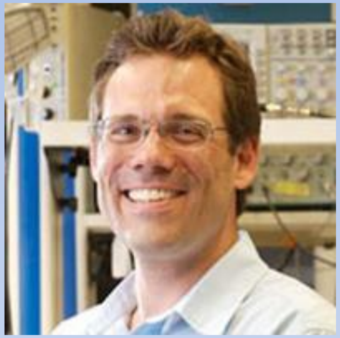
How songbirds sing birdsongs?



Michale Fee (MIT)

Liora Las

Veit et al. (*J Neurophysiol*, 2011)

Outline:

1) Introduction to songbirds as a model.
2) Neuronal circuits underlying mature song production (motor system).
3) Neuronal circuits underlying early stages of singing (learning system).

The brain is a learning machine

- Many motor and cognitive skills are learned through trail-and-error process -> i.e. playing the piano or playing tennis.
- **Human speech learning** is an sensorimotor skill that needs auditory feedback; we have brain areas that are devoted for these tasks.

Vocal learning

Mammals:
- Humans
- Bats
- Dolphins/Whales
- Elephants
- Sealions

Birds:
- Parrots
- Hummingbirds
- Songbirds

Over 4000 different species of songbirds

What do songbirds and humans have in common?

Both humans and songbirds learn their motor behavior (e.g. vocal) early in life.

Both learn to communicate by listening to their parents.

They must be able to hear their own vocalization in order to learn to sing/speak.

Both humans and songbirds have evolved a complex hierarchy of specialized brain areas essential for vocal control.

Birds sing for two main reasons:

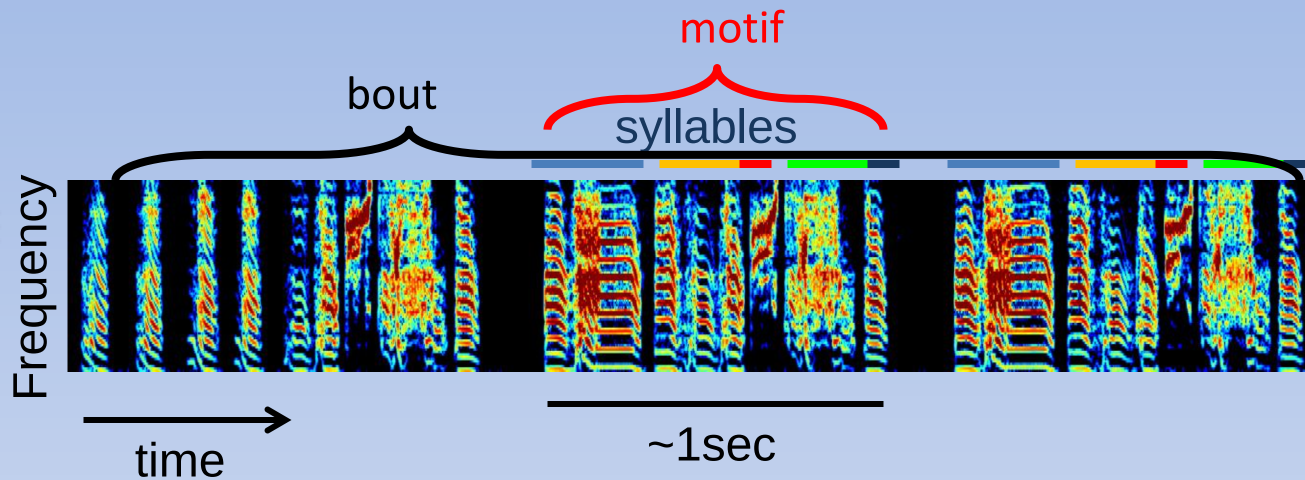
1. To attract a mate.
2. To establish and hold a territory.

Singing is mostly a male activity.

Male's brains are specialized in singing, female's brains are specialized in evaluating the song

Songbirds sing! Adult song is highly stereotyped

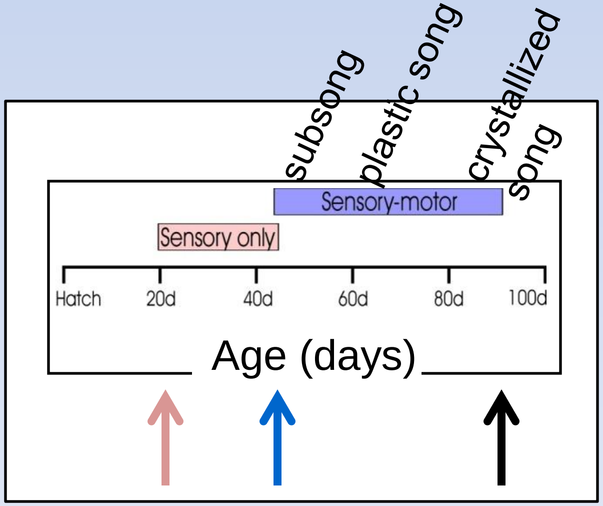
Zebra finch

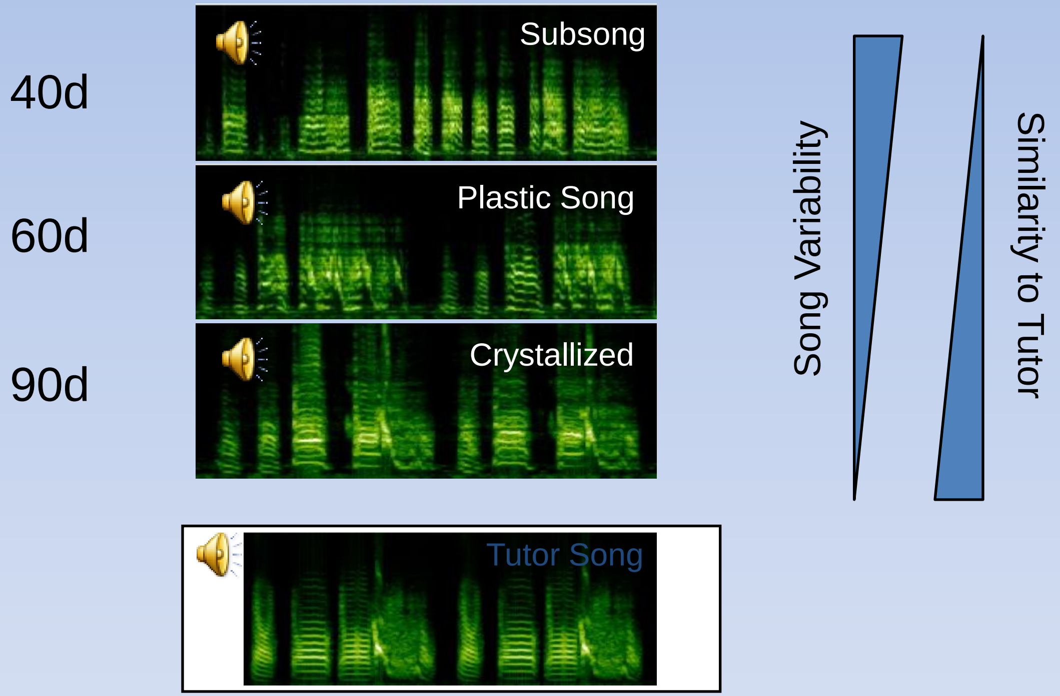


Ofer Tchernichovski's Lab (CUNY)

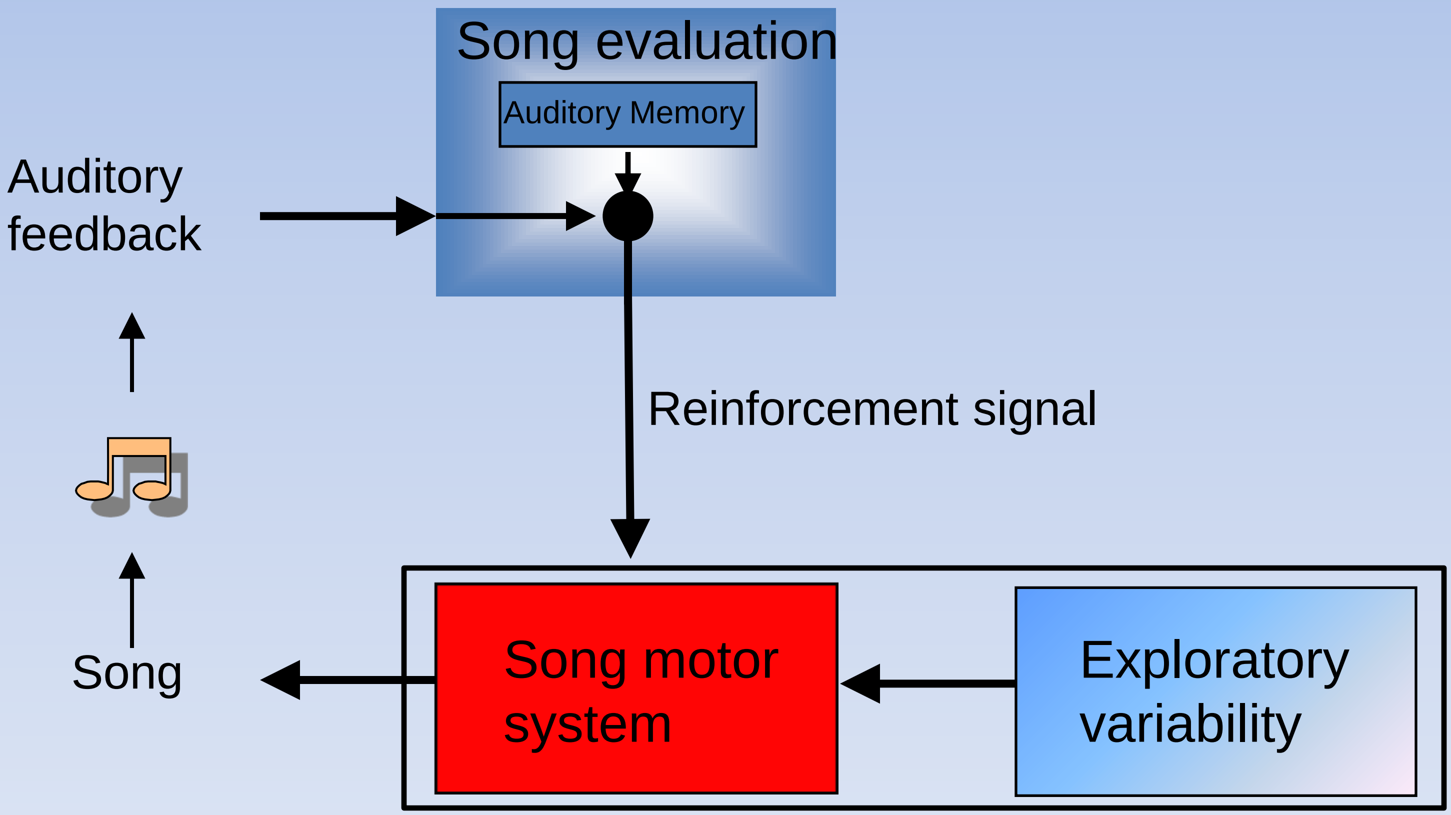
There are two modes of singing:
1) Direct singing
2) Undirected singing

Songbirds learn to sing by imitating their tutor



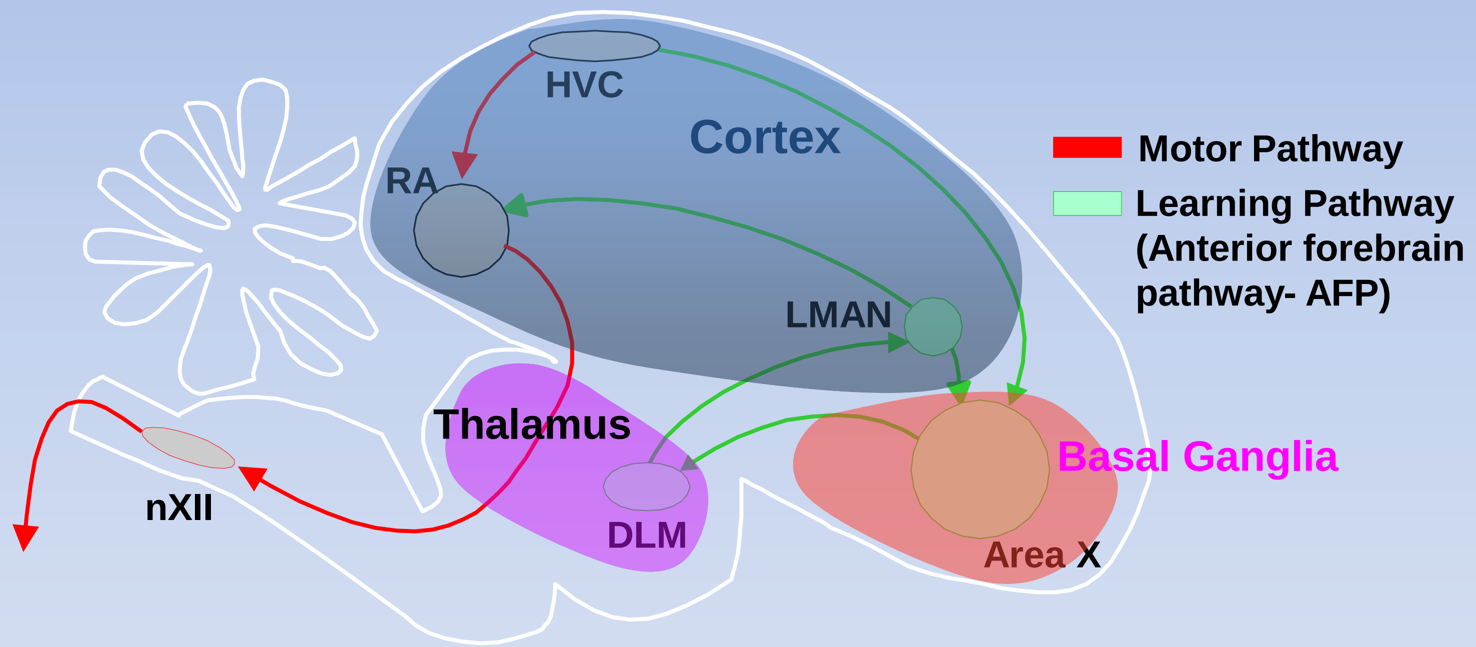


Reinforcement learning model for song acquisition



Konishi 1965; Marler 1970

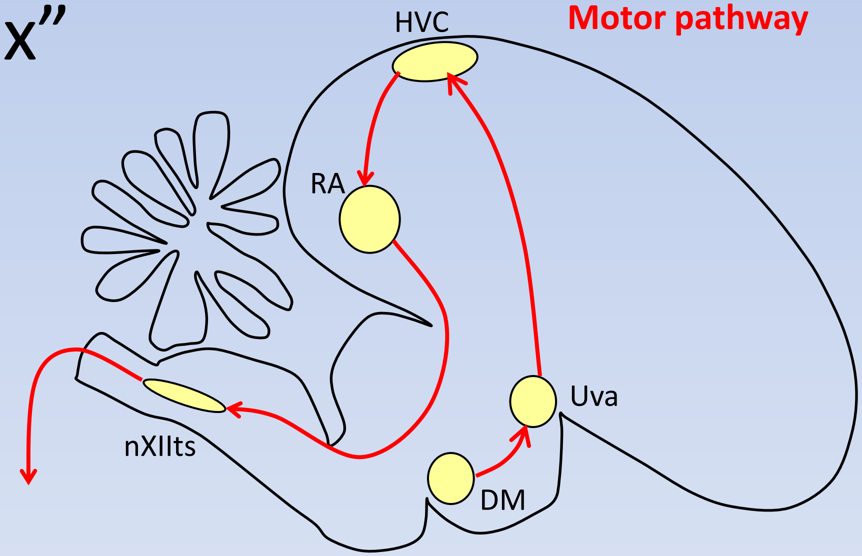
Song system



HVC
Cortex
RA
LMAN
Thalamus
DLM
Basal Ganglia
Area X
nXII
Motor Pathway
Learning Pathway
(Anterior forebrain
pathway- AFP)

Motor pathway

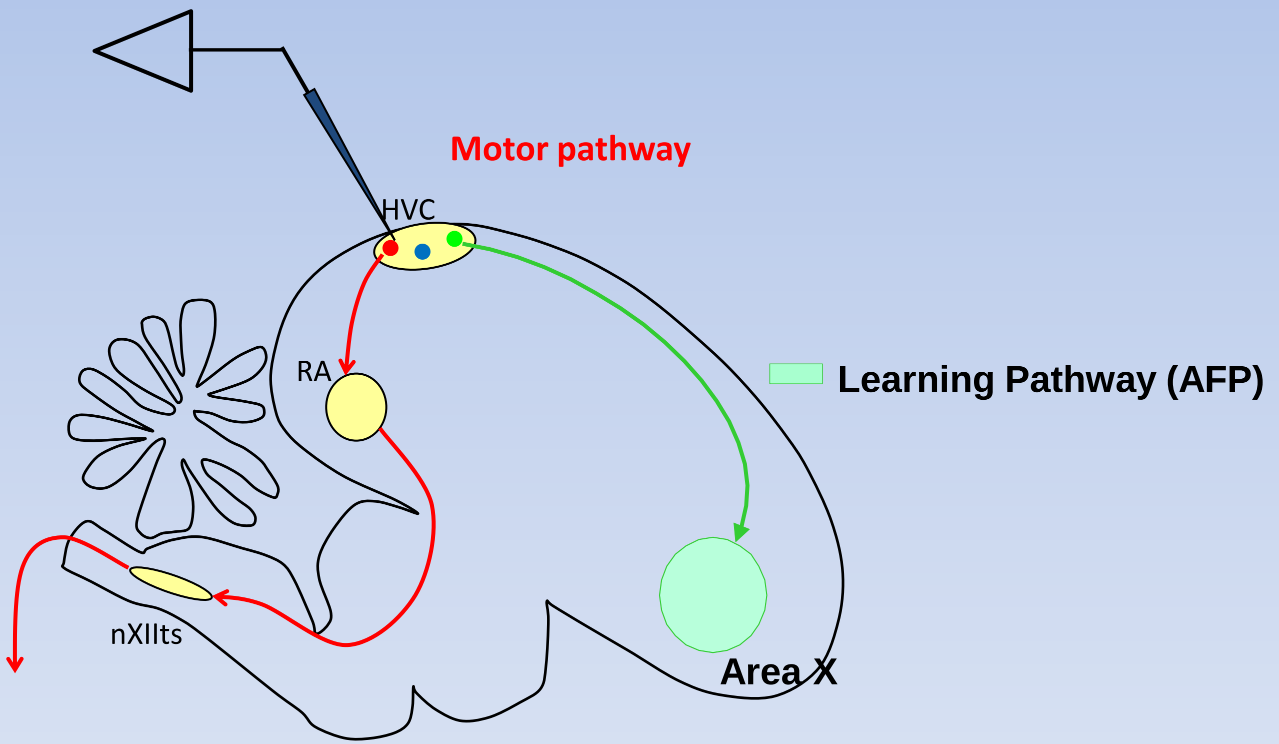
- HVC (high vocal center)
- RA: primary motor "cortex"
- brainstem motor areas
  - Muscles of the syranx
  - respiratory muscles

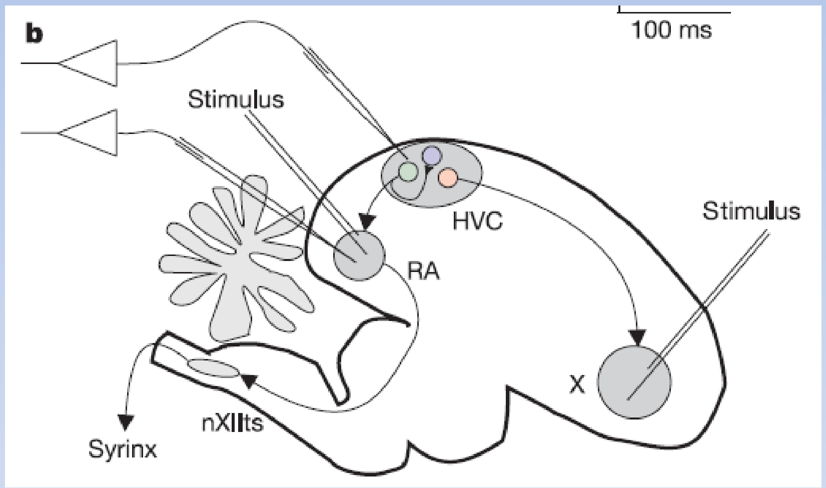


Nottebohm et al., (*J Comp Neurol*, 1976)

