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).

Vocal learning

Mammals:

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

Birds:

- Parrots
- Hummingbirds
- 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:

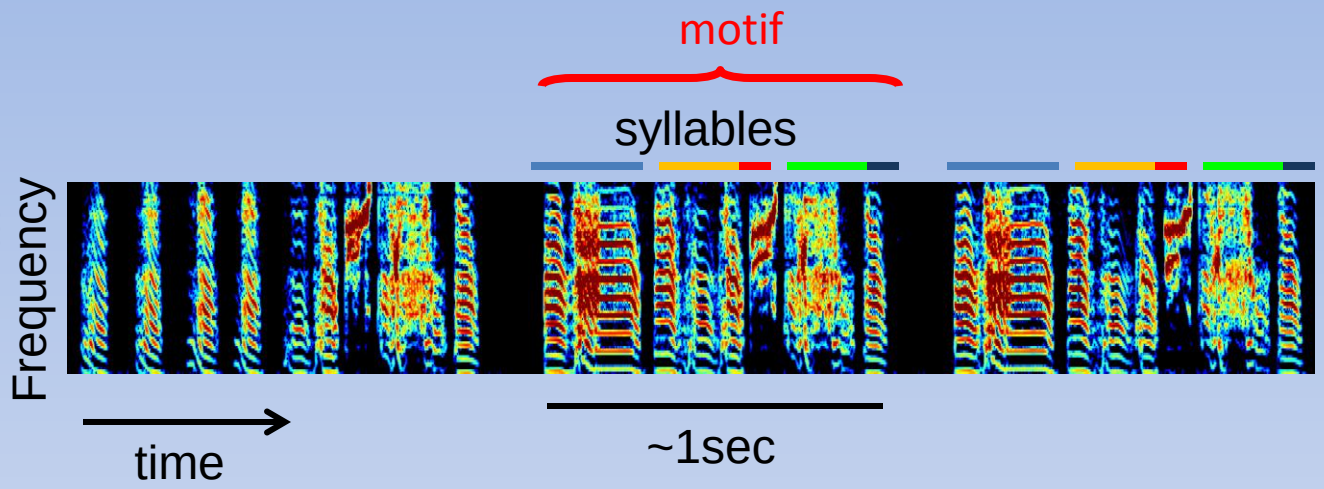
1. **To attract a mate.**
2. **To establish and hold a territory.**

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



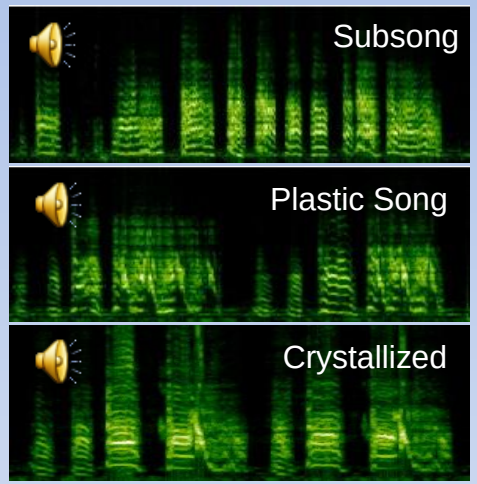
Ofer Tchernichovski's Lab (CUNY)

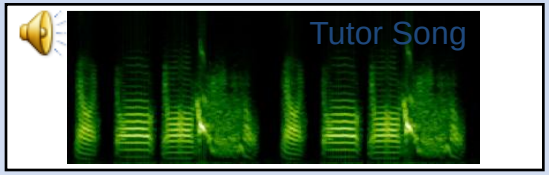
Songbirds learn to sing by imitating their tutor

