A reinforcement learning model of song acquisition in the bird

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9.54

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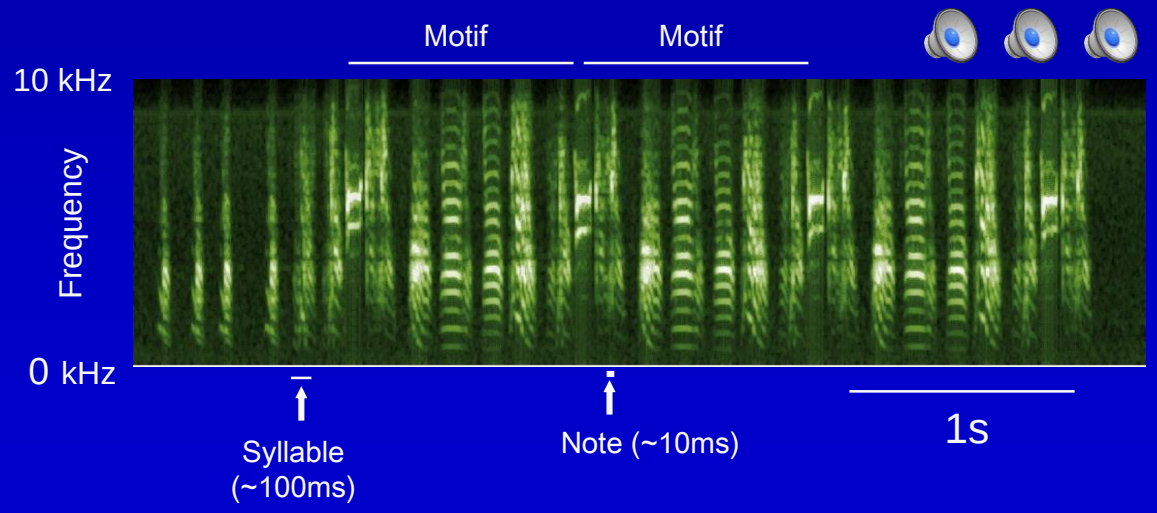
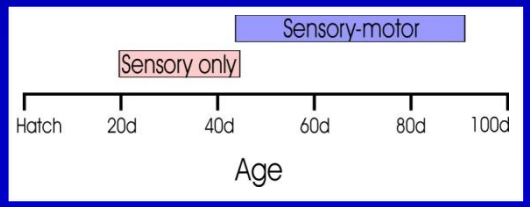
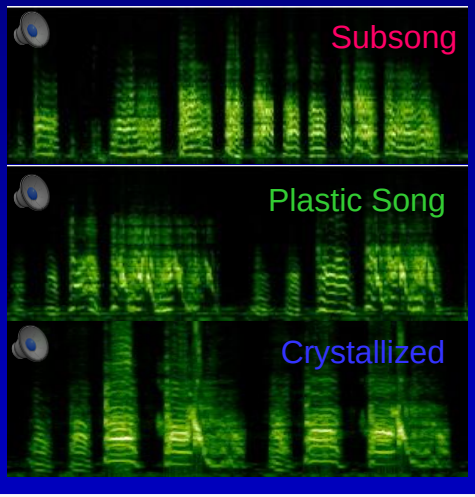
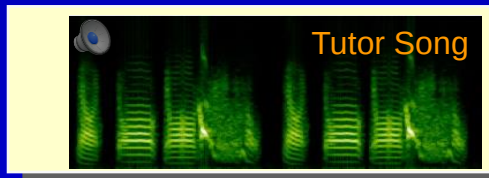
Structure of zebra finch song



Songbirds learn to sing by imitating their parents



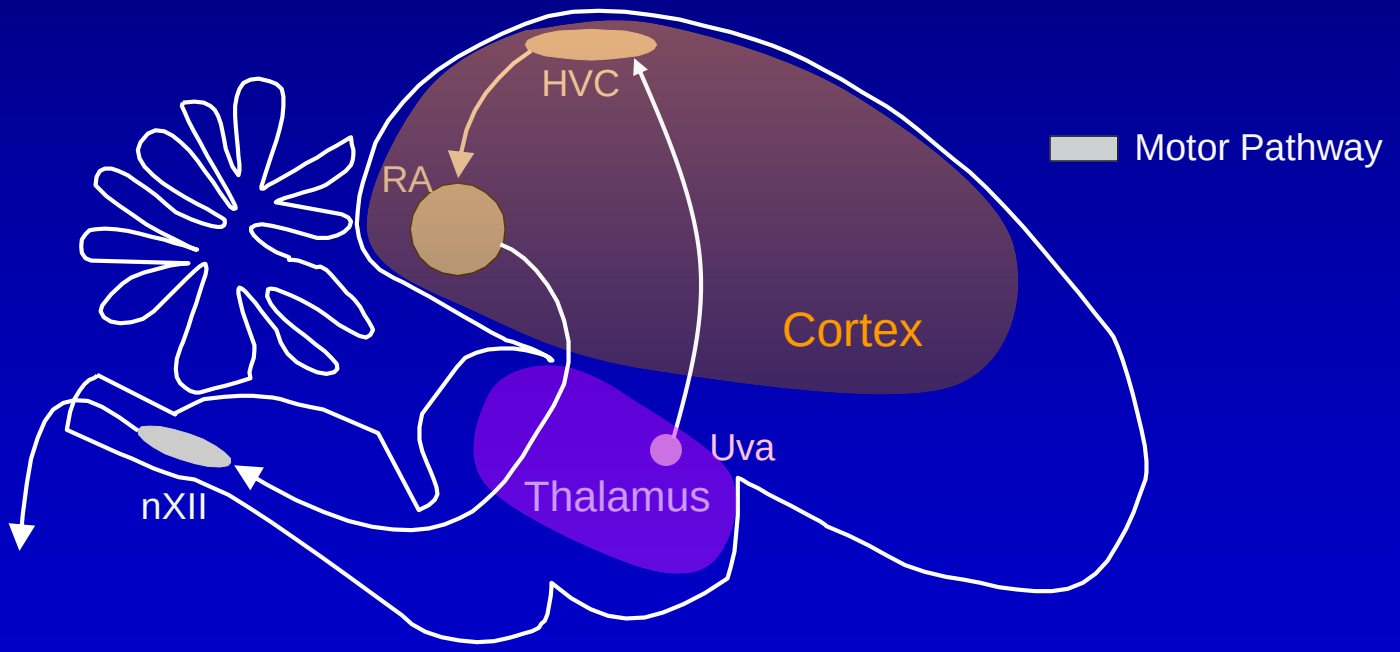




Overview

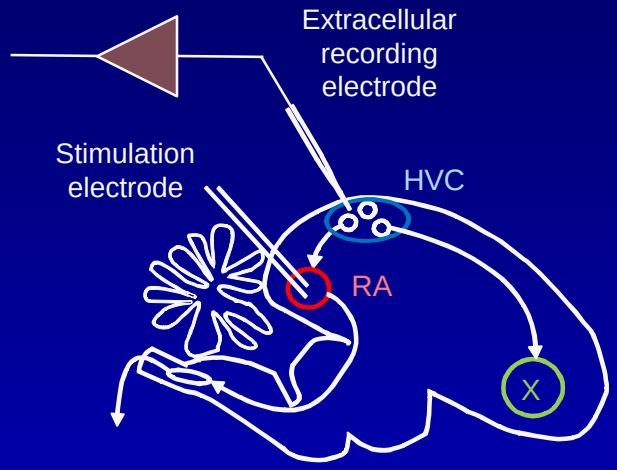
- The songbird as a model system for understanding how the brain generates and learns complex sequential behaviors
- Review some current understanding of the mechanisms of song production
- Describe progress in elucidating the role of cortical and basal ganglia circuits in song learning.
- Some speculations on how insights from the songbird may inform our understanding of mammalian BG function

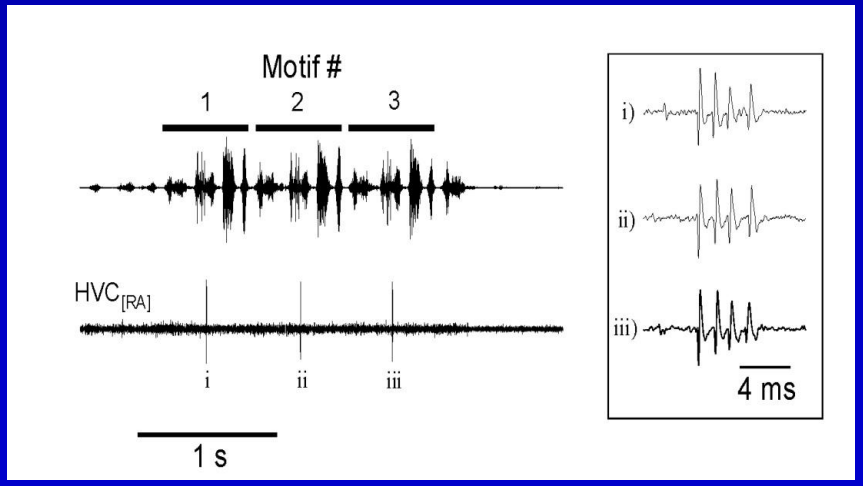
A circuit for vocal production

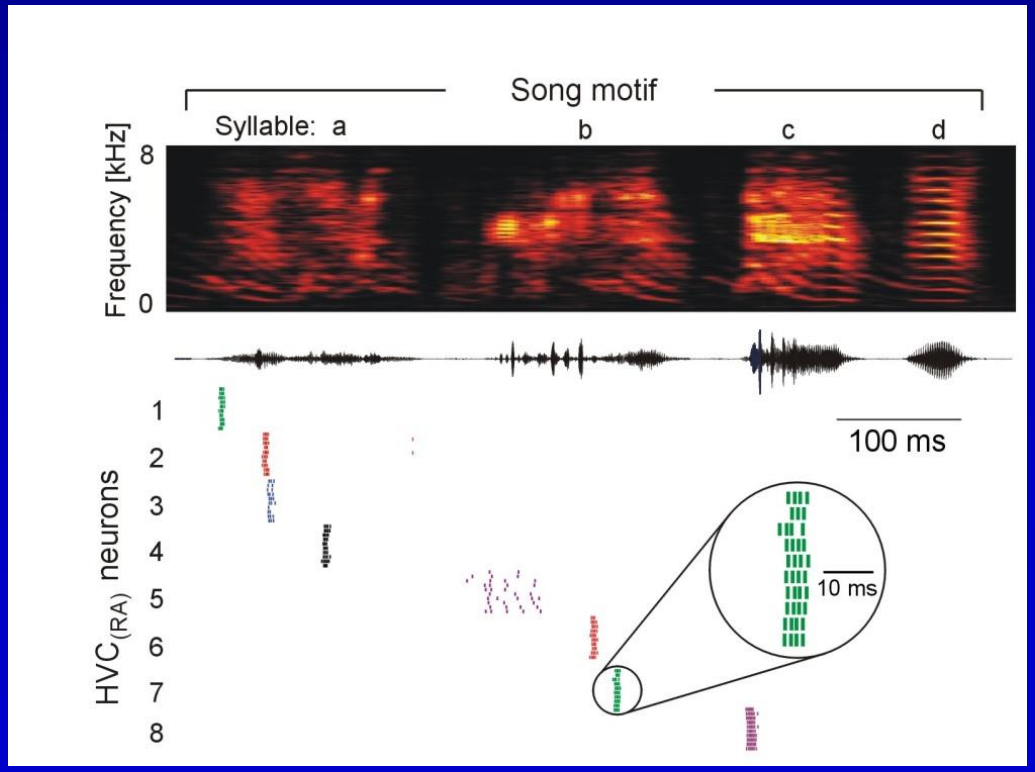


Nottebohm et al, 1976, 1982

Antidromic activation allows identification of RA-projecting neurons in HVC

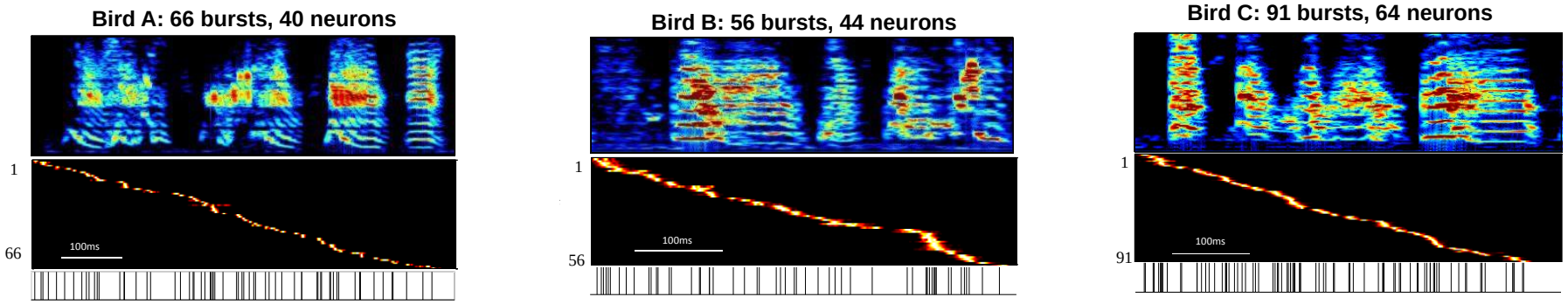




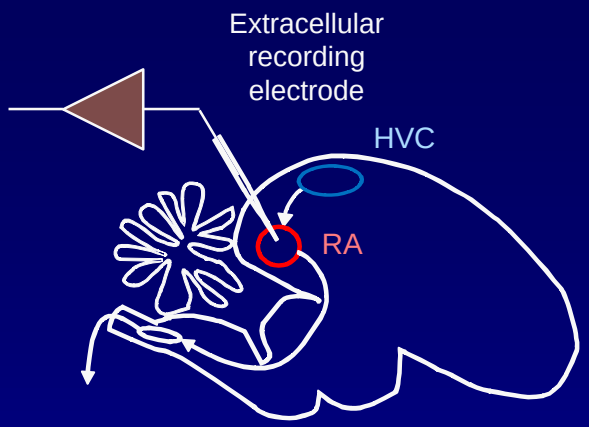


Hahnloser, Kozhevnikov and Fee, 2002

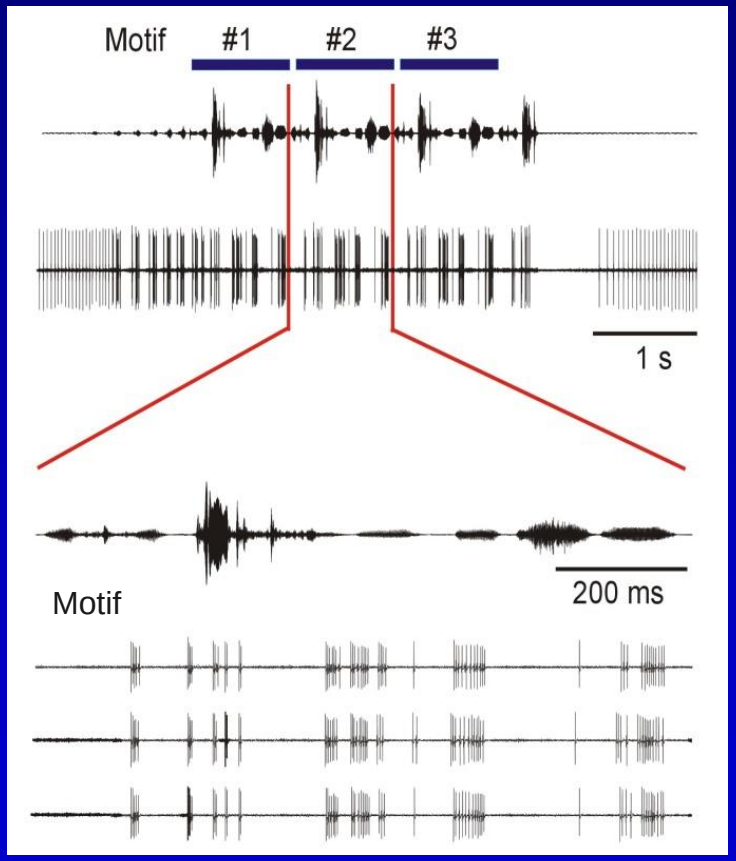
HVC neurons burst throughout the song



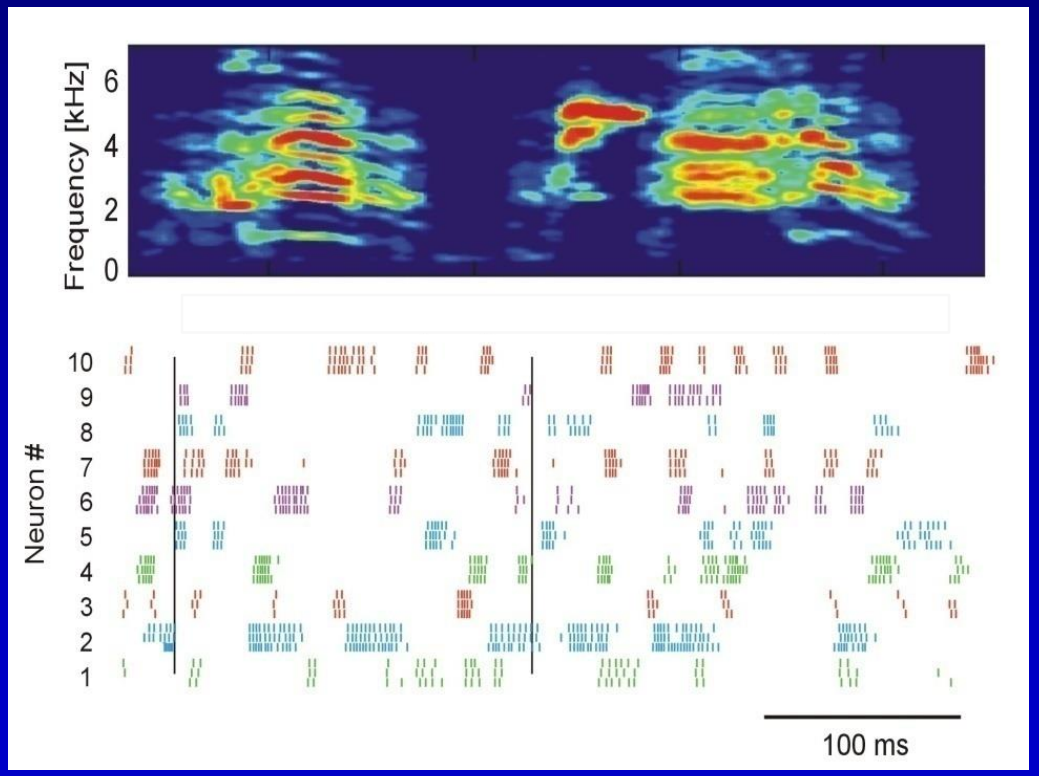
Lynch, Okubo and Fee, *in preparation*



Activity of RA neurons during singing

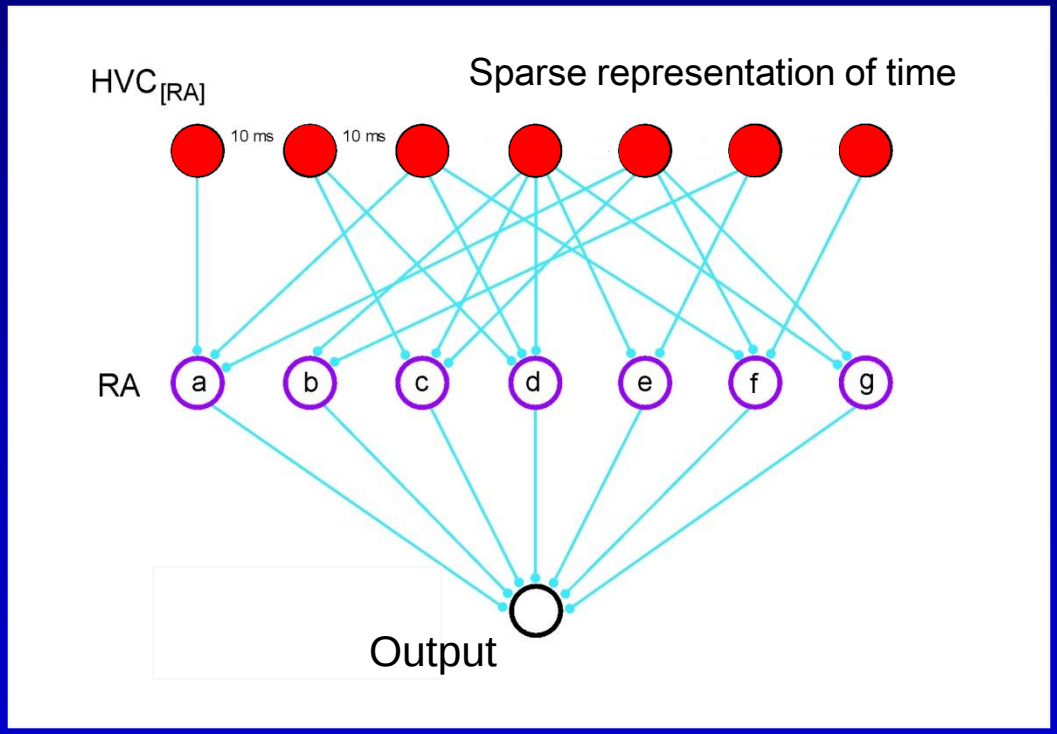


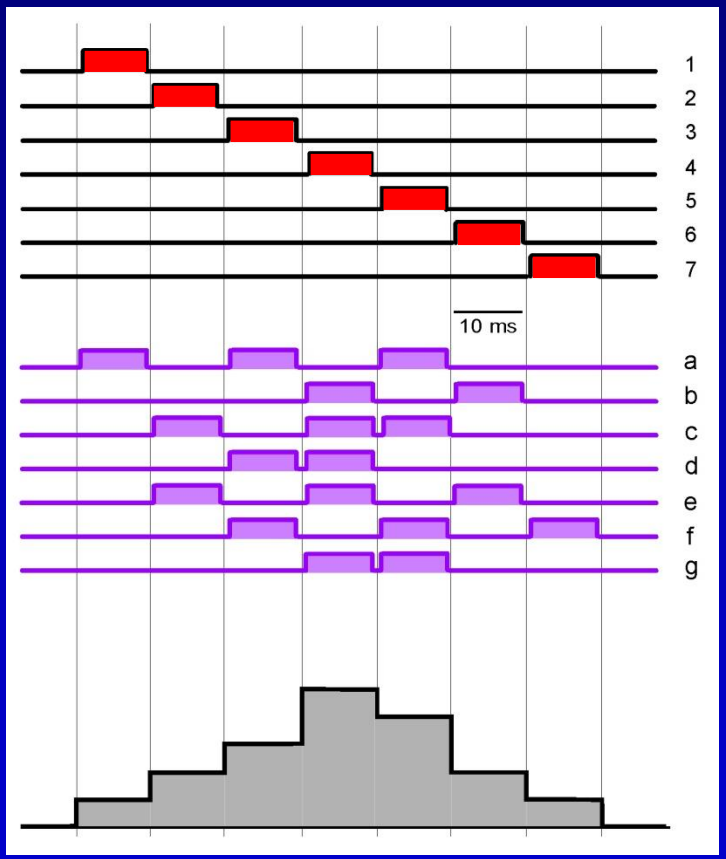
Yu and Margoliash, 1996



Leonardo and Fee, 2005

Simple sequence generation circuit





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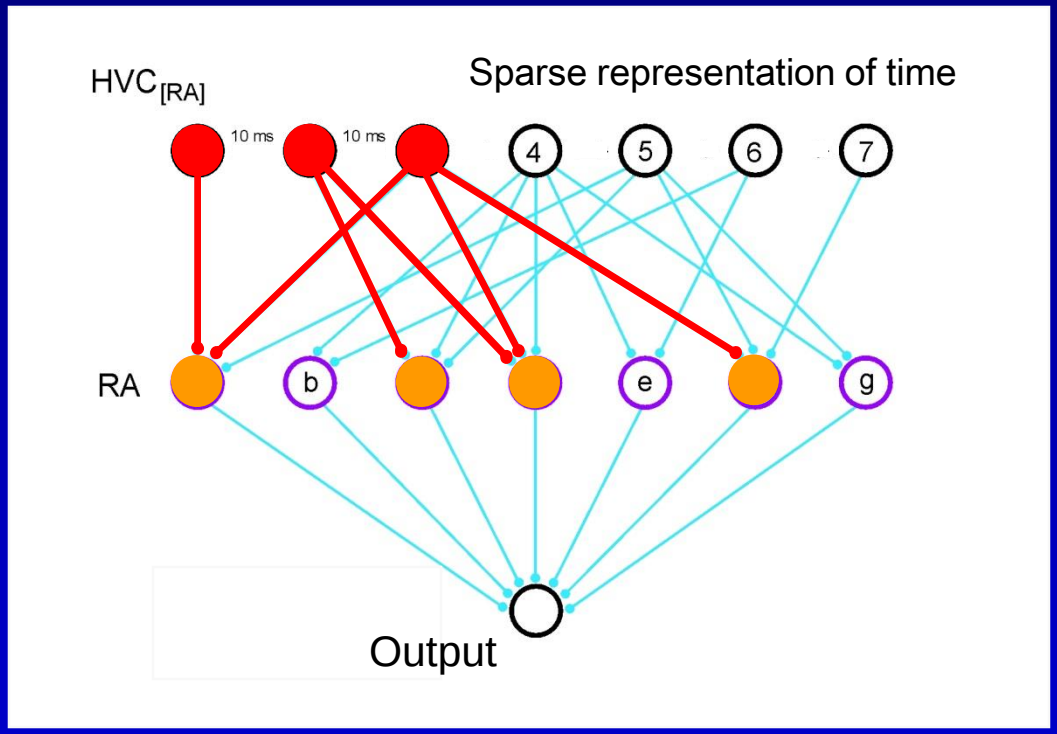
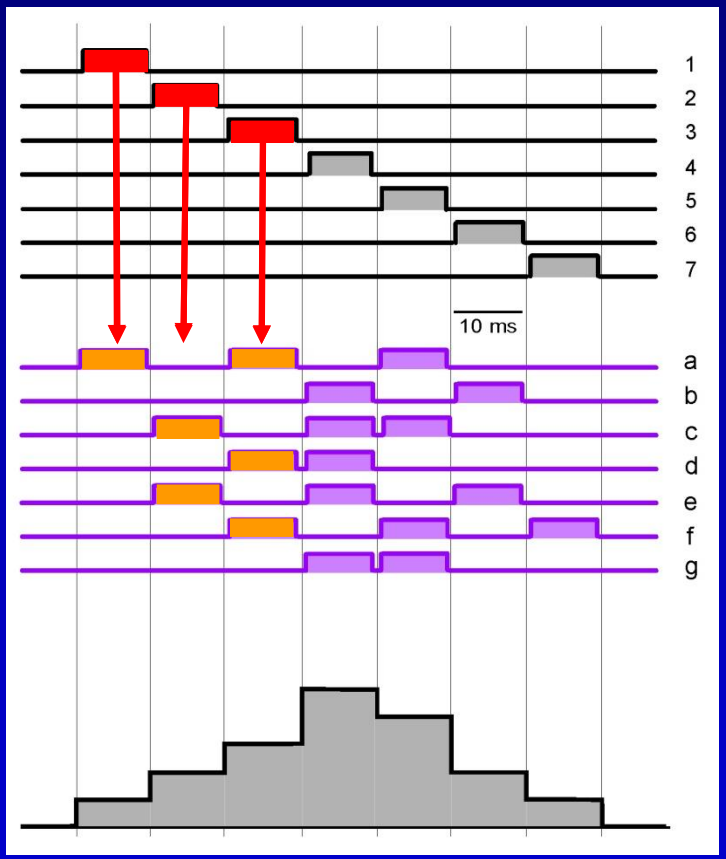
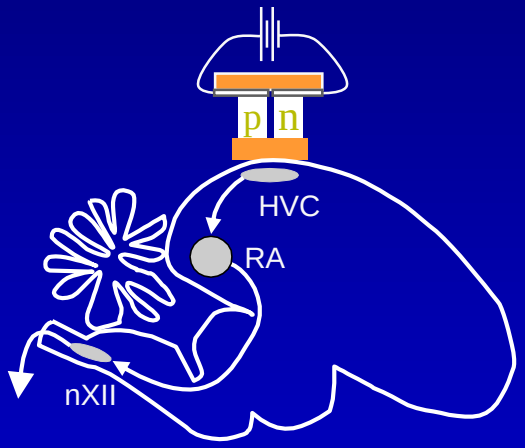


