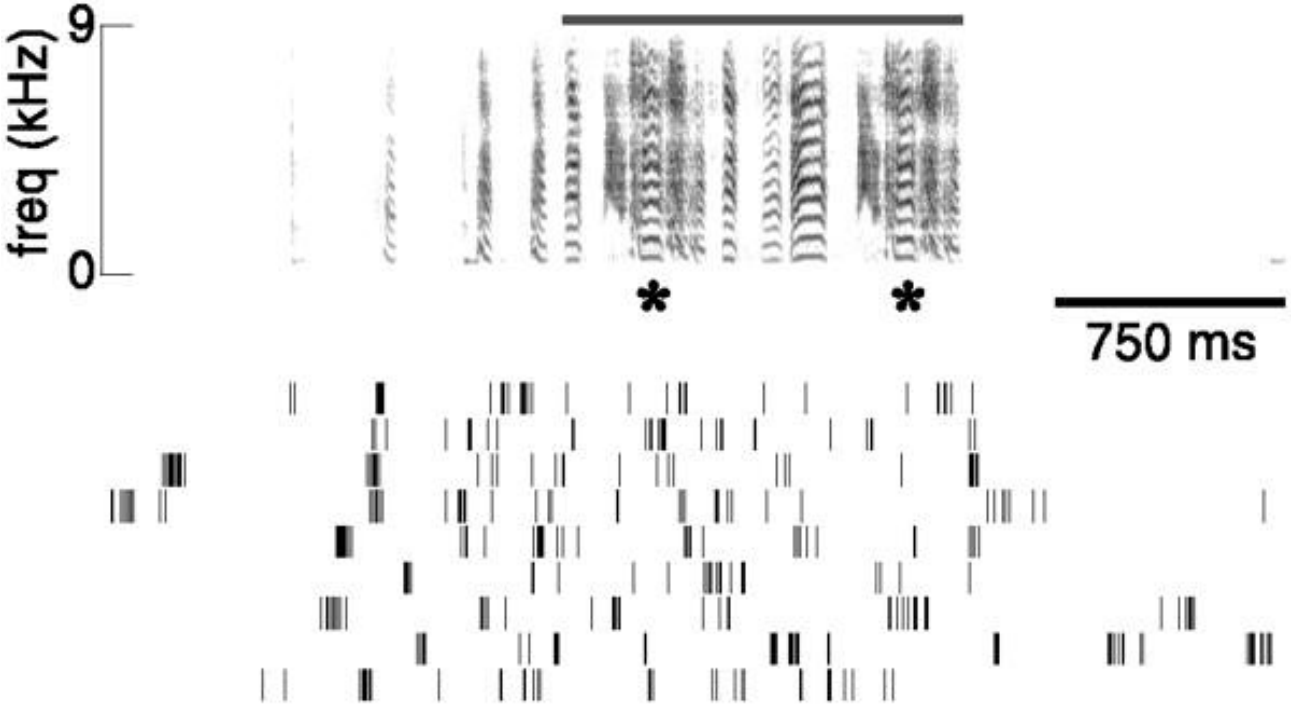


Distorted feedback
→ song becomes unstable (increasing errors)

Distorted feedback and AFP lesion
→ no song deterioration (error-based learning stops?)