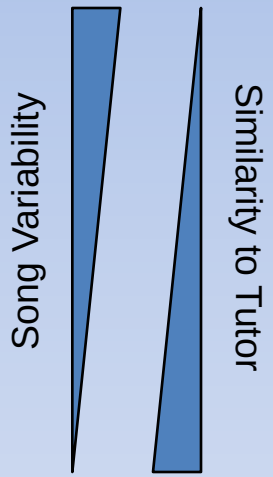
40d

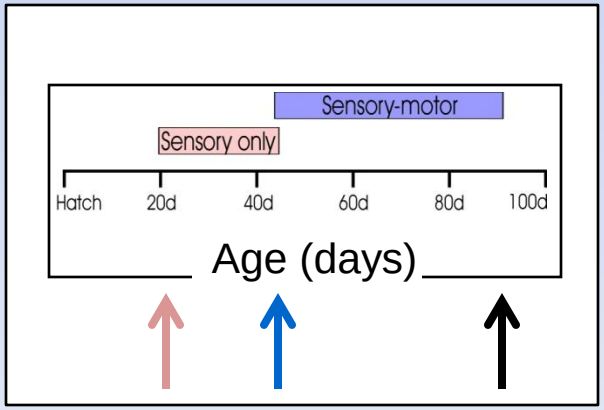
60d

90d

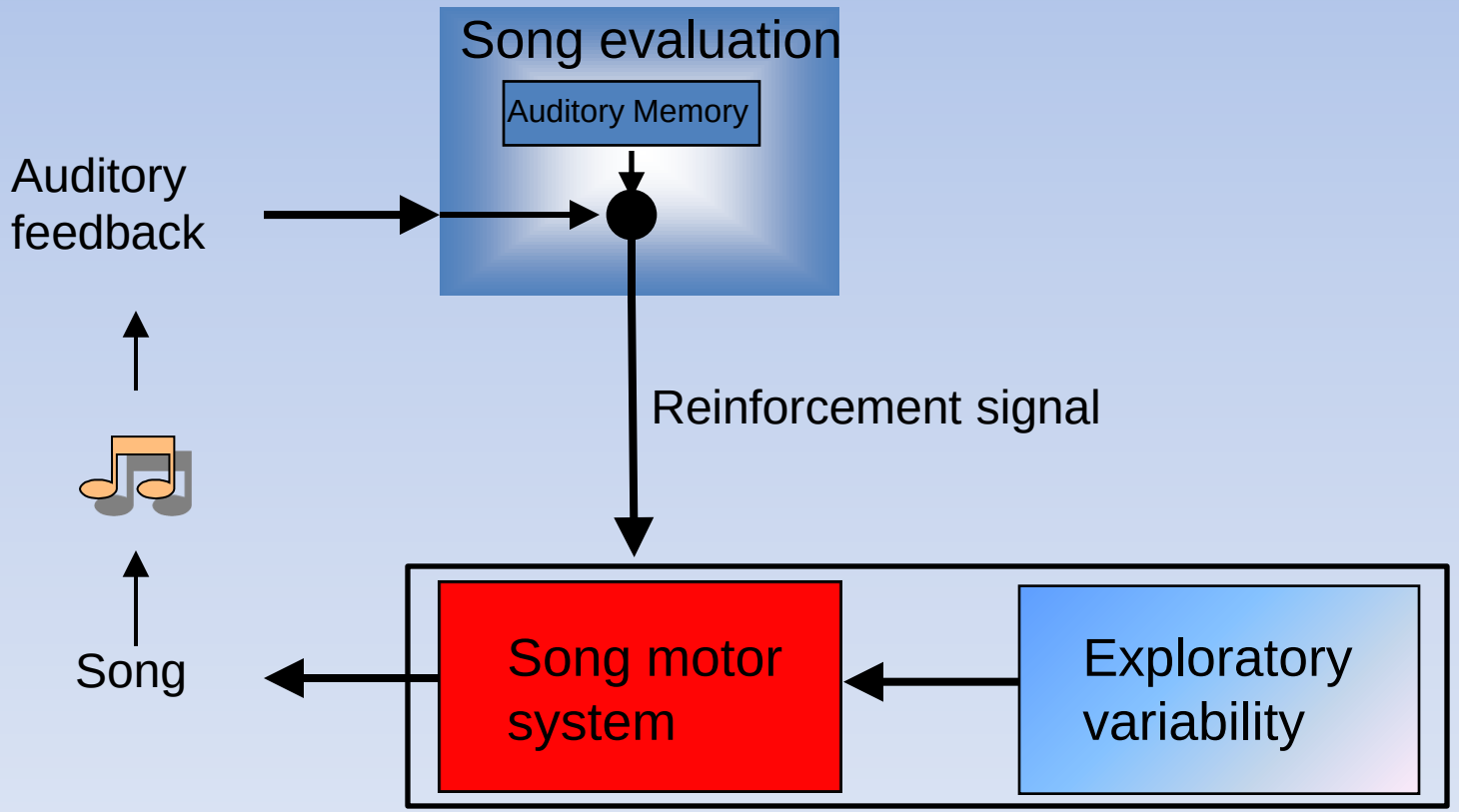






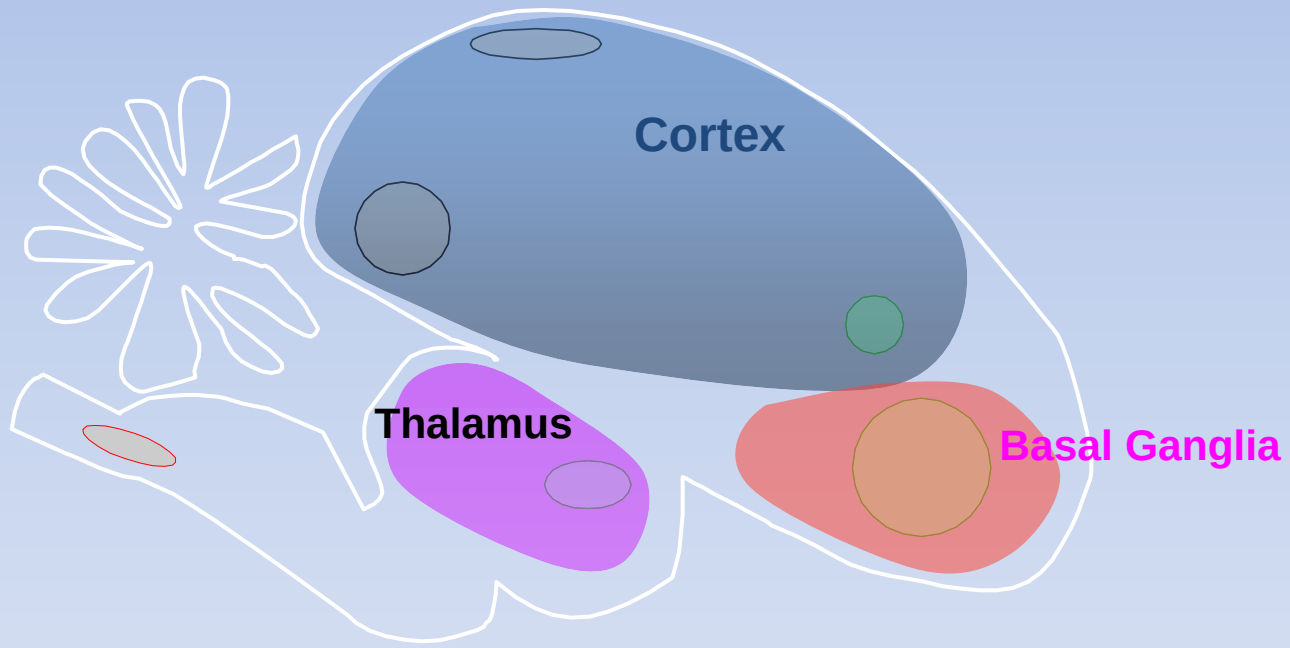


Reinforcement learning model for song acquisition



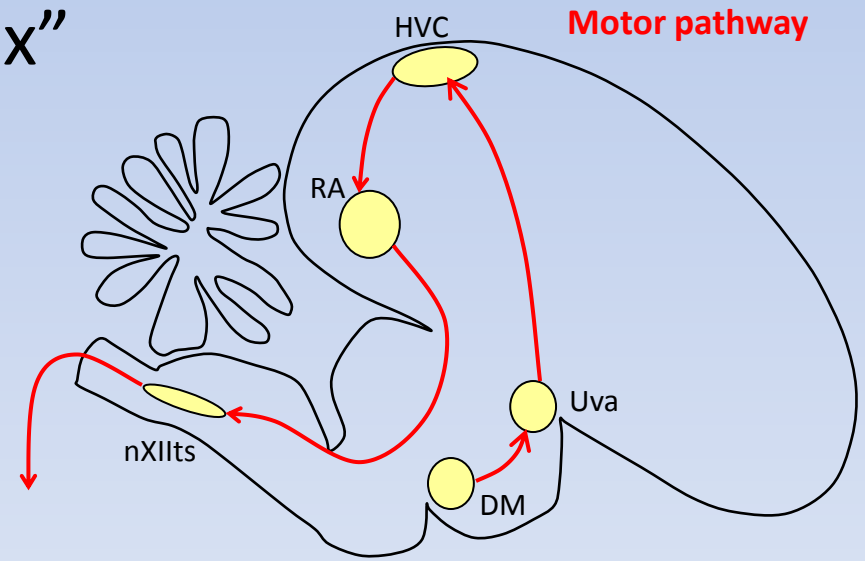
Konishi 1965; Marler 1970

Brain of Songbirds



Motor pathway

- HVC: “high vocal center”
- RA: primary motor “cortex”
- brainstem motor areas