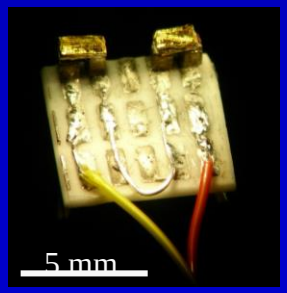


Leonardo and Fee, 2005

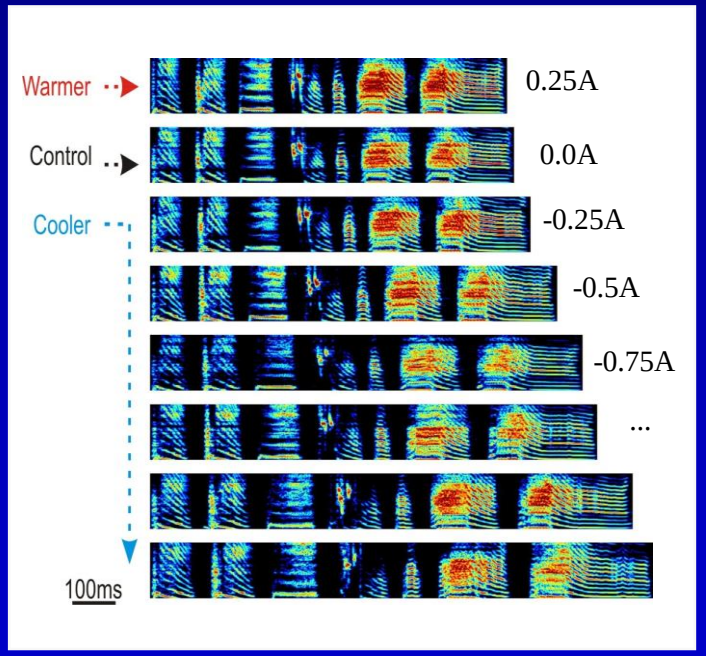
HVC is the 'clock' of the song motor pathway

Brain cooling to localize dynamics



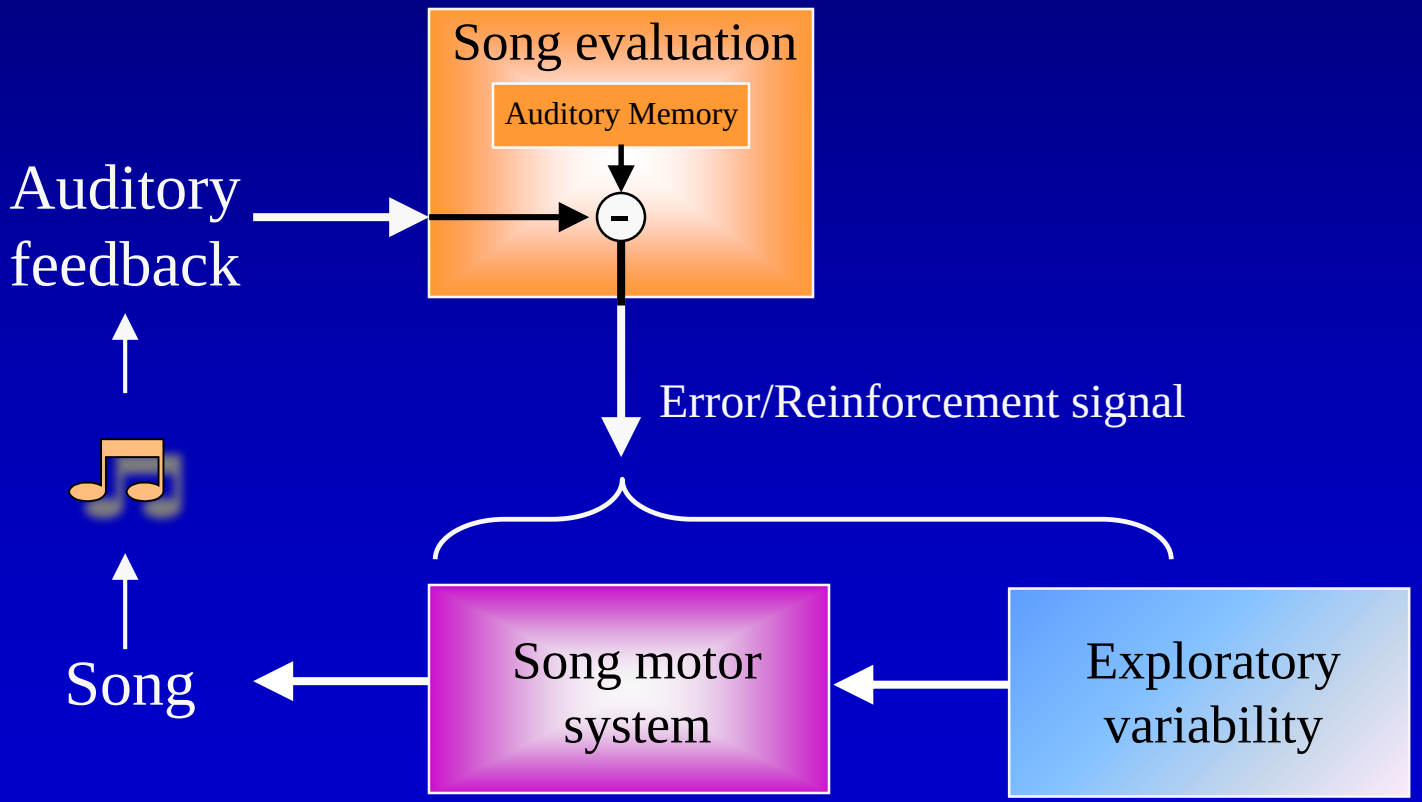


Bilateral cooling of HVC causes uniform slowing of the song



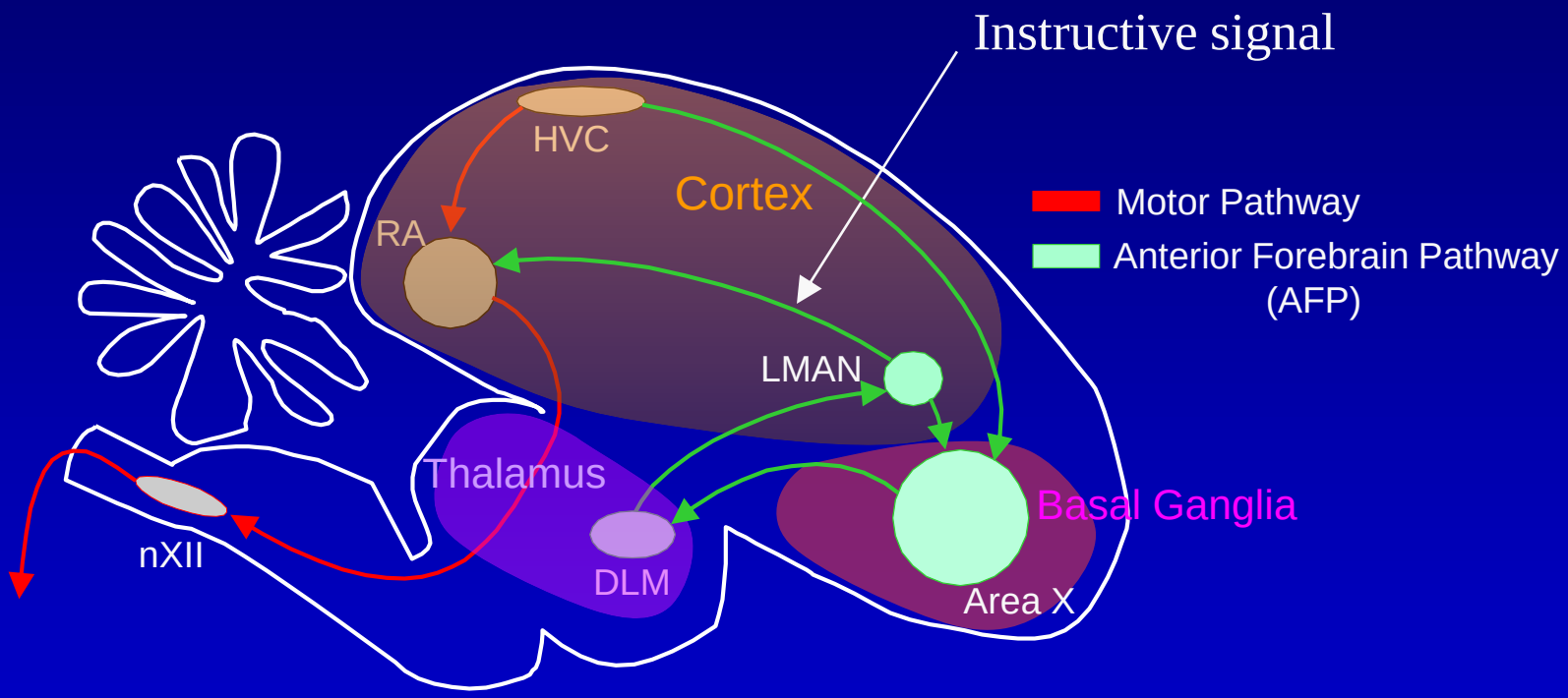
Long and Fee, Nature 2008

A simple reinforcement model of song learning



Doya and Sejnowski, 1989

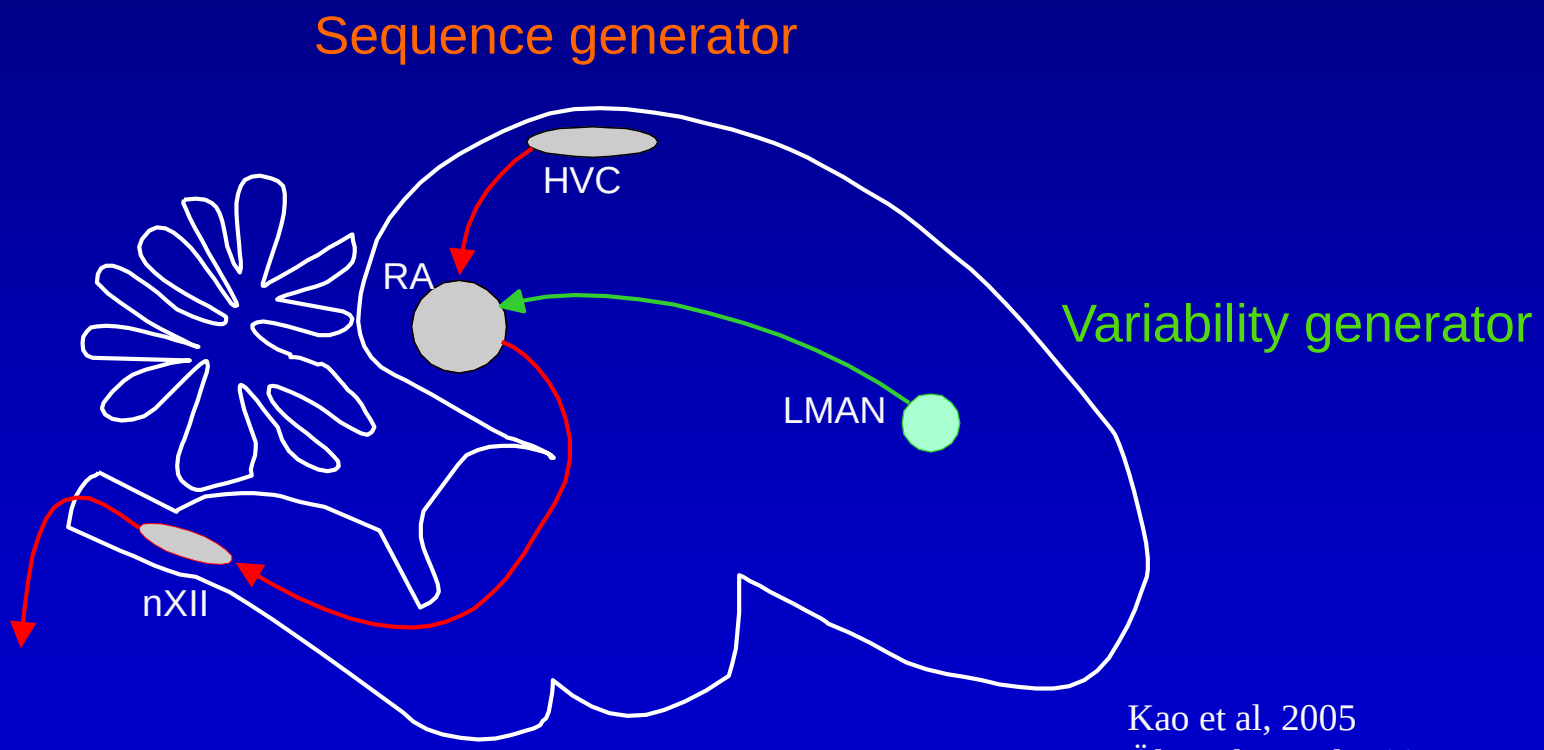
A separate circuit for song learning



•The learning pathway is not necessary for adult song production , but is required for learning (Bottjer, 1984, Scharff and Nottebohm, 1991)

•Bottjer proposed that the AFP transmits an instructive signal that guides plasticity in the motor pathway

Separate premotor pathways for stereotyped song and variability



Kao et al, 2005
Ölveczky et al, 2005
Aronov et al, 2008
Stepanek and Doupe, 2010

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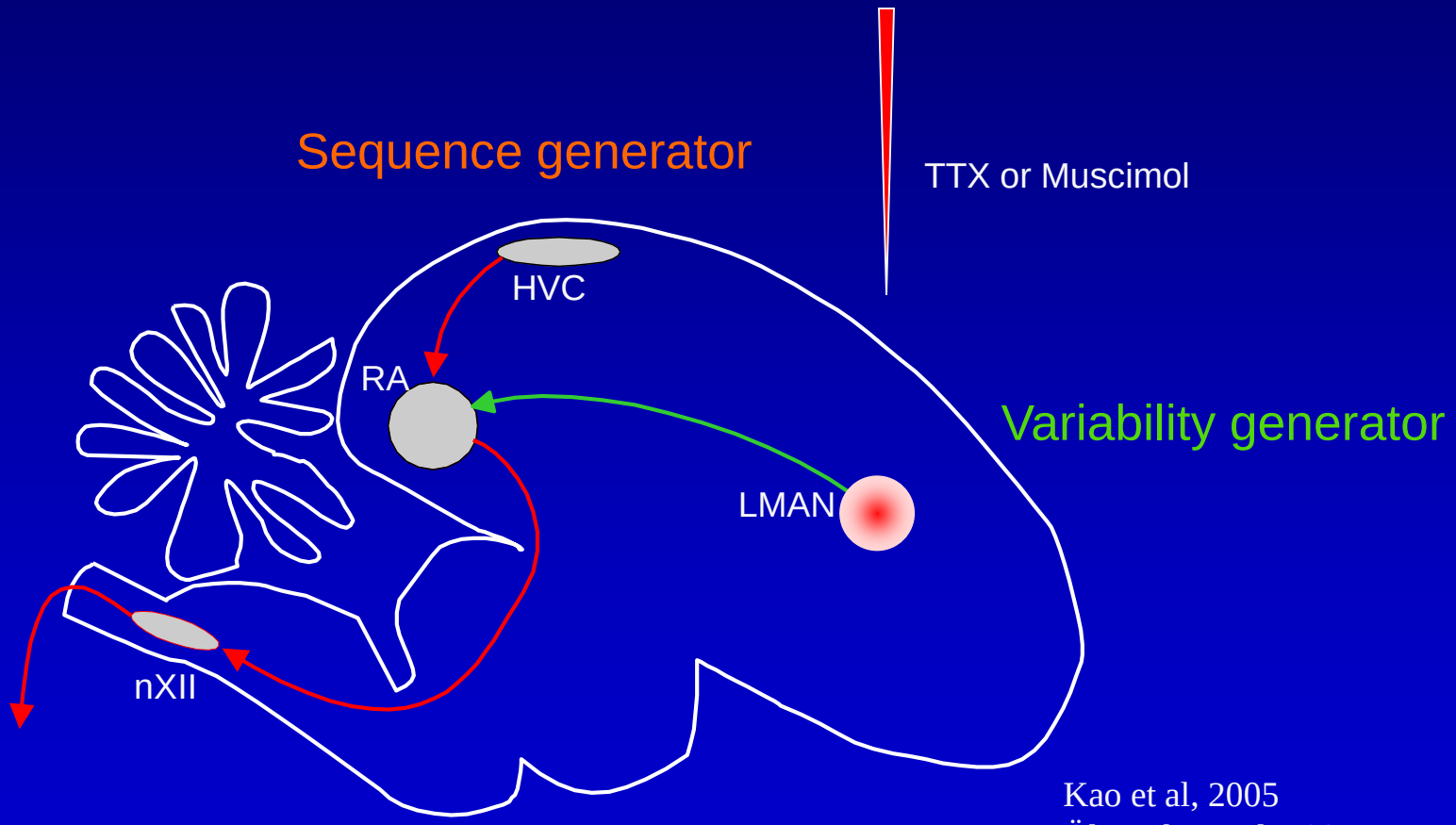

Kao et al, 2005
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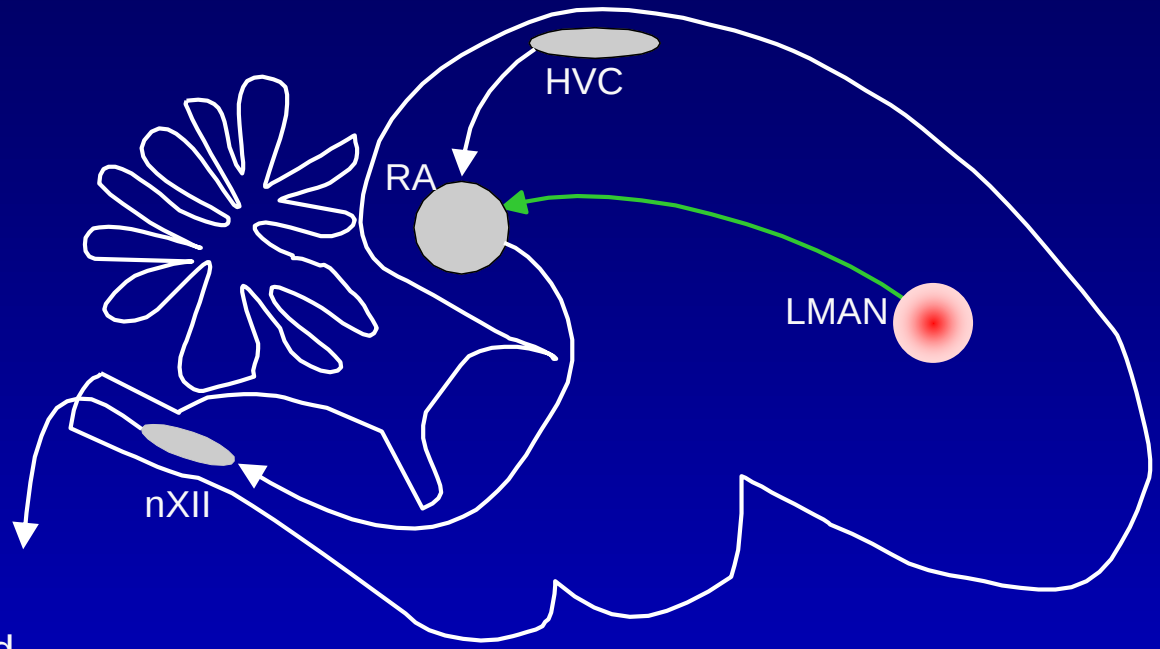
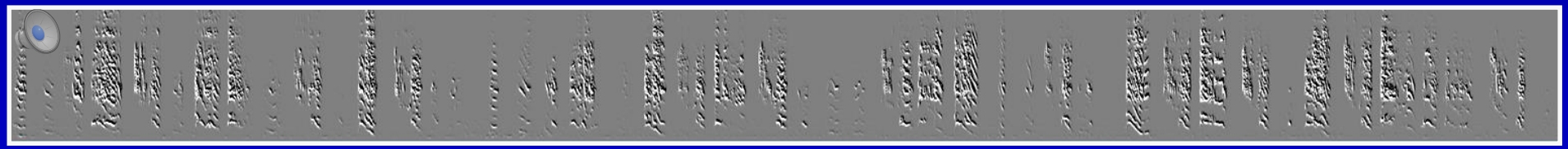
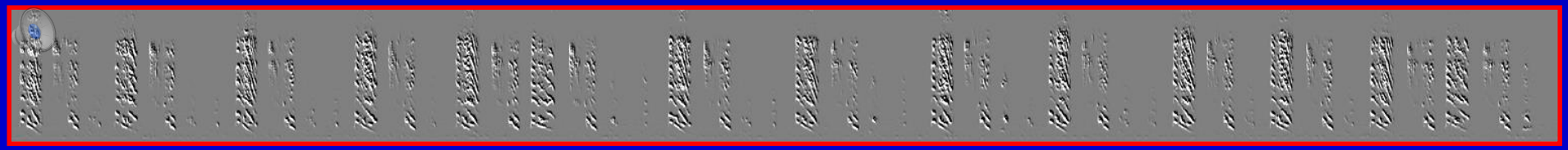
Stepanek and Doupe, 2010

Transient inactivation of the learning pathway



55 day old bird

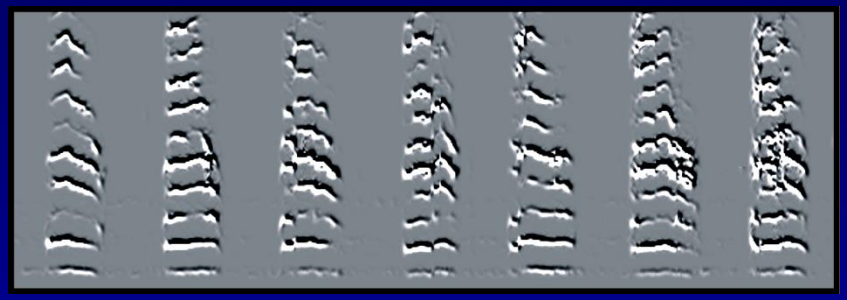




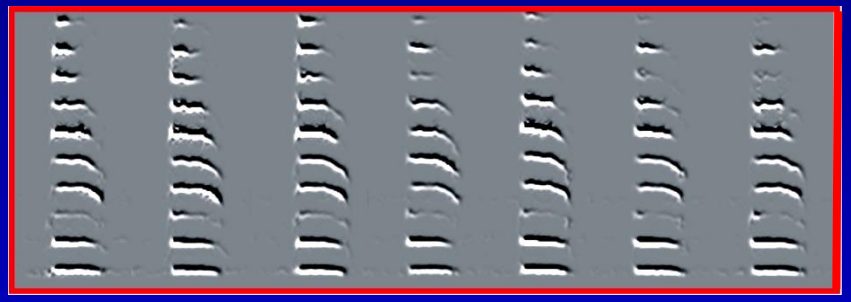
Olveczky, Andalman, and Fee, 2005

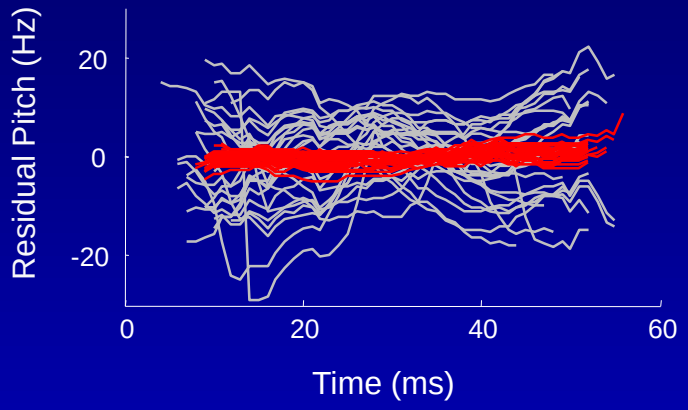
LMAN drives exploratory variability in song

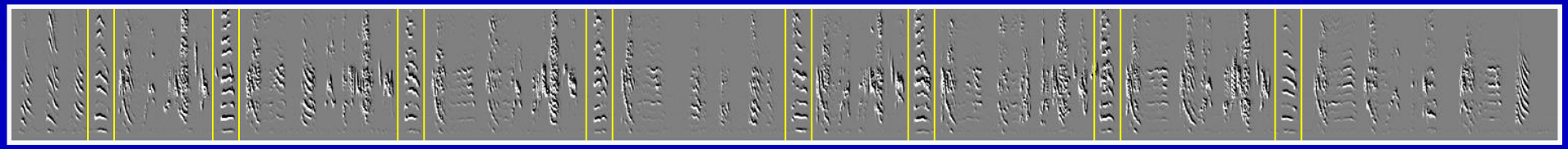
LMAN intact

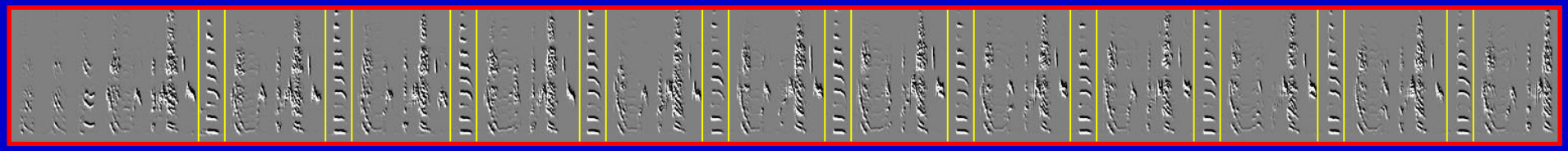


LMAN inactivated



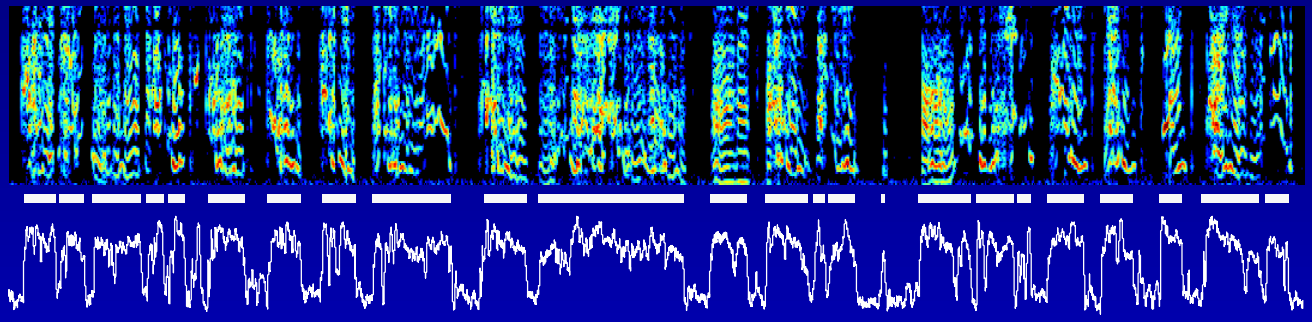




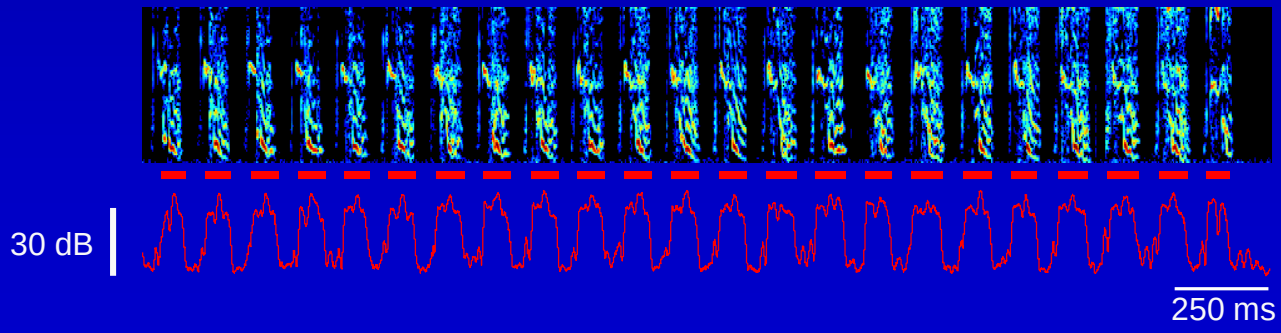


LMAN also drives early song 'babbling'