3 types of neurons in HVC –

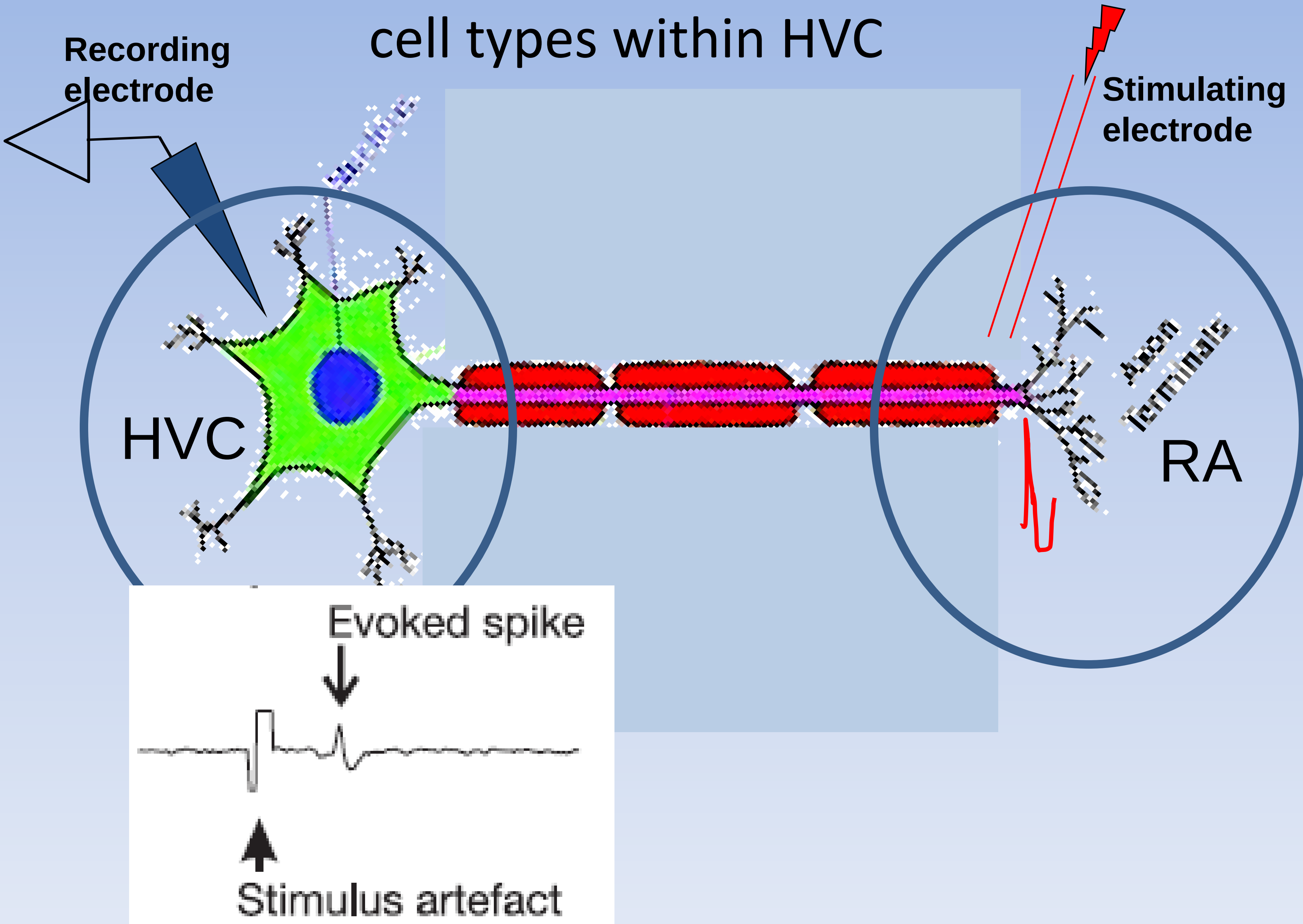
1) HVC-RA projecting neurons
2) HVC-X projecting neurons
3) interneurons

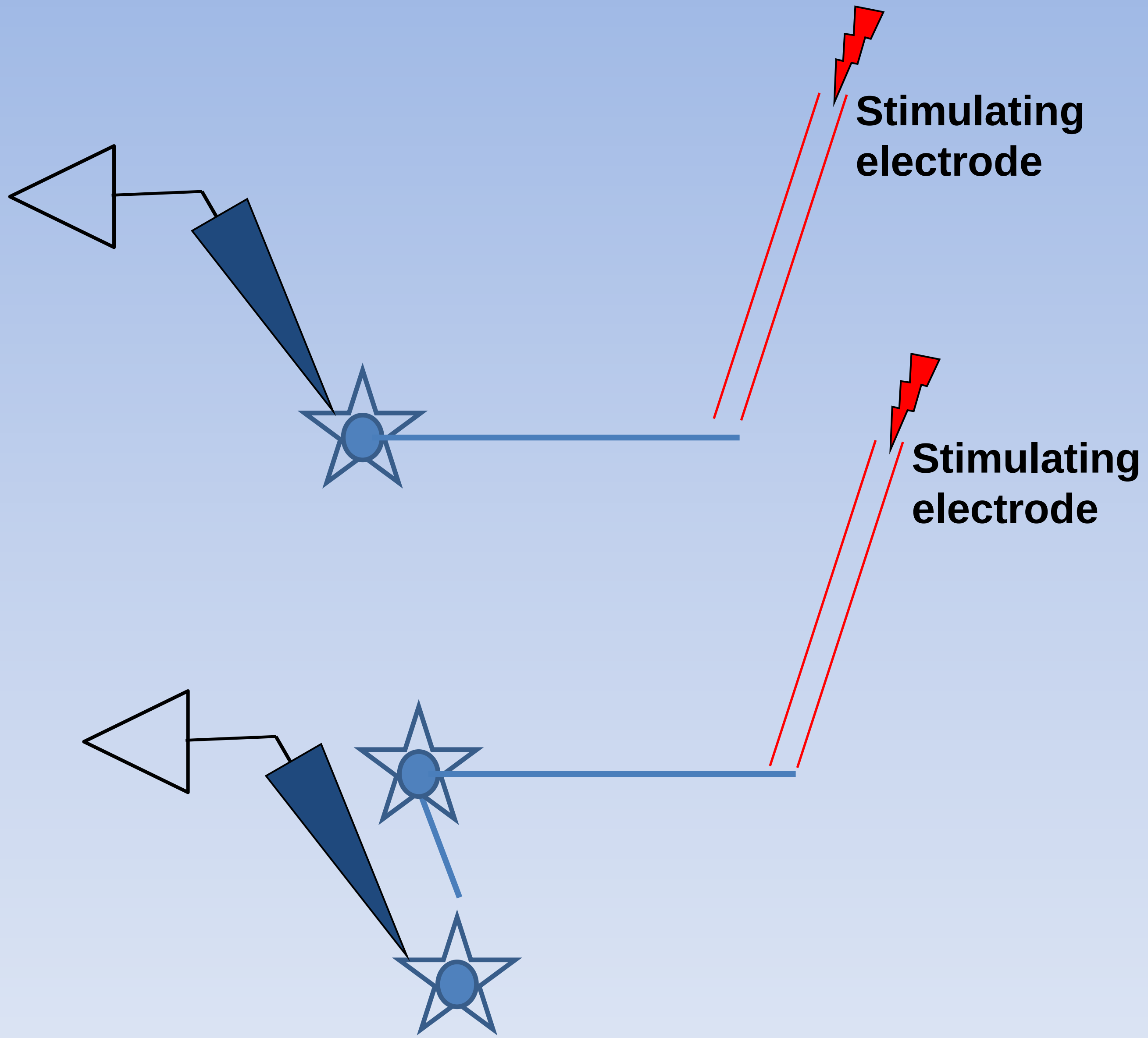




Hahnloser et al. (*Nature*, 2002)

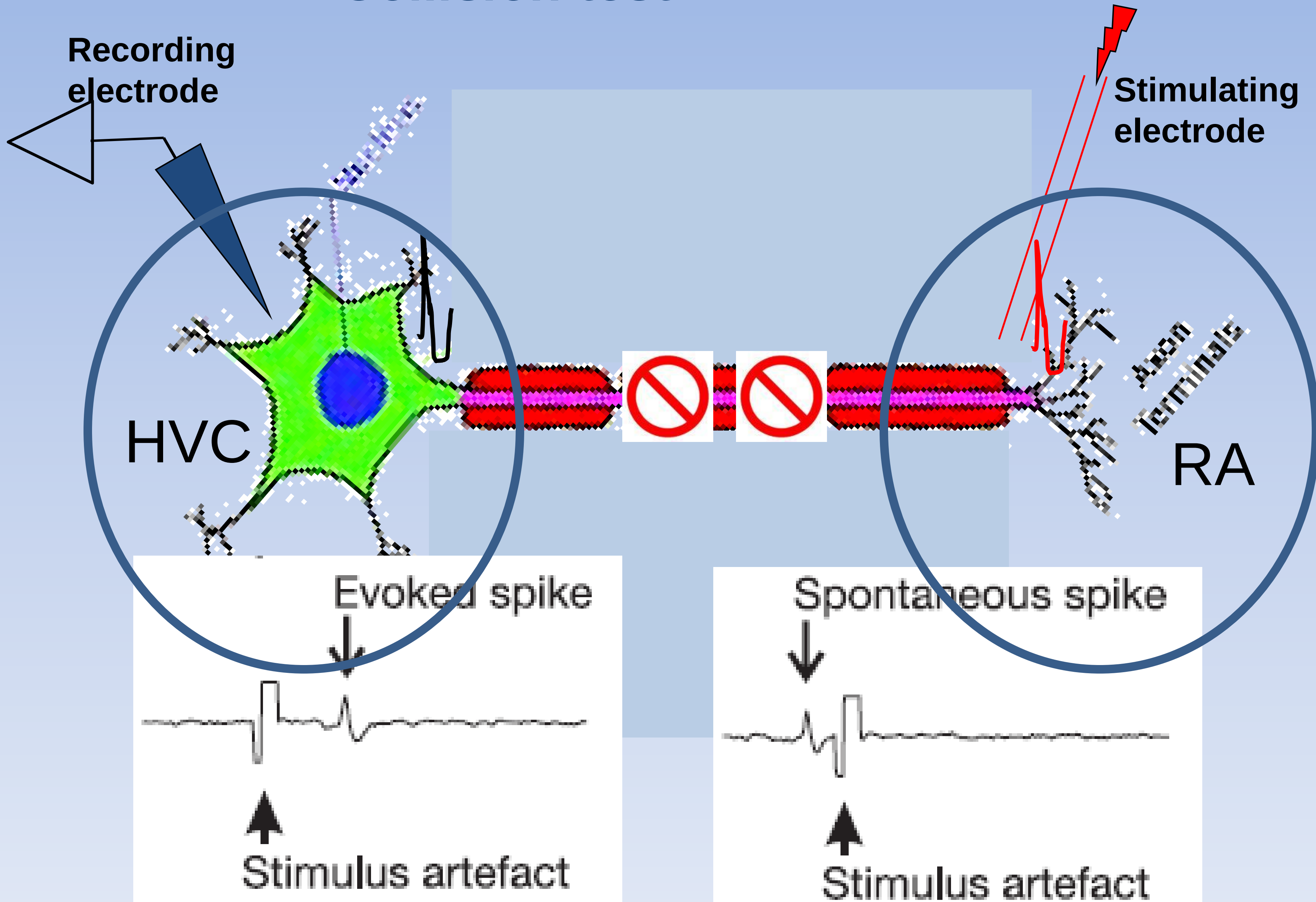
Using antidromic stimulation to identify cell types within HVC



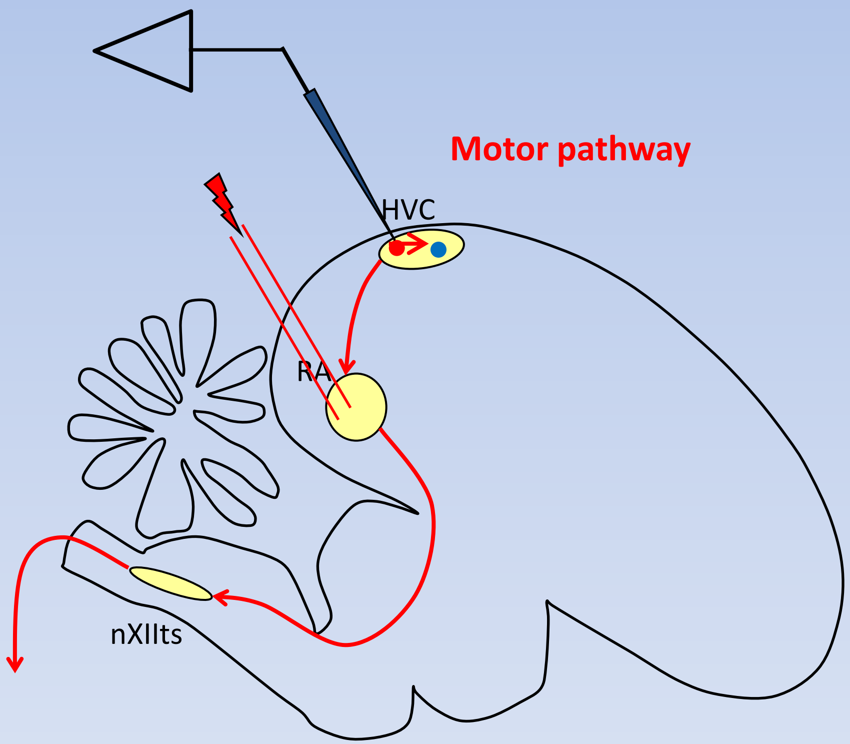


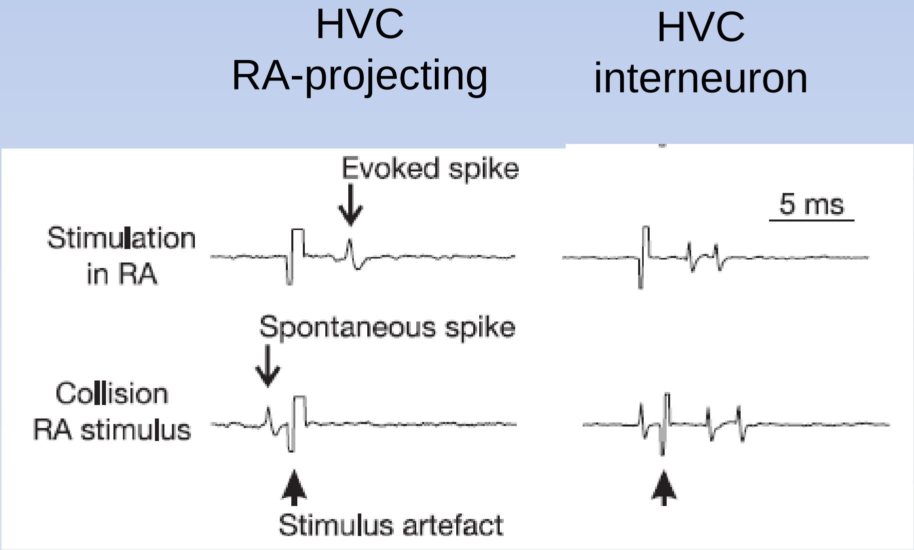
Stimulating electrode
Stimulating electrode

Collision test



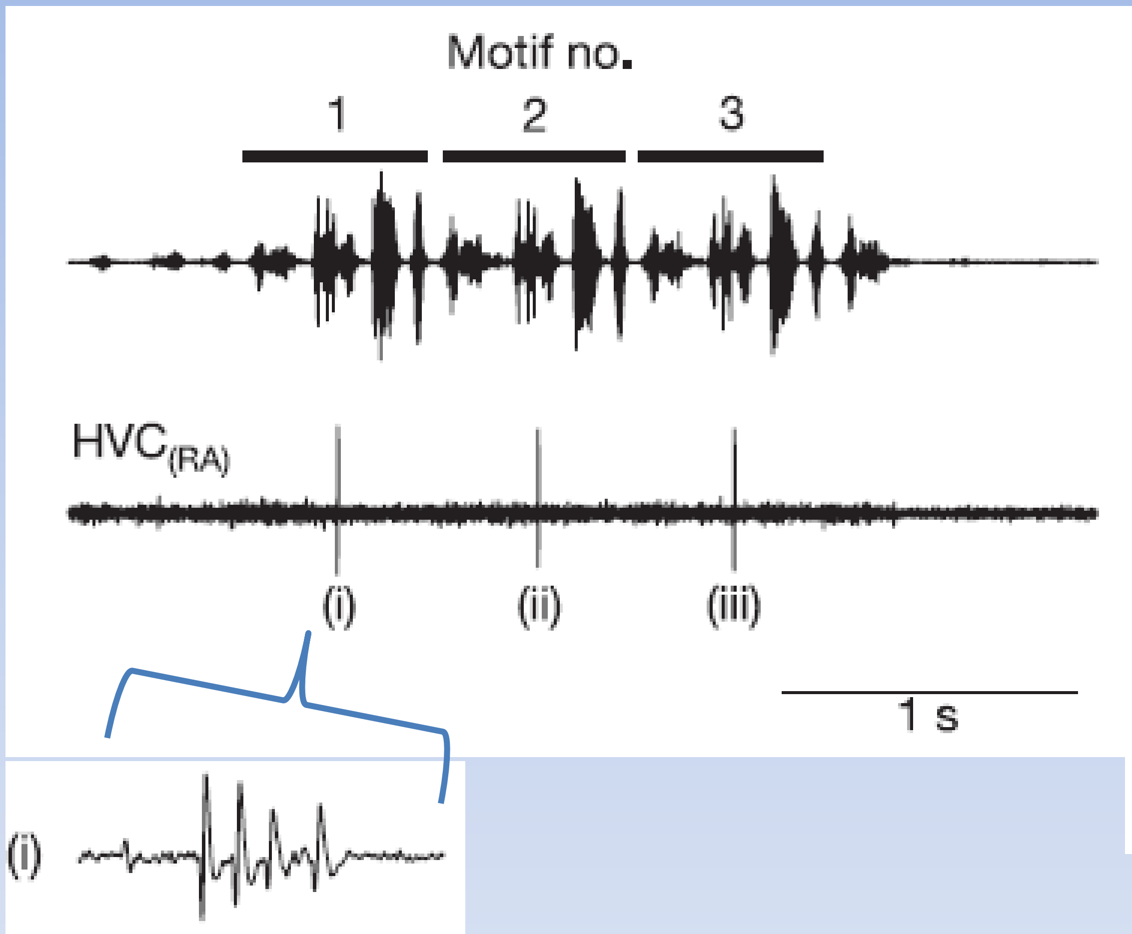
Using antidromic stimulation to identify cell types within HVC