  - Muscles of the syranx
  - respiratory muscles



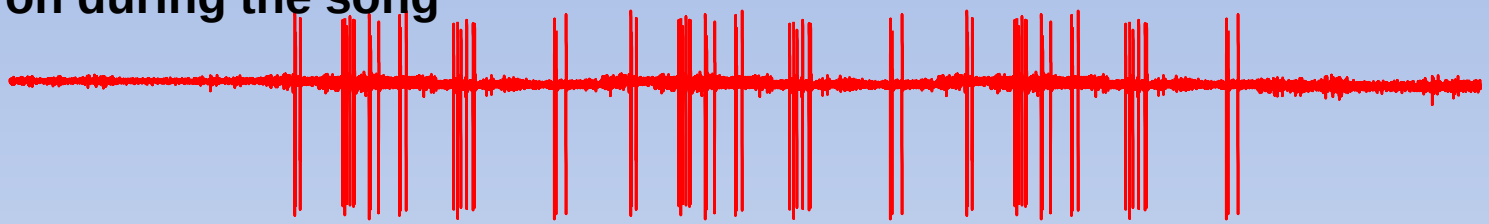
Nottebohm et al., (*J Comp Neurol*, 1976)

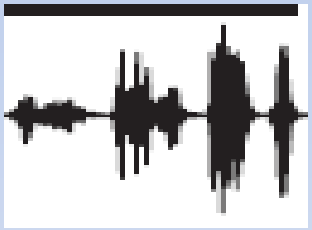
- **Question**:

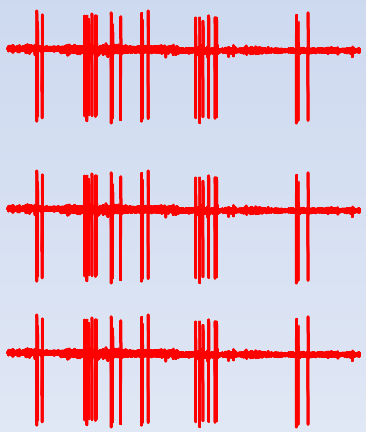
How do these circuits work to produce a song?

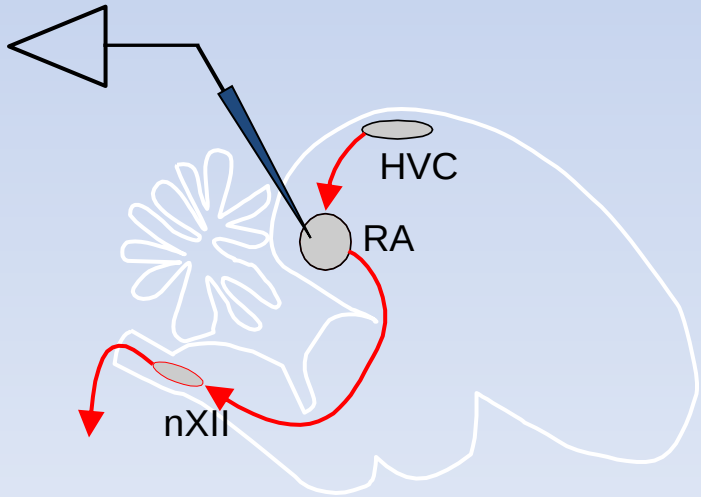
Record from brain areas and see what are the firing patterns of these neurons during singing.