LMAN intact

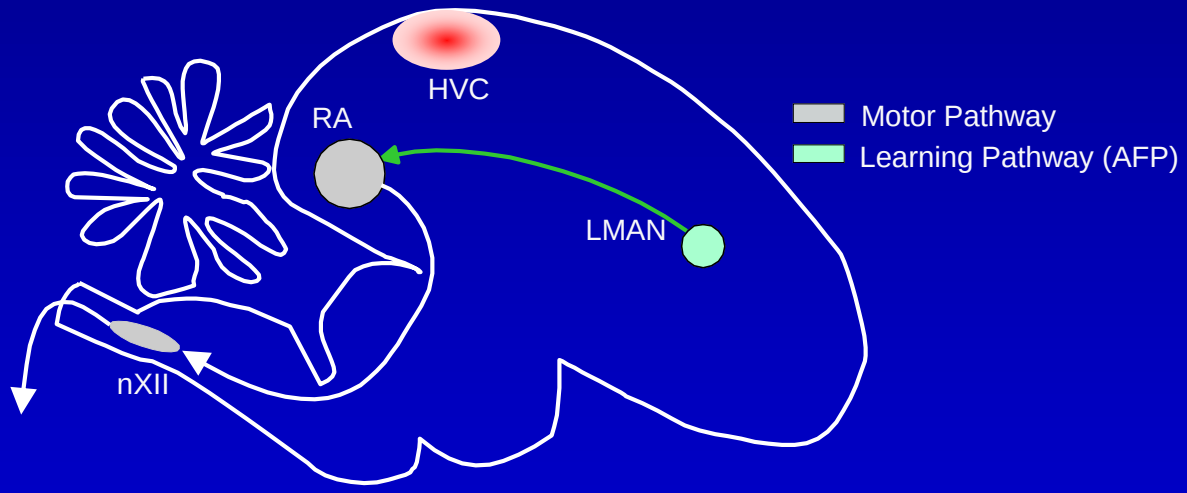


LMAN inactivated

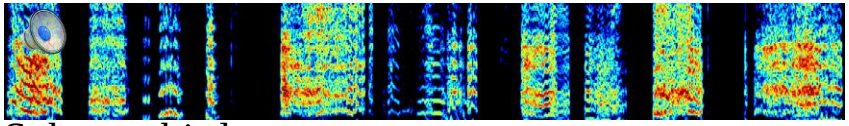
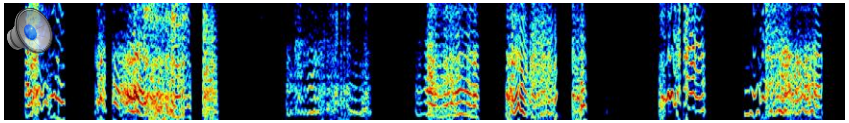
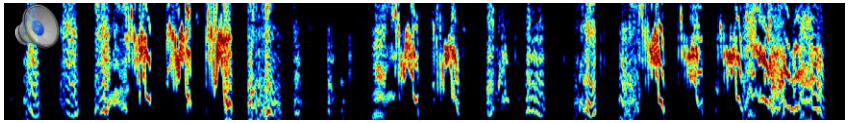
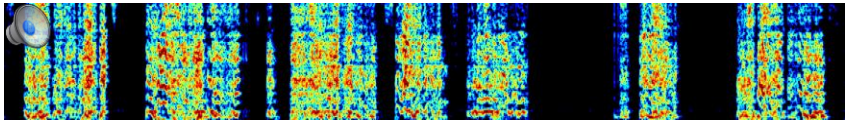
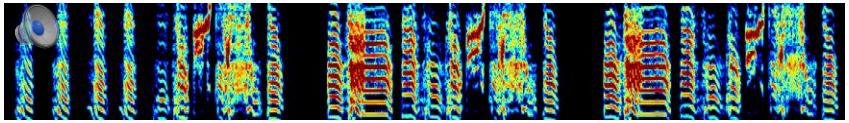
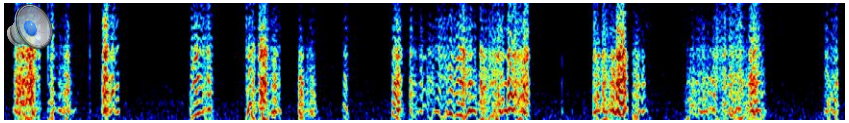


Goldberg and Fee, 2011

HVC lesions abolish all stereotyped song structure



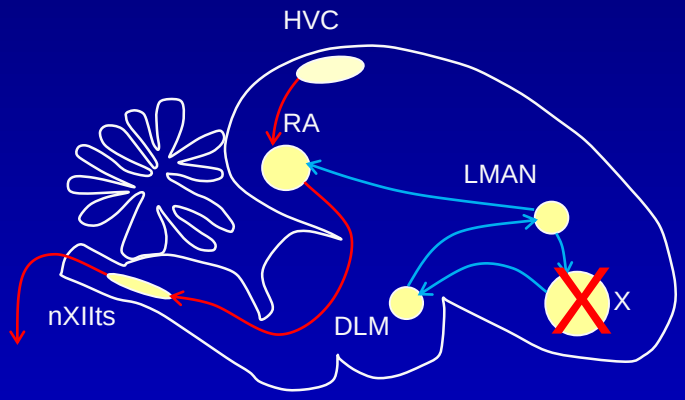
HVC lesions abolish all stereotyped song structure

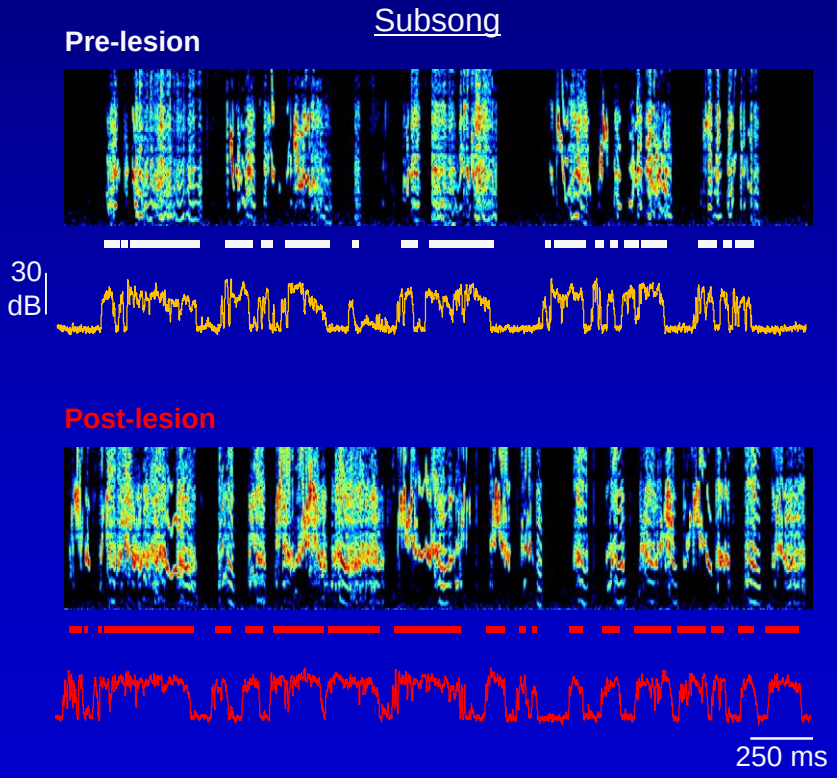
Pre HVC lesion	Post HVC lesion
 Subsong bird	
 Plastic song bird	
 Adult bird	

Aronov, Andalman and Fee, Science 2008,

- Transient pharmacological inactivation of HVC produces the same effect

The basal ganglia are not necessary for subsong or vocal variability in juvenile birds

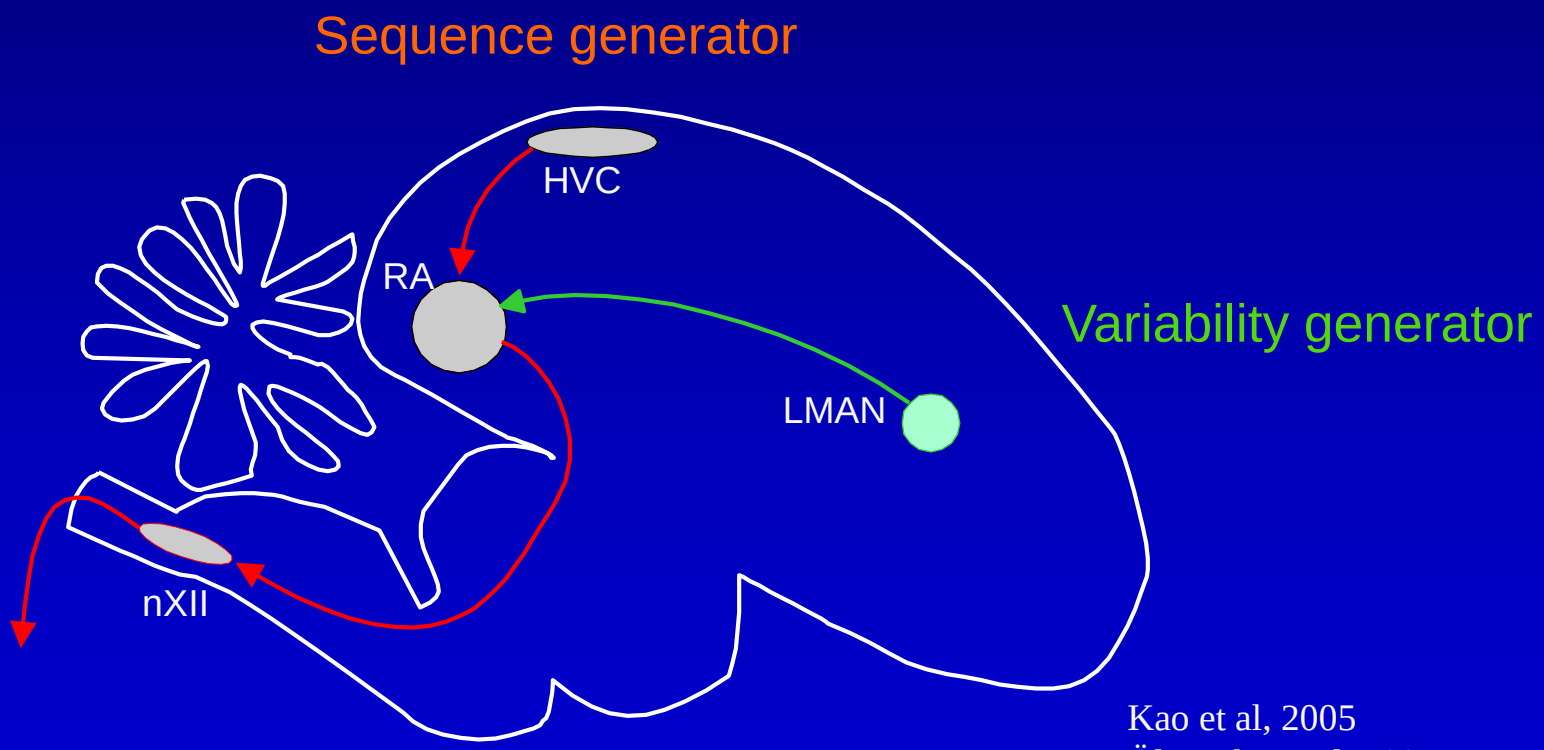




- Lesions of the BG have little or no acute effect on juvenile song variability.
- Local cooling in LMAN slow timescales of babbling ➔ exploratory vocal variability is generated by local circuit dynamics *within LMAN*.

Goldberg and Fee, 2011

Separate premotor pathways for stereotyped song and variability



Kao et al, 2005
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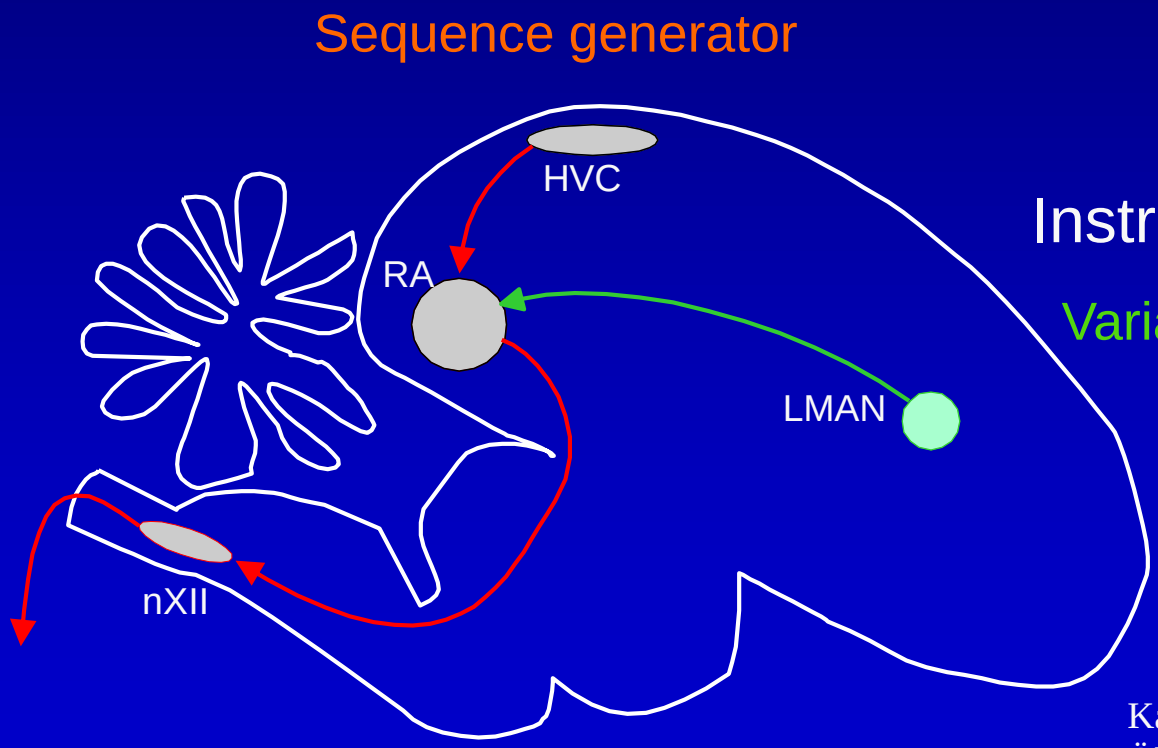

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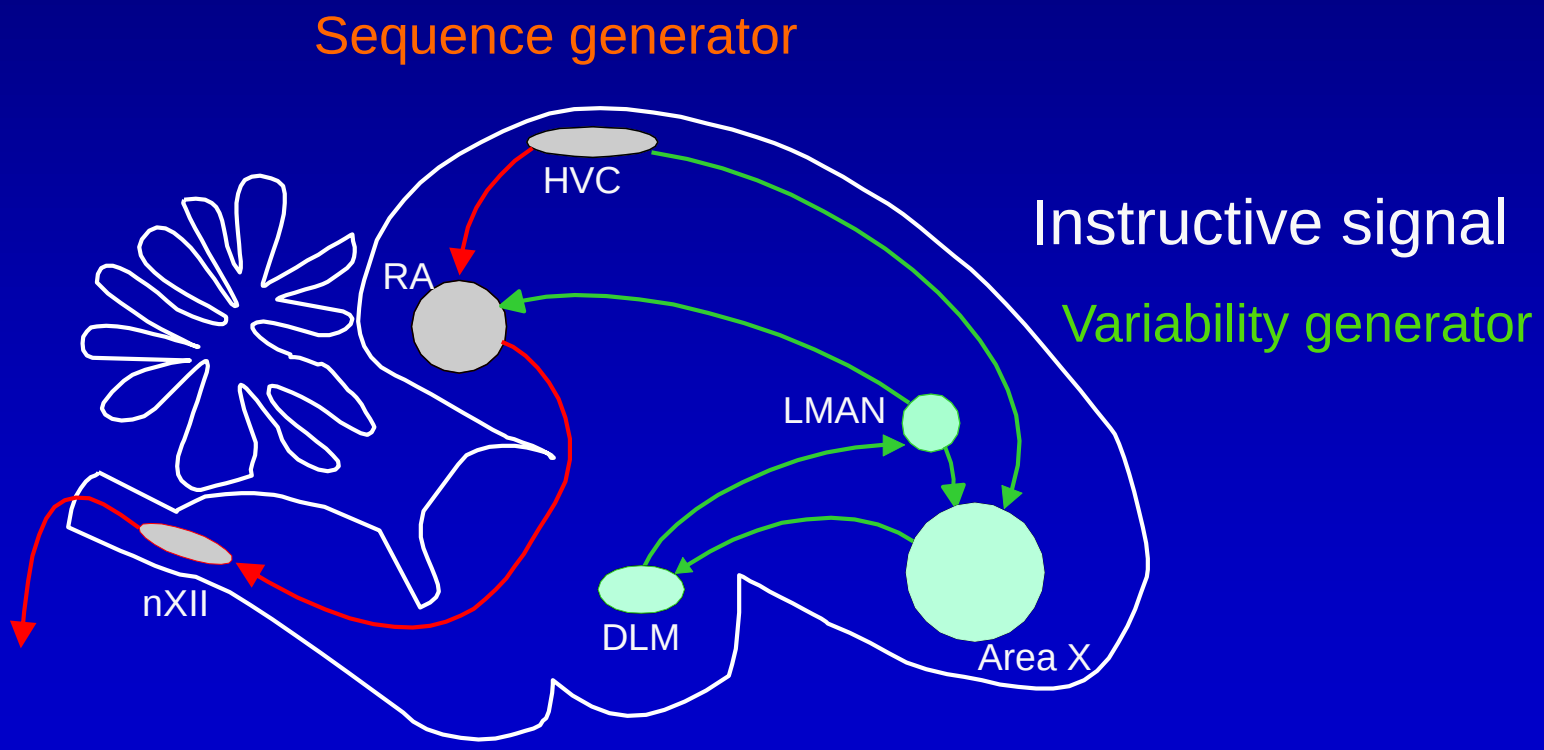
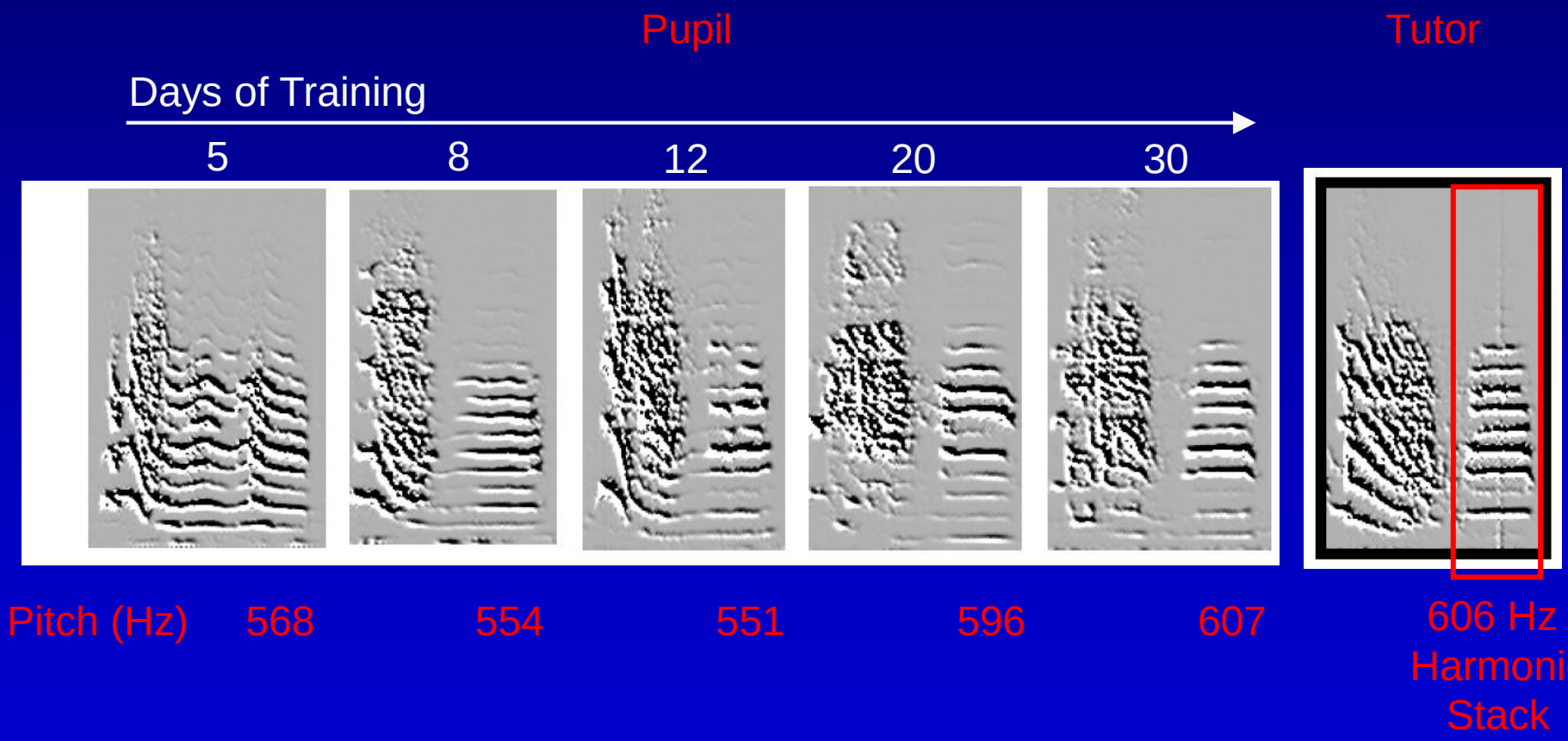
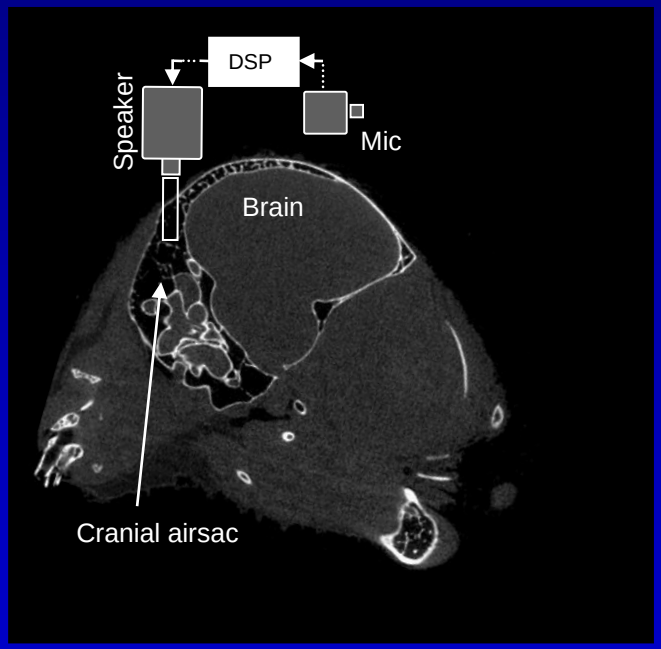