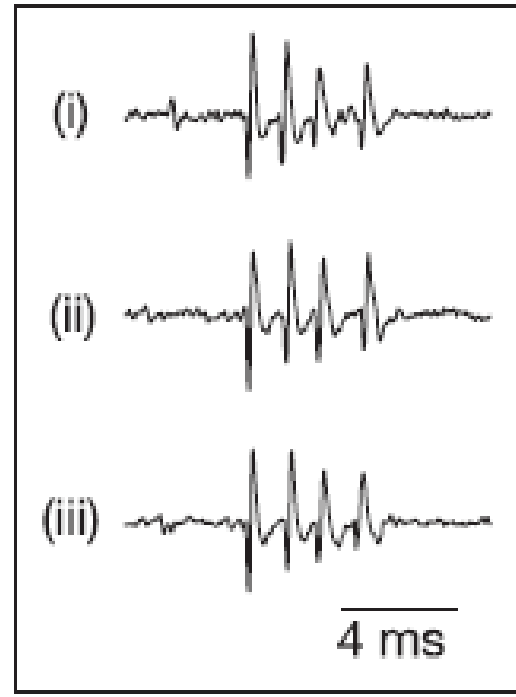




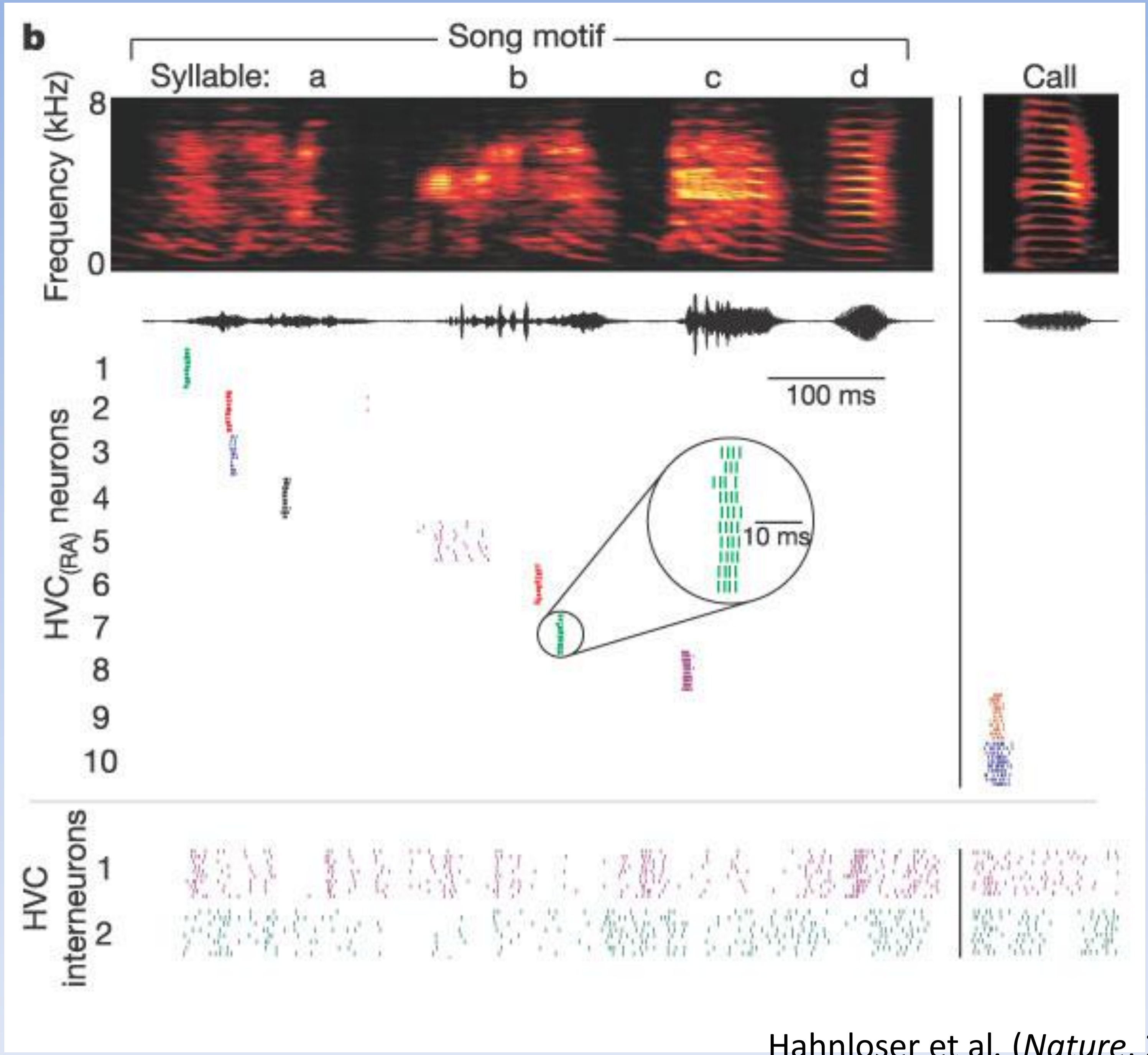
Hahnloser et al. (*Nature*, 2002)

Activity of HVC-RA neurons during singing





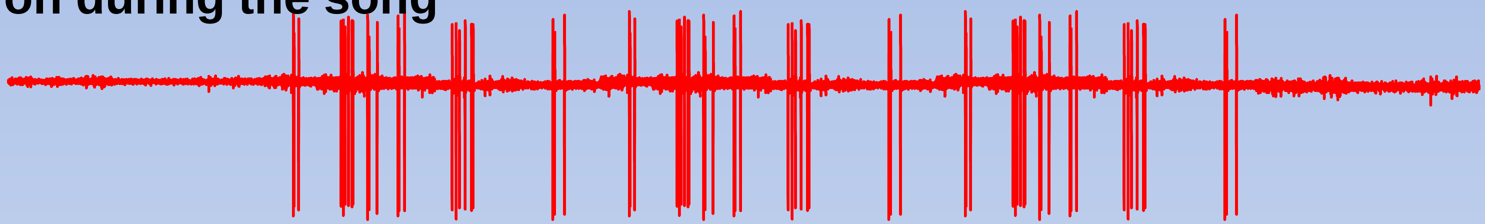
Hahnloser et al. (*Nature*, 2002)

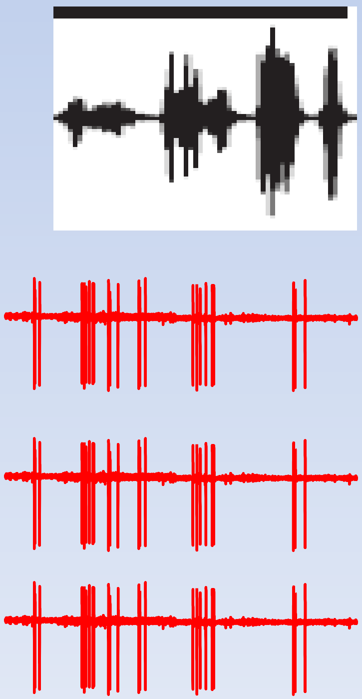


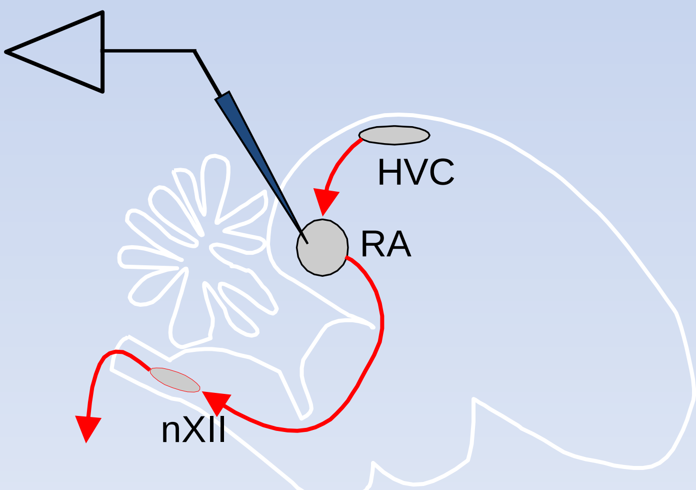
Hahnloser et al. (*Nature*, 2002)

The song

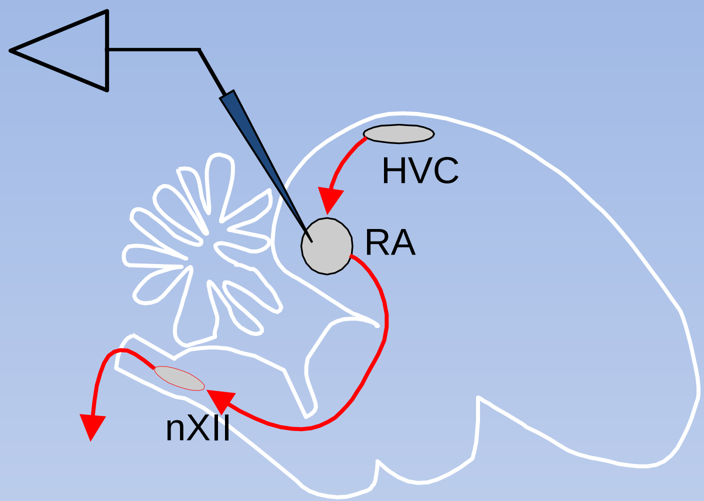
Recordings from RA neuron during the song



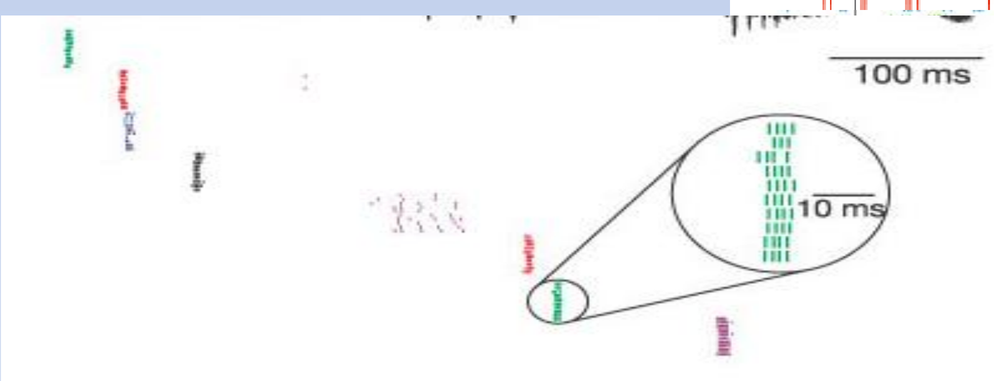


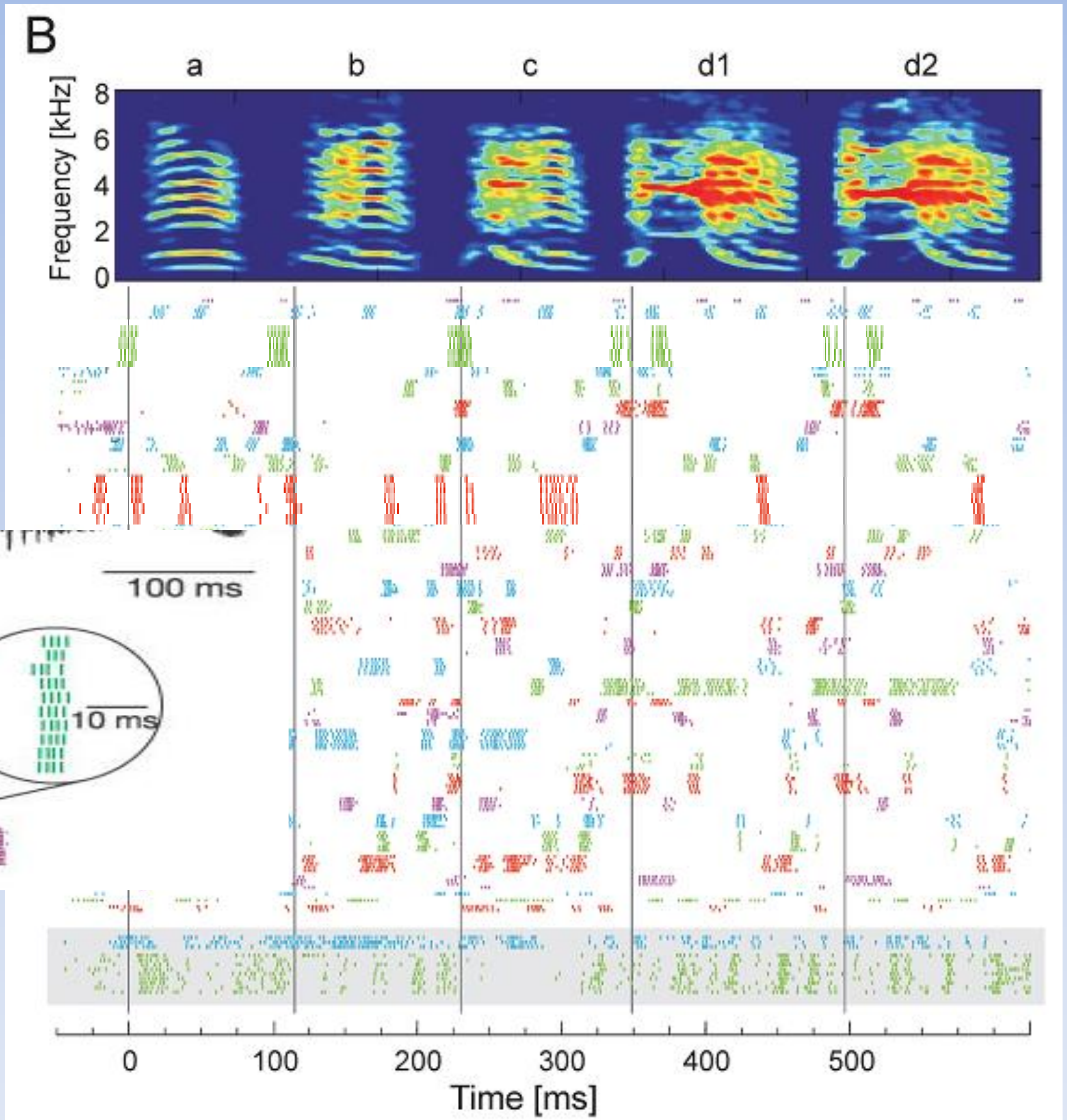


RA activity during singing



HVC-RA neurons

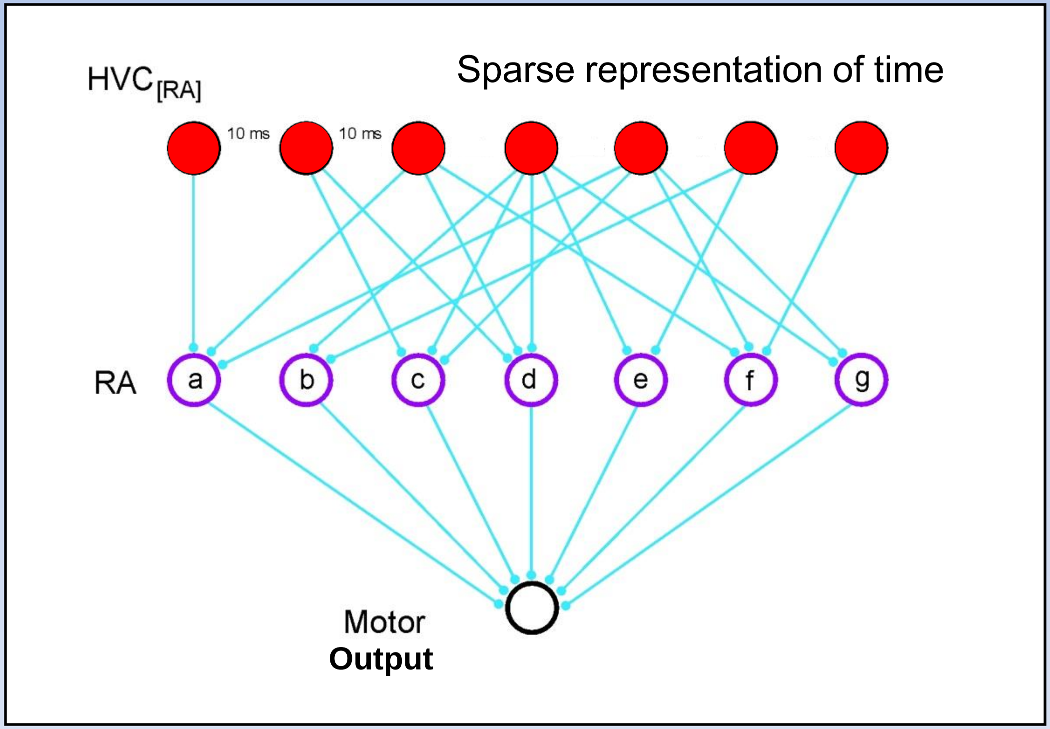


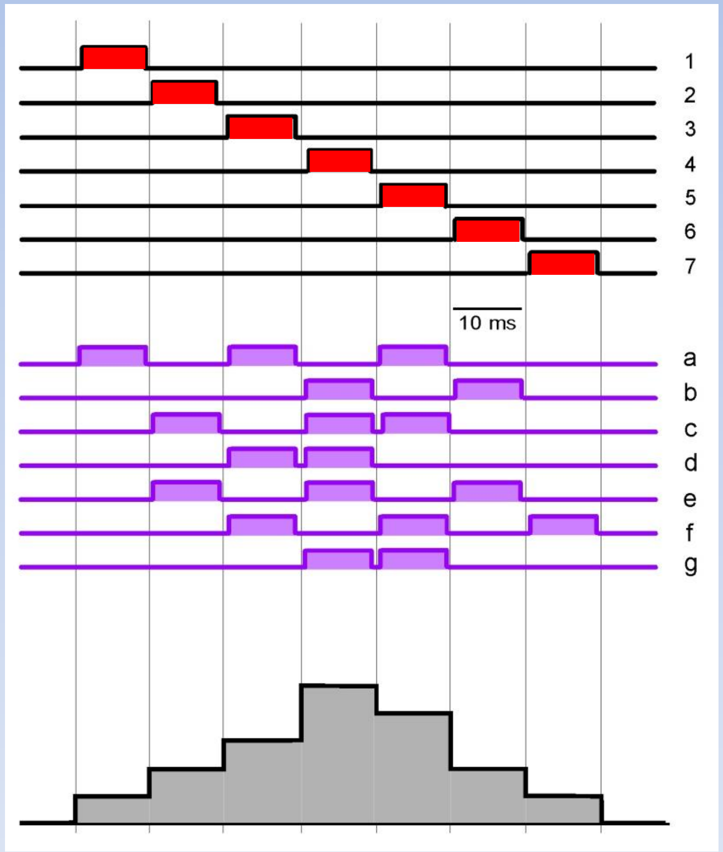


Leonardo & Fee (*J Neurosci*, 2005)

Simple sequence generation circuit

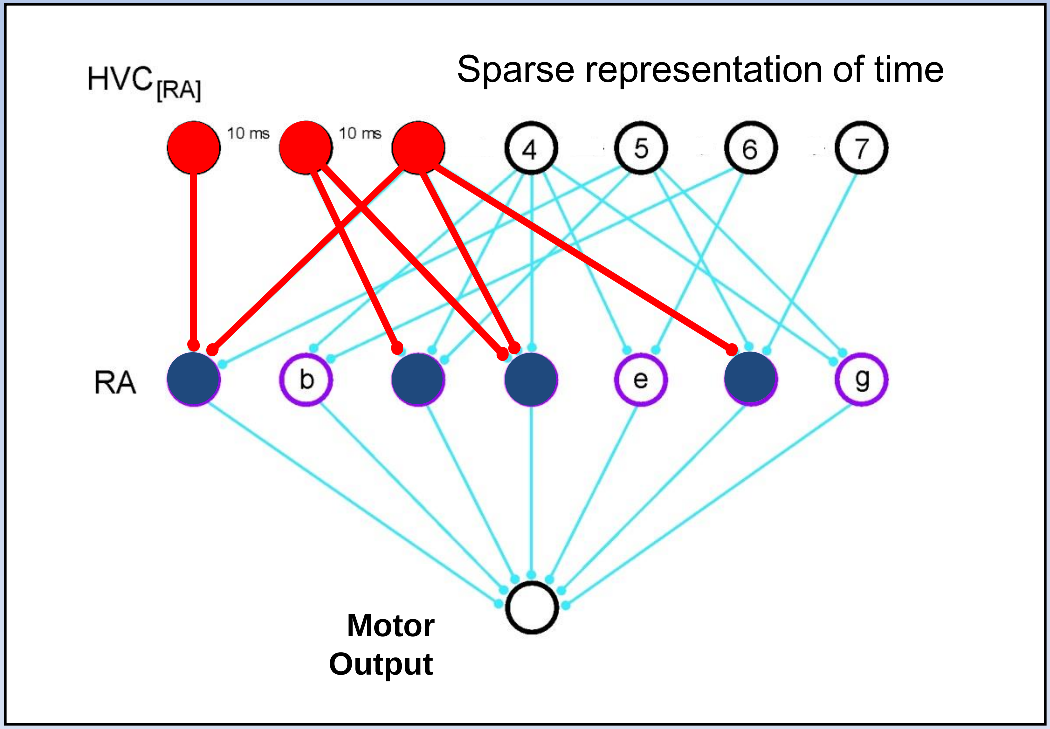
bursting activity propagates through a chain of synaptically connected HVC_{RA} neurons (like falling dominoes), creating a timing signal that spans the entire motif.