Recordings from RA neuron during the song

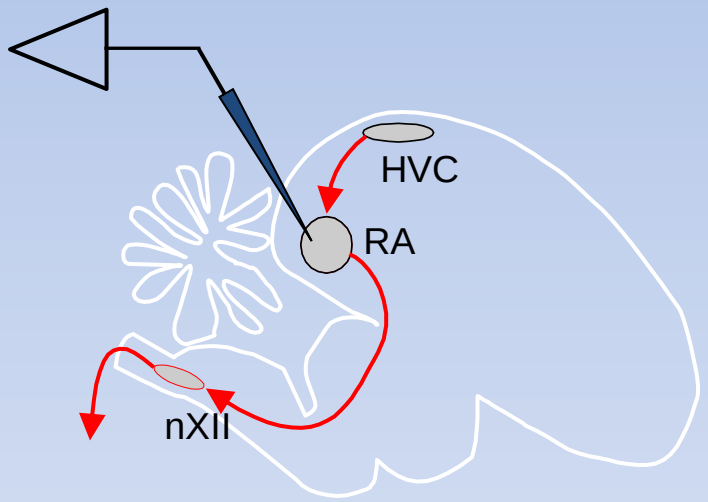


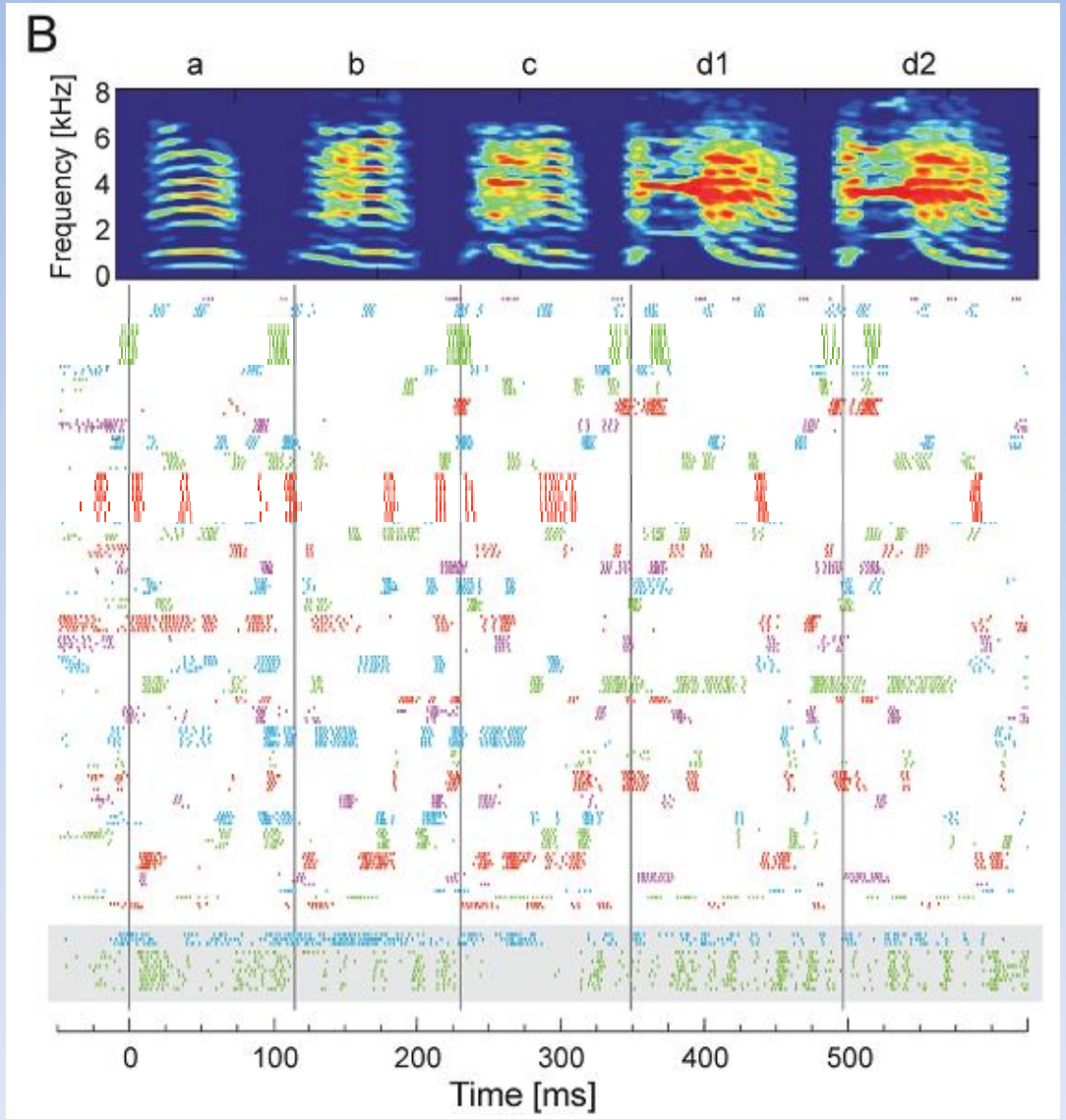




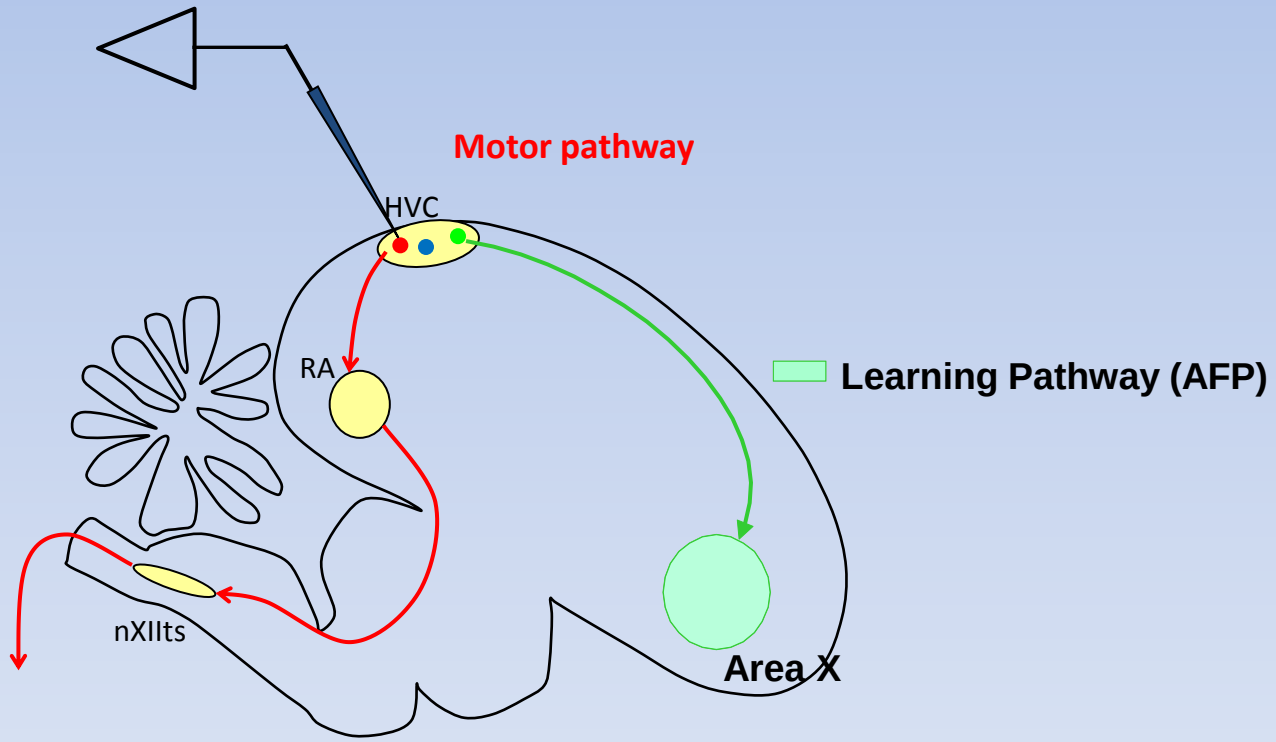