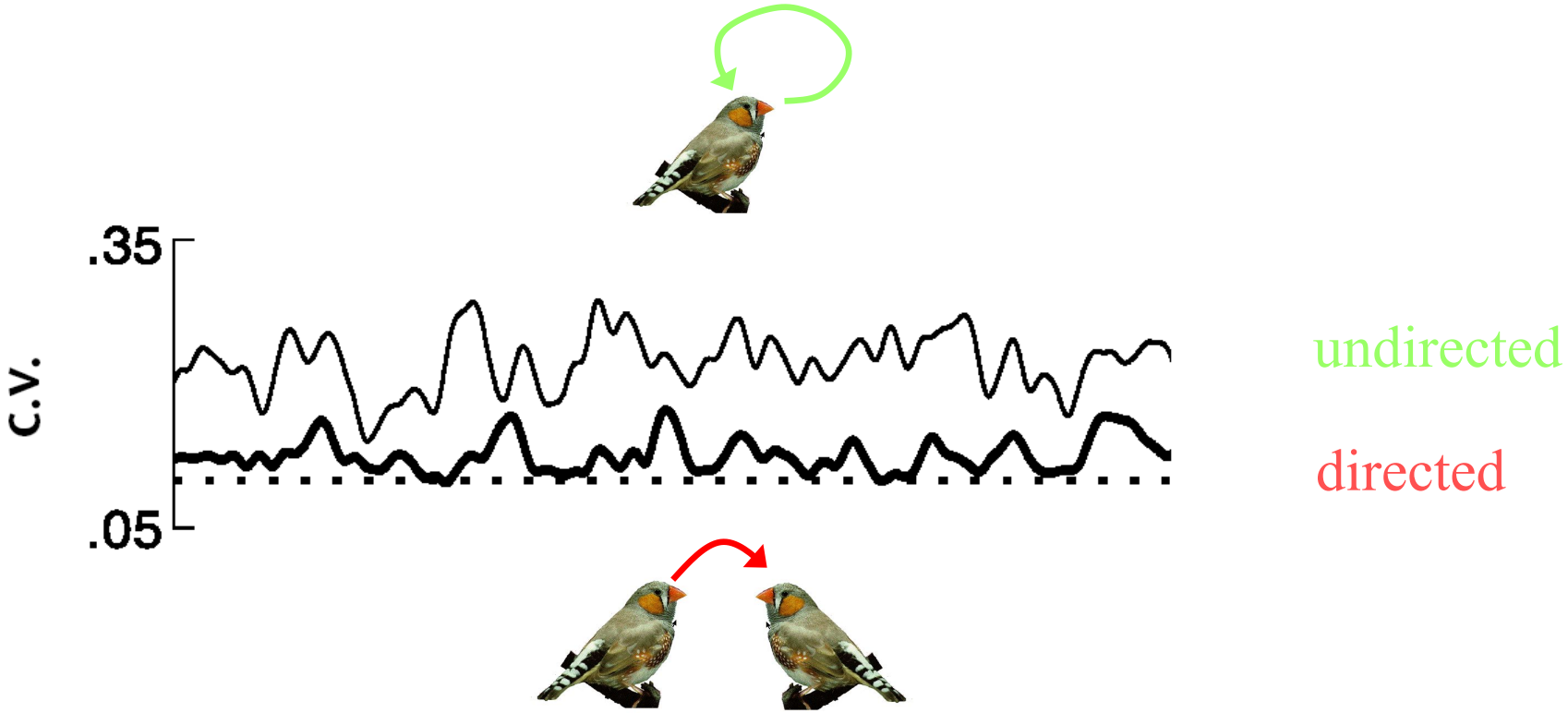
AFP important for error-based learning.