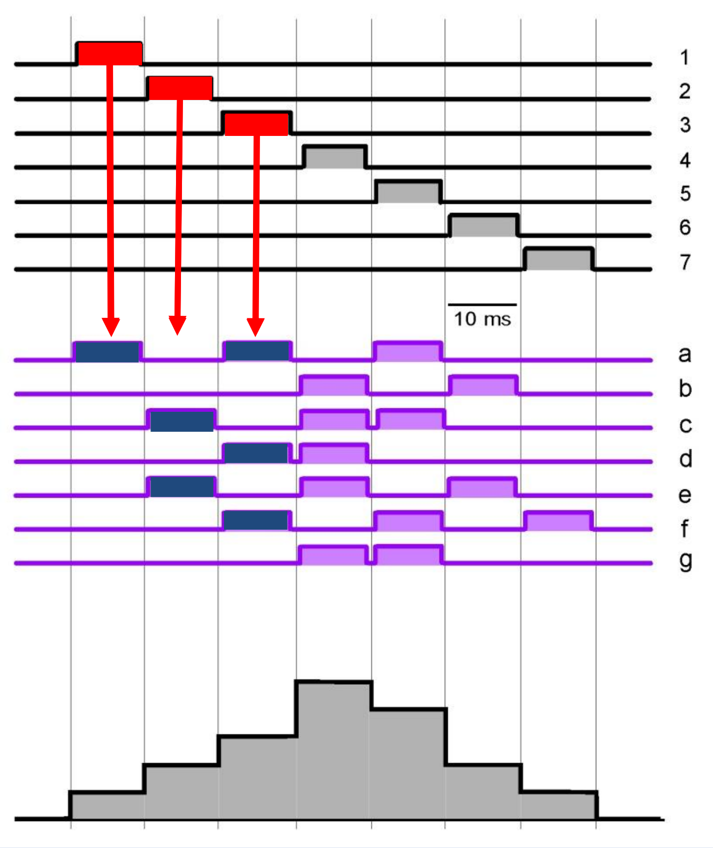




Leonardo and Fee, 2005

Simple sequence generation circuit

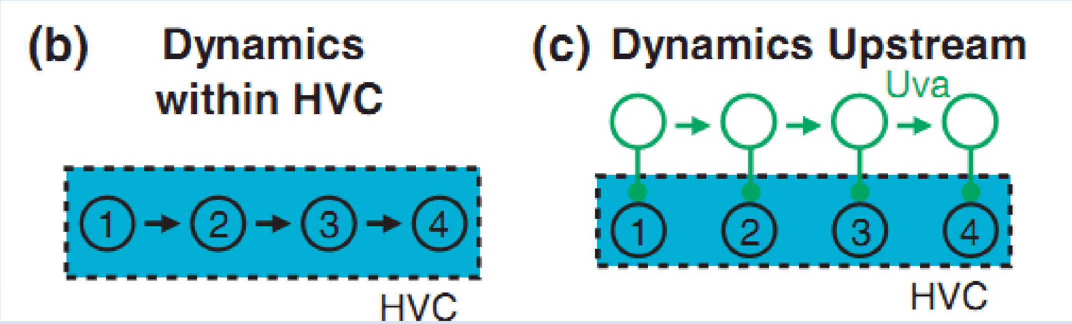


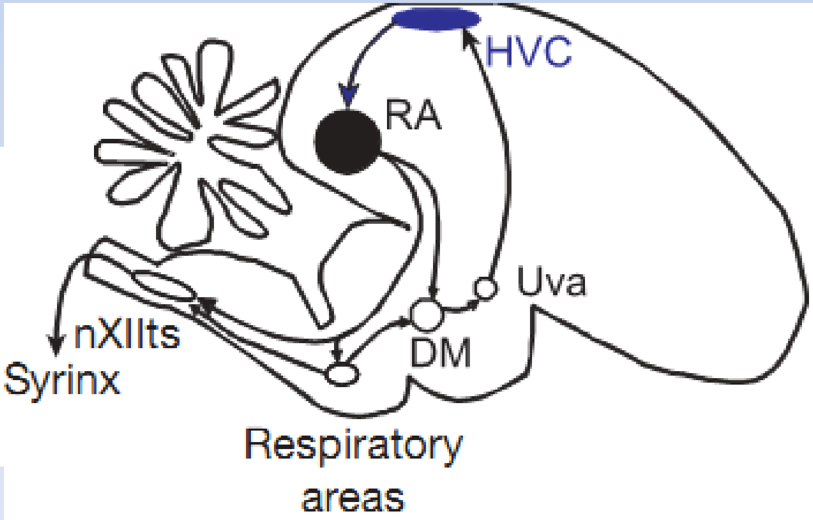


Leonardo and Fee, 2005

Part 1: Summary

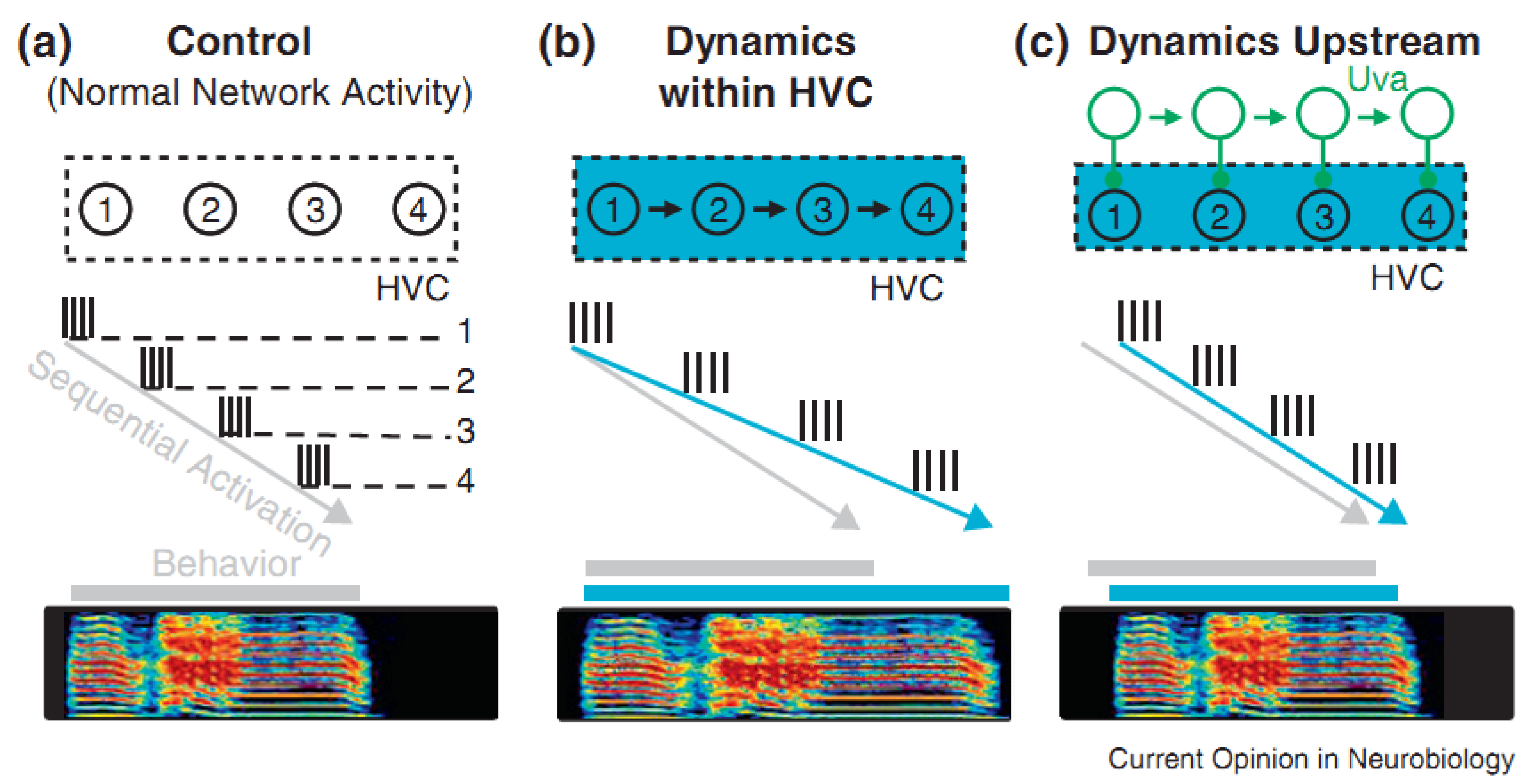
- HVC exhibits sparse bursts during singing.
- RA transforms the sparse code into multiple bursts which then drive motoneurons.
- BUT: Where are these patterns of activity coming from? What is driving HVC to fire at a particular moment?





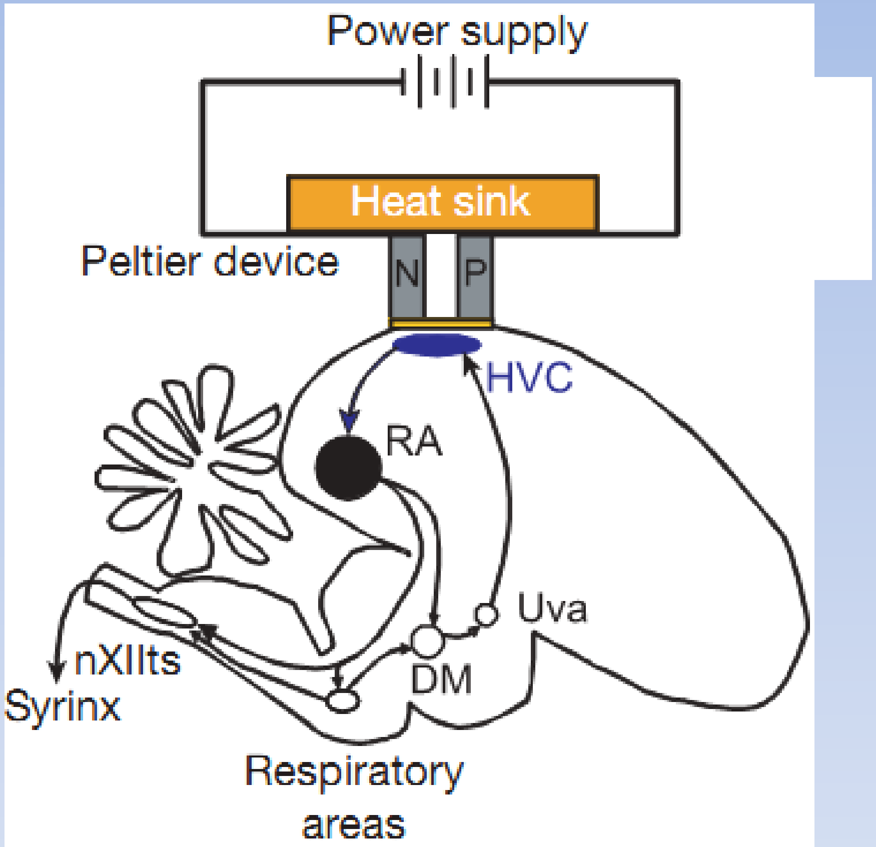
What and where is the mechanism that determines tempo? Are the dynamics generated within HVC?

If song tempo is determined by the activity of the HVC local network, then song should slow as HVC is cooled.



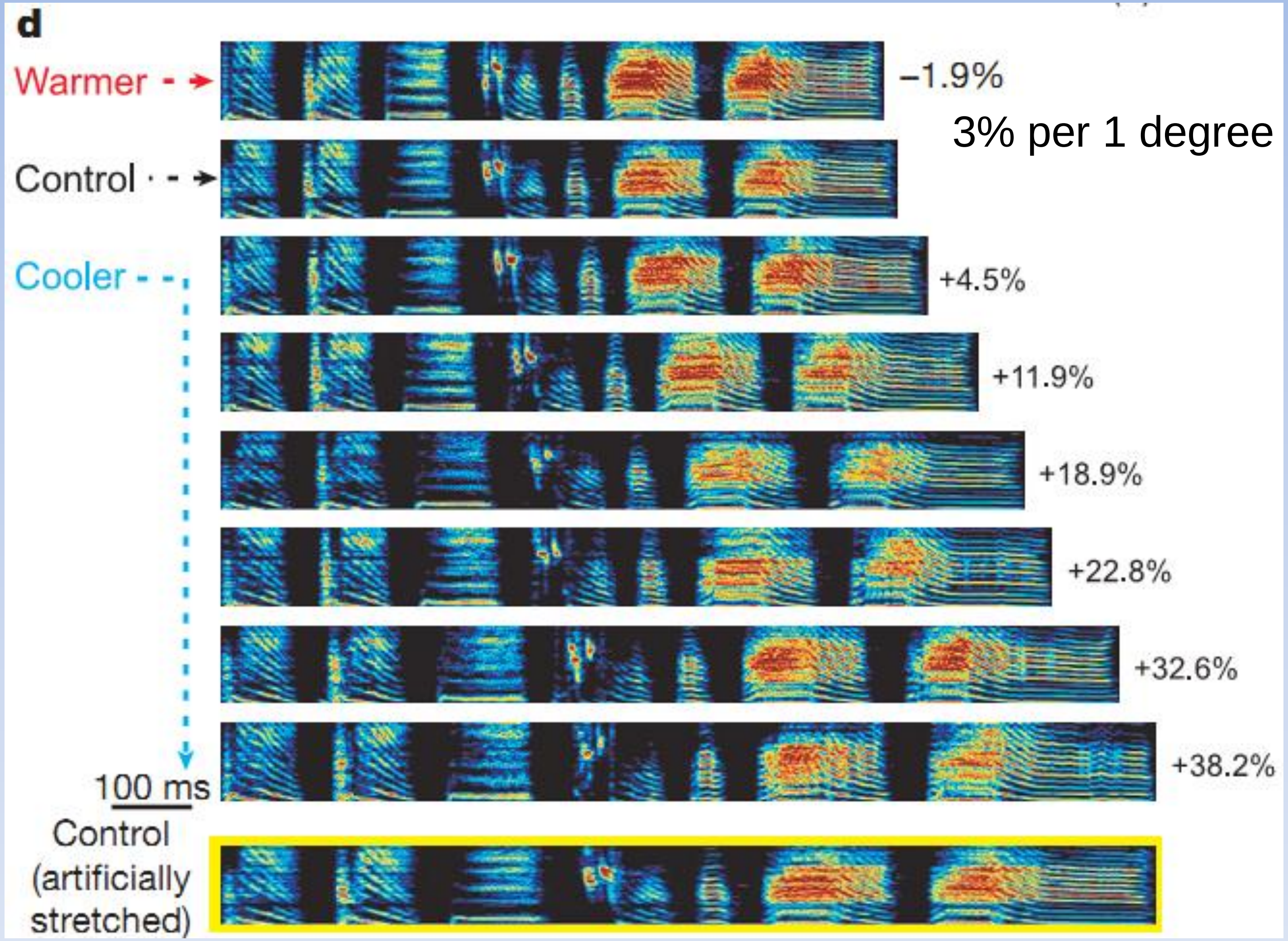
Fee & Long (*Curr Opin Neurobiol*, 2011)

Local manipulation of brain temperature



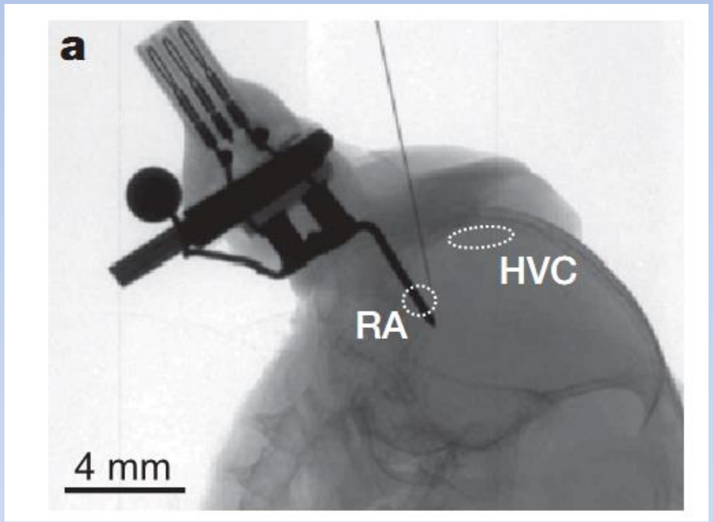
Long & Fee (*Nature*, 2008)

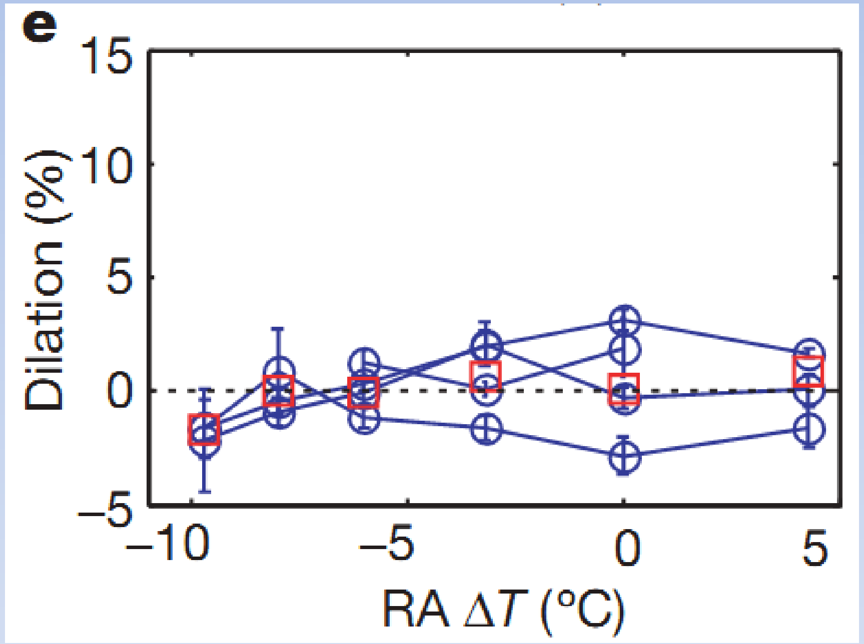
Cooling of HVC: song tempo slowed similarly across all timescales: individual notes (~10 ms), entire motif (~1s) and the silent gaps



Long & Fee (*Nature*, 2008)

Cooling RA has no effect on song speed



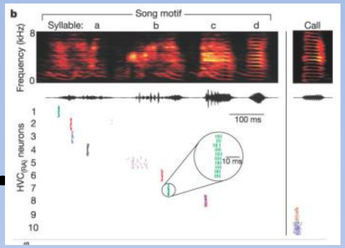


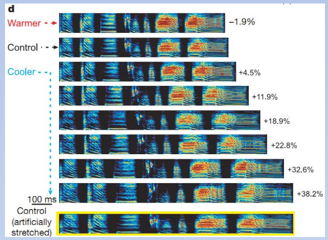
Long & Fee (*Nature*, 2008)

Part 1: Summary

HVC:

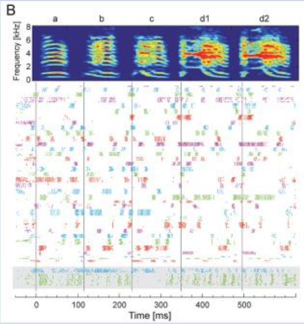
- HVC exhibits sparse bursts during singing.
- Song timing is controlled within HVC.