RA activity during singing

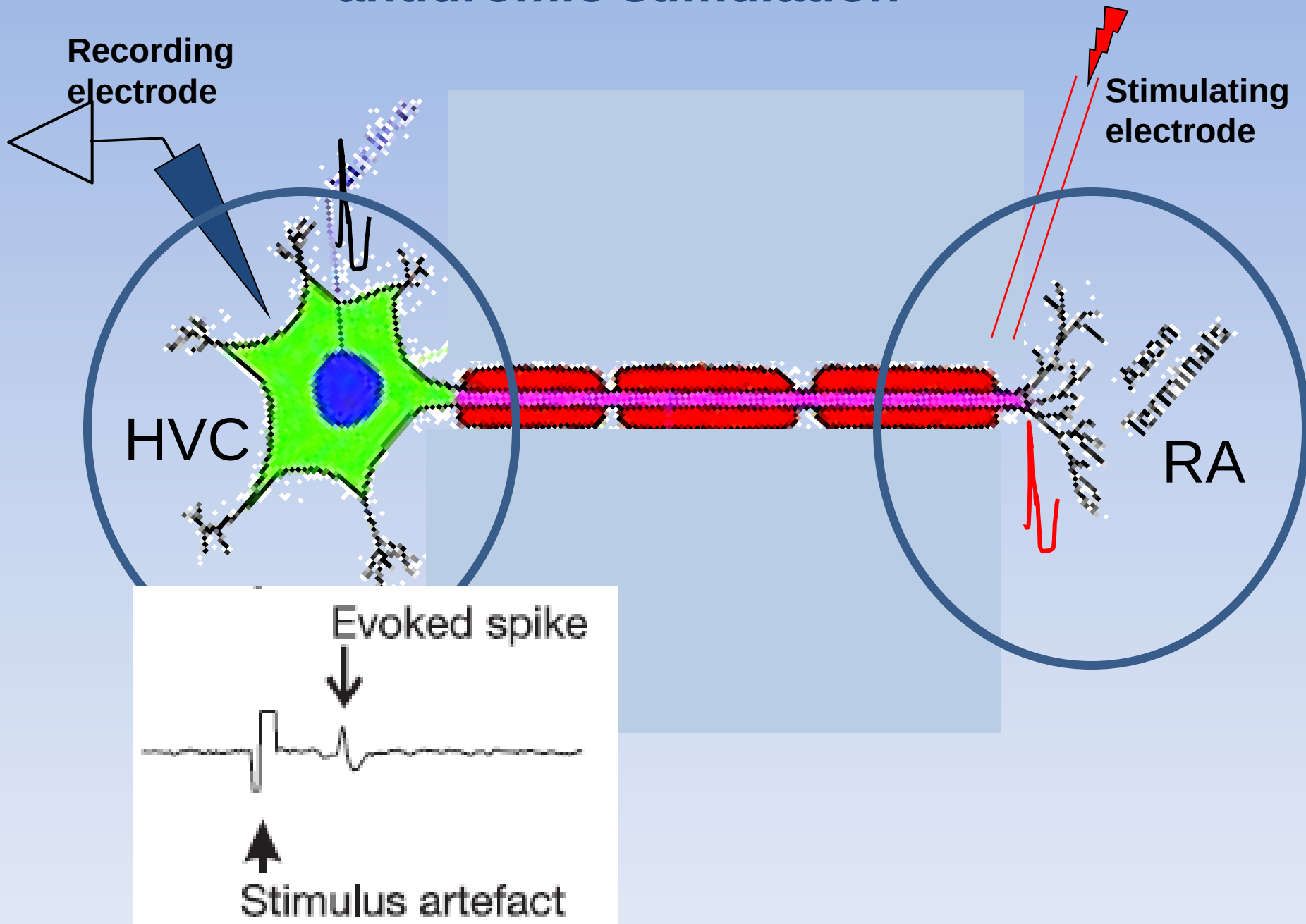


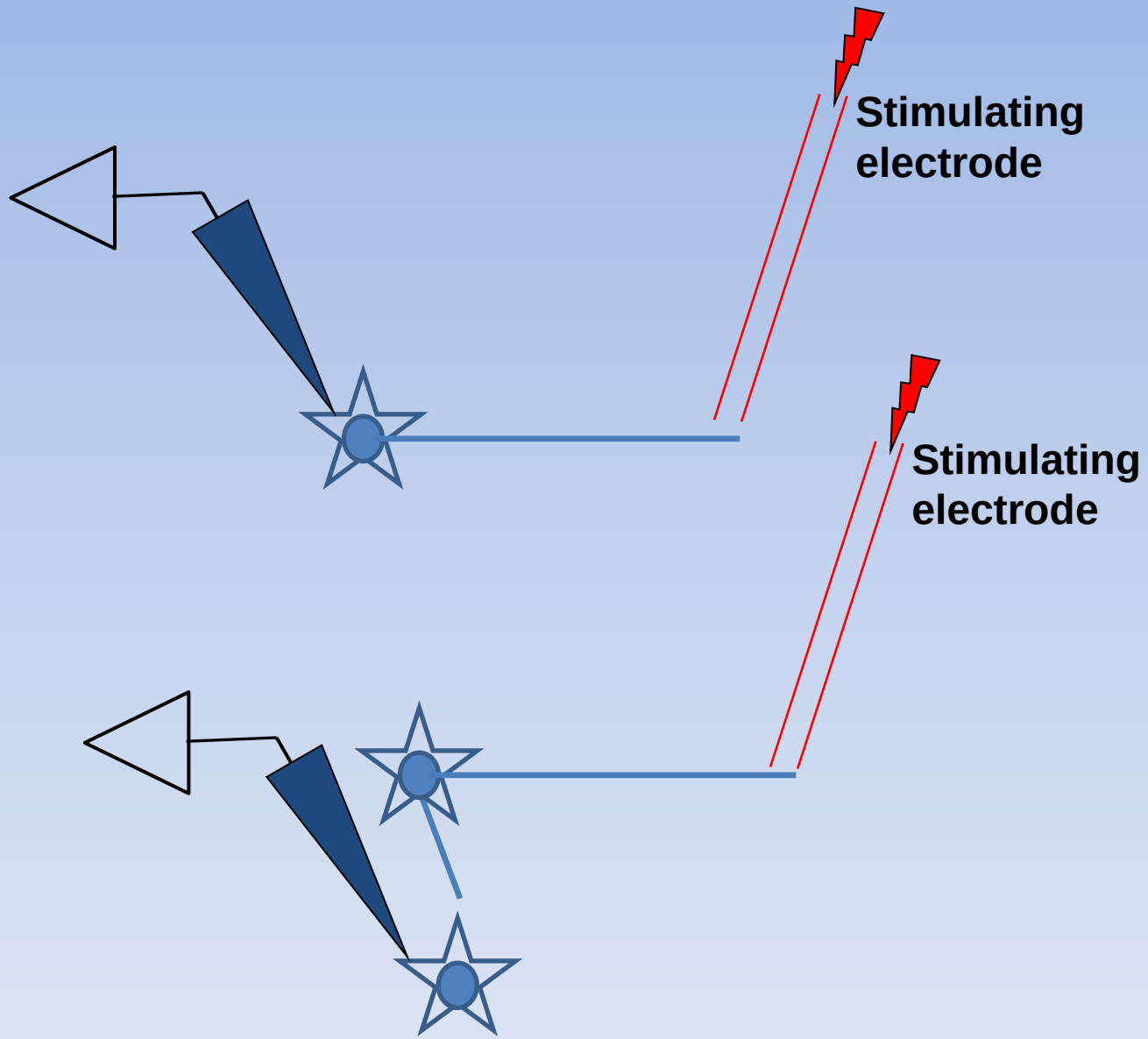


Leonardo & Fee (*J Neurosci*, 2005)