Looking inside the AFP: LMAN activity is variable



Hessler & Doupe

LMAN variability in practice vs performance



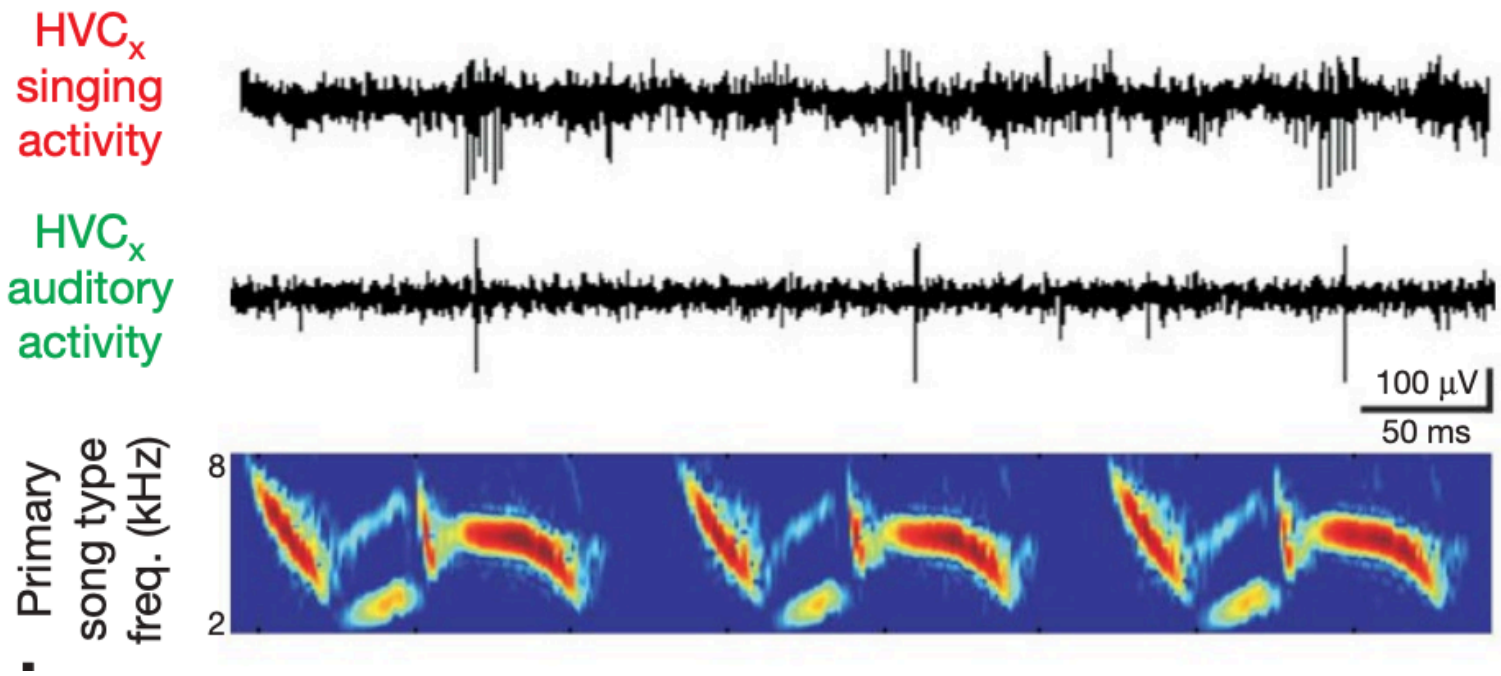
Hessler and Doupe, 1999

LMAN lesion in adult

- No immediate change in song.
- Gradual degradation of song.

→ AFP important in keeping the system tuned-up.

A forward model? Songbird mirror neurons



Singing (unaffected by auditory distortion so likely motor efference not auditory)

Listening

Prather,…, Mooney 2008

Songbirds and motor sequence learning

- Zebra finch do not seem to use an inverse model: they learn through an extended period of sensorimotor matching.
- Forward model: potentially exists – songbird mirror neurons
- HVC a simple reservoir?

A preview: Learning rules in the brain (biologically plausible learning rule models)

Central idea of learning by reinforcement

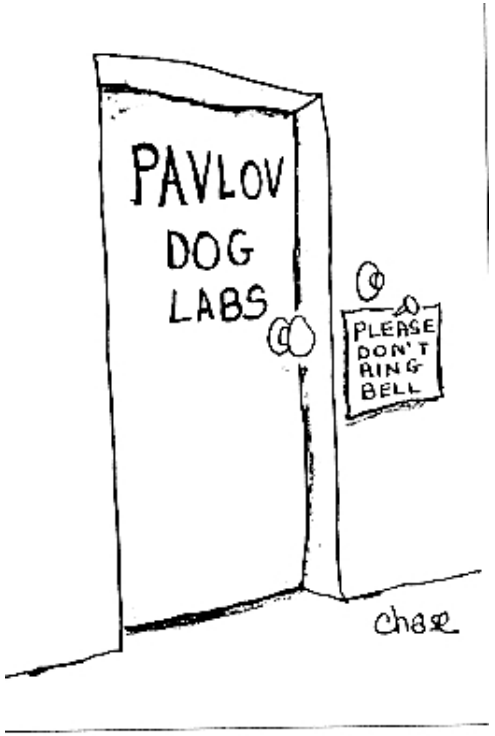
Exploratory neuronal activity (driven by noise), coupled with a reward dependent on activity leads to the reinforcement of rewarded (desired) behaviors.

Simple algorithm

1) *Neuronal responses are often 'noisy'.*
2) *Compute outcome due to noisy output.*
3) *If outcome better than past or expected outcomes, reinforce parameters so future neuronal responses more likely to resemble the recent activity.*

Reinforcement vs Hebbian learning

Classical conditioning – Pavlov's dog:
Reward not contingent on behavior



Operant conditioning –
Reward administered based on behavior

Reinforcement loop