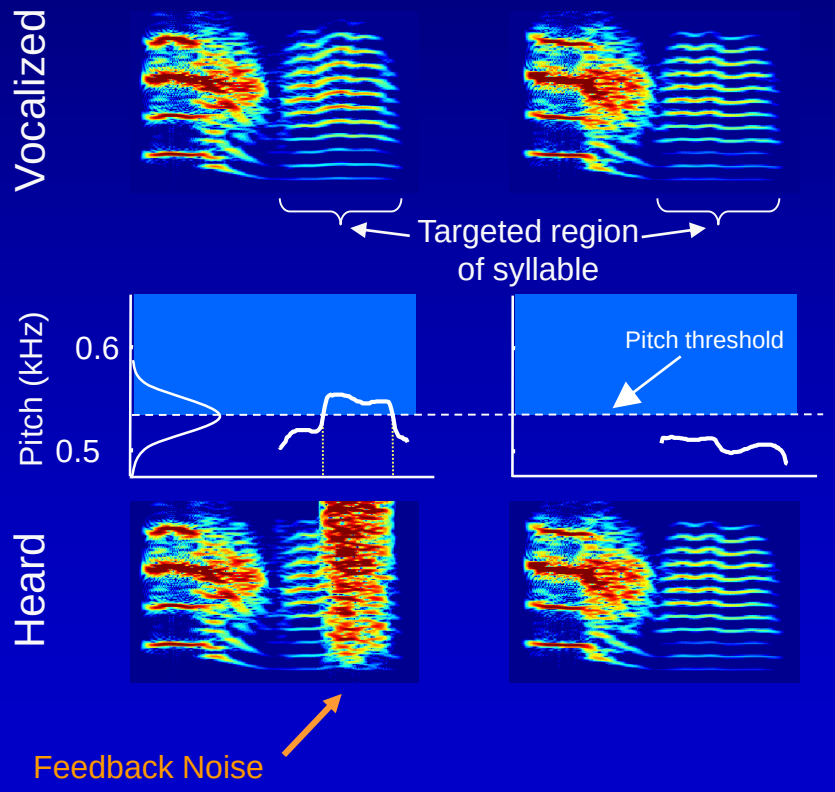
Song learning is slow



Tchernichovski, Mitra, Lints, Nottebohm, 2001

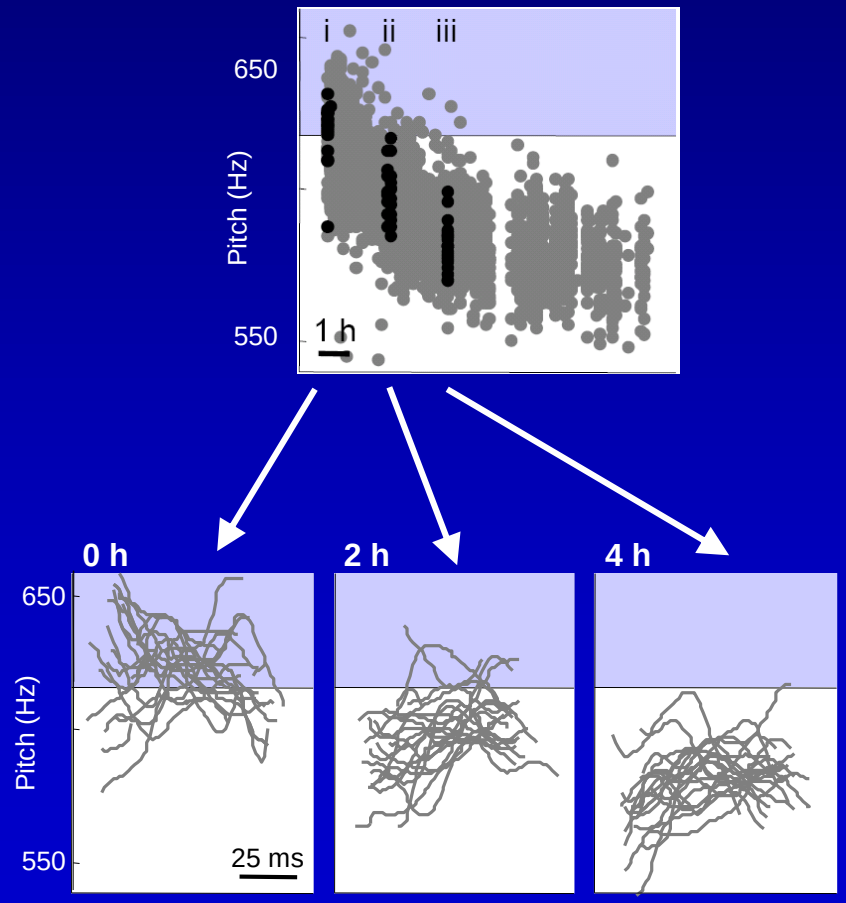
Experimental control of song learning



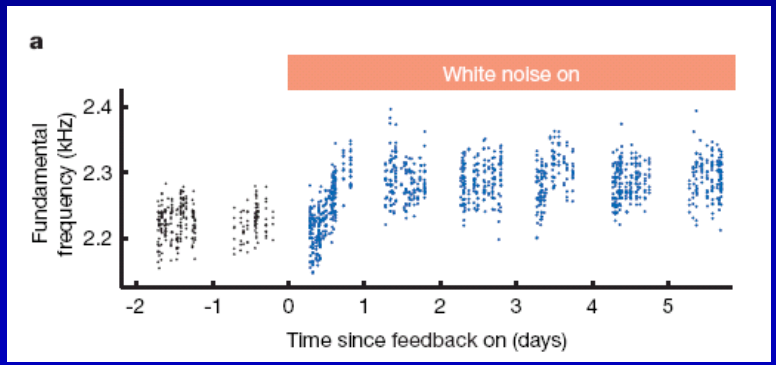


Andalman and Fee 2009; Tumer and Brainard 2007

Conditional auditory feedback drives pitch learning

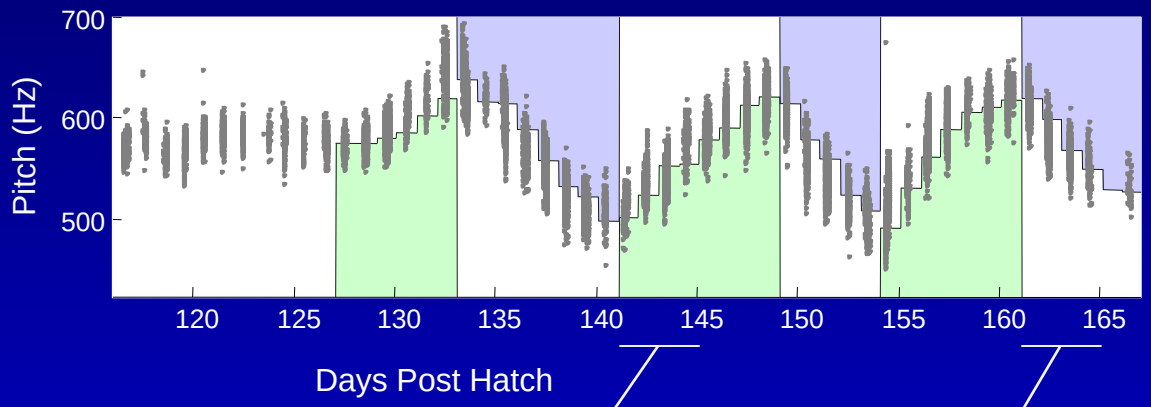


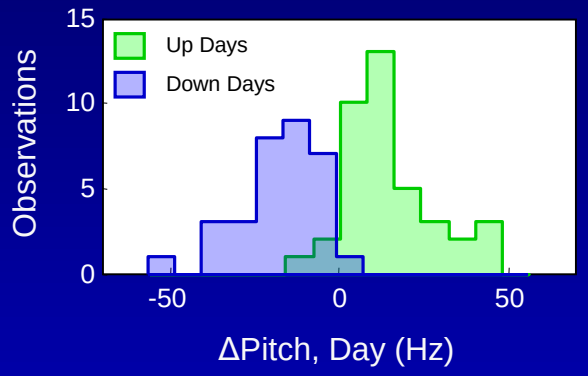
Andalman and Fee 2009

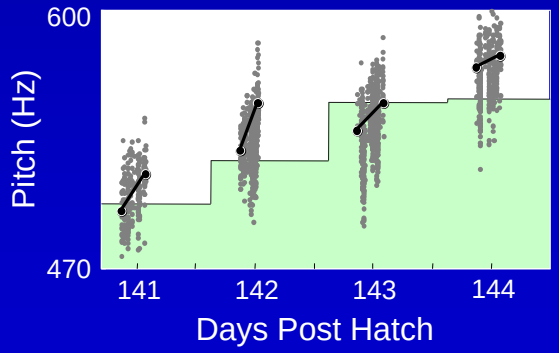


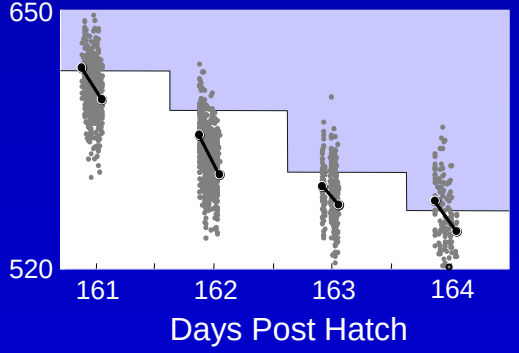
Tumer and Brainard 2007

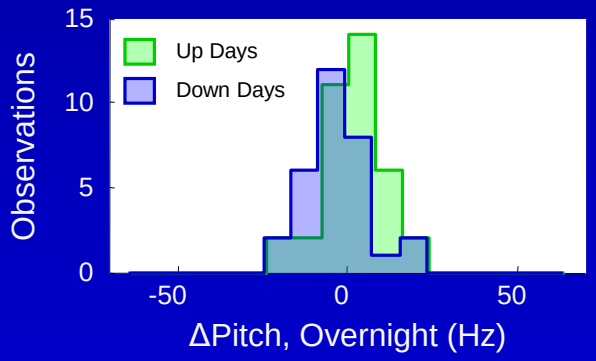
Many days of sequential learning



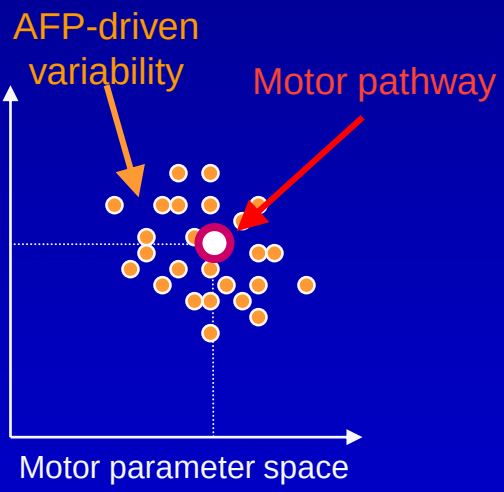




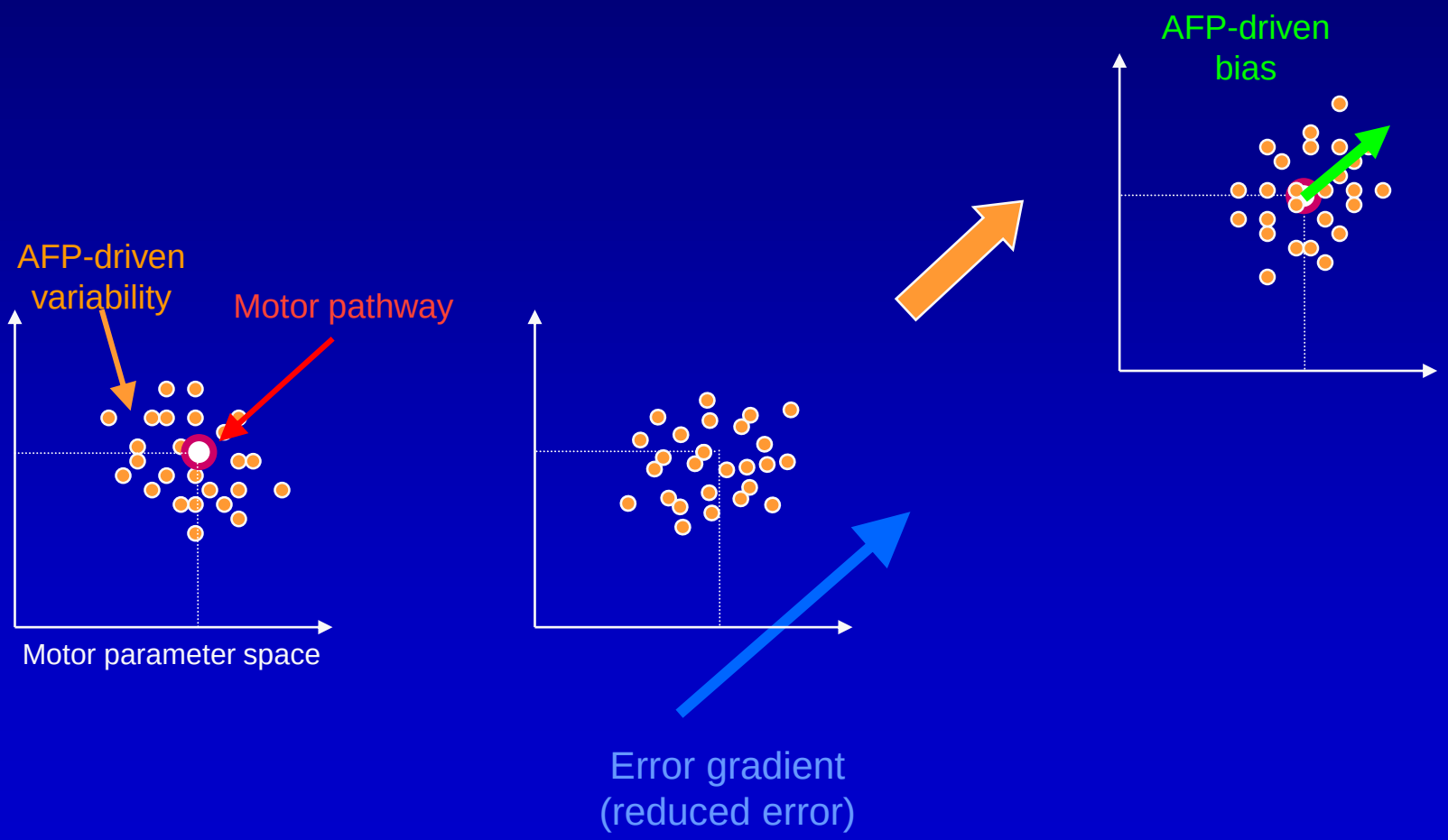




Where does this learning occur in the song control circuit?



Where does this learning occur in the song control circuit?



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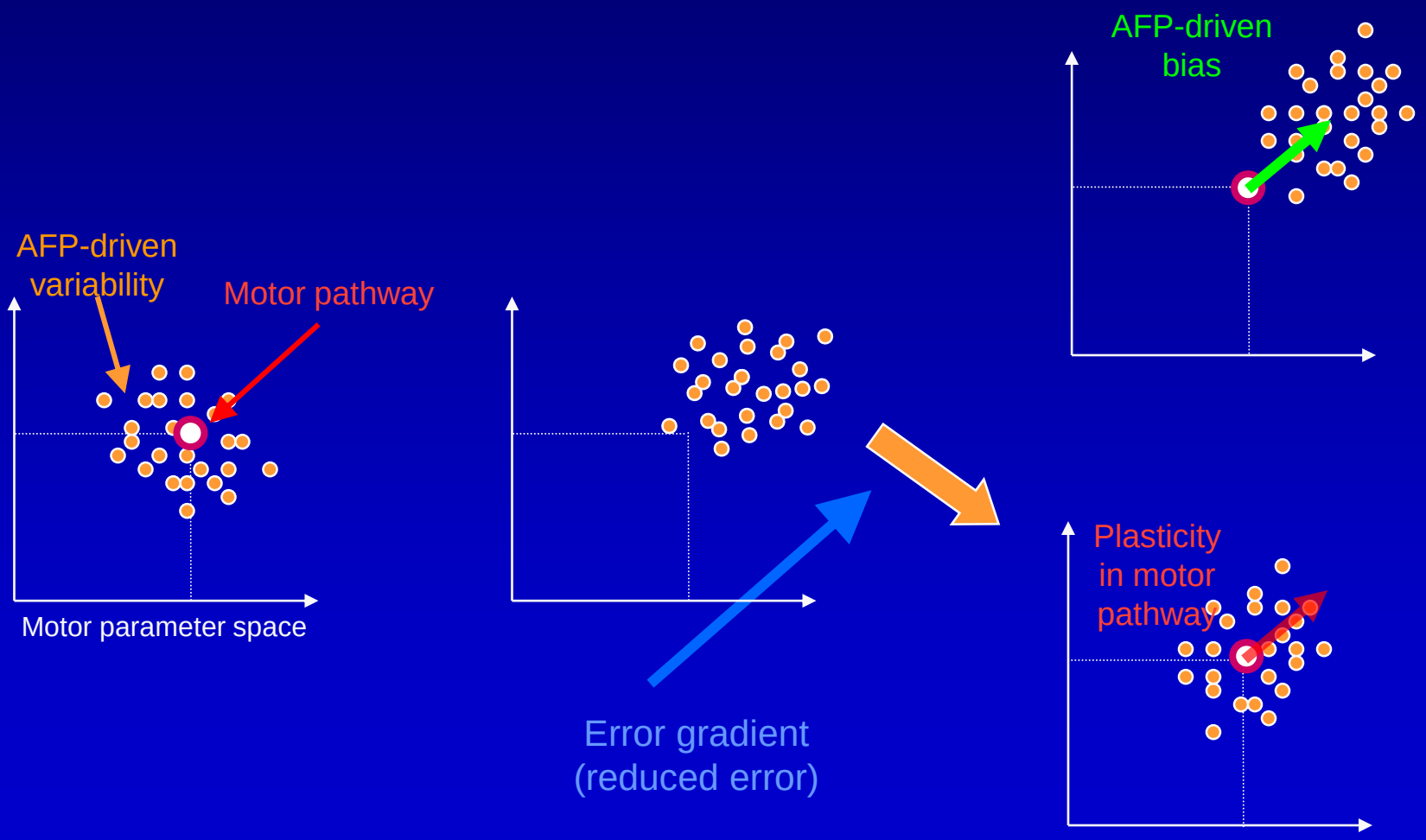

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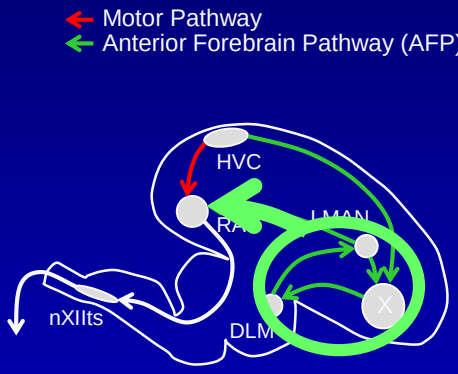
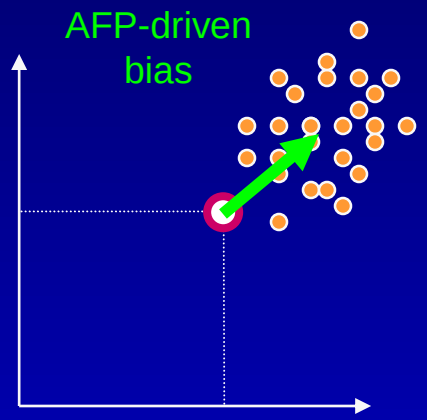
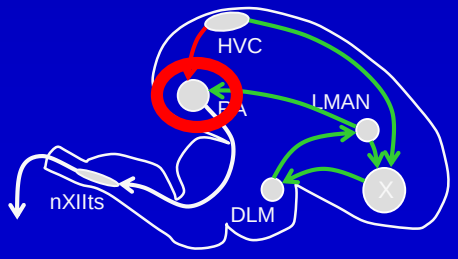
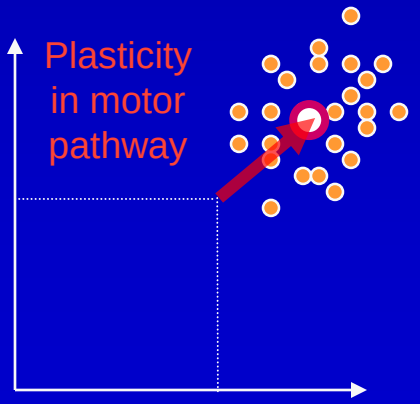
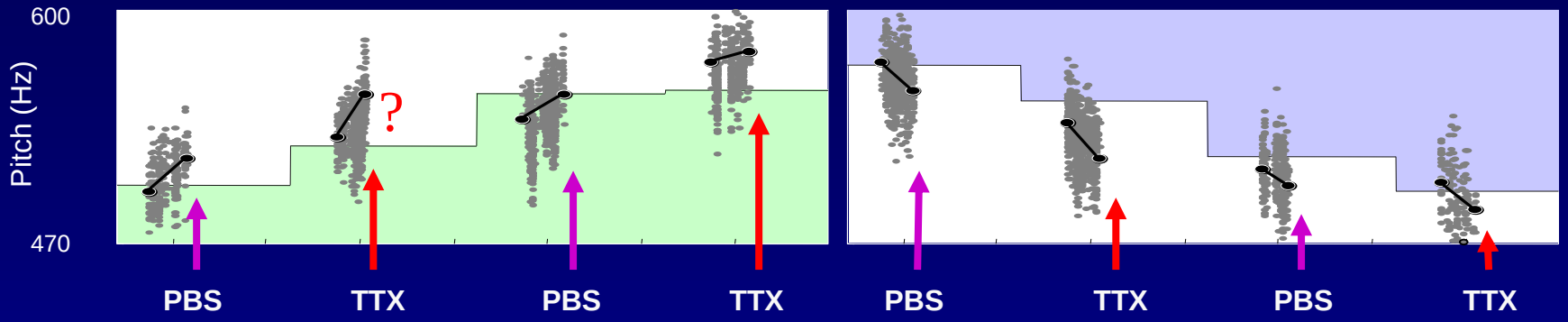
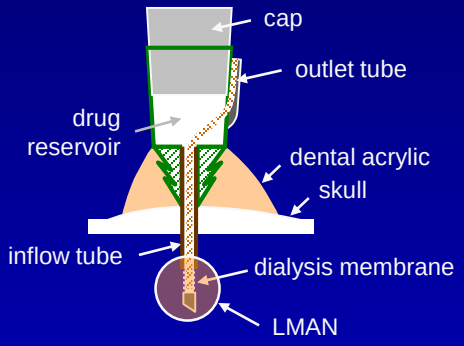


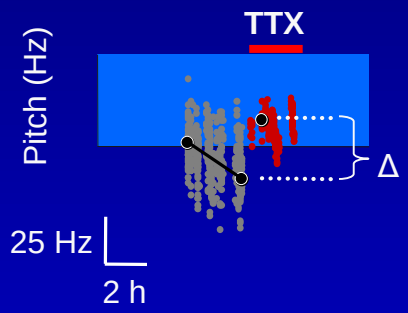


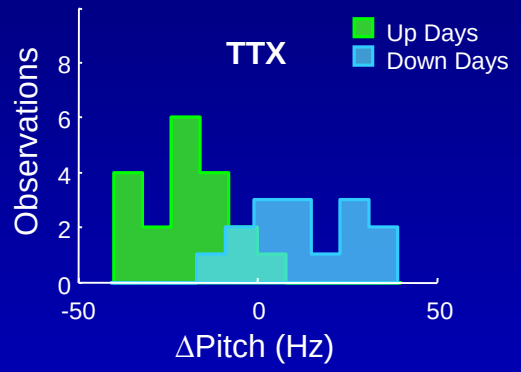


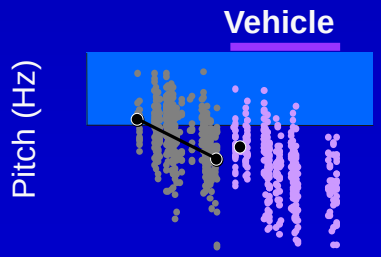


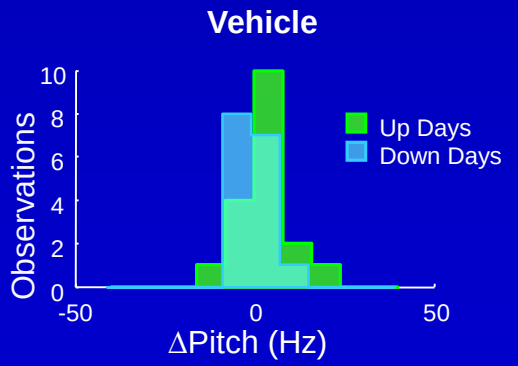








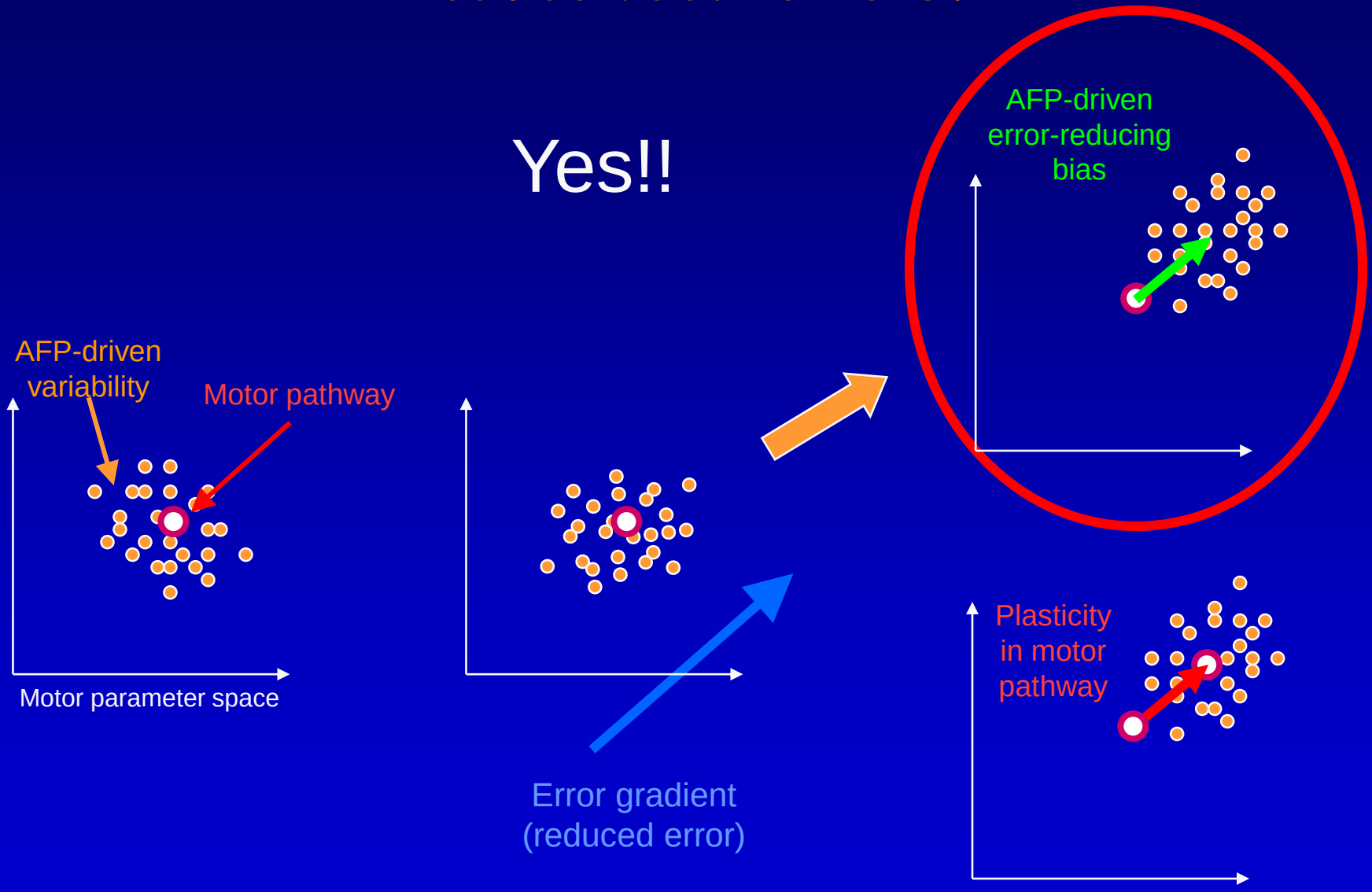




Andalman and Fee, PNAS 2009

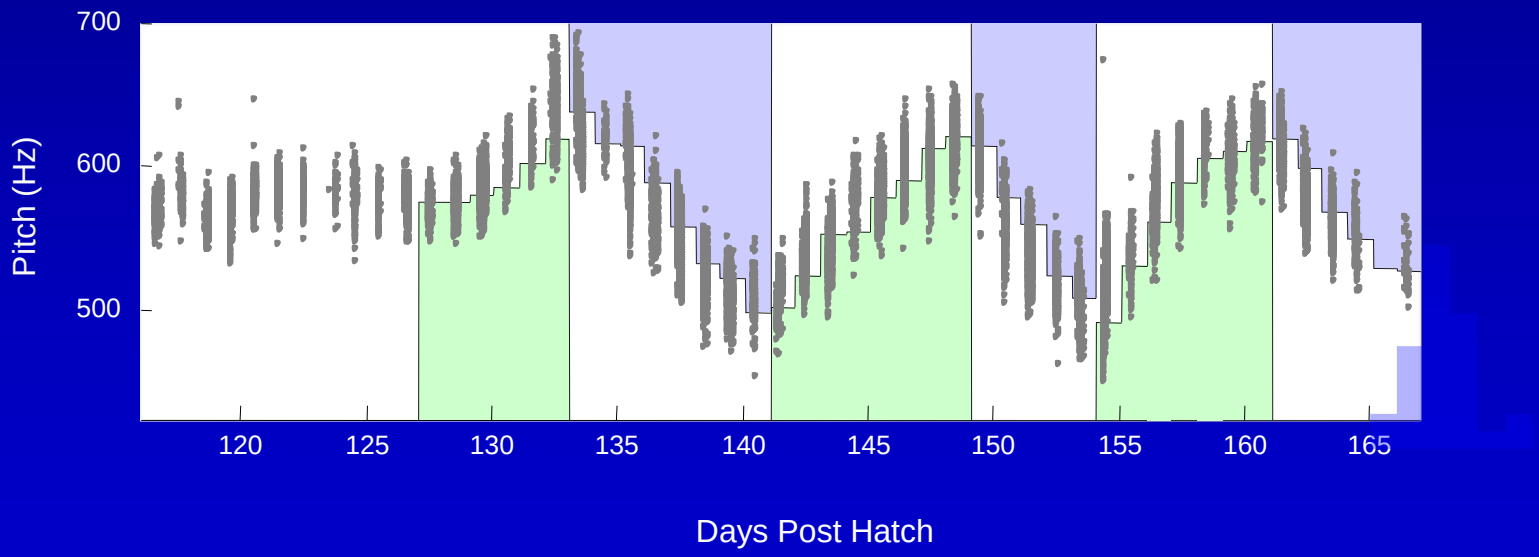
Does AFP-driven variability become biased to reduce vocal errors?

Yes!!



Is all song learning mediated by AFP bias?

Many days of sequential learning



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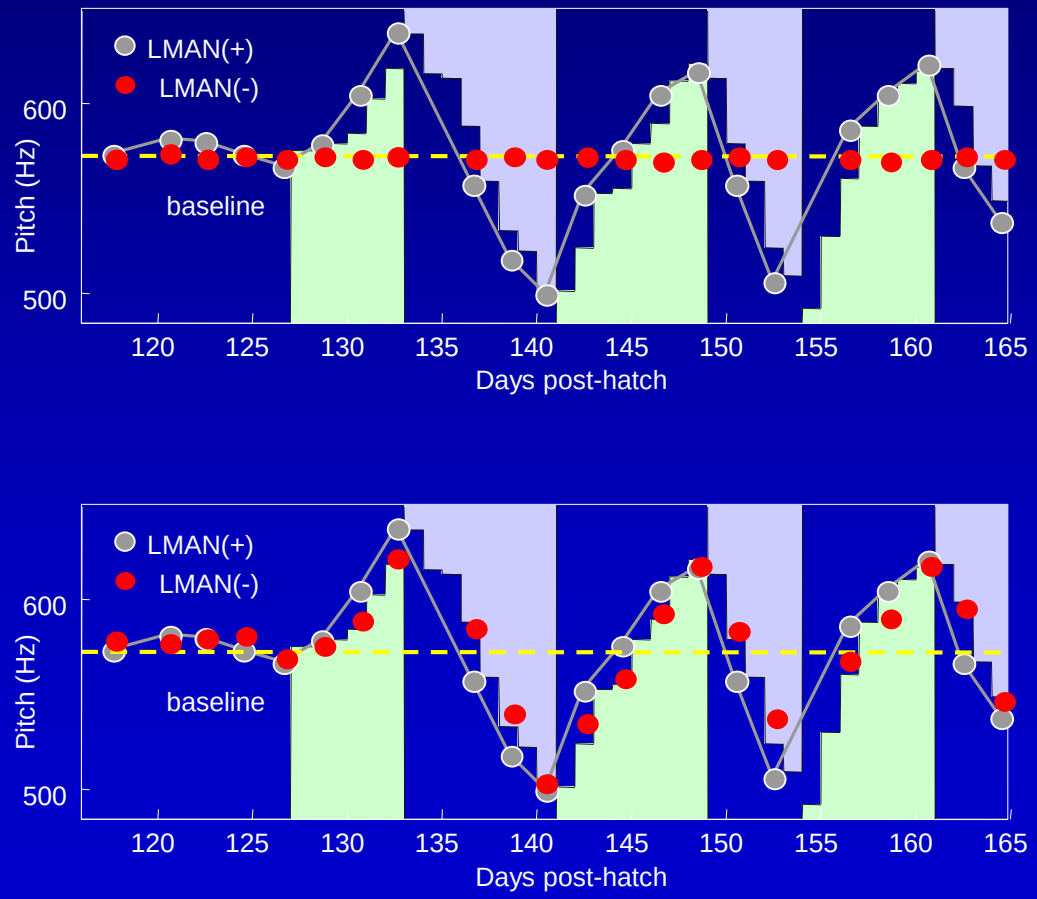
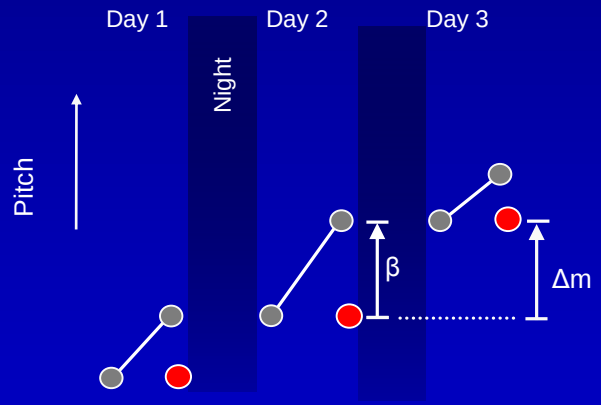
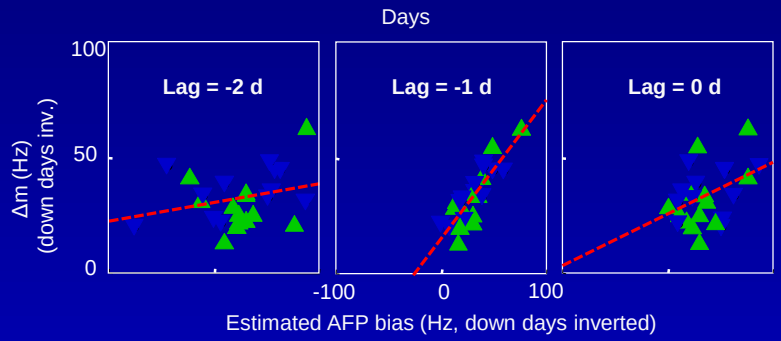
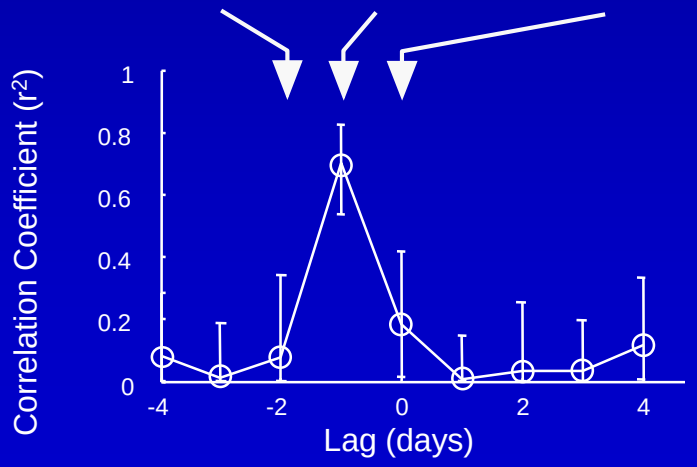