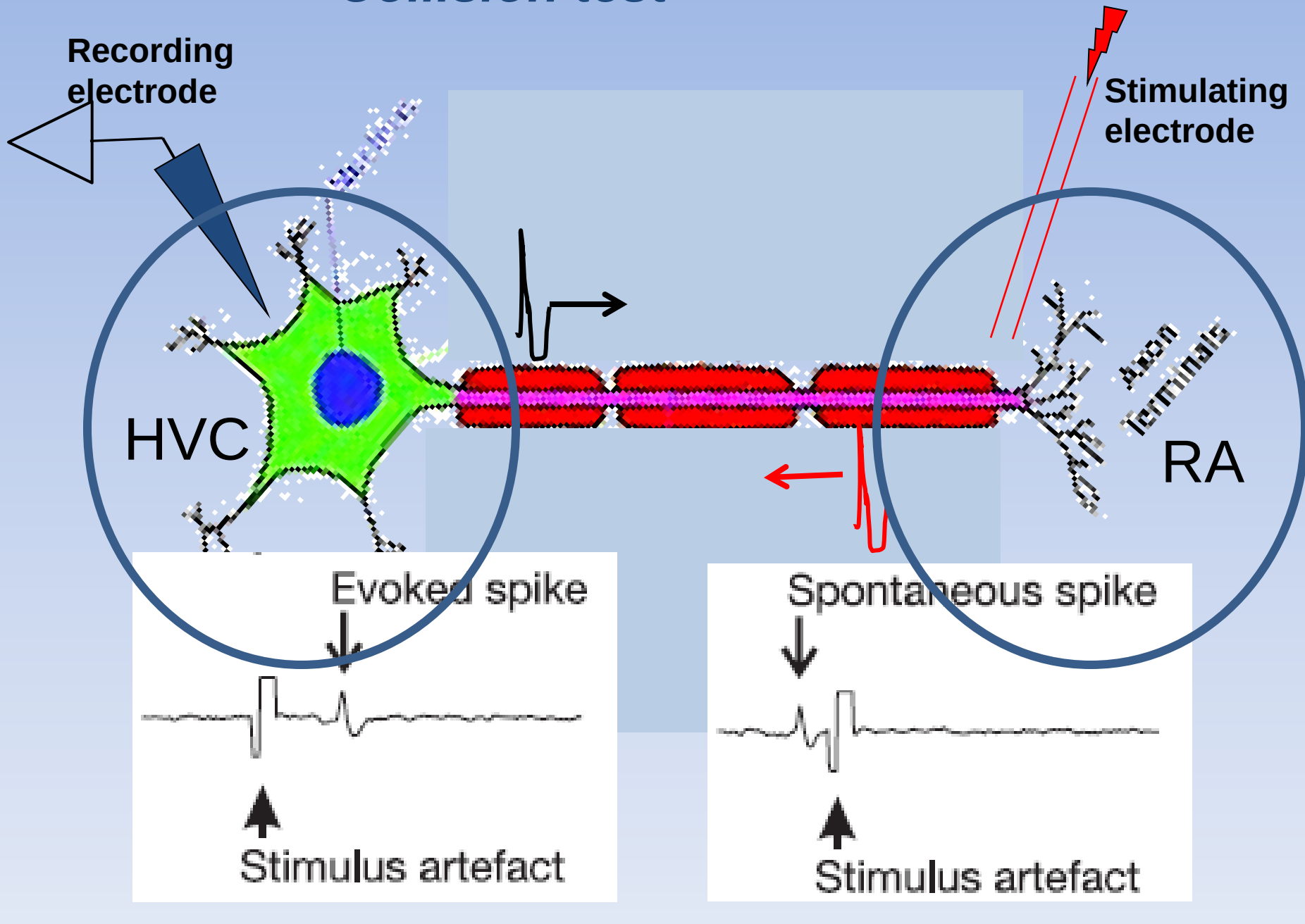

Motor pathway
HVC
RA
nXIIts
Area X
Learning Pathway (AFP)