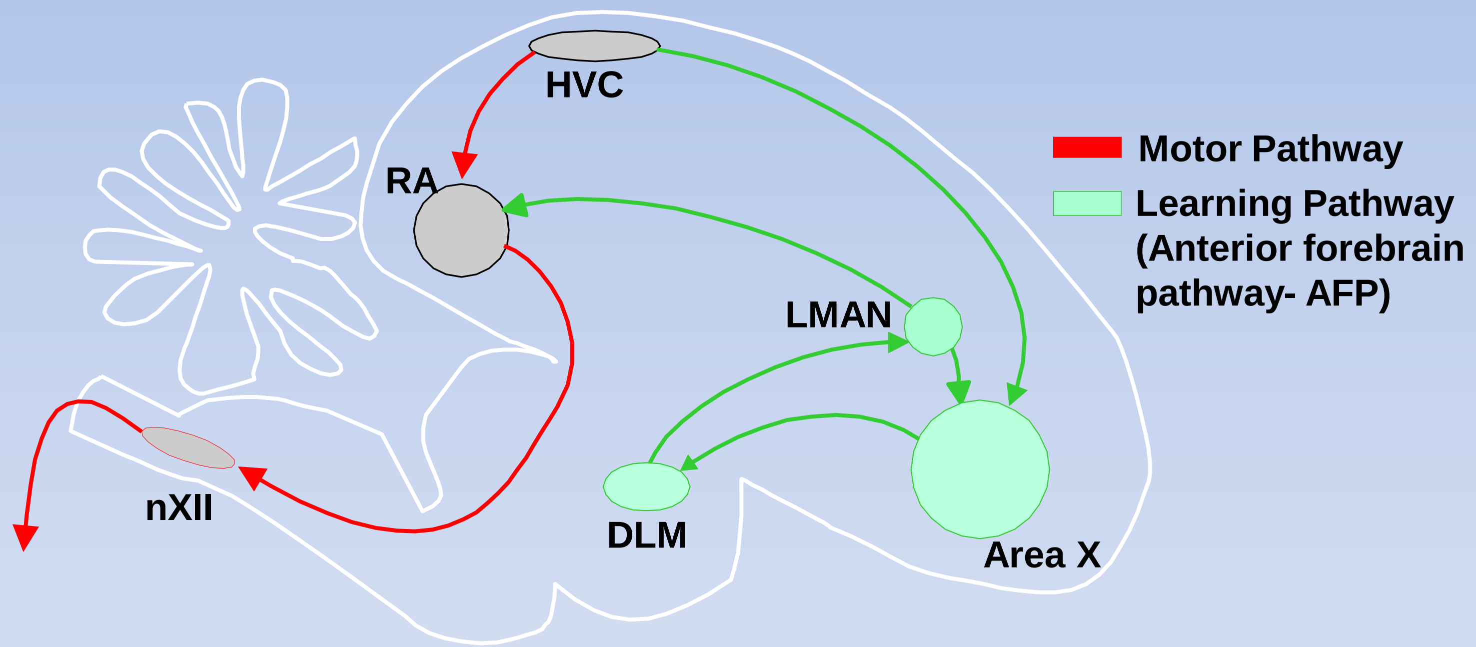


RA:

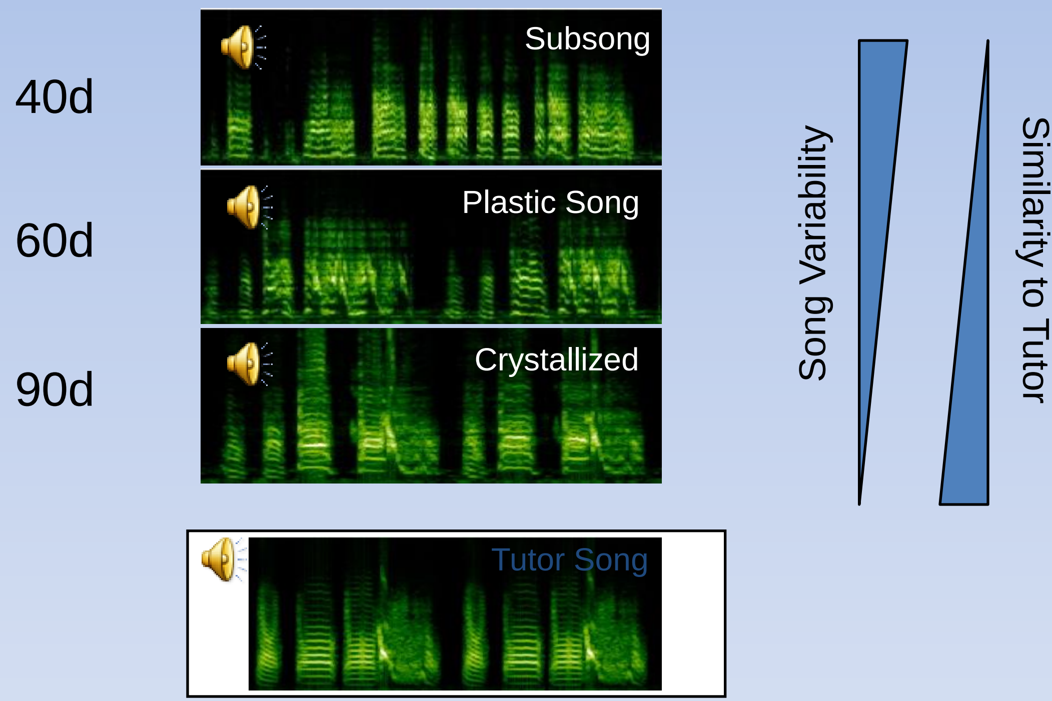
- RA transforms the sparse code into multiple bursts which then drive motoneurons.

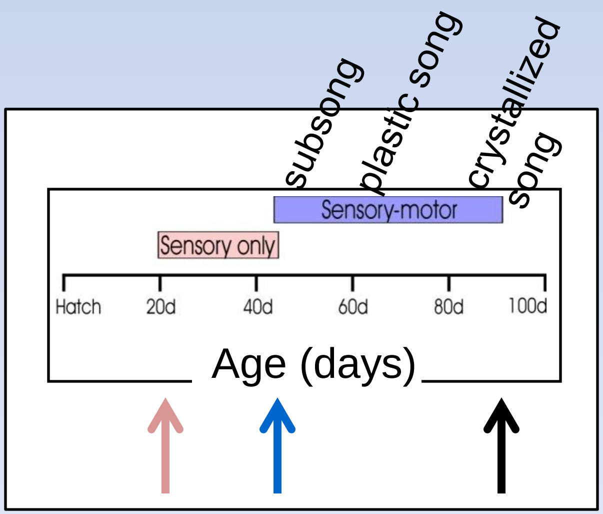


RA also gets input from LMAN!
What is the role of the learning pathway?



Subsong (“babbling”) – i.e., the highly variable song in very young juveniles

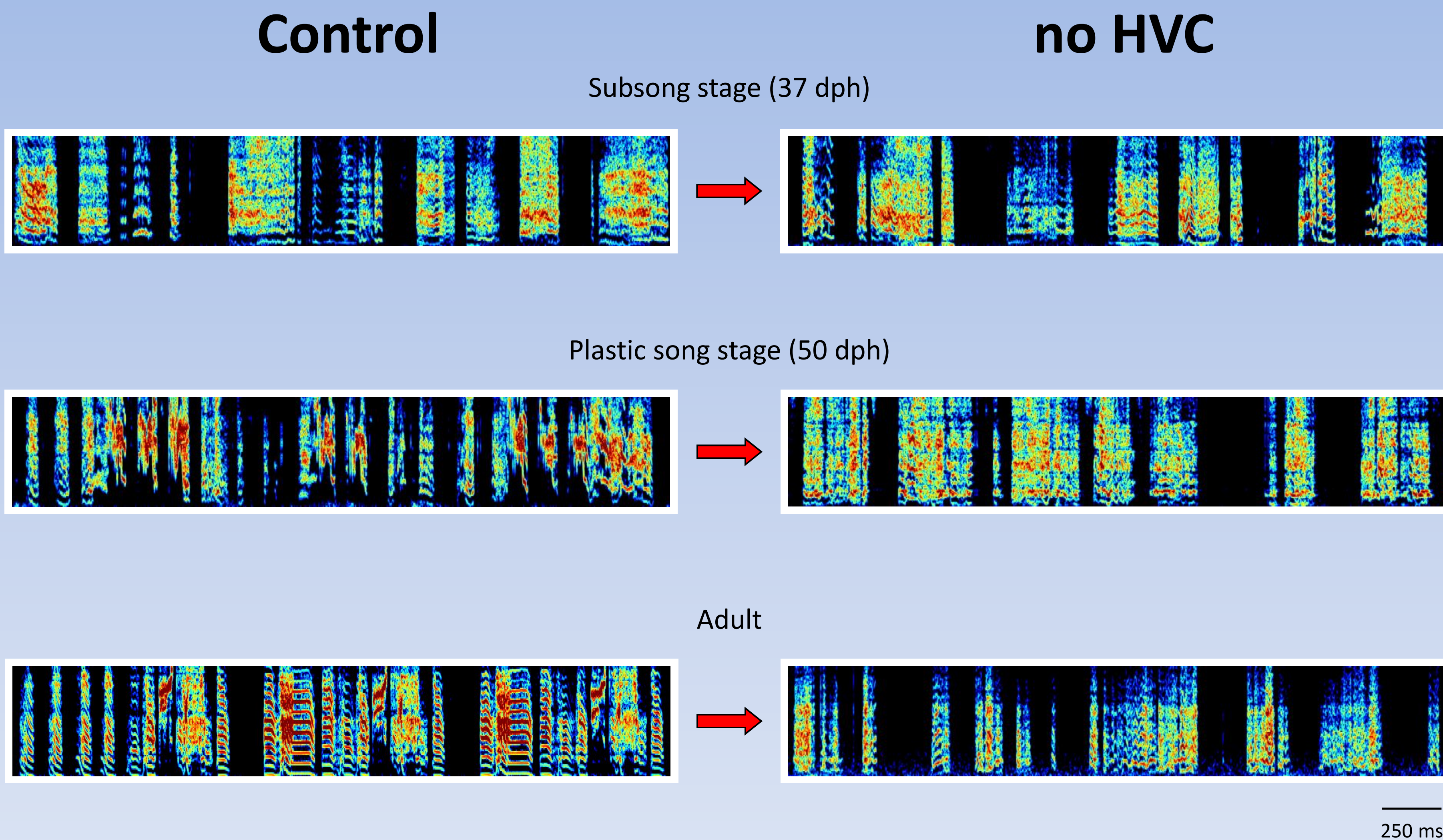




- **Question**:

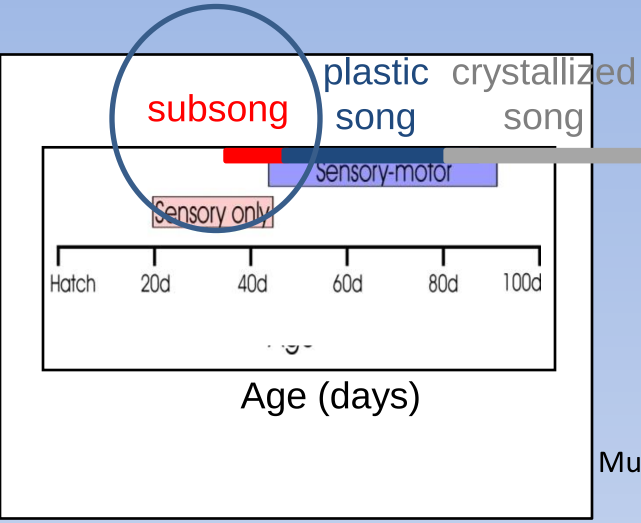
What are the mechanisms that produce subsong (“babbling”) – i.e., the highly variable song in very young juveniles?

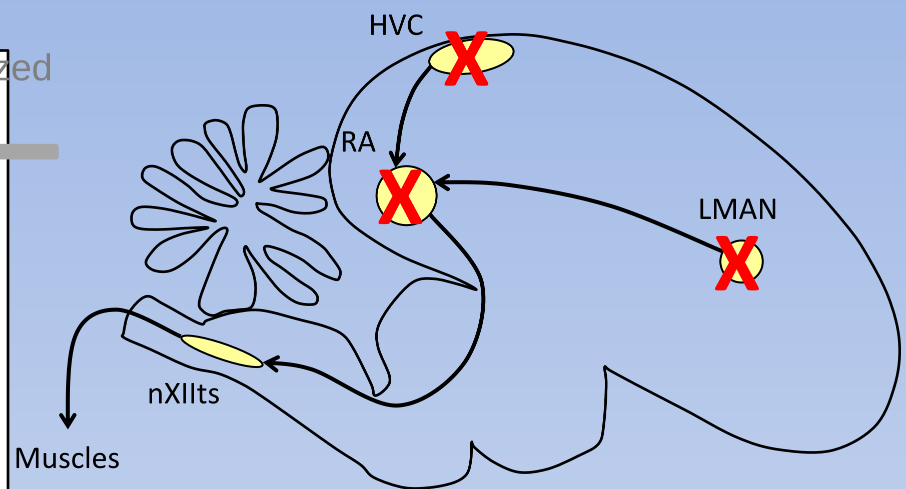
HVC-lesioned birds could still produce subsong!

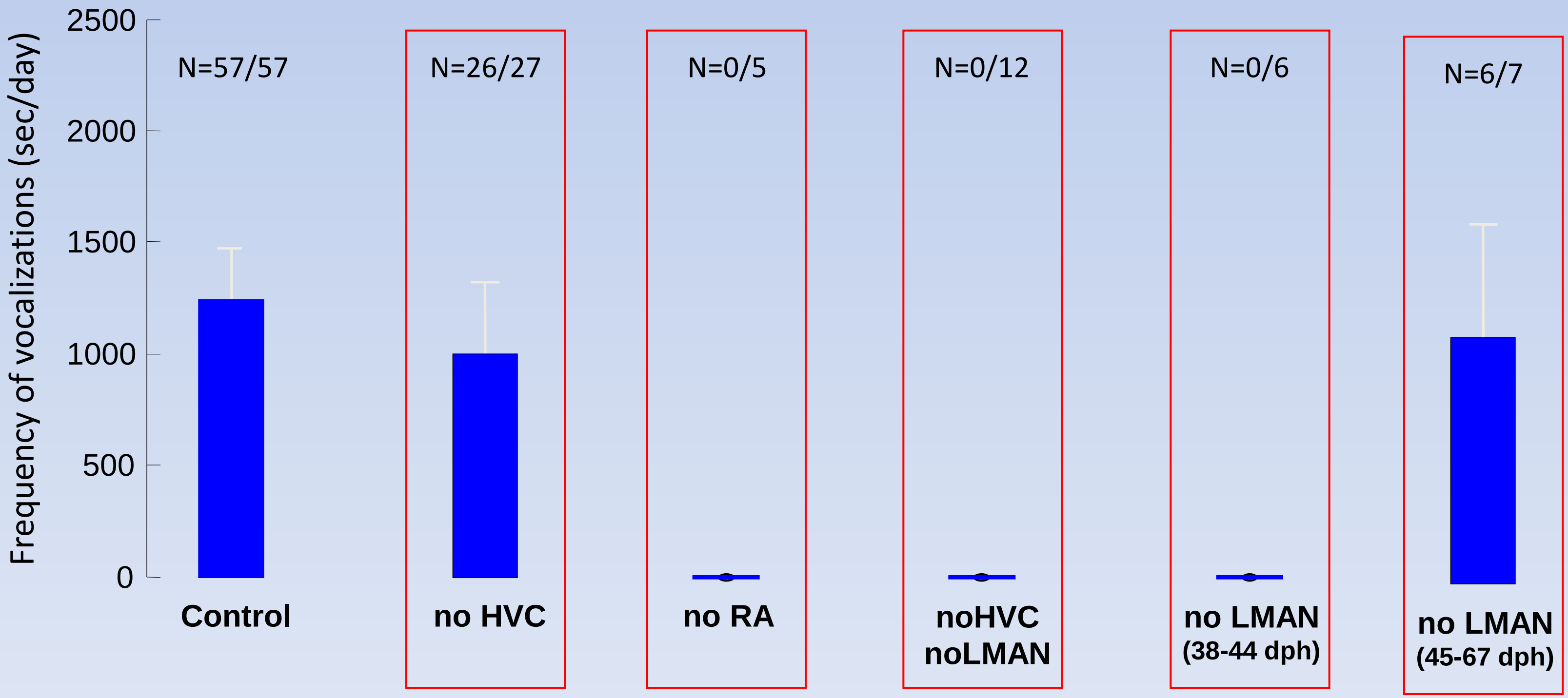


Aronov et.al. (2008) *Science*

What drives subsong production?

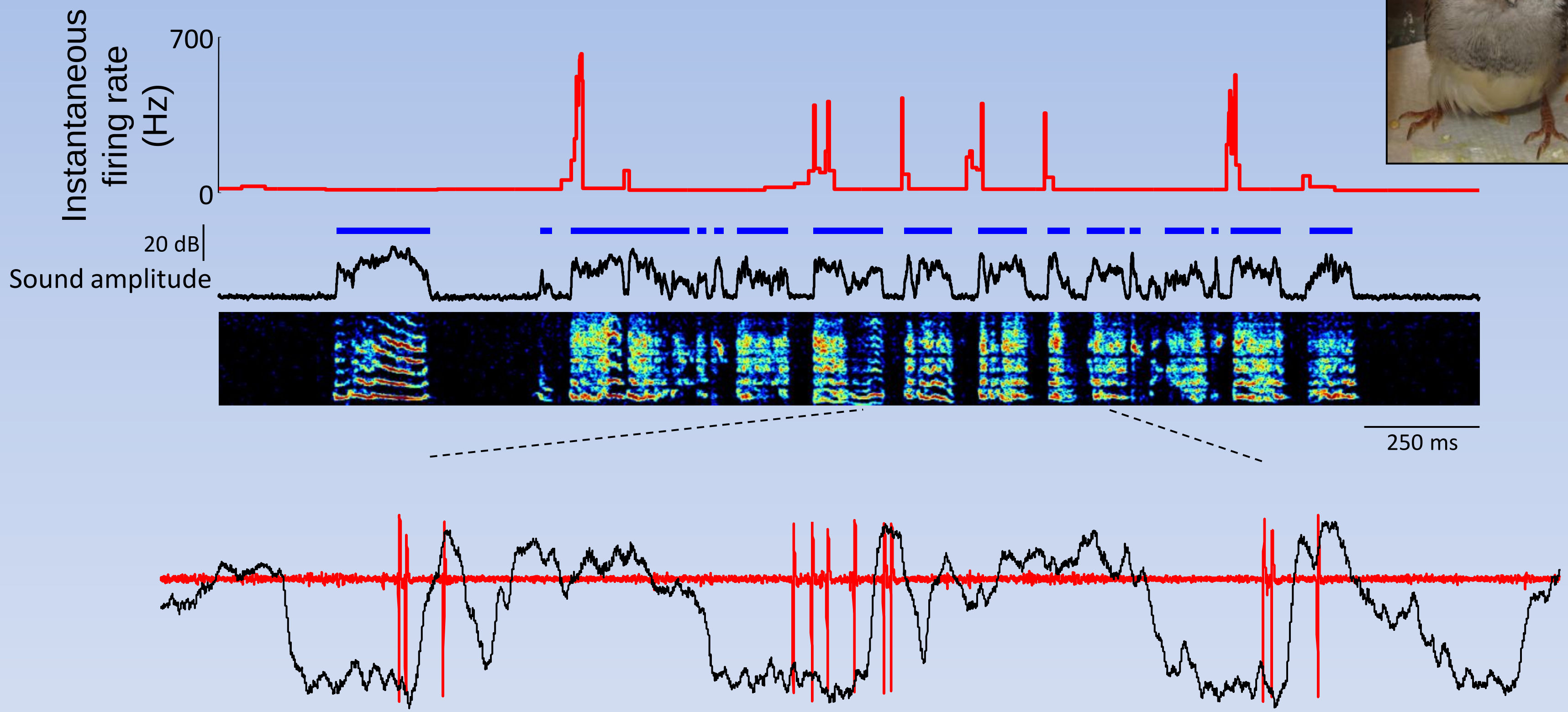






Aronov et.al. (2008) *Science*

LMAN-RA projecting neurons exhibit activity primarily prior to subsong syllable onsets

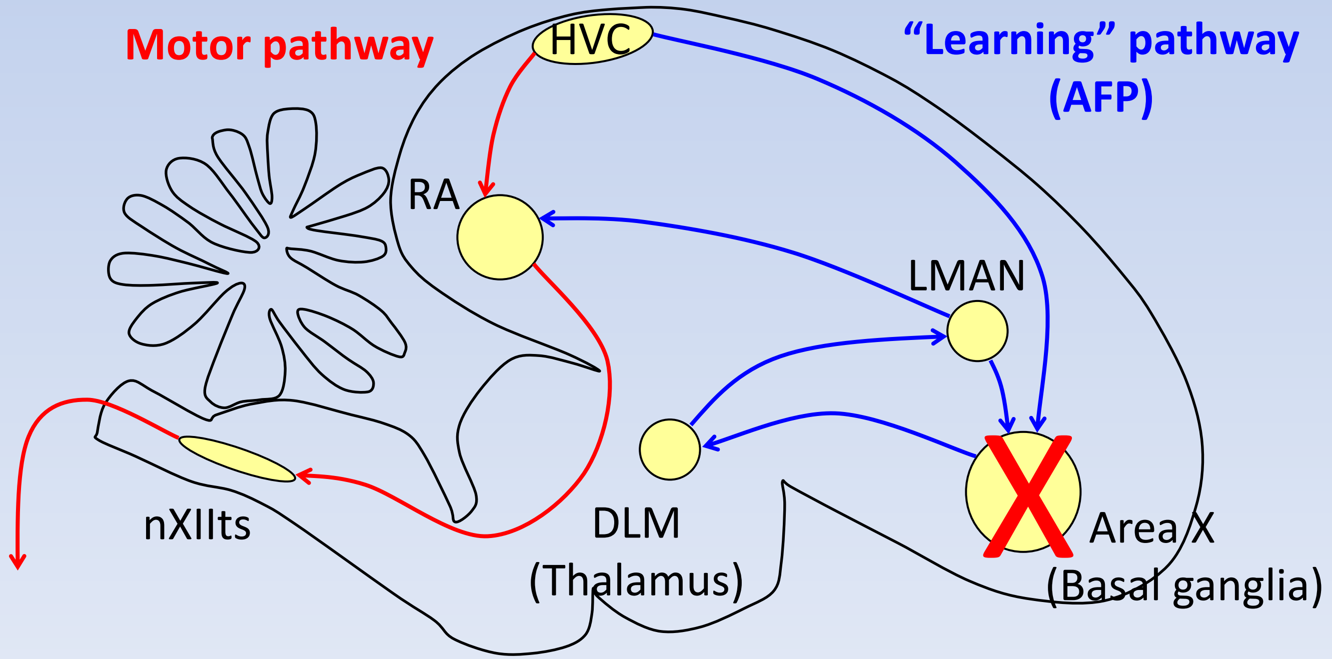


this suggest that babbling is not a result of immature motor pathway but it is actually deriving by this learning circuit

Aronov et.al. (2008) *Science*

- AFP (anterior forebrain pathway) is necessary for producing subsong, suggesting that this circuit is important for vocal variability.
- Which part of AFP is necessary?