AFP bias is highly predictive of motor pathway plasticity within the next 24 hours



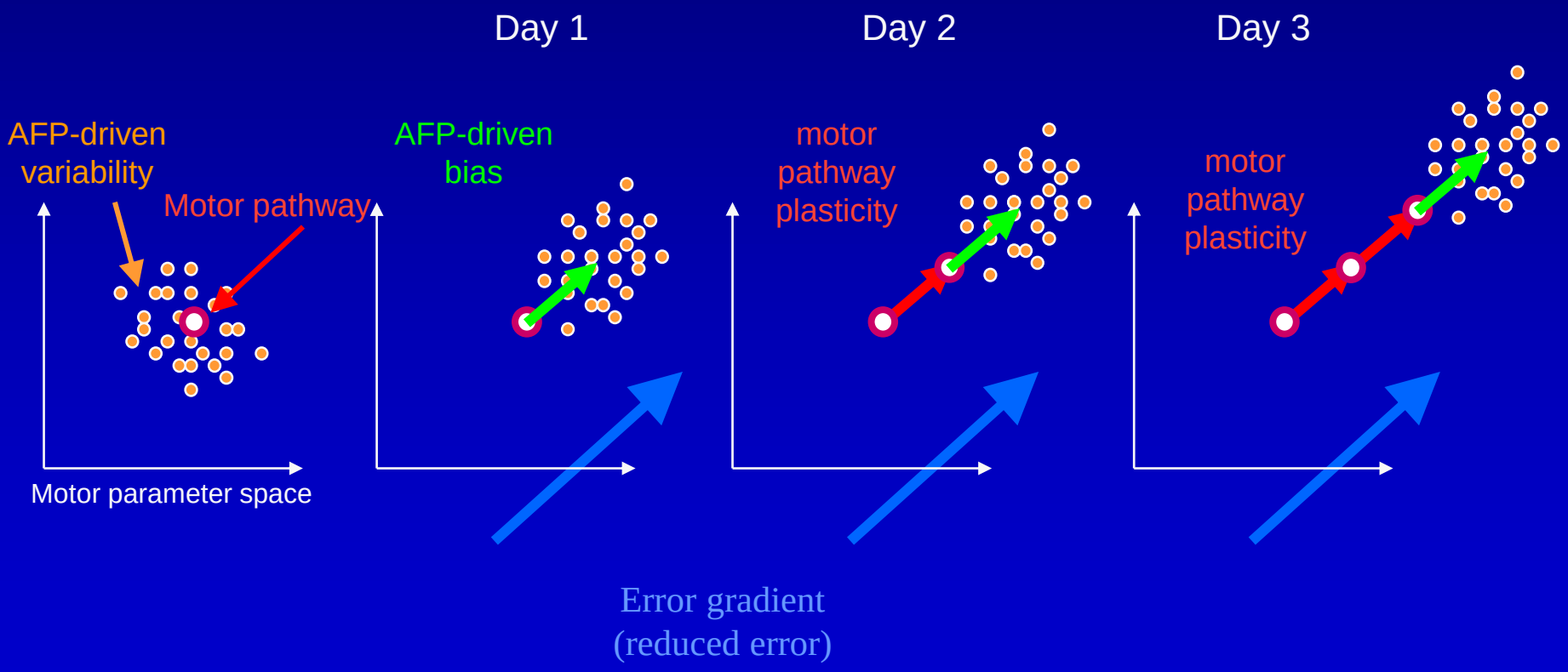




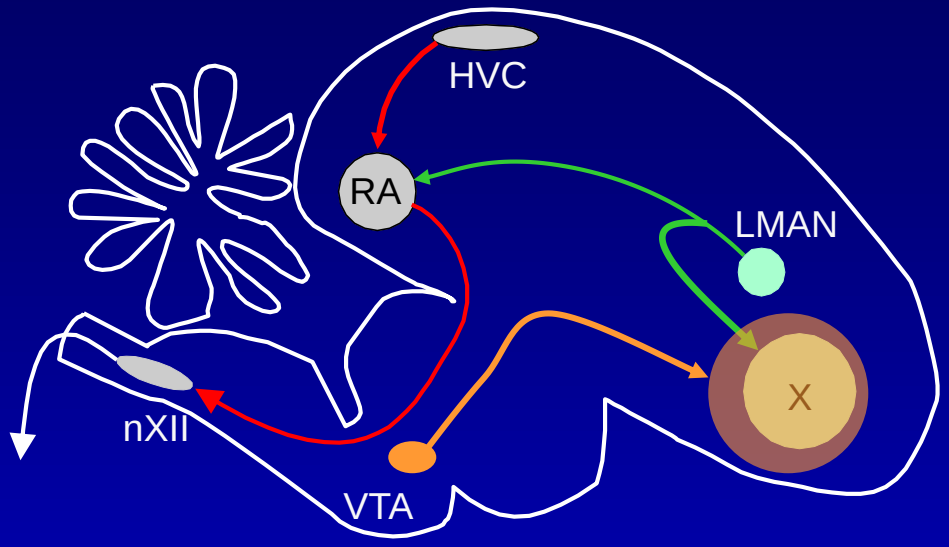
Andalman and Fee, 2009

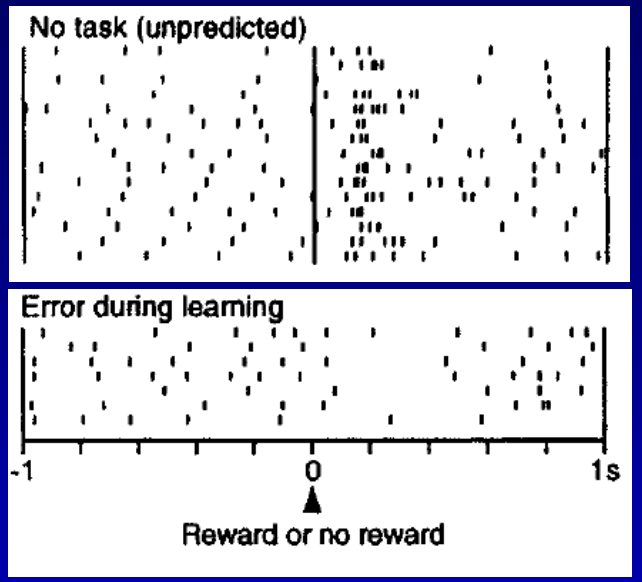
Warren et al, 2011

Motor pathway plasticity appears to 'integrate' AFP bias



How is AFP bias generated?

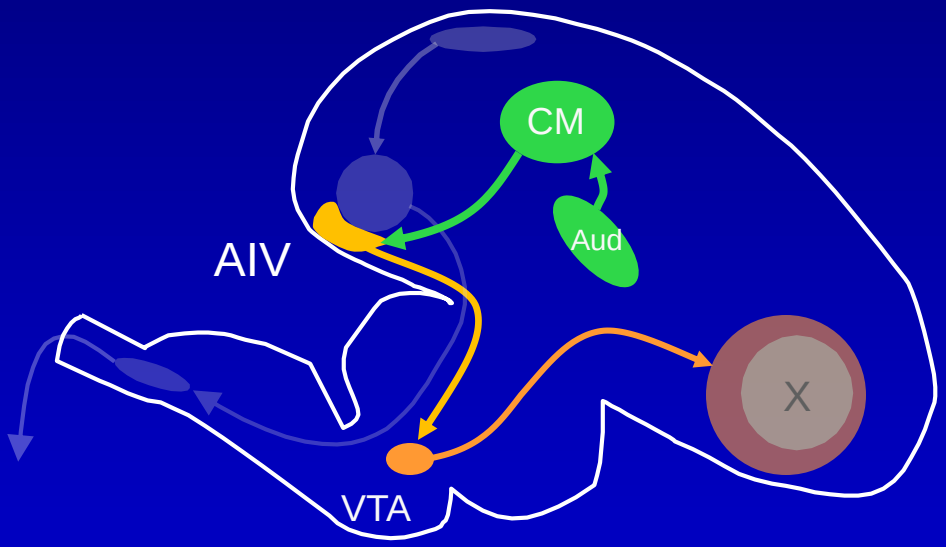




Schultz, 2000

- Area X receives an efference copy of variability signals sent to RA.
- If Area X also receives an evaluation signal, then X could figure out which variations lead to better song performance.
- Dopaminergic midbrain (VTA) has been shown to signal reward prediction error
- Do X-projecting VTA neurons carry error-related signals?

A descending pathway from higher-order auditory areas to VTA/SNc

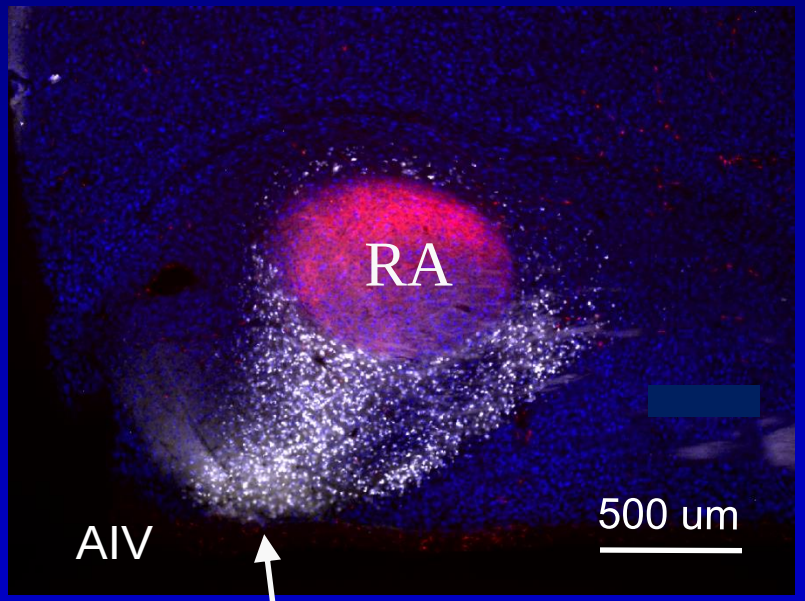


Keller and Hahnloser, 2008

Gale, Perkel 2008

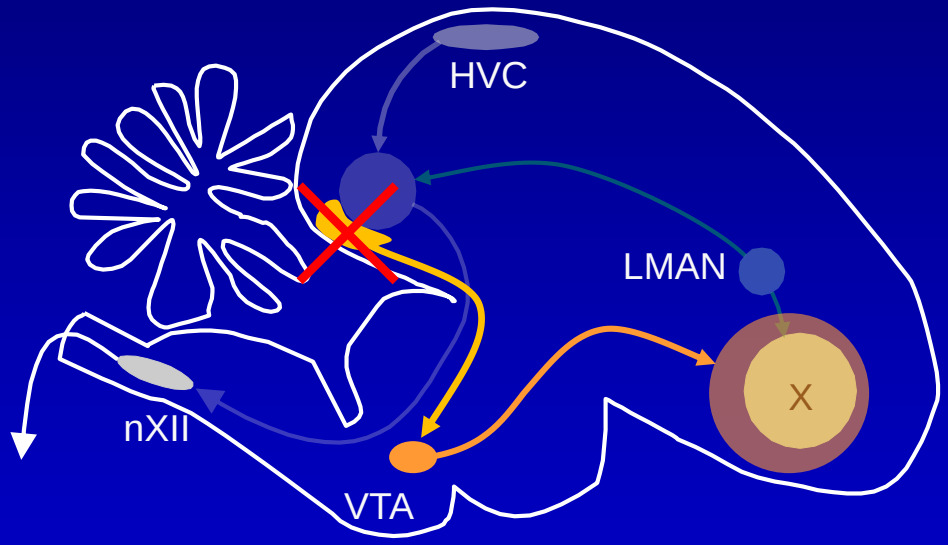
Mandelblat-Cerf et al, 2014

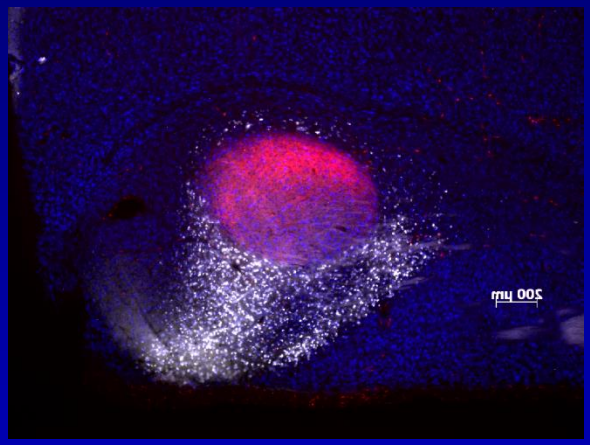
Ventral Intermediate Arcopallium (AIV)

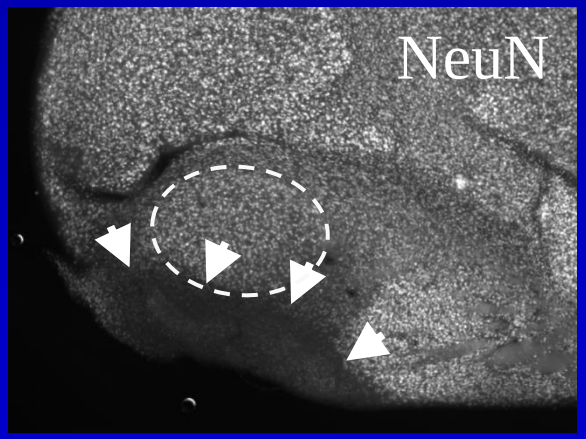


Retrograde label from VTA

Is AIV necessary for song learning?







Las, Denisenko, Mandelblat-Cerf, eLife, 2014

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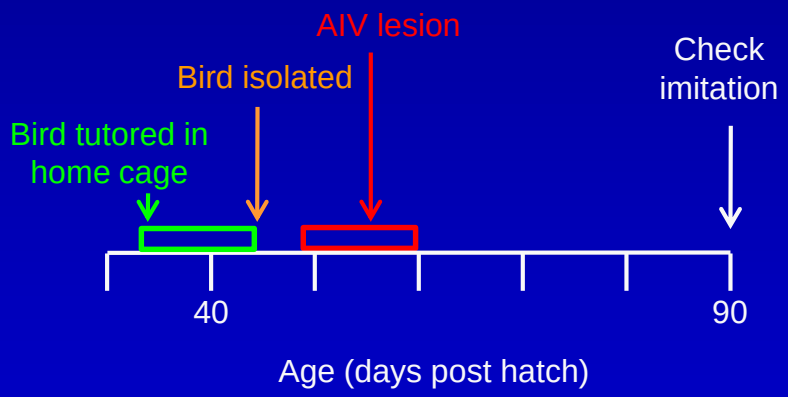
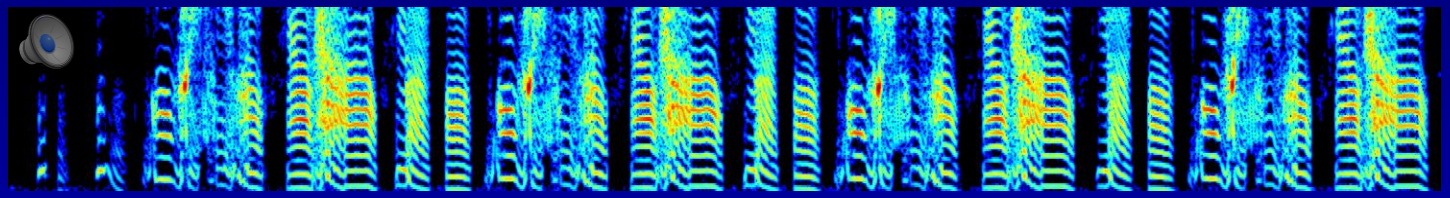


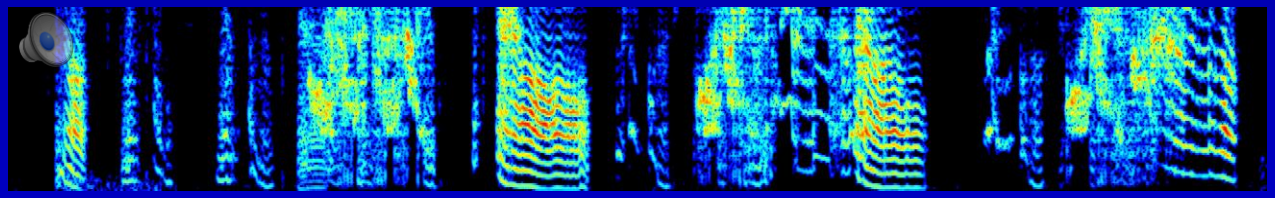
AIV lesion produces profound song learning deficits

Tutor

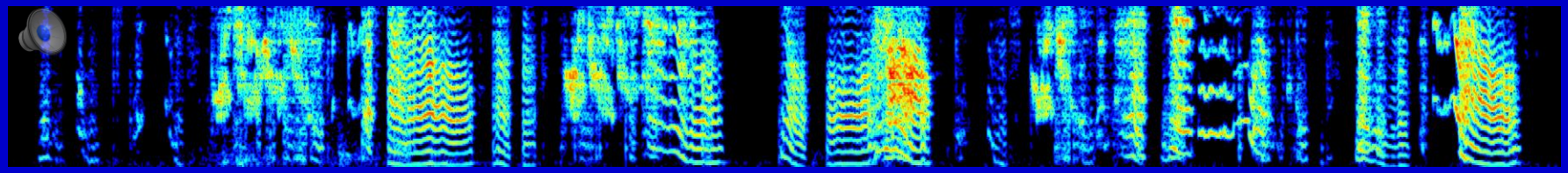


AIV lesioned pupil #2 – Adult song

Example 1



Example 2



AIV lesions produce profound song learning deficits

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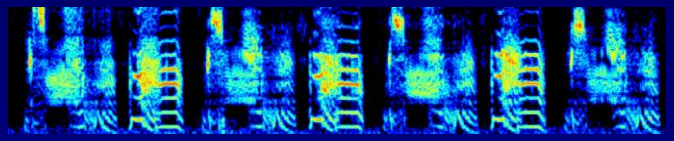
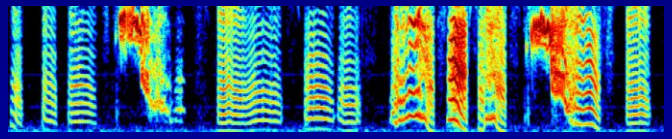
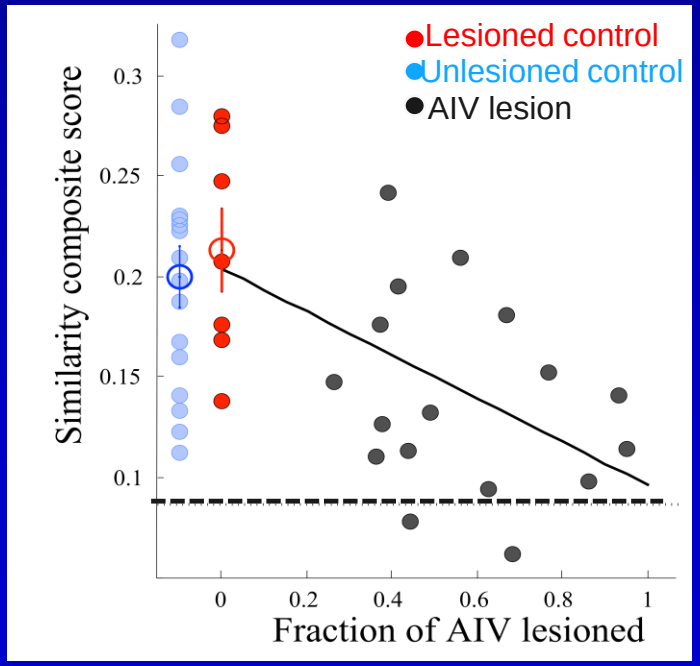


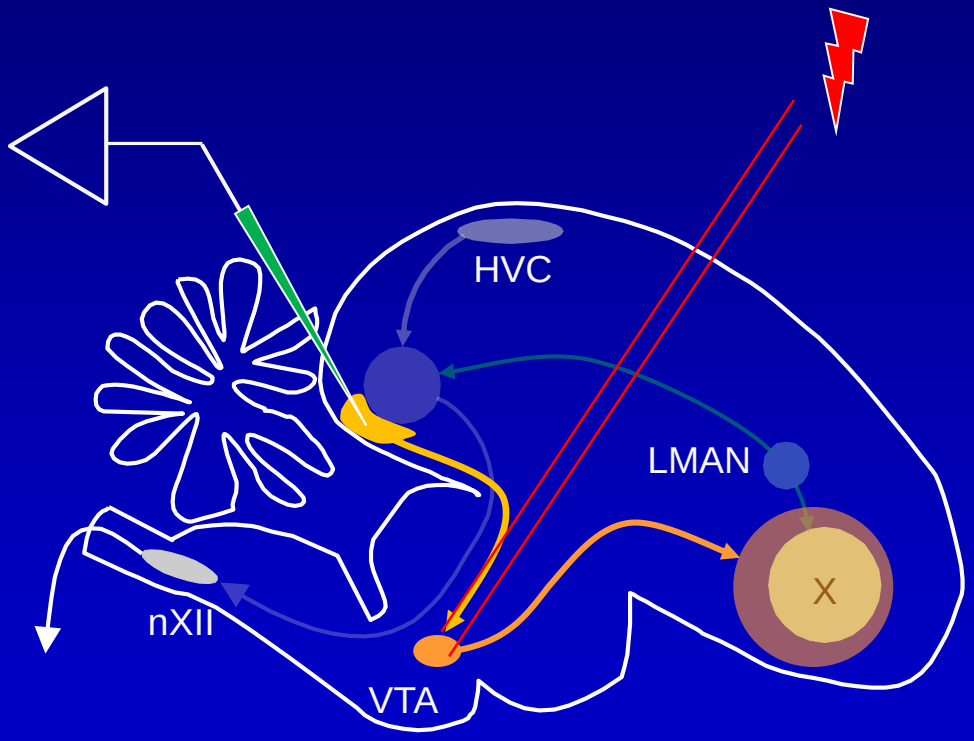
AIV lesioned – adult song

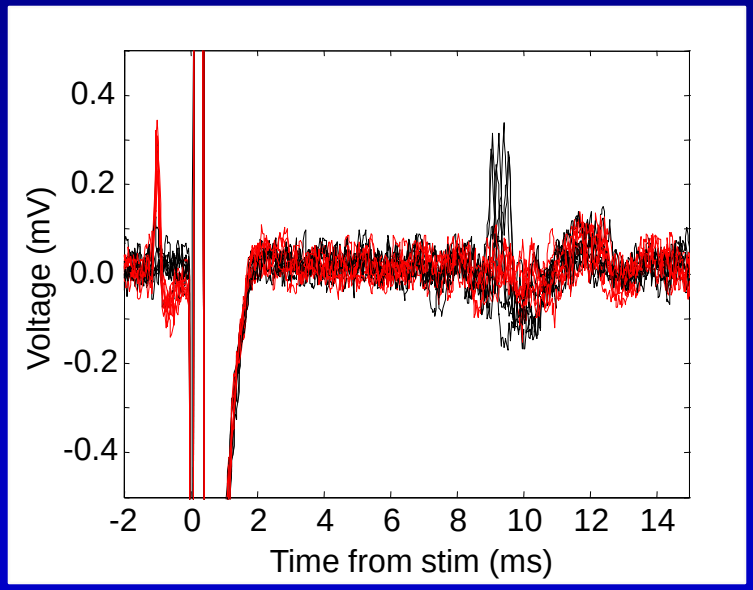




Similarity of unrelated birds

Do AIV neurons transmit an 'error' signal to VTA during singing?





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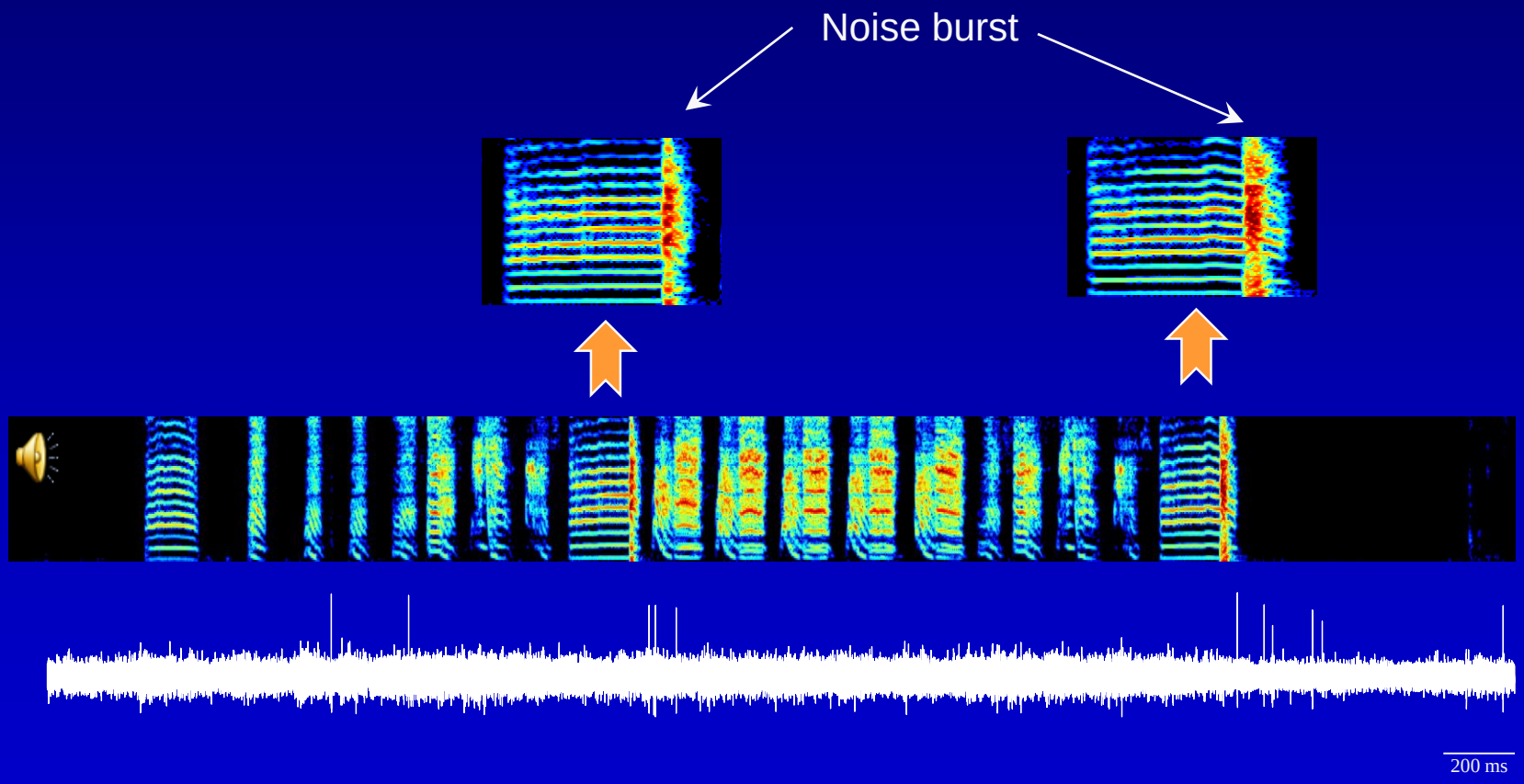
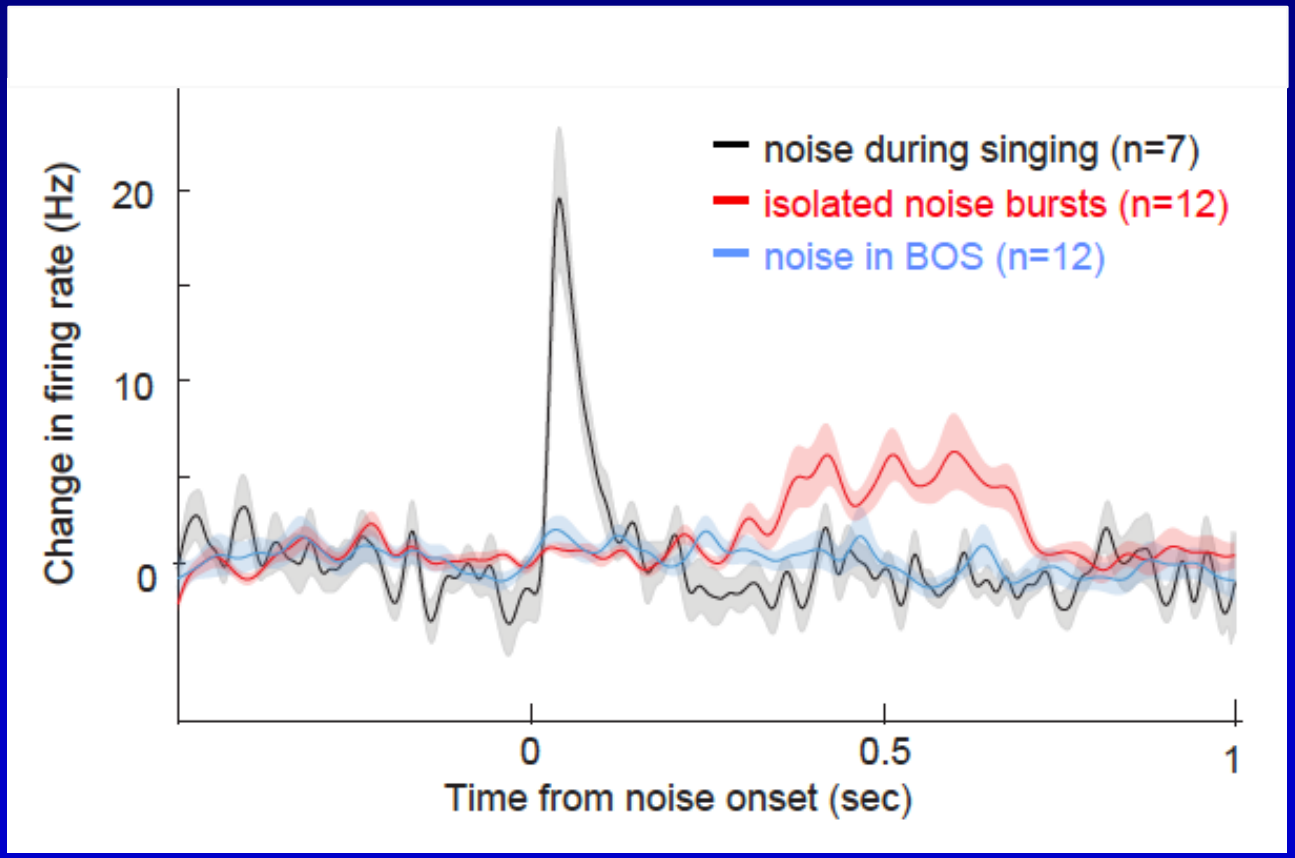
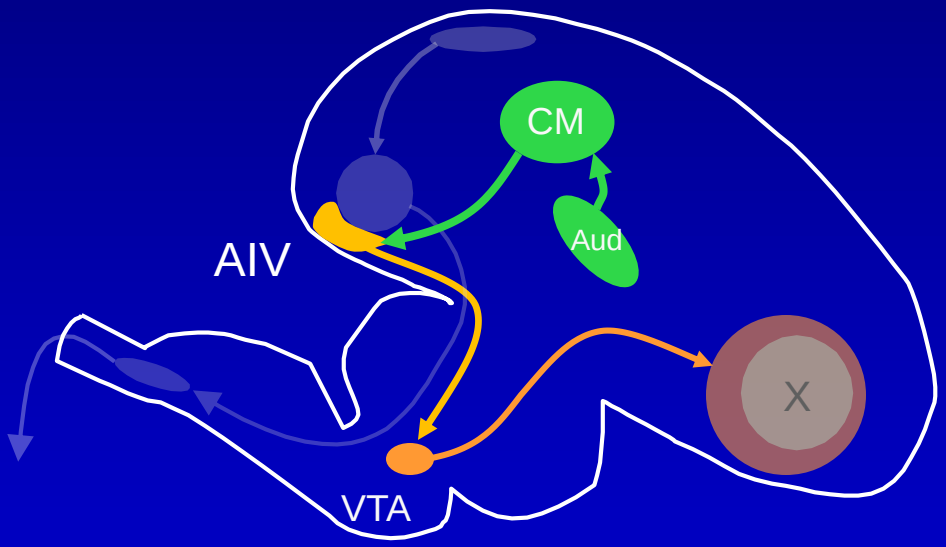