antidromic stimulation

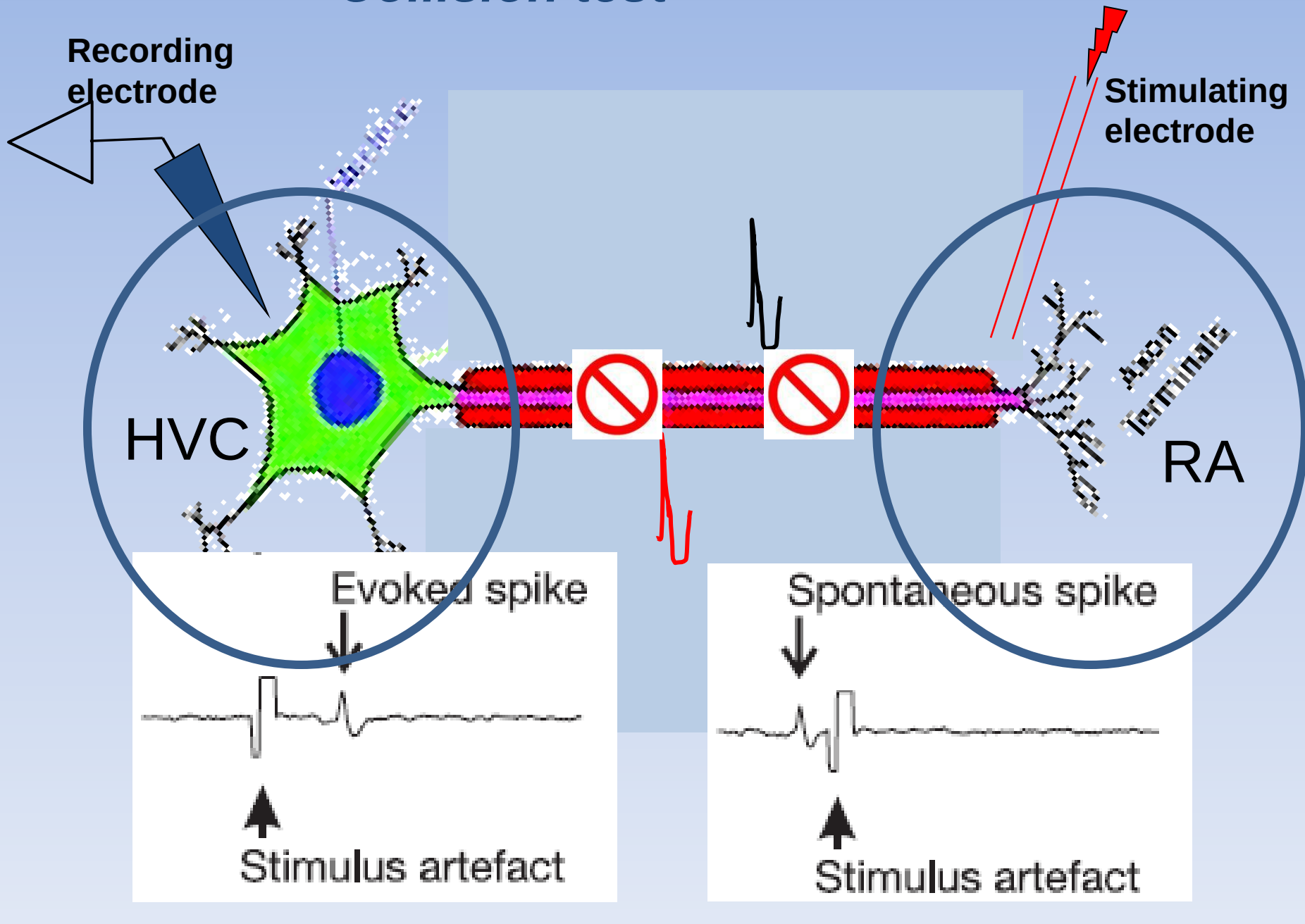



Stimulating electrode
Stimulating electrode

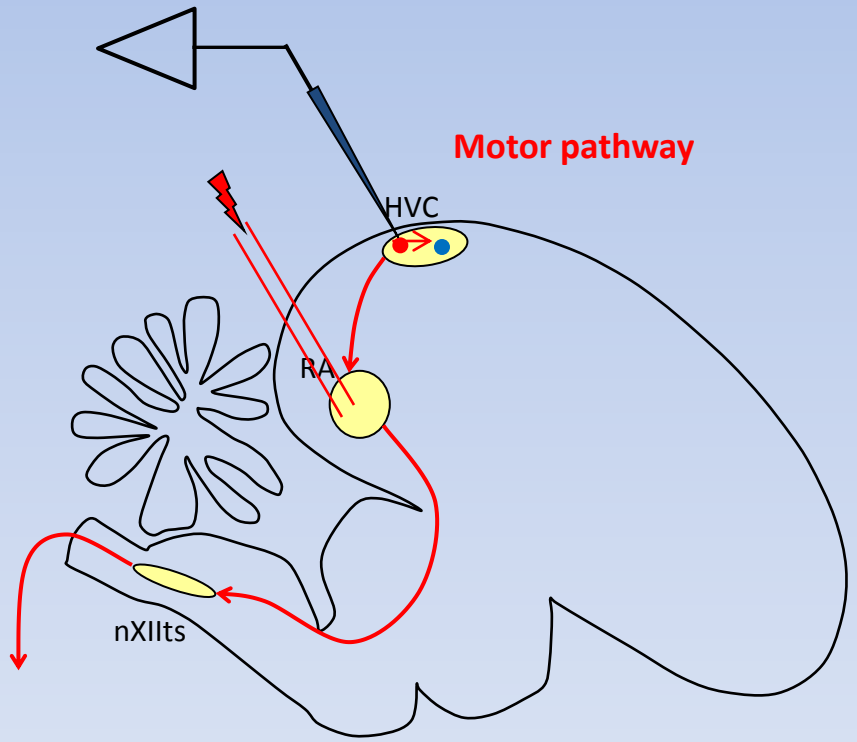
Collision test