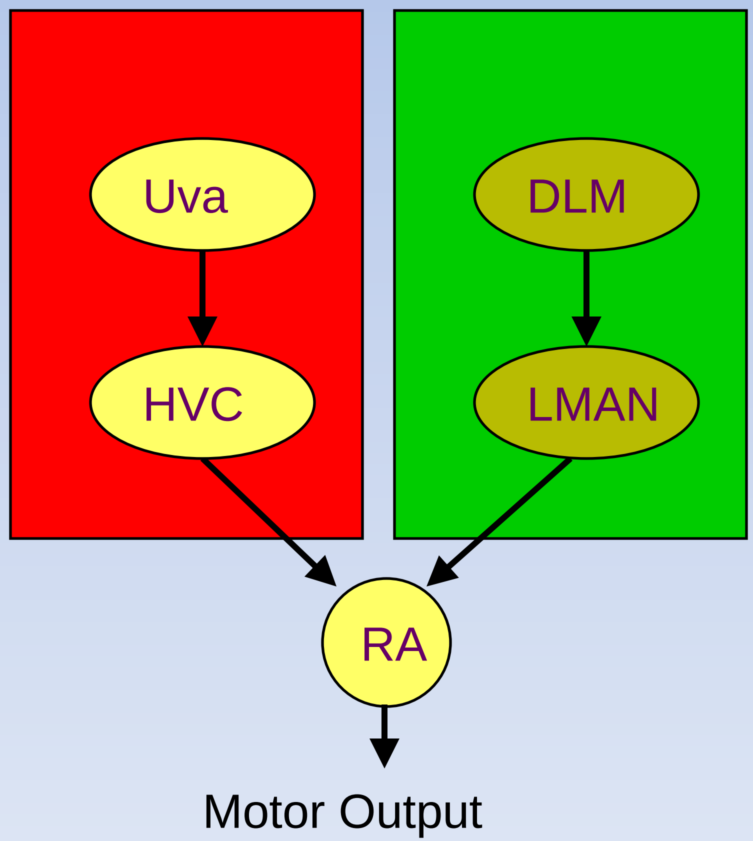
Lesion of area X does not lead to elimination of subsong.
DLM is necessary for the production of subsong.
LMAN → RA pathway cannot generate subsong like vocalizations independent of DLM.



Separate premotor pathways for stereotyped song and babbling

Sequence
Stereotypy
Precision

Adult song



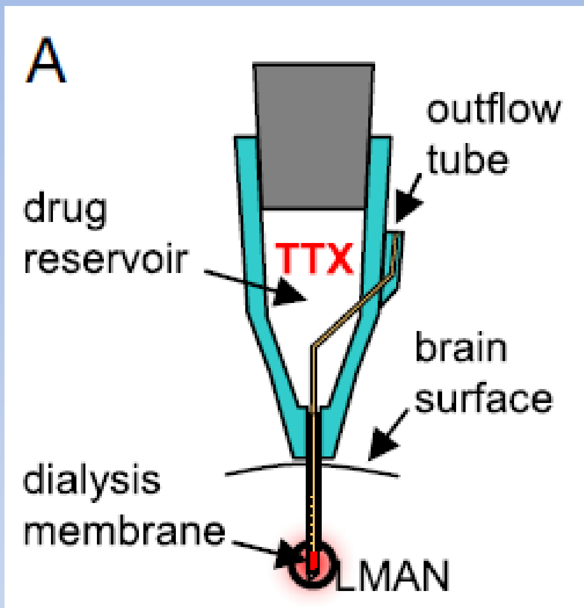
Randomness
Variability
Exploration

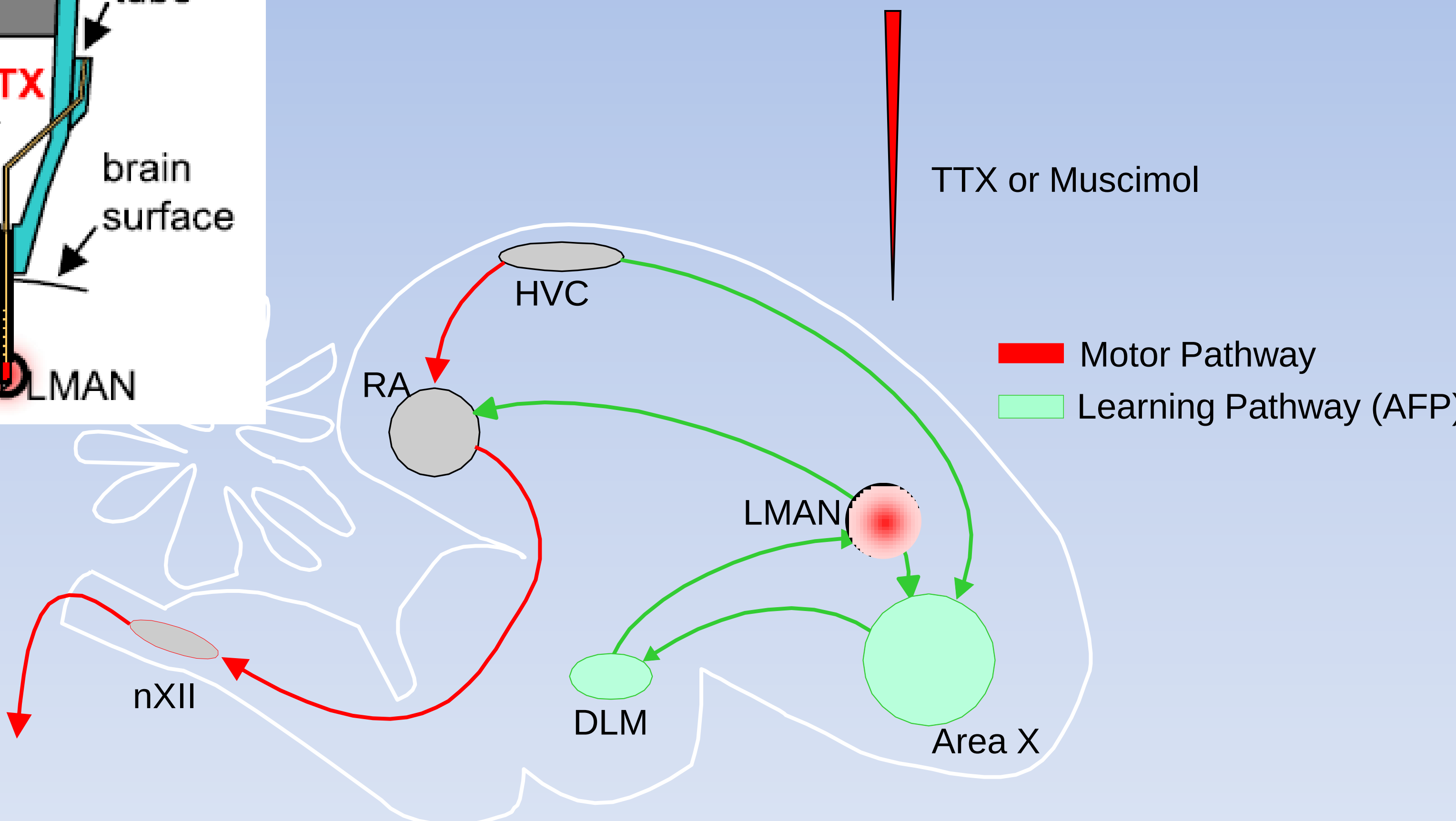
Subsong

- **Question**:

  What is the role of LMAN in older juveniles?

Role of LMAN in older juveniles

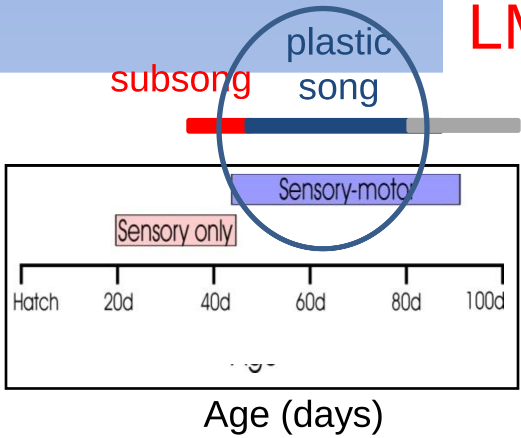


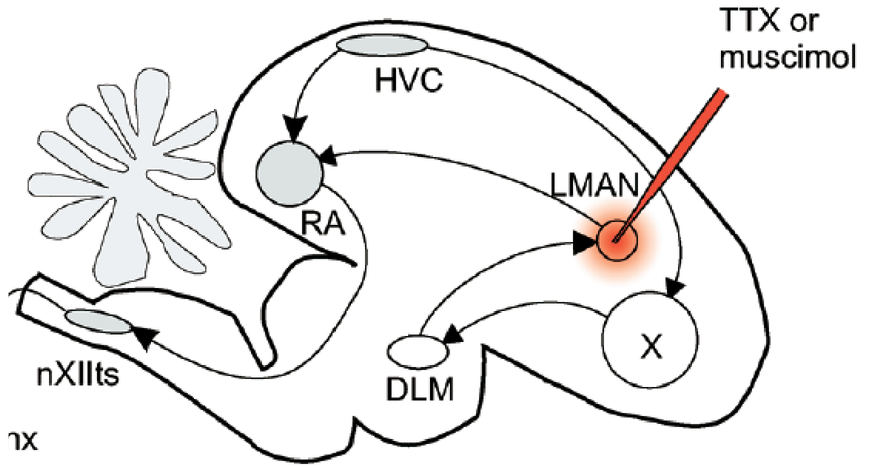


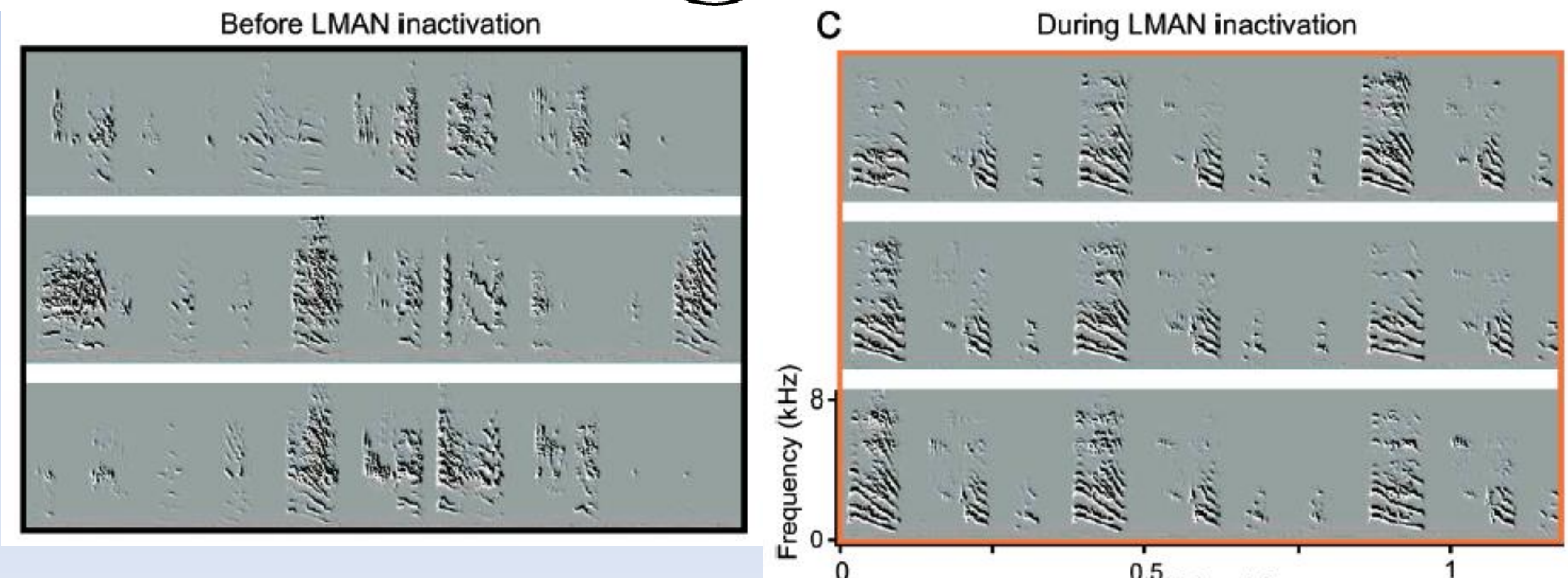
Ölveczky BP, Andalman AS, Fee MS (2005) Vocal Experimentation in the Juvenile Songbird Requires a Basal Ganglia Circuit. PLoS

Role of LMAN in older juveniles

LMAN is a generator of variability

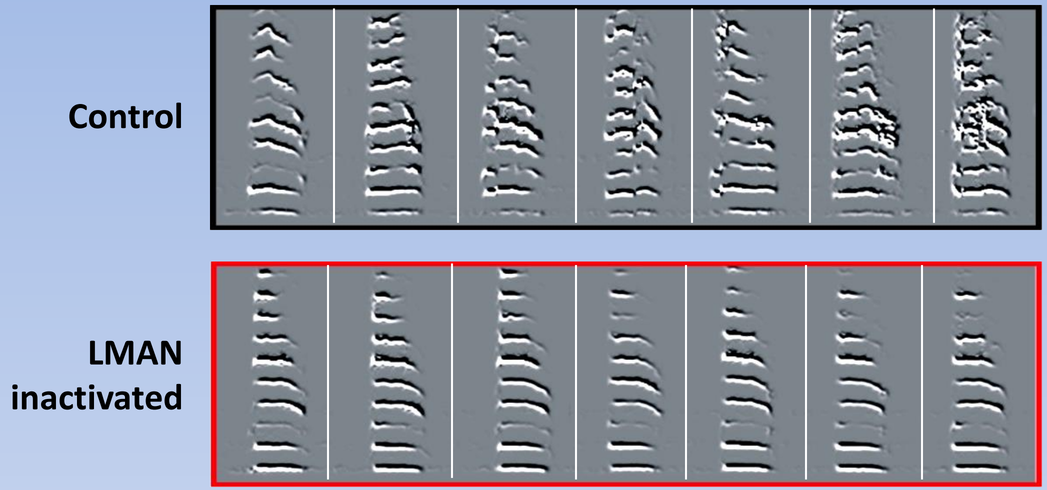




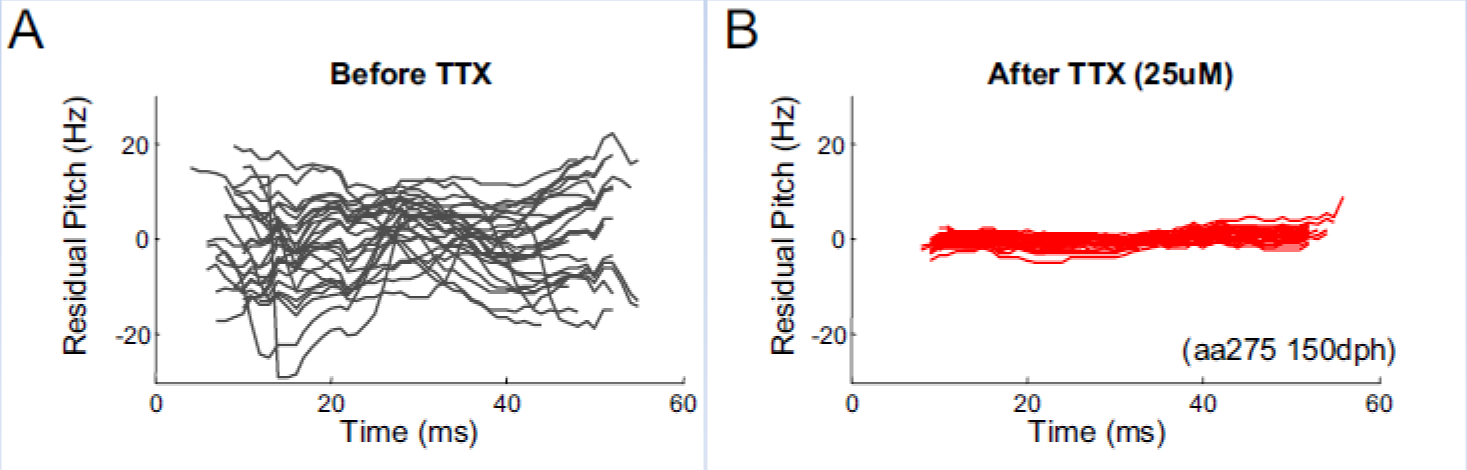


Ölveczky BP, Andalman AS, Fee MS (2005) Vocal Experimentation in the Juvenile Songbird Requires a Basal Ganglia Circuit. PLoS Biol 3(5): e153. doi:10.1371/journal.pbio.0030153

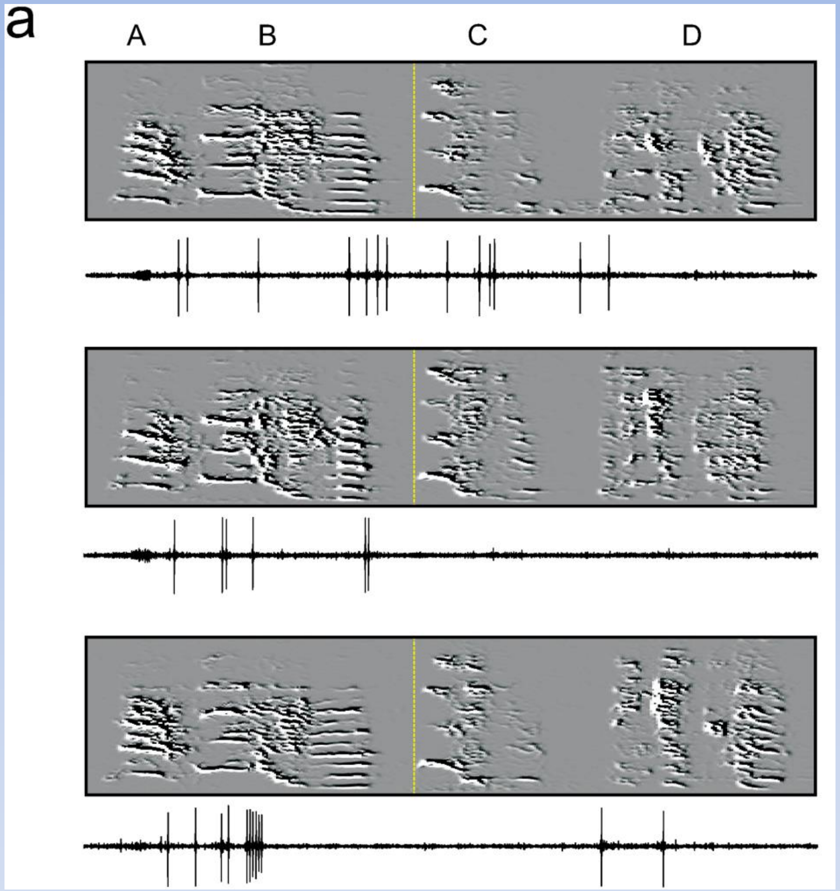
Reduced variability in pitch after LMAN inactivation during crystalized song

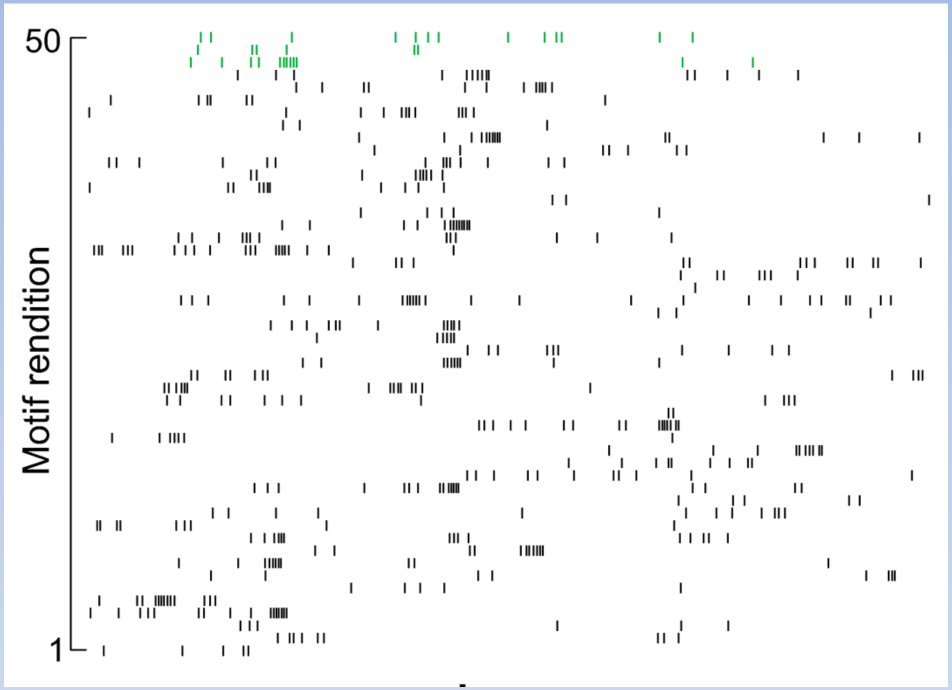


LMAN involves in injecting stochastic noise into the naive behavior so to have more variation on which to select the better performance.