AIV neurons show error-related signals



Mandelblat-Cerf, Las, Denisenko, under review

A descending pathway from higher-order auditory areas to VTA/SNc



Keller and Hahnloser, 2008

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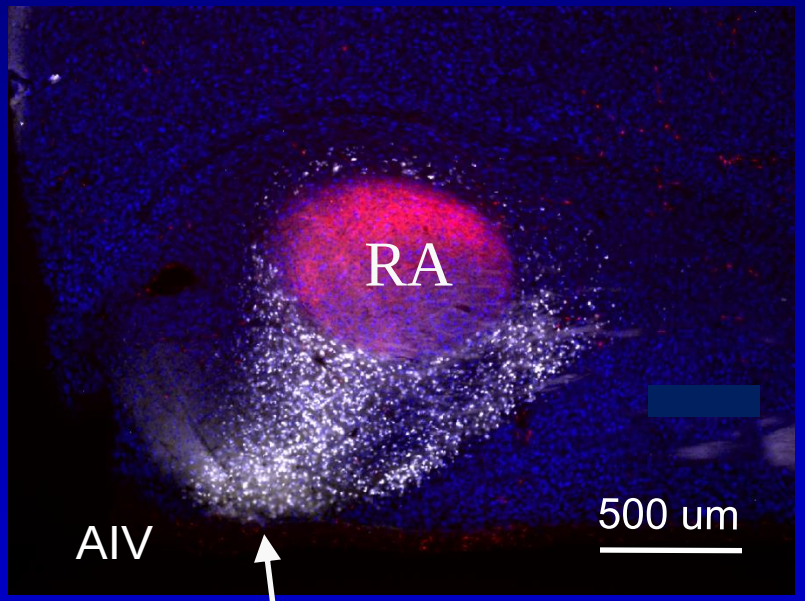
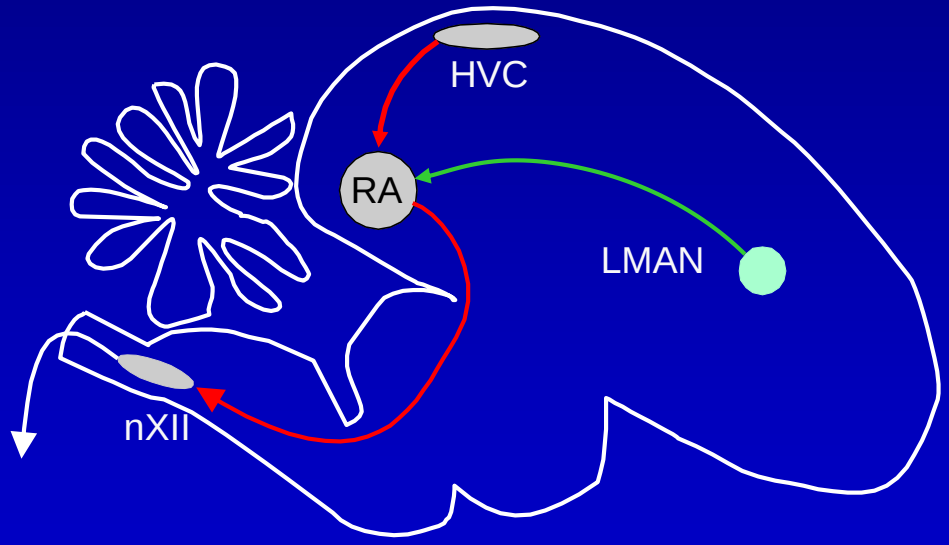
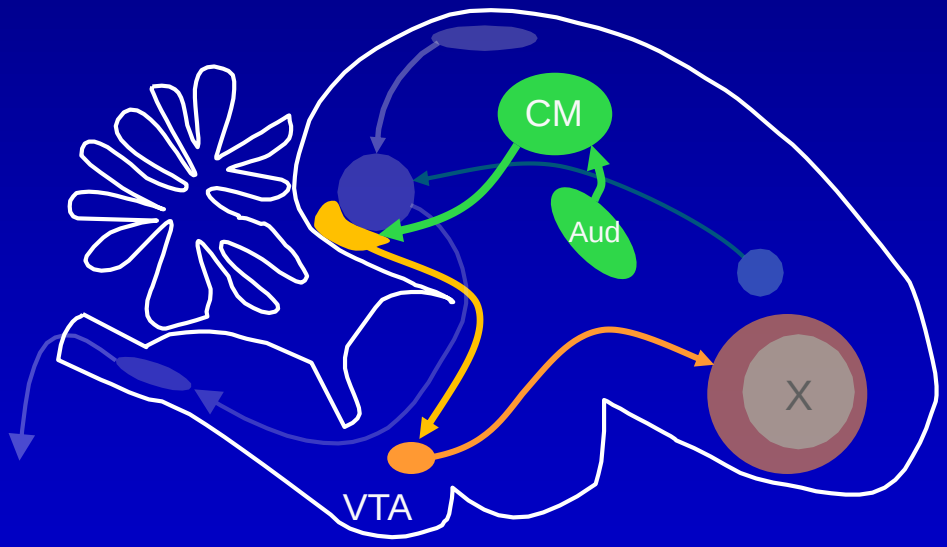


Retrograde label from VTA

How it all works: a hypothesis



How it all works: a hypothesis



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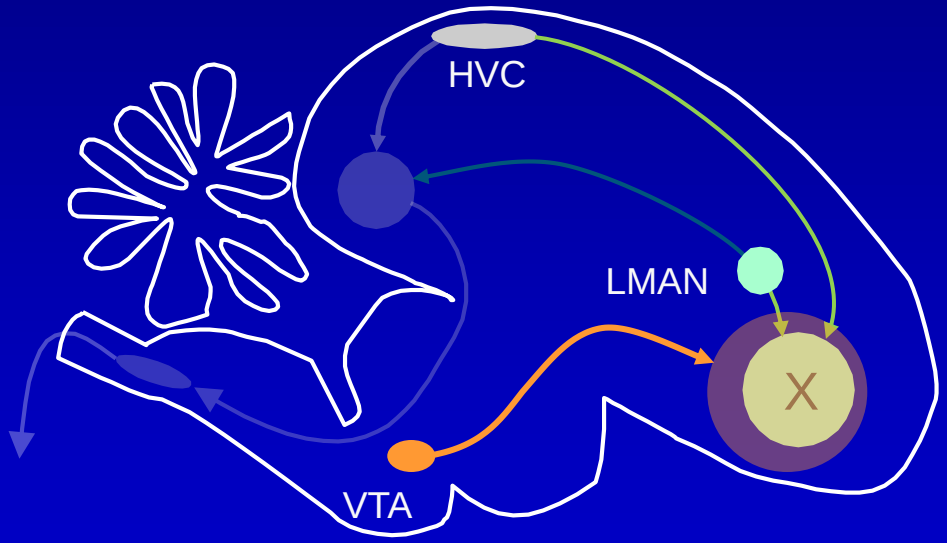
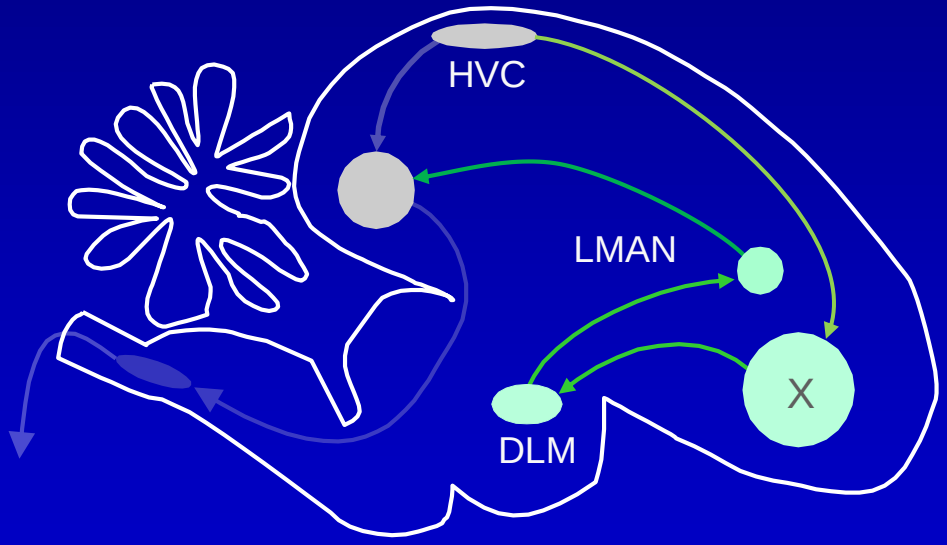


How it all works: a hypothesis



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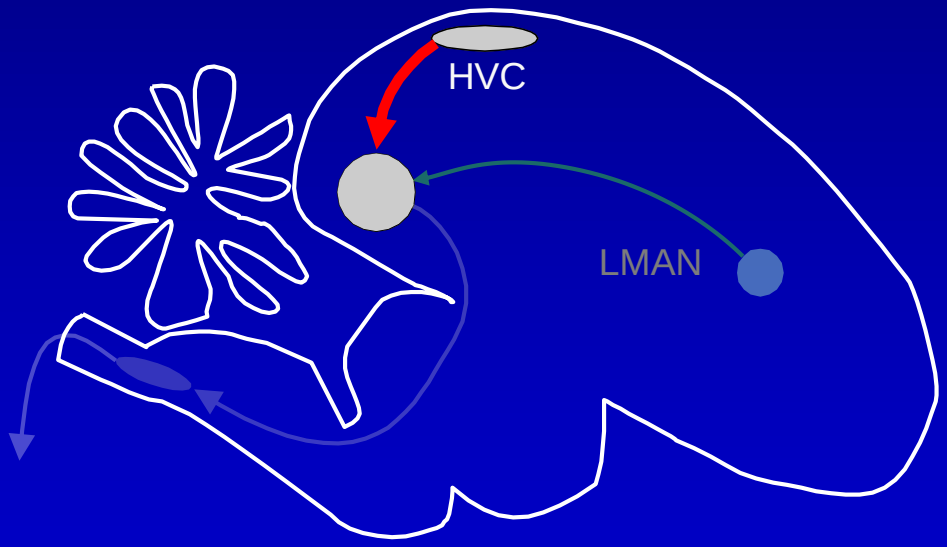
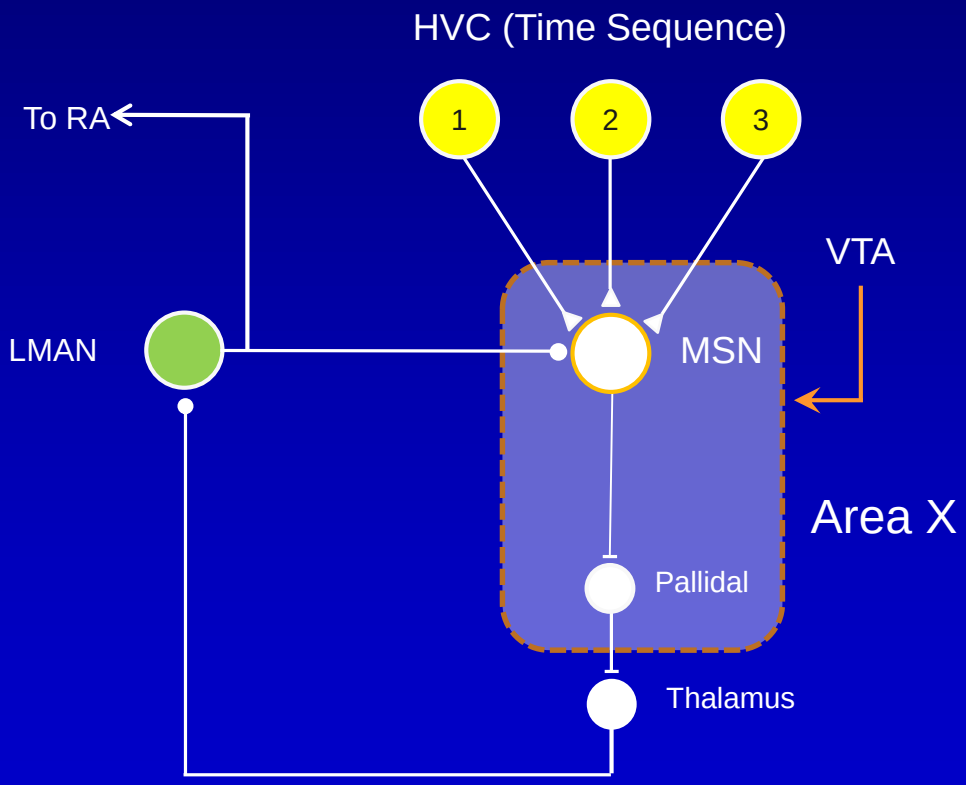
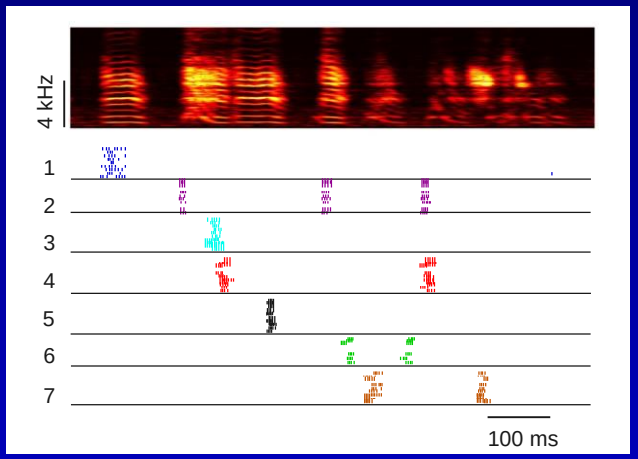


A model of basal ganglia function with functionally distinct inputs for context, motor efference copy, and reward

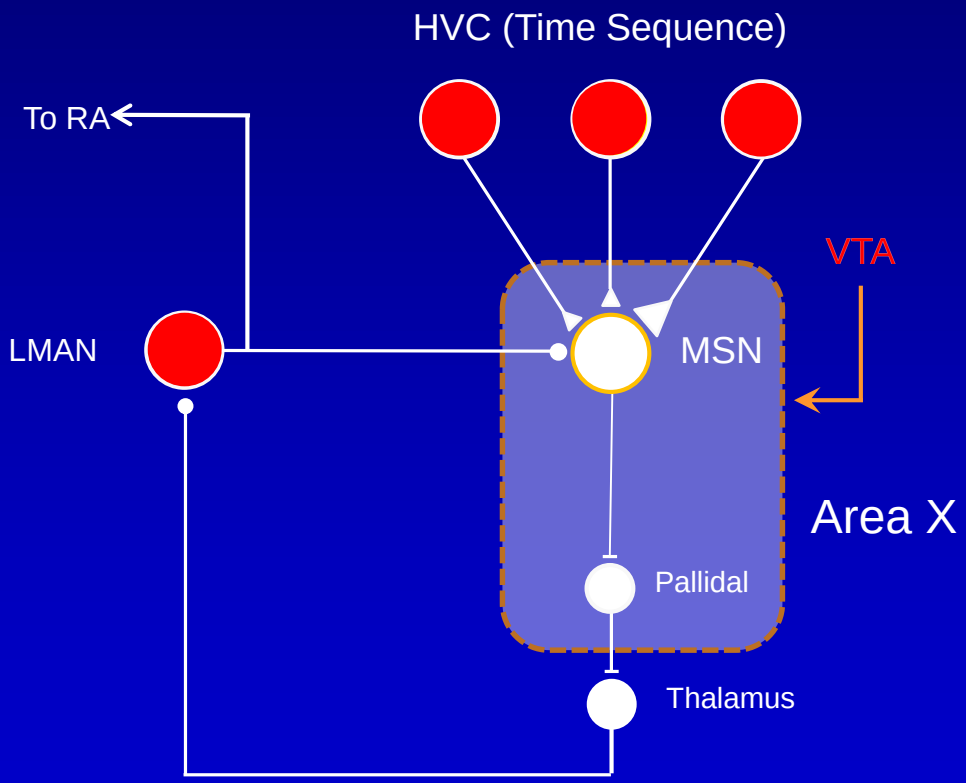


HVC$_{(X)}$ firing patterns



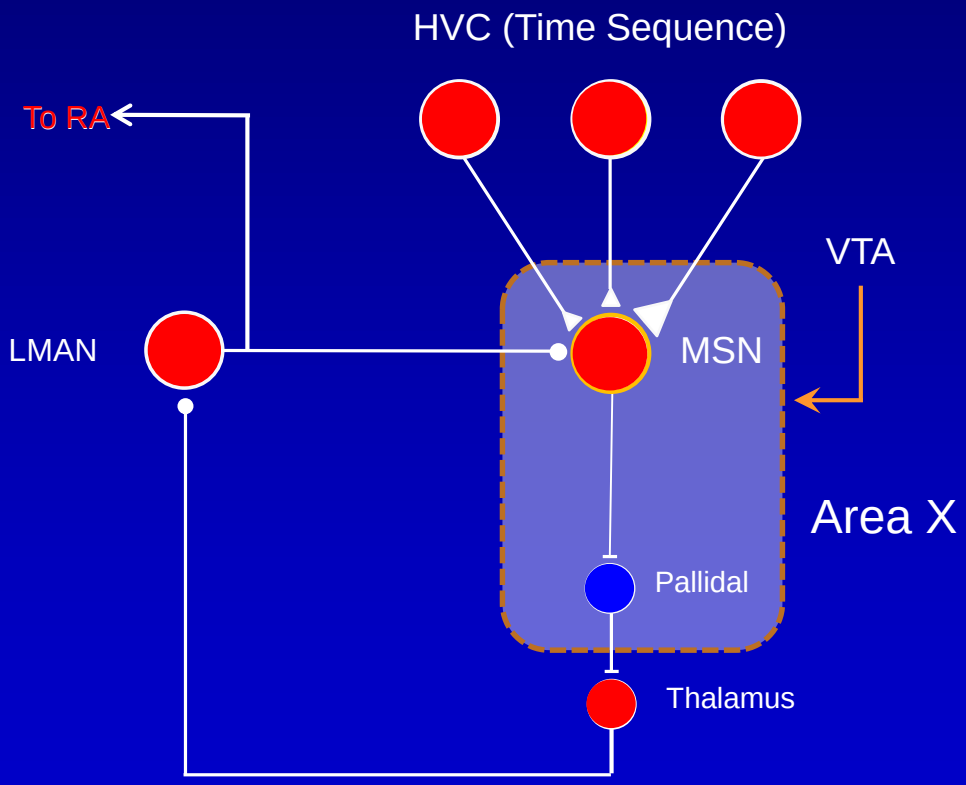
The AFP forms a classic cortical-BG-thalamo-cortical loop

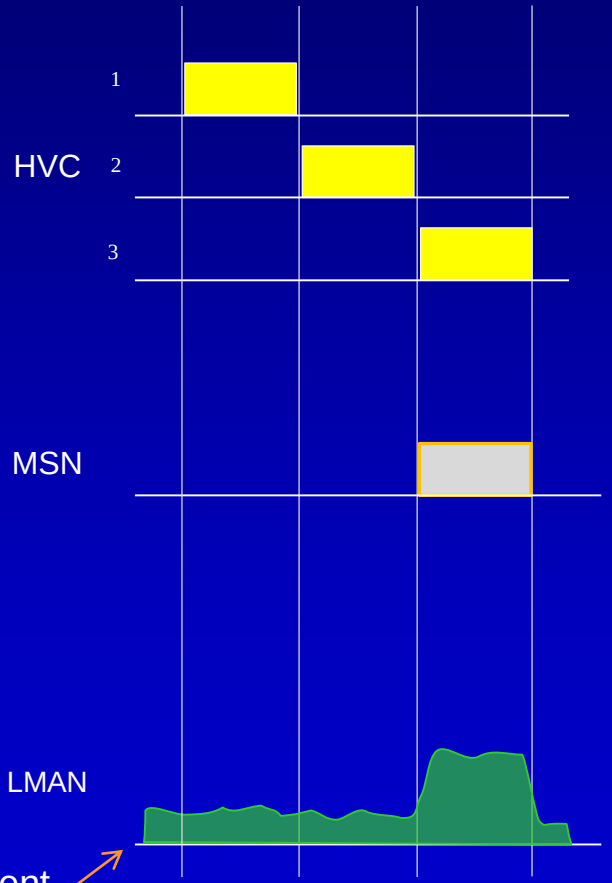
A model of basal ganglia function with functionally distinct inputs for context, motor efference copy, and reward



Learning rule:
Strengthen HVC synapse
after coincidence
of LMAN, HVC and DA inputs

A model of basal ganglia function with functionally distinct inputs for context, motor efference copy, and reward

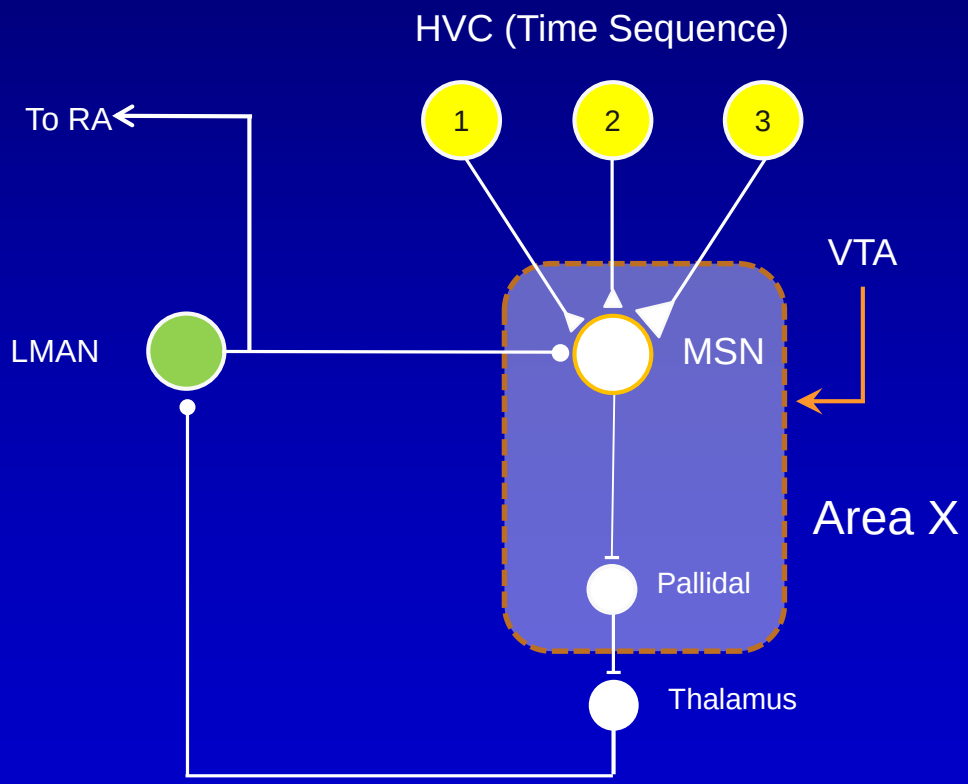




Time-dependent bias of one LMAN neuron

Goldberg and Fee 2010

A model of basal ganglia function with functionally distinct inputs for context, motor efference copy, and reward