Ölveczky BP, Andalman AS, Fee MS (2005) Vocal Experimentation in the Juvenile Songbird Requires a Basal Ganglia Circuit. PLoS Biol 3(5): e153. doi:10.1371/journal.pbio.0030153





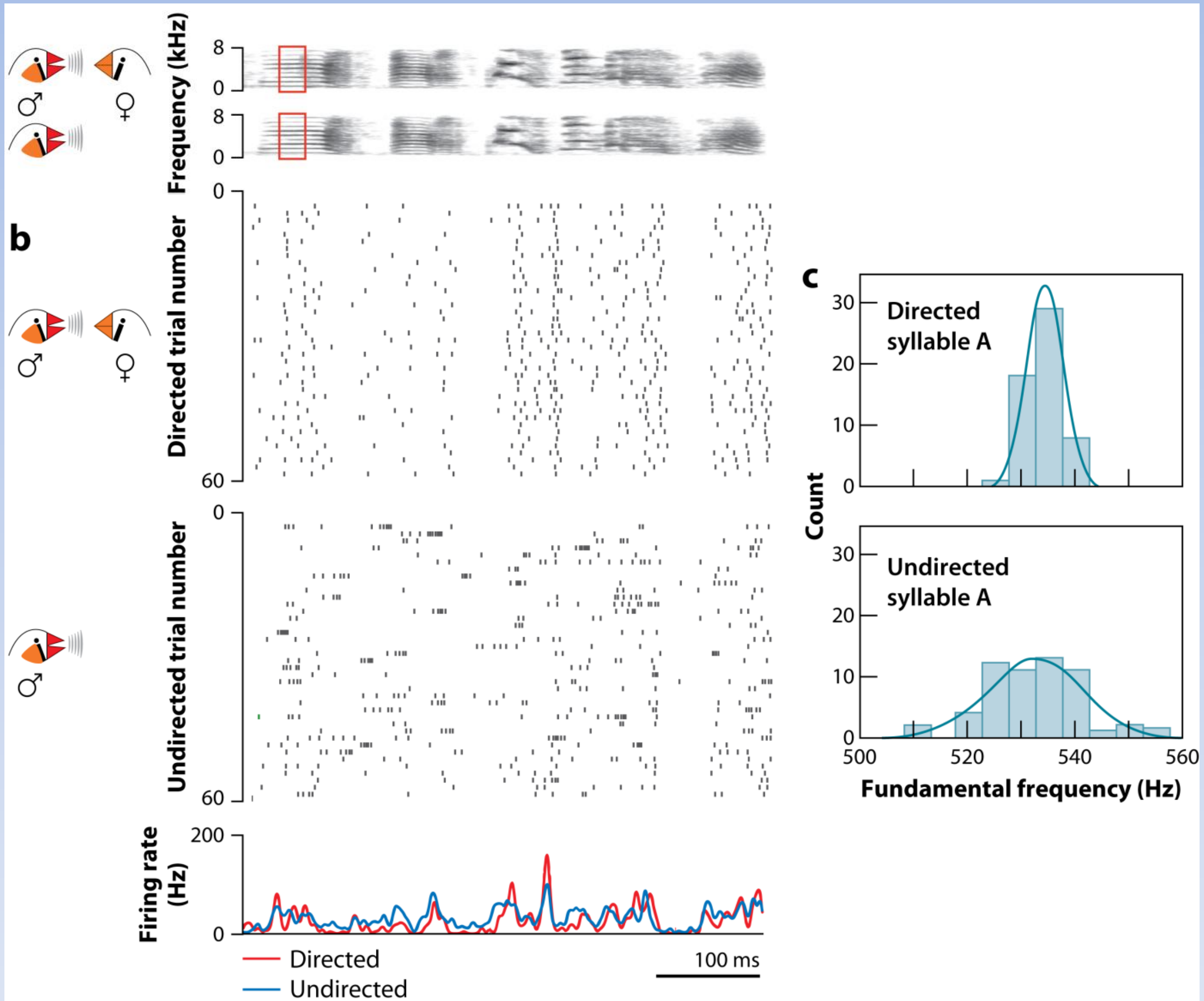
Ölveczky BP, Andalman AS, Fee MS (2005) Vocal Experimentation in the Juvenile Songbird Requires a Basal Ganglia Circuit. PLoS Biol 3(5): e153. doi:10.1371/journal.pbio.0030153

The crystallized songs of male zebra finches display different amounts of acoustic variability depending on social context

Directed singing

Undirected singing

rehearsal?



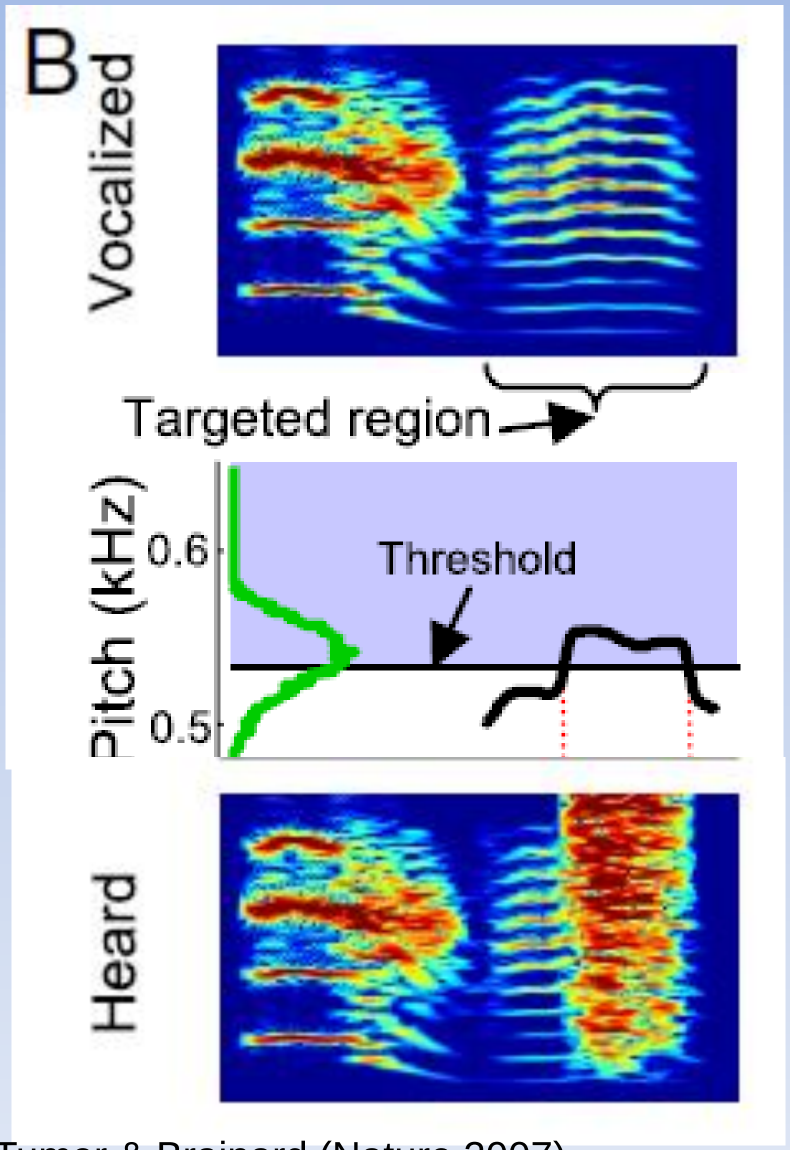
Brainard MS, Doupe AJ. 2013.
Annu. Rev. Neurosci. 36:489–517

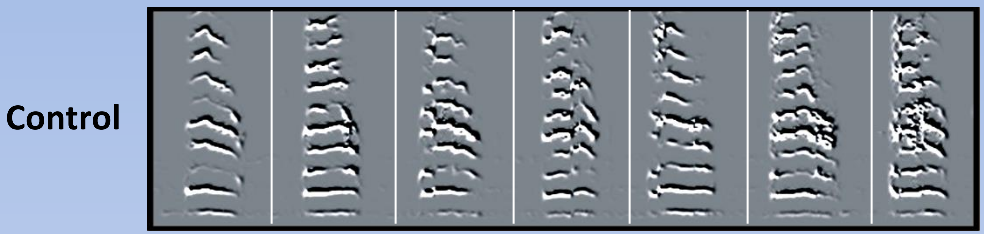
Kao et al. (Journal of Neuroscience, 2008)

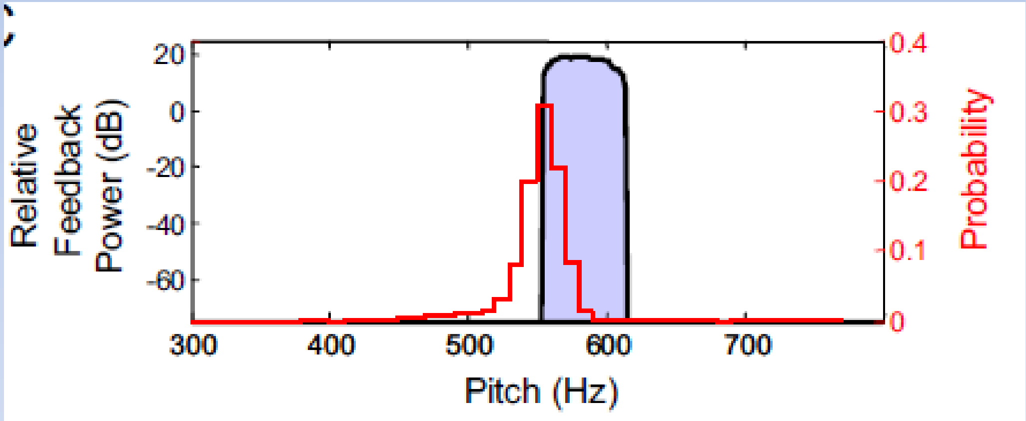
Role of LMAN in learning

- Question
  - Is variability purely random or is it biased?
- Difficulty
  - Song learning is a slow process.
- Strategy
  - Use real-time feedback to induce error in the song artificially.

Conditional auditory feedback

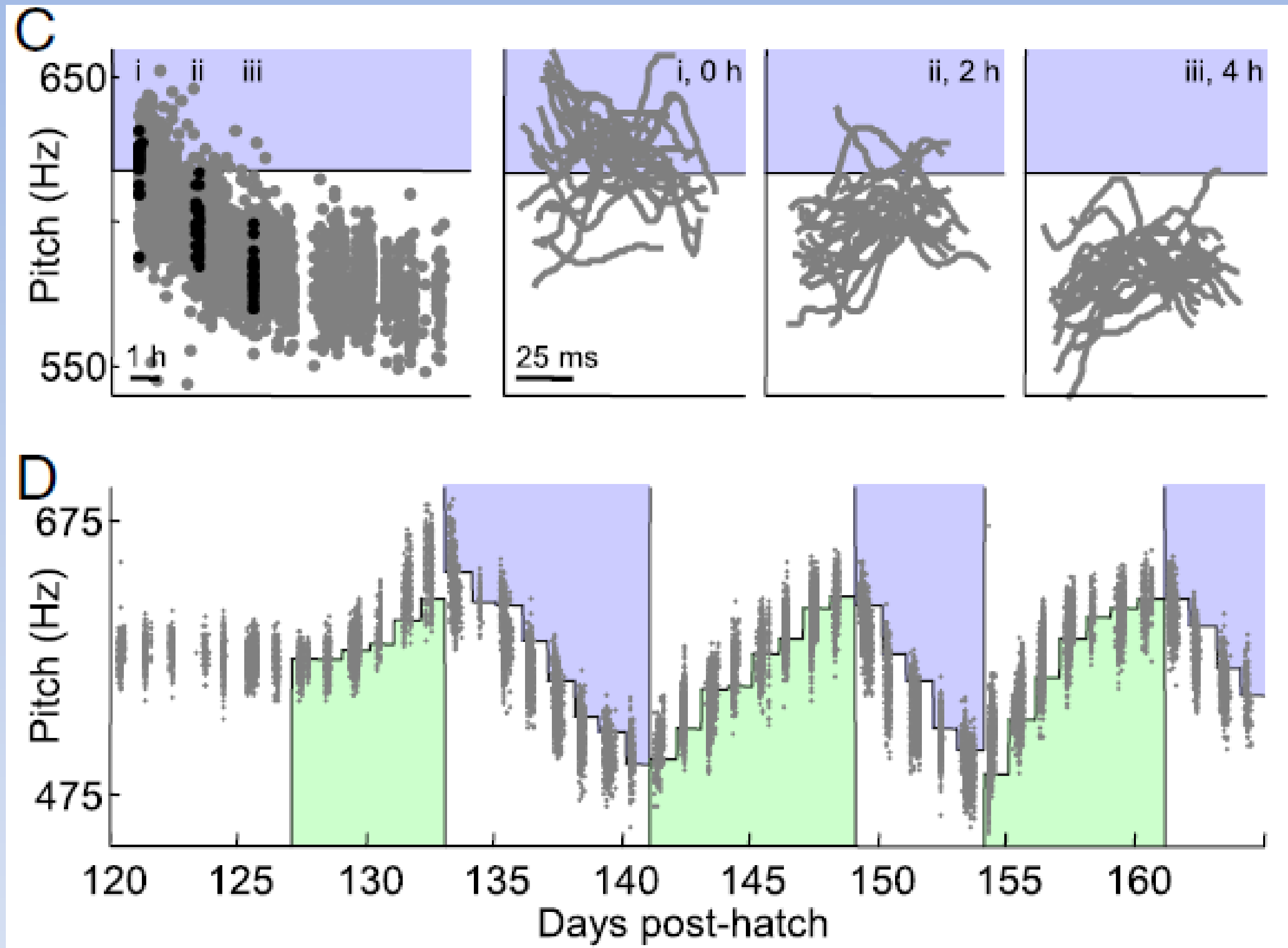






Tumer & Brainard (Nature 2007)
Andalman & Fee (PNAS, 2009)

Behavioral results



Andalman & Fee (PNAS, 2009)

Two possibilities

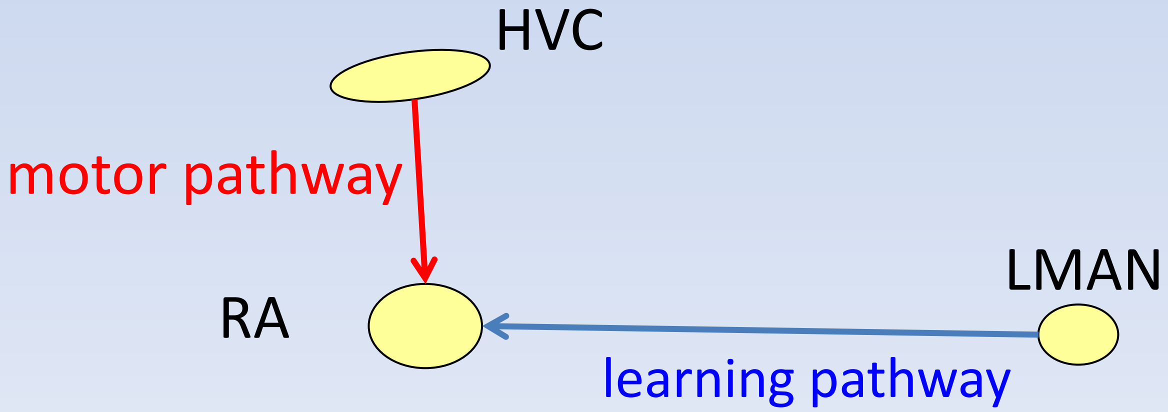
Where does the learning take place?

- Hypothesis 1: motor pathway

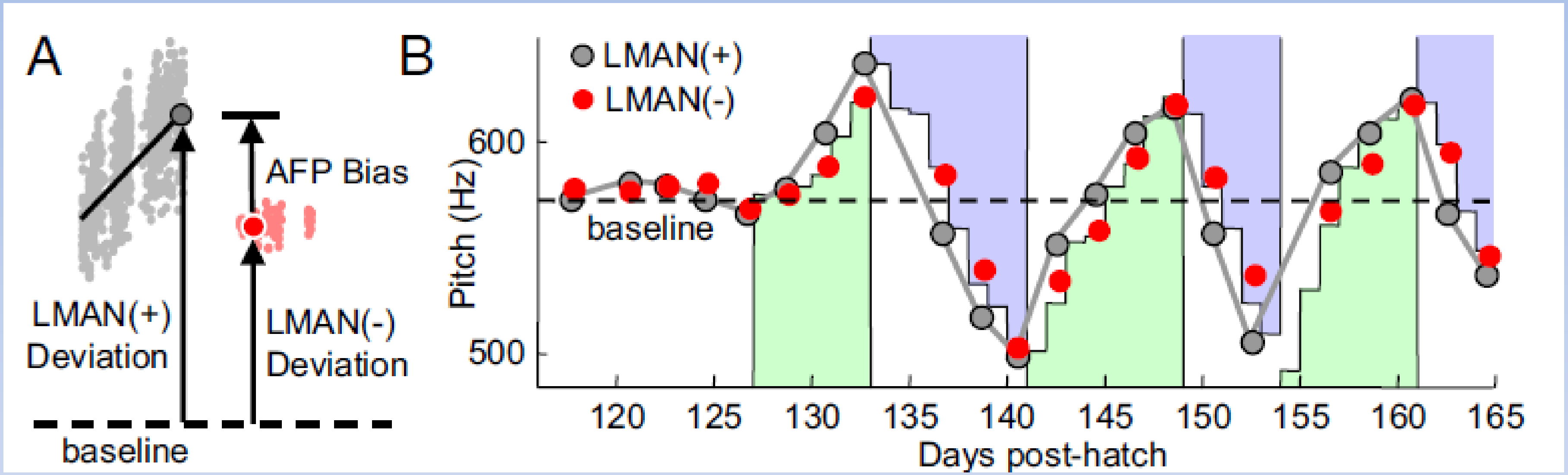
  → LMAN inactivation will not change the pitch.

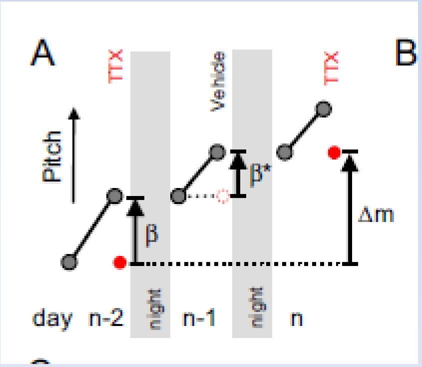
- Hypothesis 2 : learning pathway

  → LMAN inactivation will change the pitch to go back.



Motor pathway consolidation





This variability produced by the learning pathway is not purely random, but instead biased.