HVC synapses

Timing
Drive MSNs
Plastic
Selective for single synapses

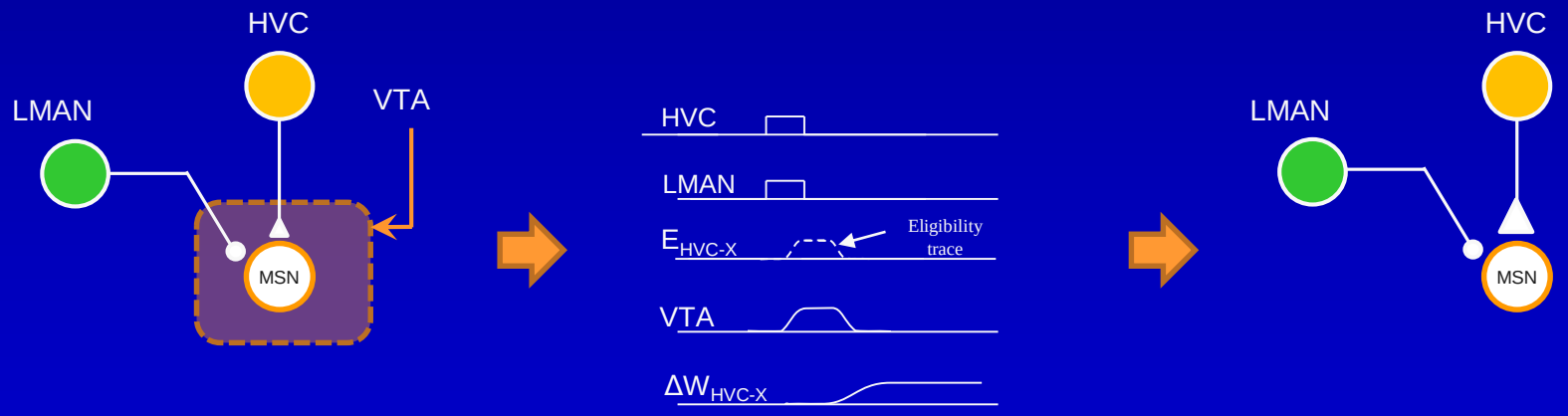
LMAN synapses

Action
Do NOT drive MSNs
Not plastic
Global signal

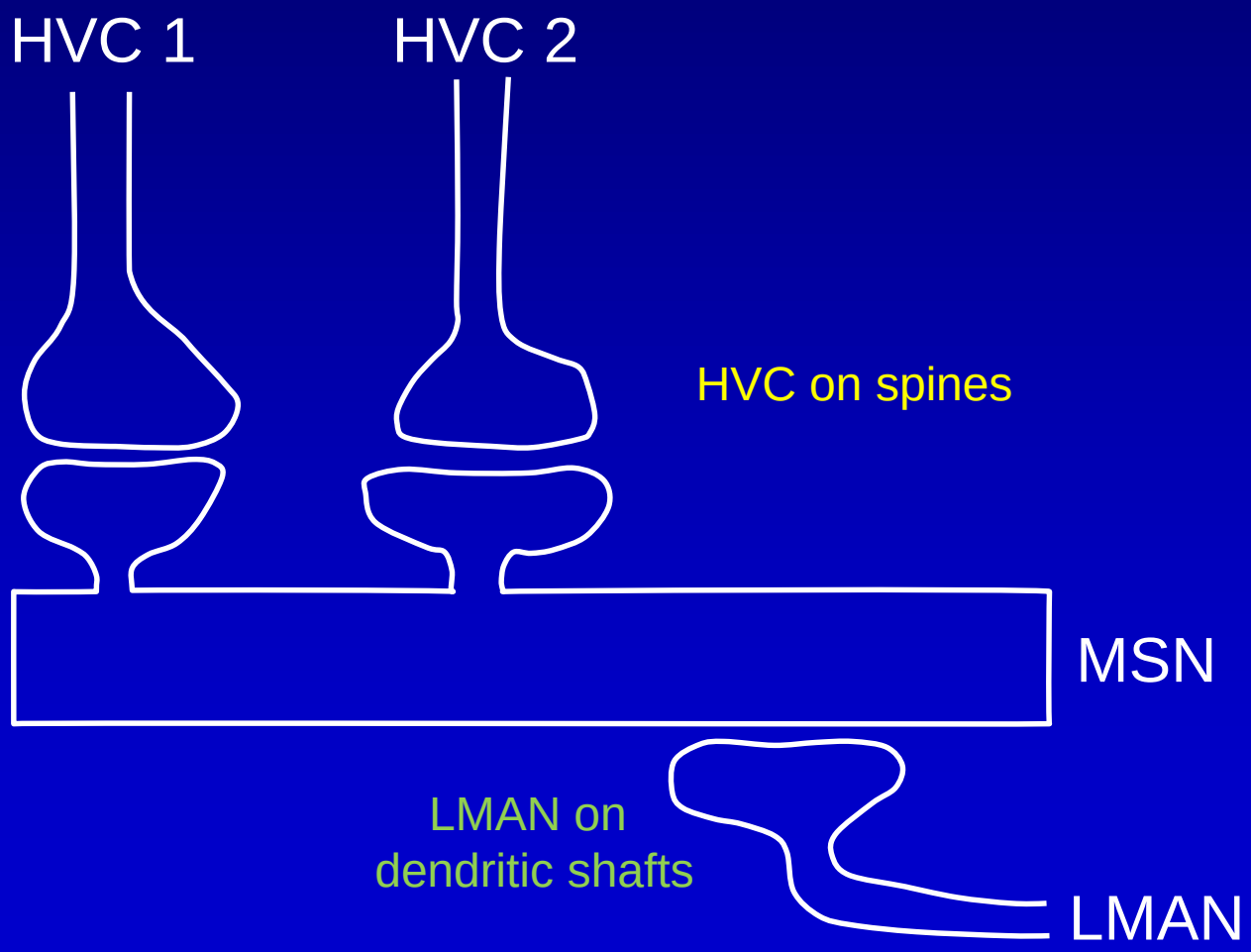
A learning rule with an eligibility trace allows delayed reward

$$E_{HVC-X} = LH$$

$$\Delta W_{HVC-X} = bE_{HVC-X}R$$



Hypothesis for HVC-LMAN synaptic interaction on striatal MSNs



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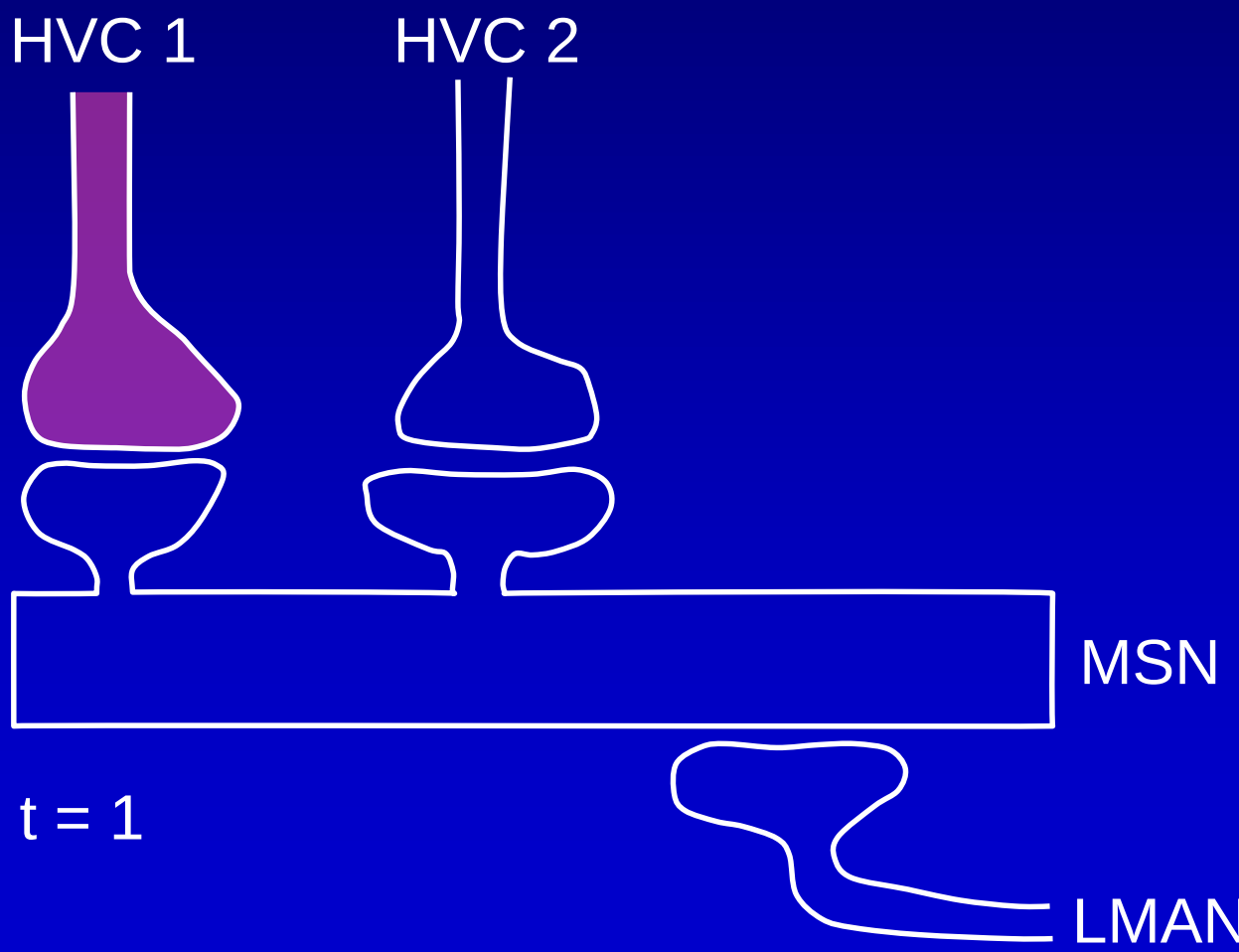

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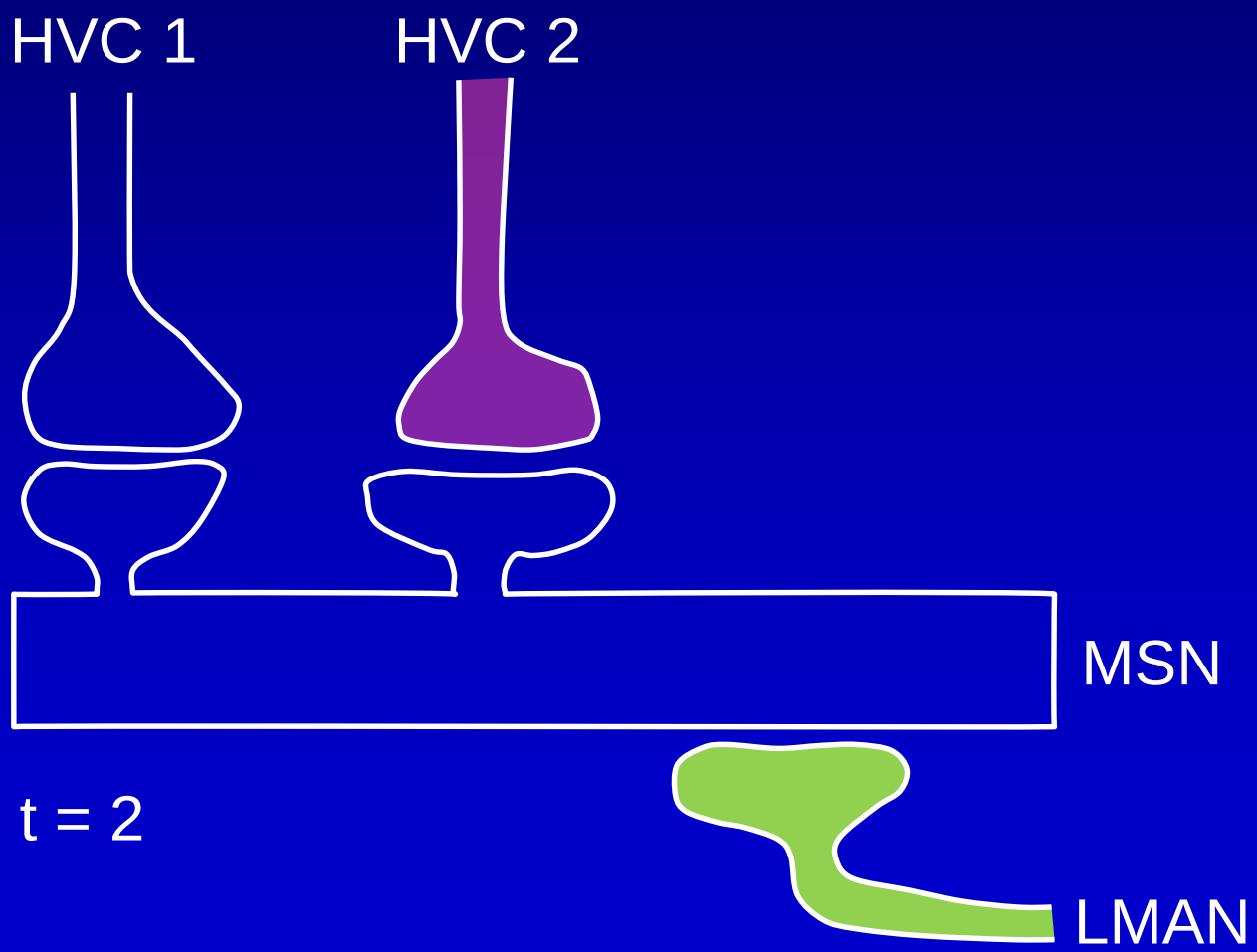

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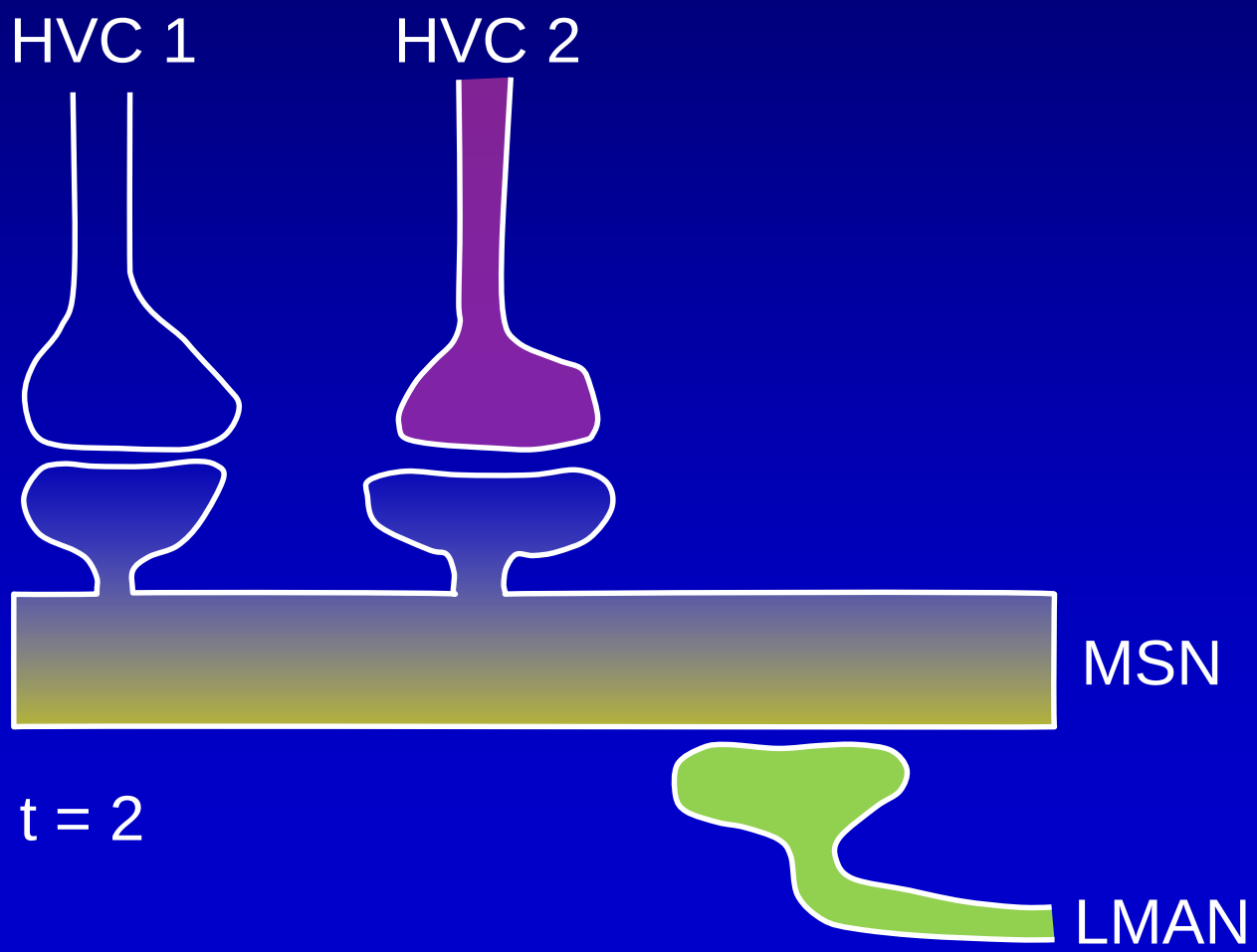
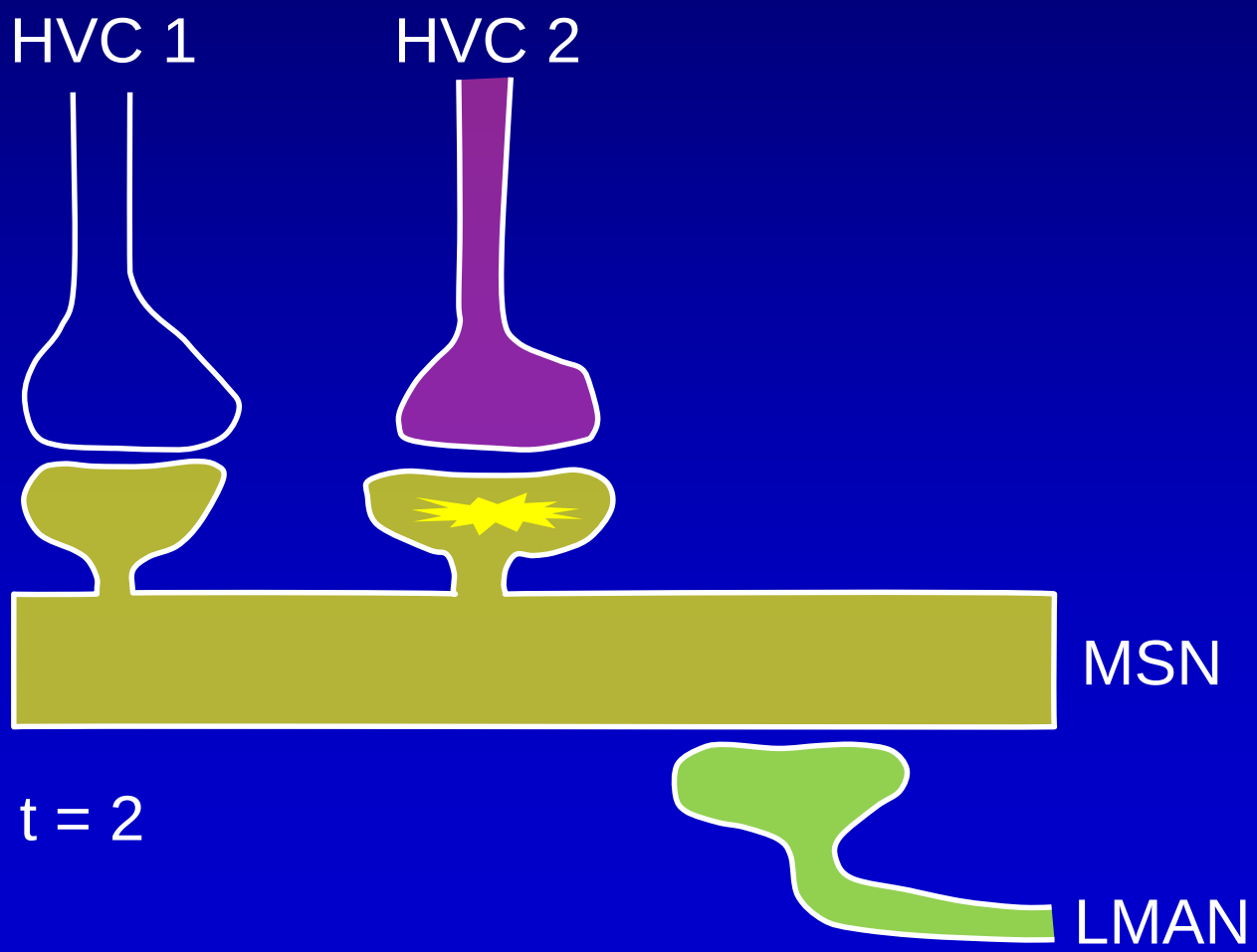
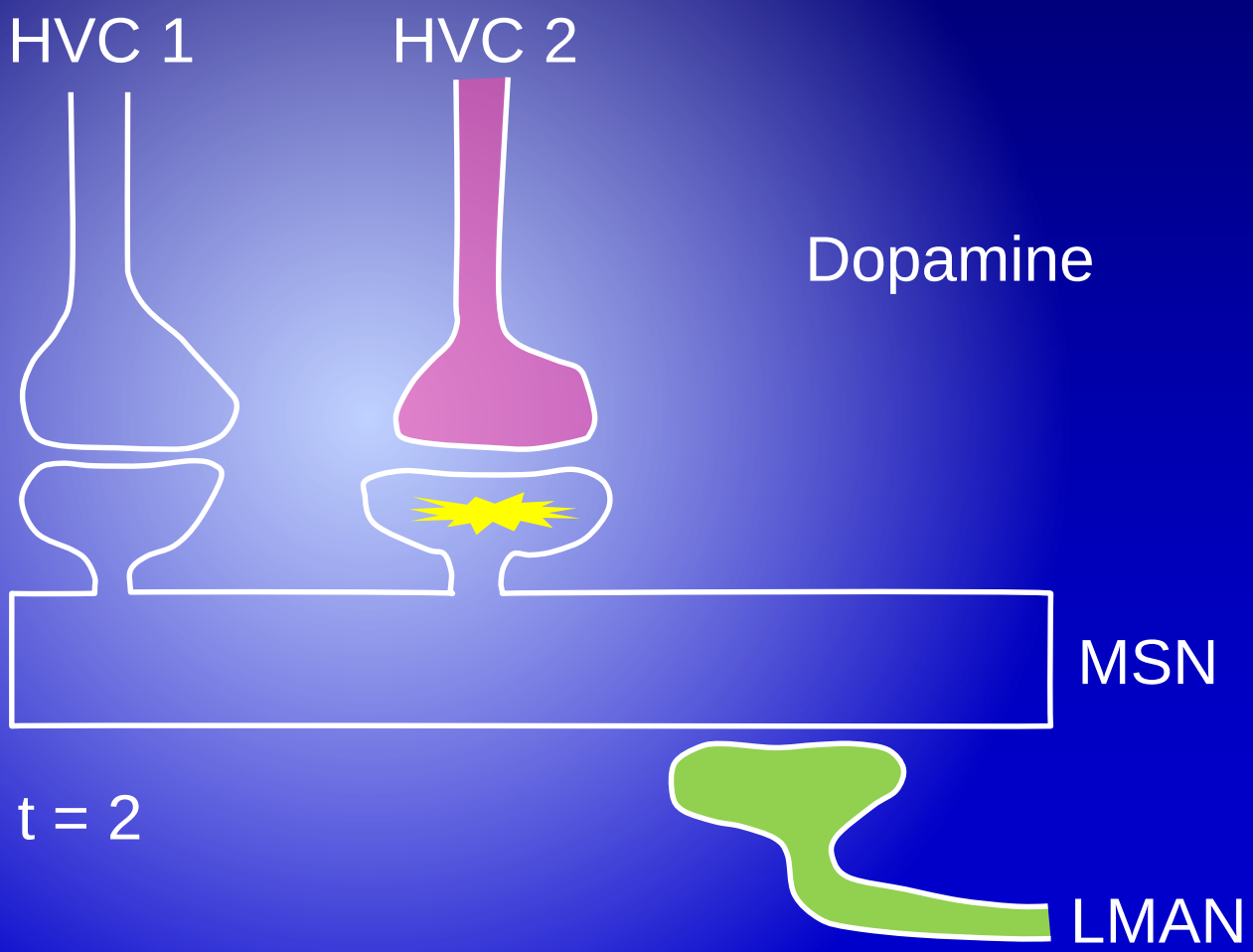


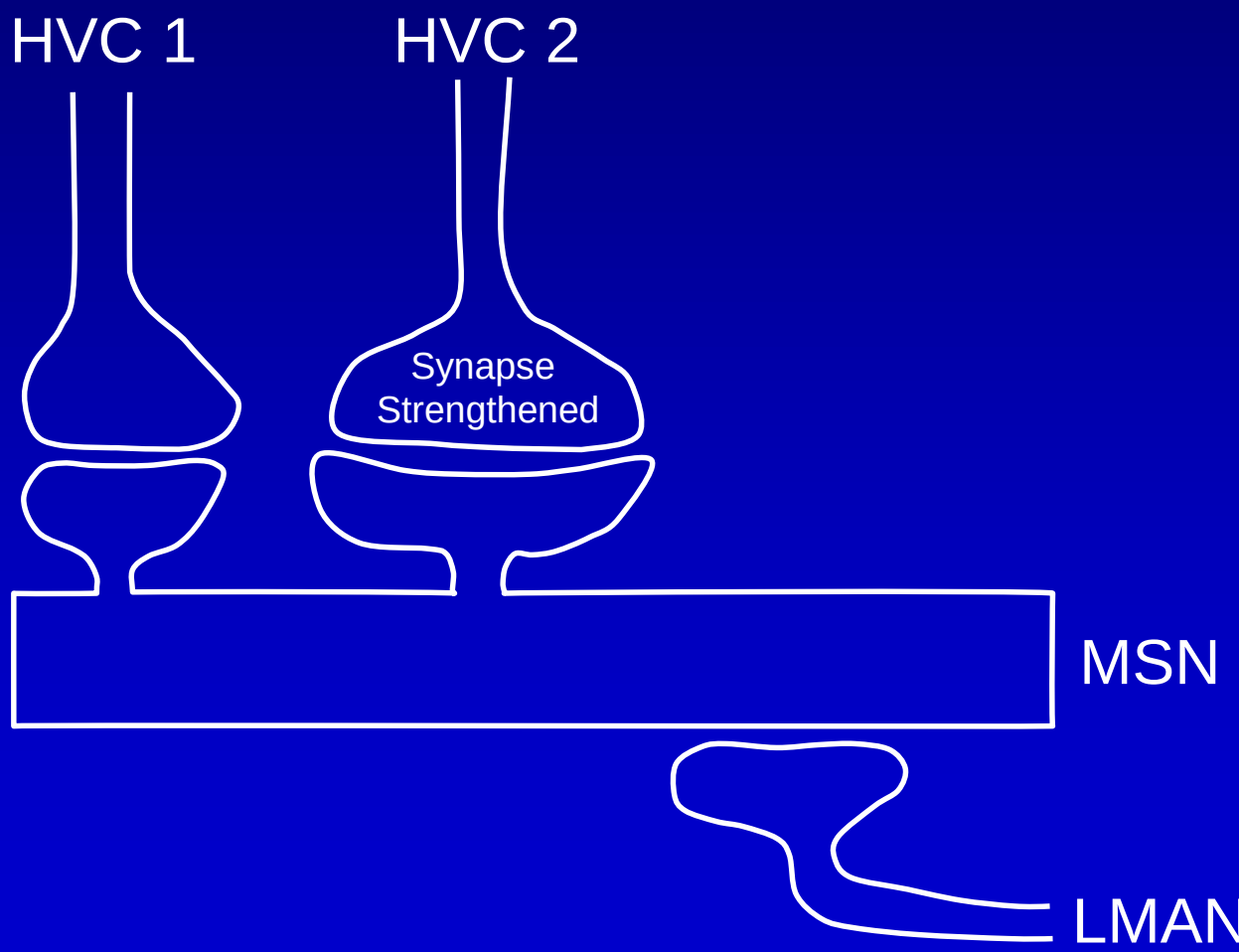
Hypothesis for HVC-LMAN synaptic interaction on striatal MSNs



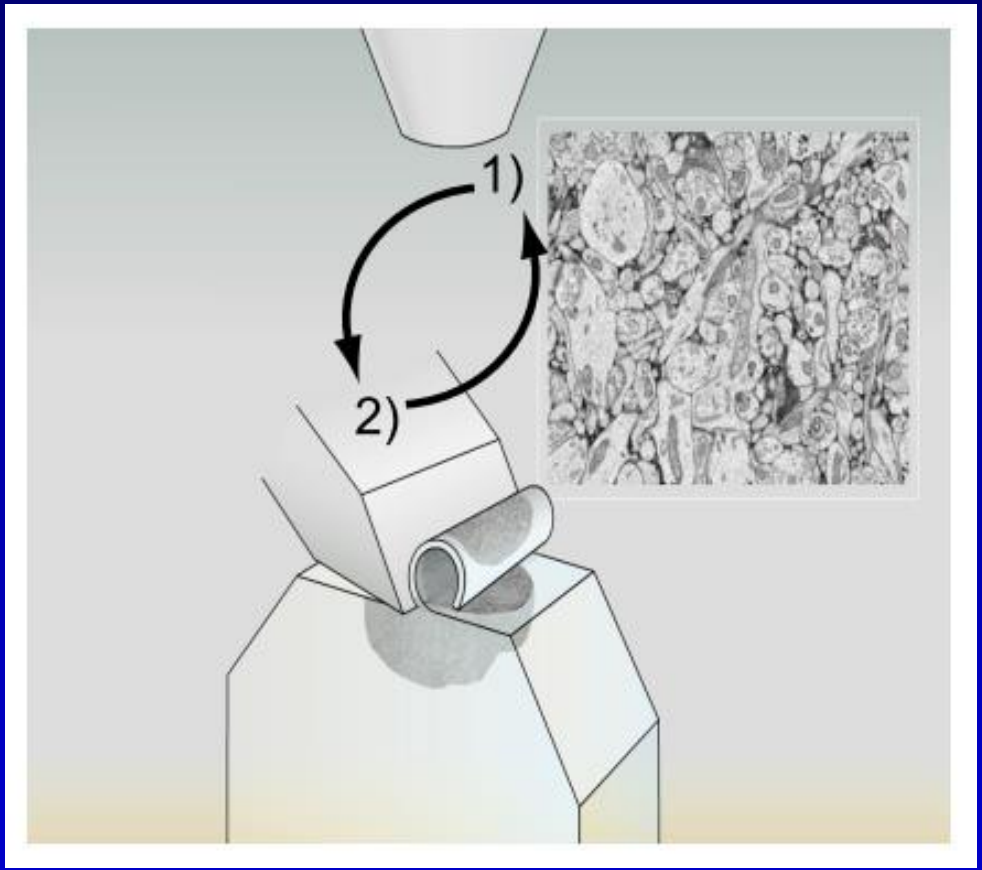
Hypothesis for HVC-LMAN synaptic interaction on striatal MSNs

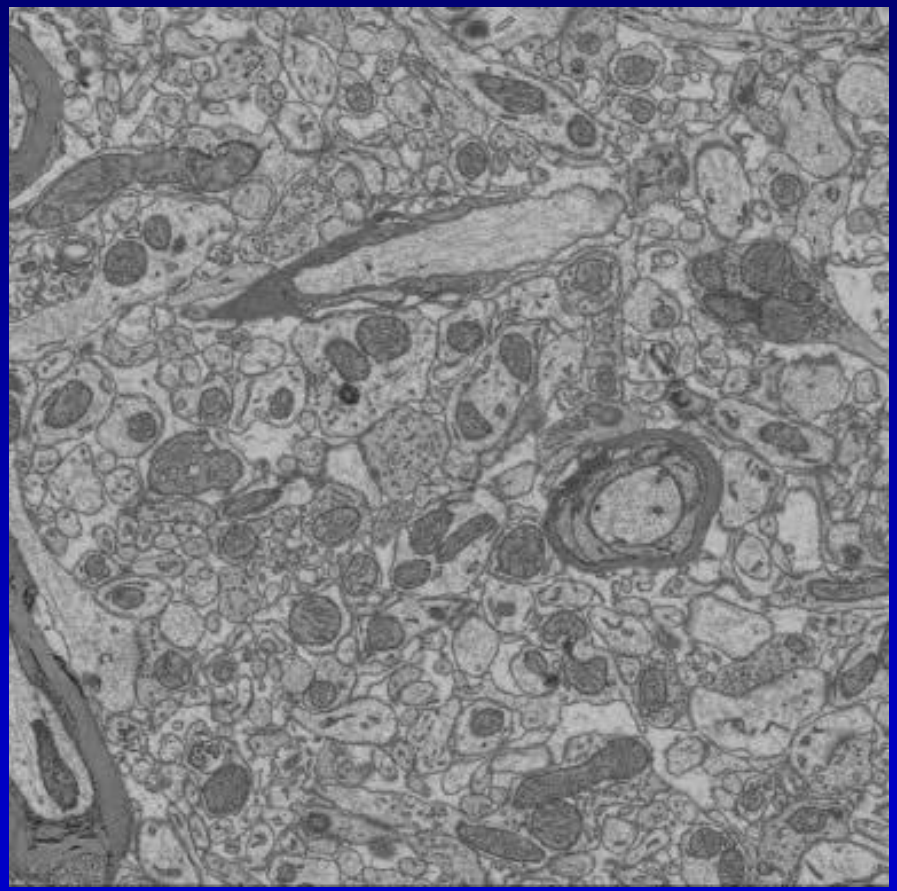


Hypothesis for HVC-LMAN synaptic interaction on striatal MSNs



Serial Block Face Scanning EM

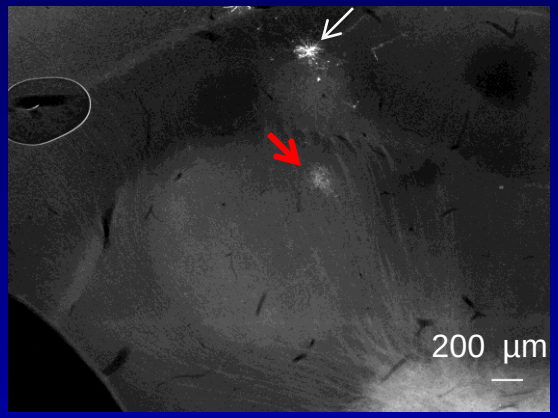




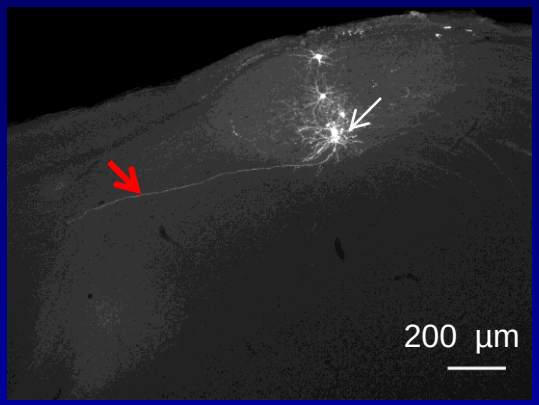
Collaboration with Winfried Denk and Jörgen Kornfeld

Distinct morphology of HVC and LMAN axons

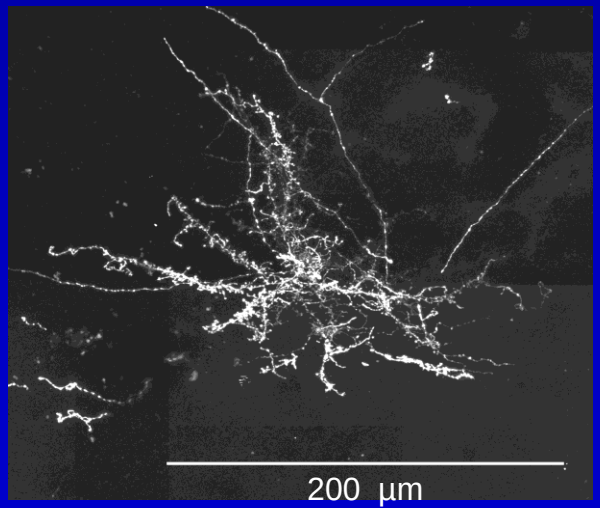
LMAN



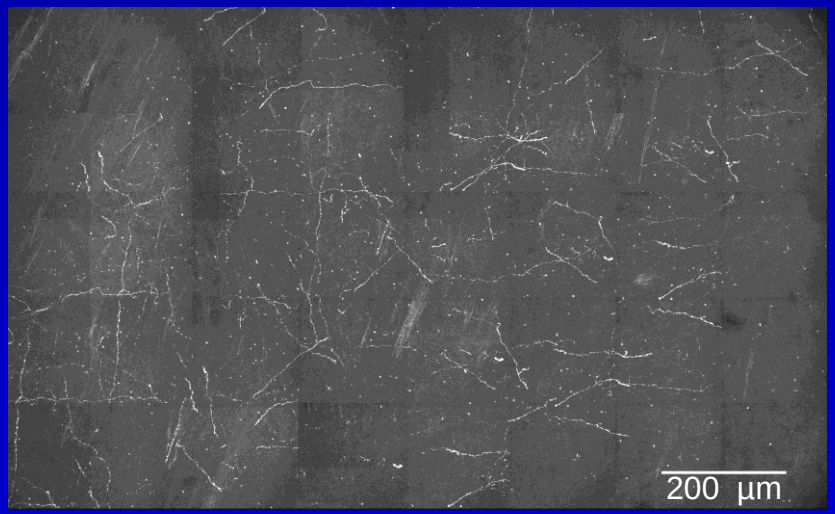
HVC



Axonal arbor of LMAN neuron in Area X



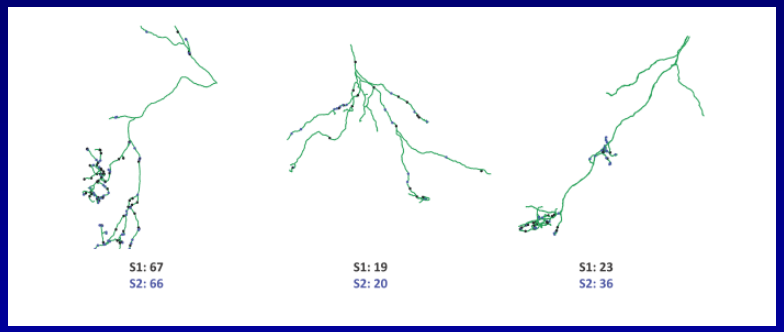
Axonal arbor of HVC neuron in Area X



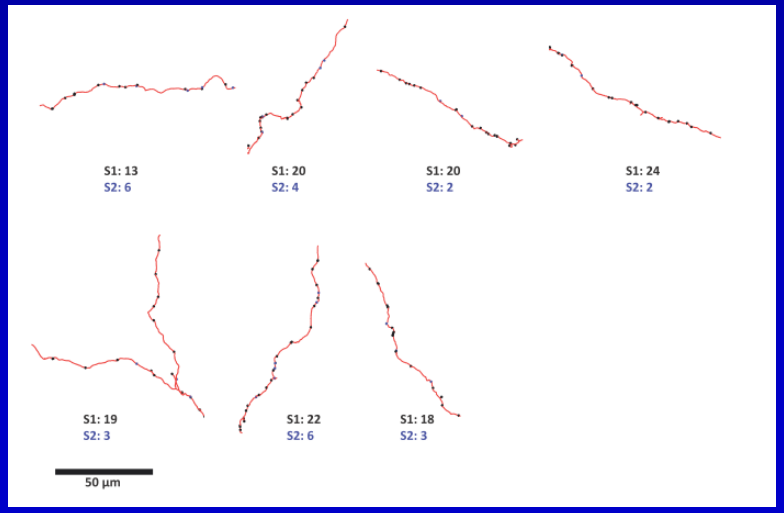
Michael Stetner

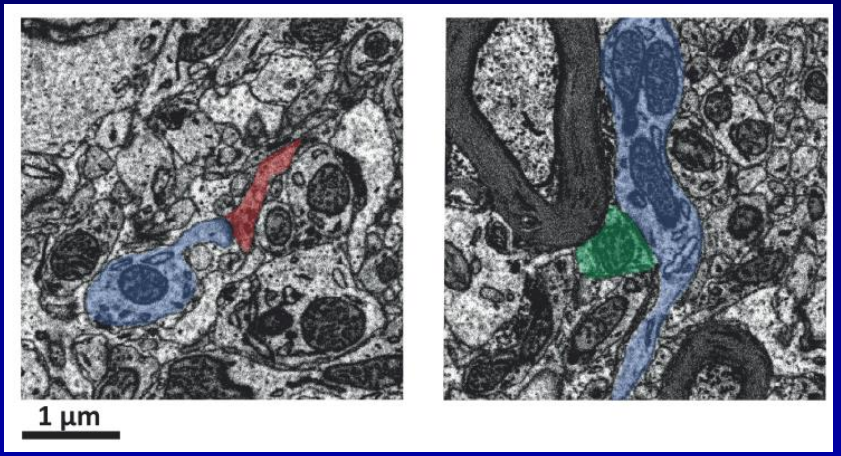
Inputs onto MSN spines originate primarily from HVC

Putative LMAN axons



Putative HVC axons





MSN HVC-like LMAN-like

~94% of synapses onto spines are from HVC-like axons

The role of the basal ganglia in songbird vocal learning

- LMAN directly drives ‘exploratory variability’ in the song motor pathway.
- LMAN-driven variability becomes biased during learning, in the direction of improved song performance.
- We have found evidence that a dopaminergic pathway to the songbird BG may carry ‘performance’ error-related information.
- We hypothesize that the basal ganglia determine which song variations lead to better performance and bias the variability in the direction of improved performance.
- We have proposed a testable model of basal ganglia function that explicitly incorporates an efference copy of cortically-generated motor actions.

The Fee Lab

Current Lab Members

- Anusha Narayan
- Natalia Denissenko
- Tatsuo Okubo
- Michael Stetner
- Emily Mackevicius
- Galen Lynch

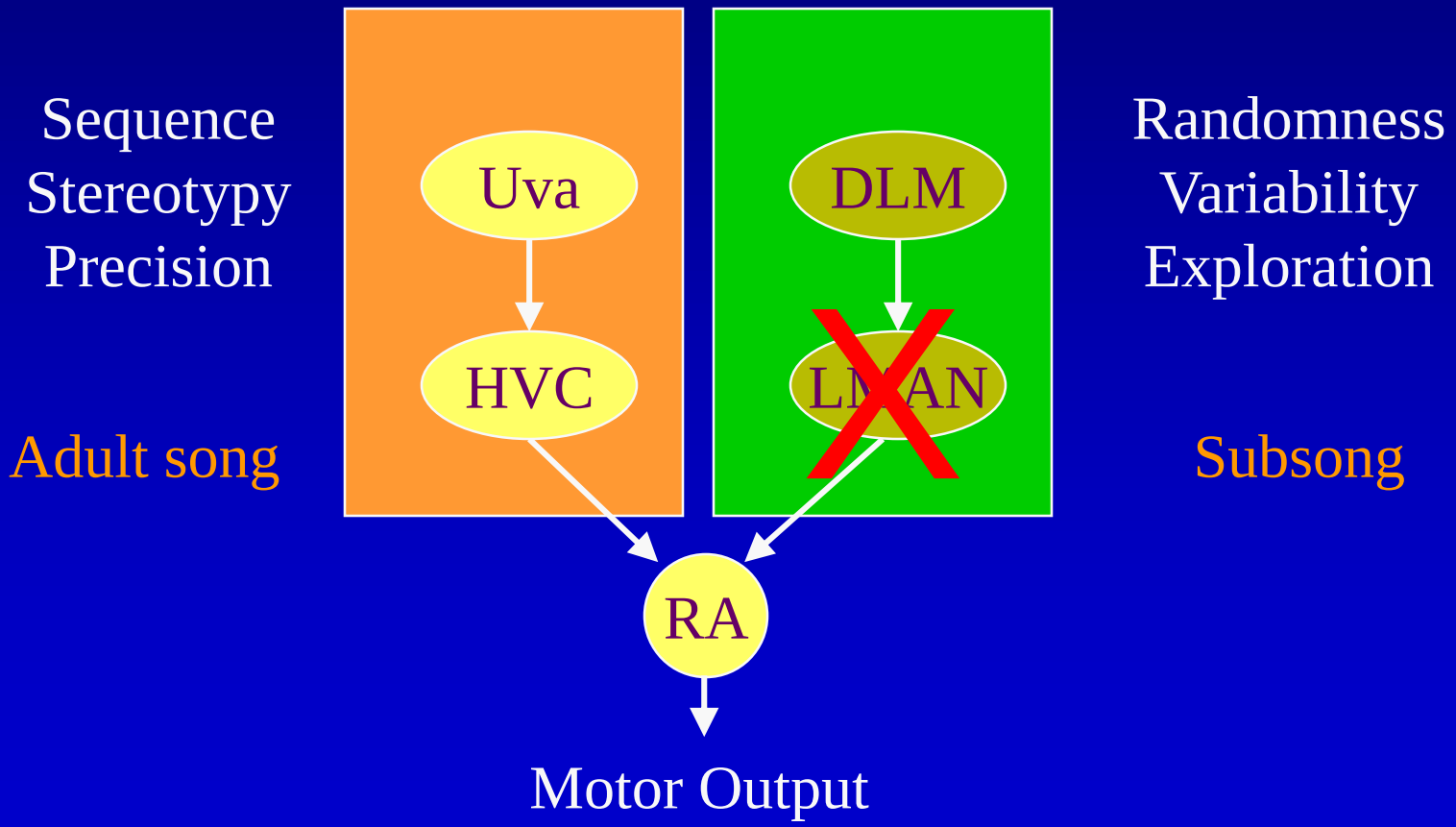
Former Lab Members

- Richard Hahnloser
- Alexay Kozhevnikov
- Anthony Leonardo
- Michael Long
- Bence Ölveczky
- Dmitriy Aronov
- Aaron Andalman
- Lena Veit
- Jakob Förster
- Liora Las
- Jesse Goldberg
- Yael Mandelblat

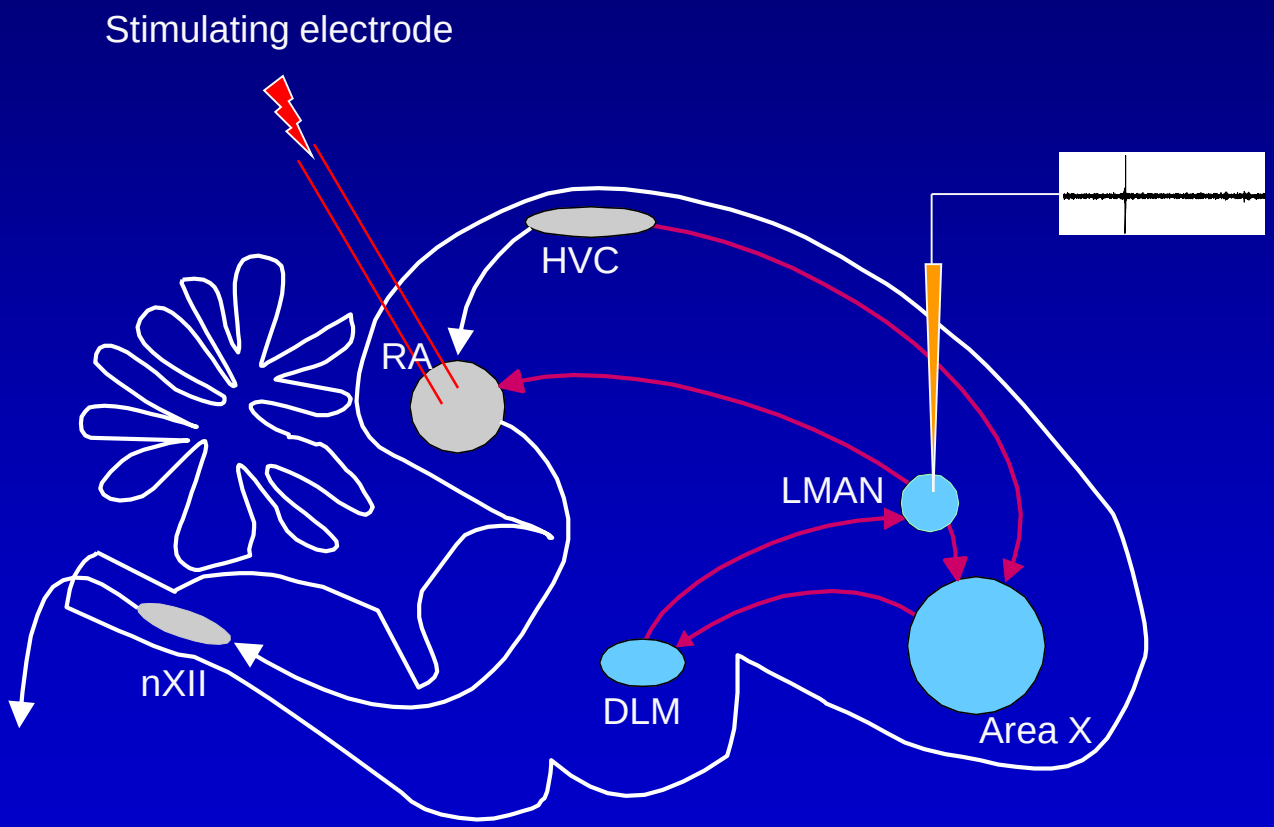
web.mit.edu/feelab

Funding:
National Institutes of Health - NIMH, NIDCD

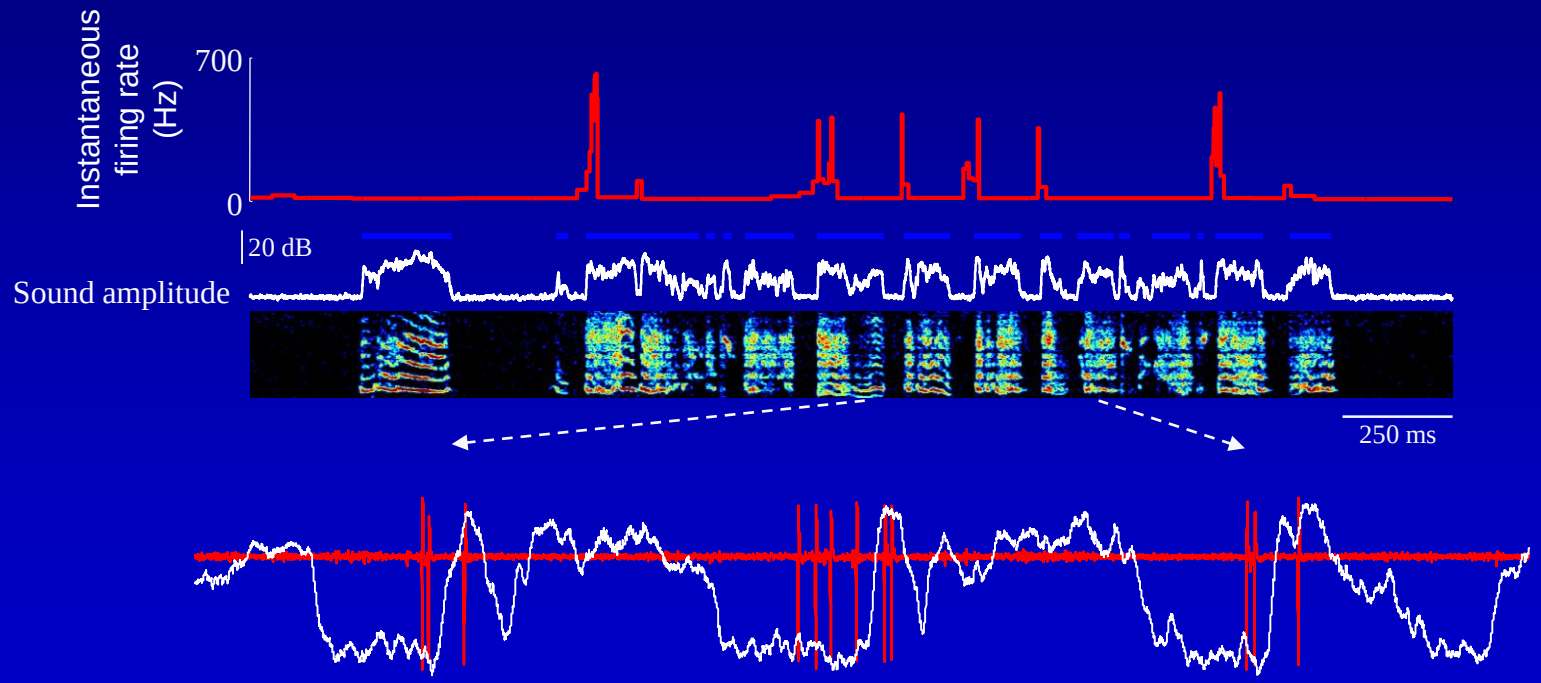
Separate premotor pathways for stereotyped song and variability



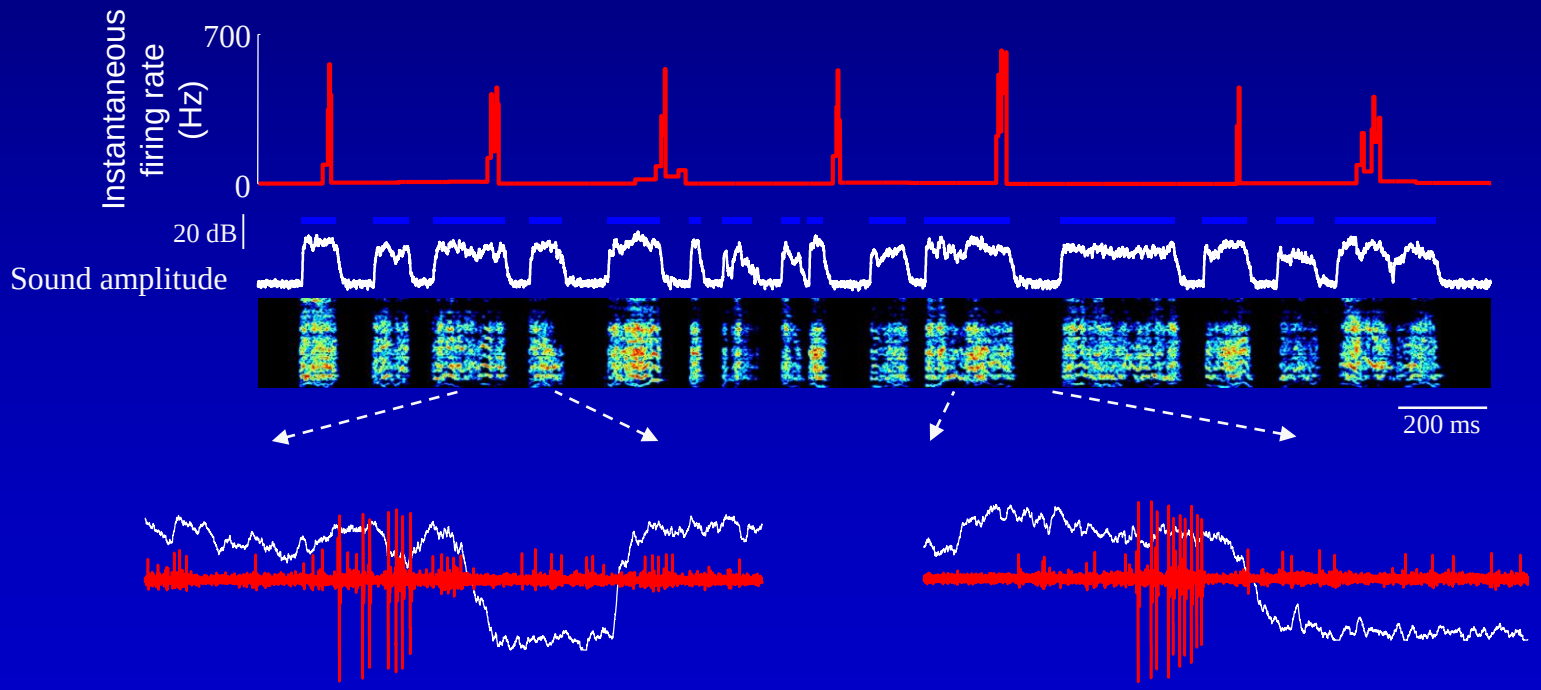
LMAN drives subsong



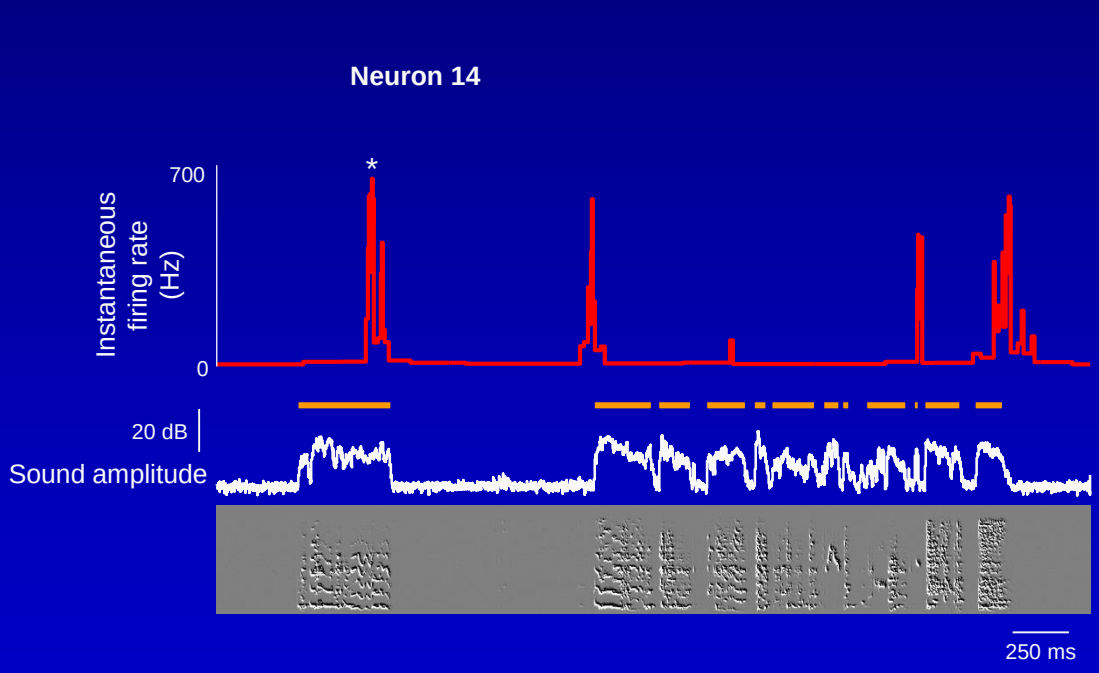
LMAN(RA) neurons exhibit premotor correlation with subsong syllables

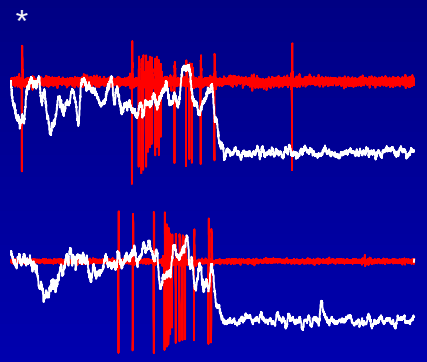


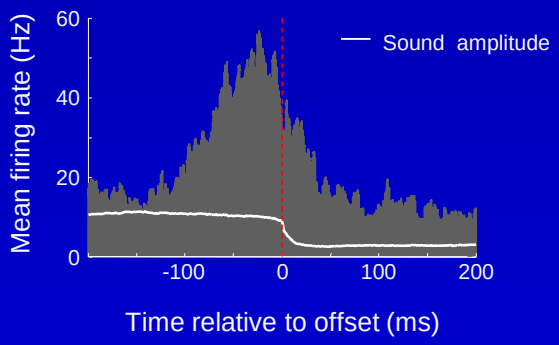
LMAN(RA) neurons exhibit premotor correlation with subsong syllables



LMAN(RA) neurons exhibit premotor correlation with subsong acoustic structure







Summary

- The AFP can generate a direct premotor bias that reduces vocal errors.
- The learning accumulated across many days of training is encoded primarily in plasticity in the motor pathway.
- The contribution of the AFP is limited to the learning that occurred most recently (during the same day).
- AFP bias is predictive of subsequent plasticity in the motor pathway within the next 24 hours