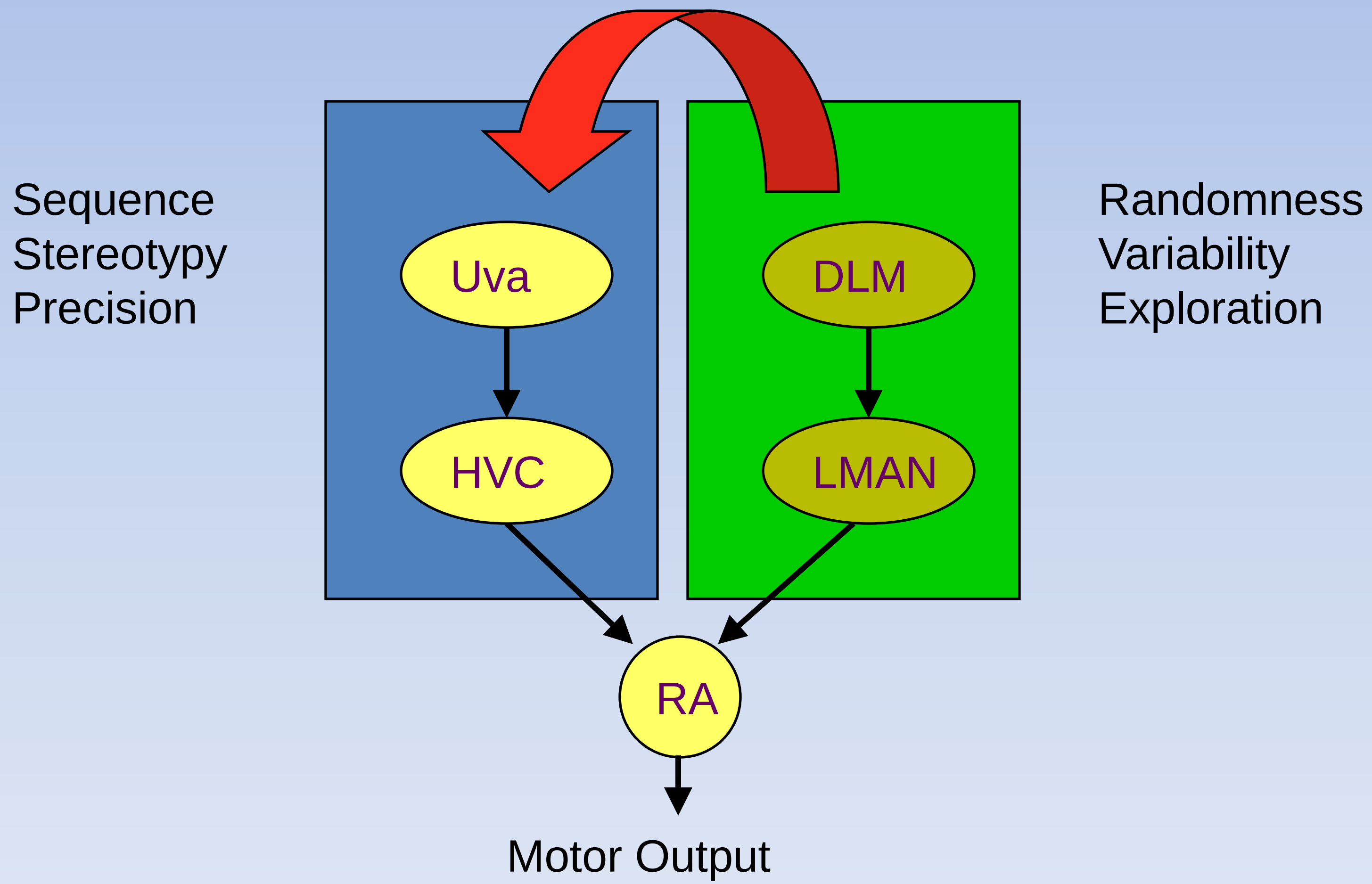
This bias is consolidated in the motor pathway after one day delay.

Andalman & Fee (PNAS, 2009)

LMAN is a generator of variability

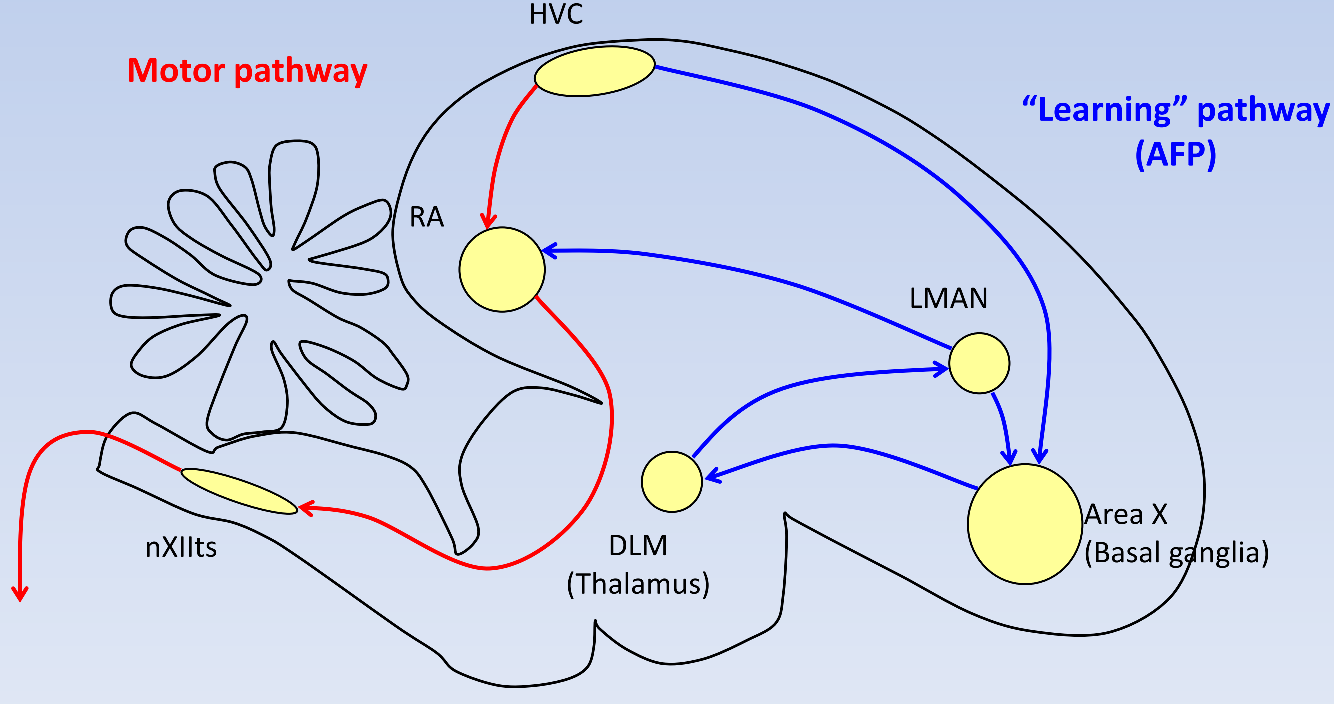
- LMAN is the essential premotor nucleus for the earliest 'babbling' vocalizations (Aronov and Fee, 2008).
- LMAN may serve an essential role in song learning by driving variability: in subsong, plastic song, and even in adult song (Kao et al, 2005).
- LMAN adds variability to enable exploration. This variability produced by the learning pathway is not purely random, but instead biased.
- This bias is consolidated in the motor pathway after one day delay.

Separate premotor pathways for stereotyped song and babbling

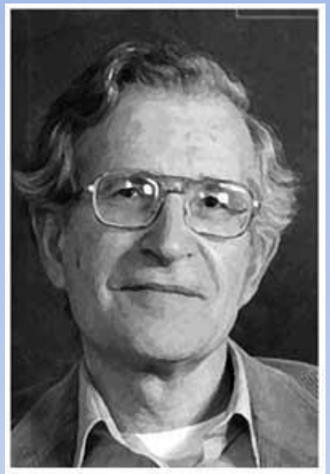


Summary

- Activity of the motor pathway is stereotyped.
- Activity of the learning pathway is variable.
- These two signals are combined at RA.



Chomsky



The basis to Chomsky's linguistic theory is that the principles underlying the structure of language are biologically determined and hence genetically transmitted. He therefore argues that all humans share the same underlying linguistic structure (syntactic), irrespective of socio-cultural difference.

In other words: genes constrain language diversity.

Ofer Tchernichovski:
Do genes constrain song diversity?

The City University of New York

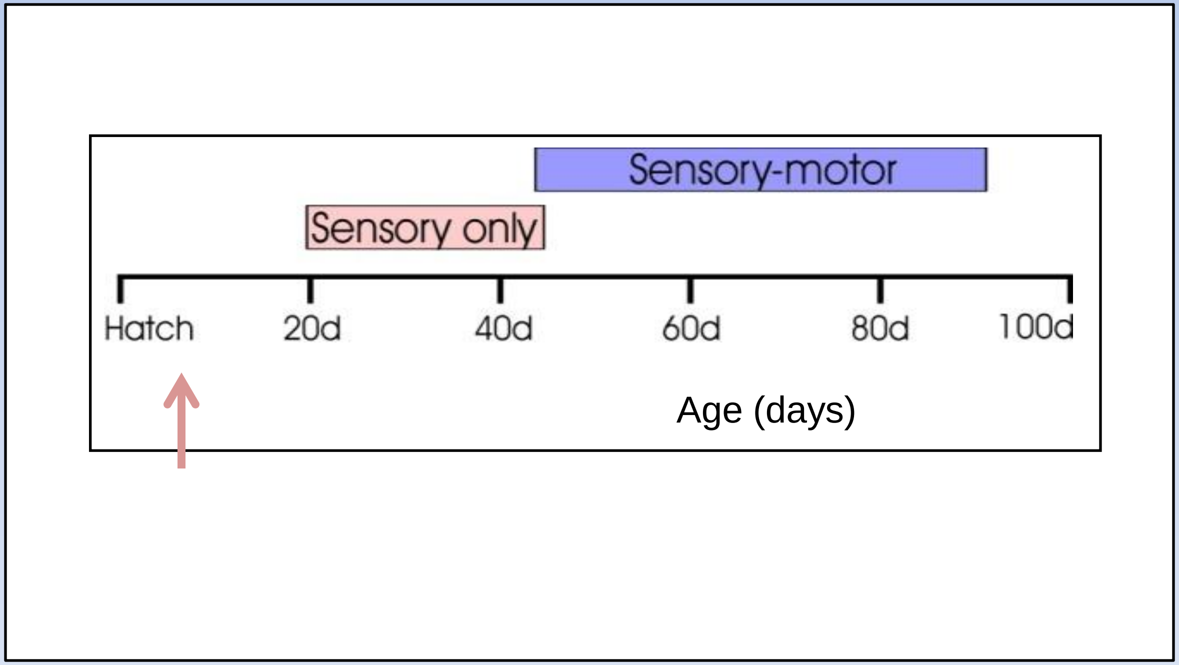
Song culture in birds

- Some songbirds provide biologically tractable models of culture:

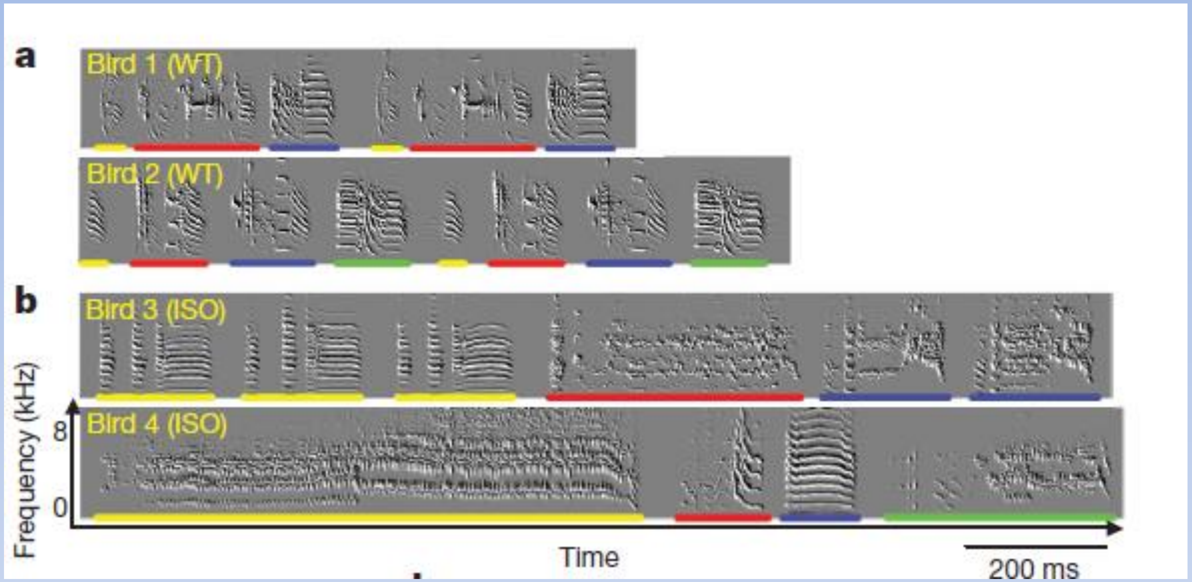
geographically separated groups have local song dialects- just like humans.

- But the variety is not infinite: different species exhibit distinct song cultures, suggesting genetic constraints.

What happens when you isolate a bird from his father before the sensory period?



Can we rise a colony from isolates?



Birds are establishing the 'song template' very early, during the sensory period.

The experiment: to determine whether normal wild-type song culture might emerge over multiple generations in an isolated colony founded by isolates.

Konishi 1965; Marler 1970

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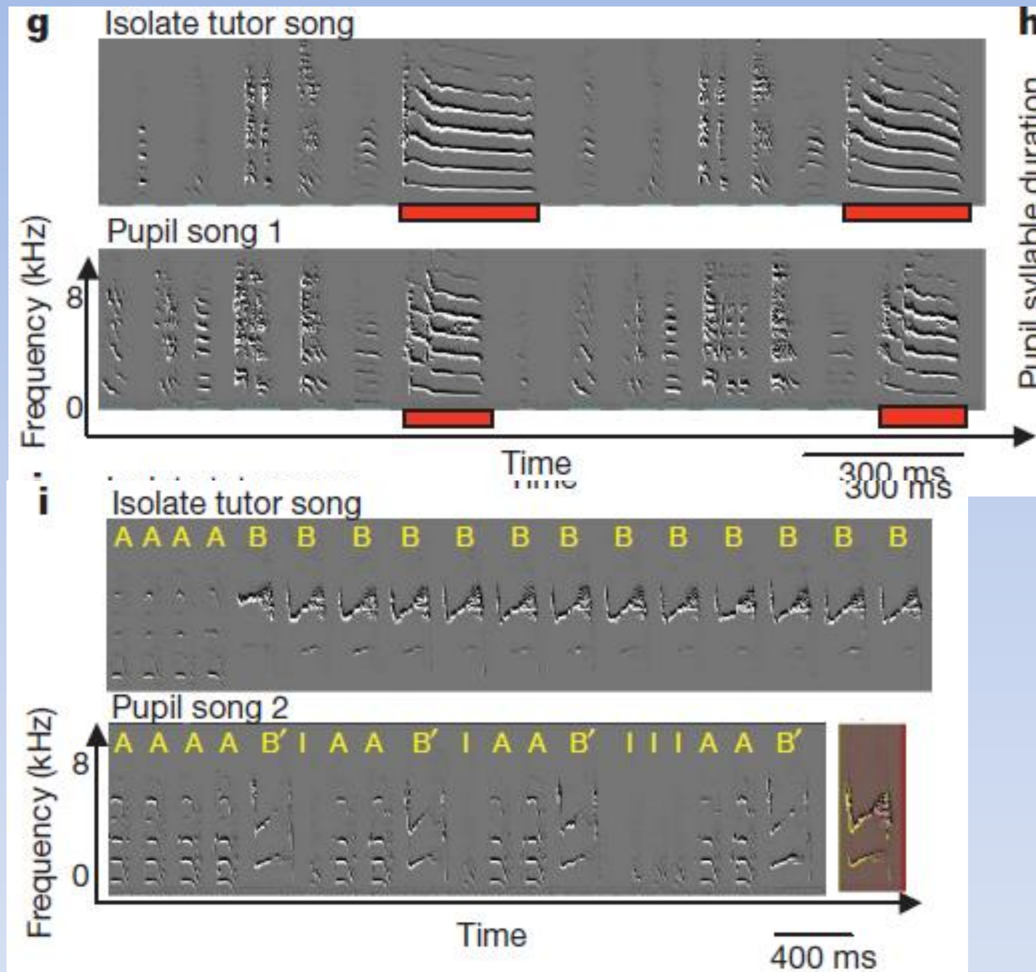
Culture in the lab: development of song culture in the zebra finch



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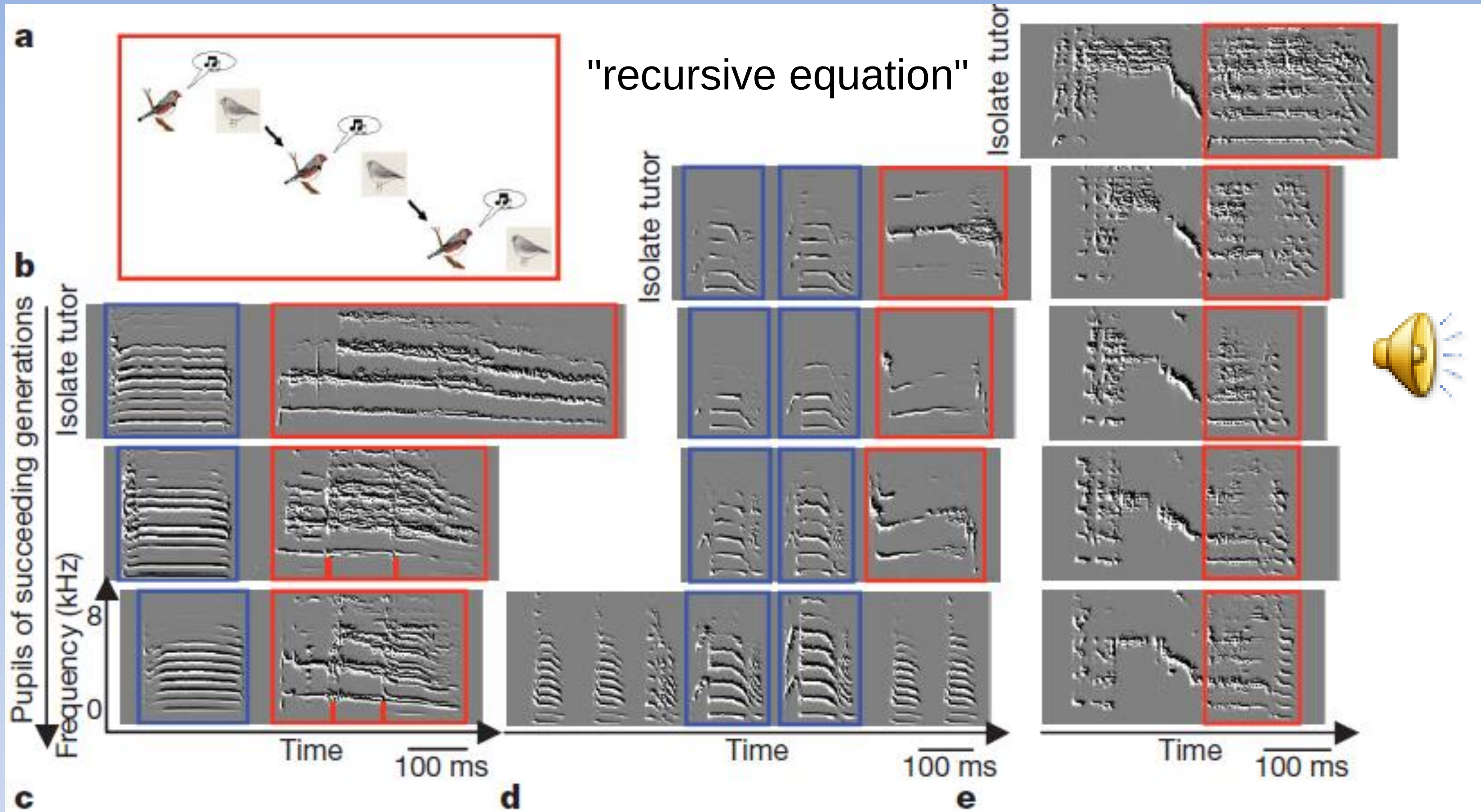

Song evolved towards the wild-type in three to four generations. Thus, species-typical song culture can appear de novo.

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