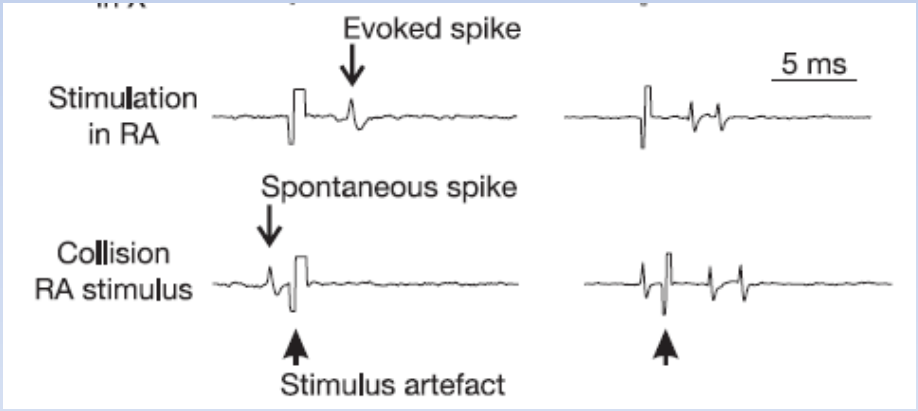


Collision test



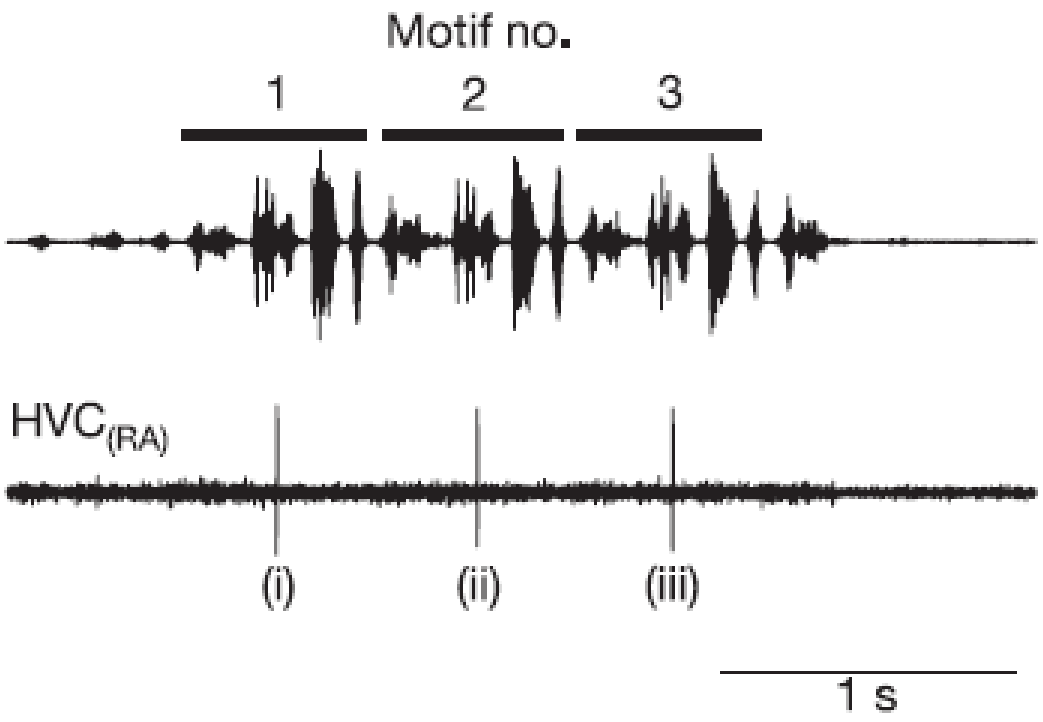
Using antidromic stimulation to identify cell types within HVC

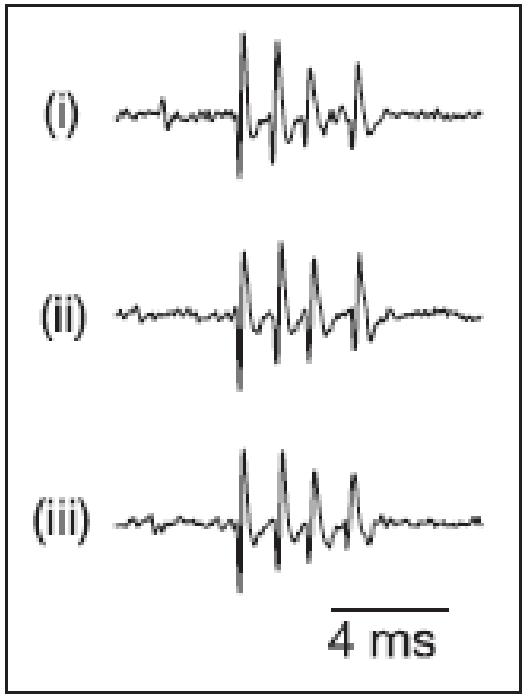




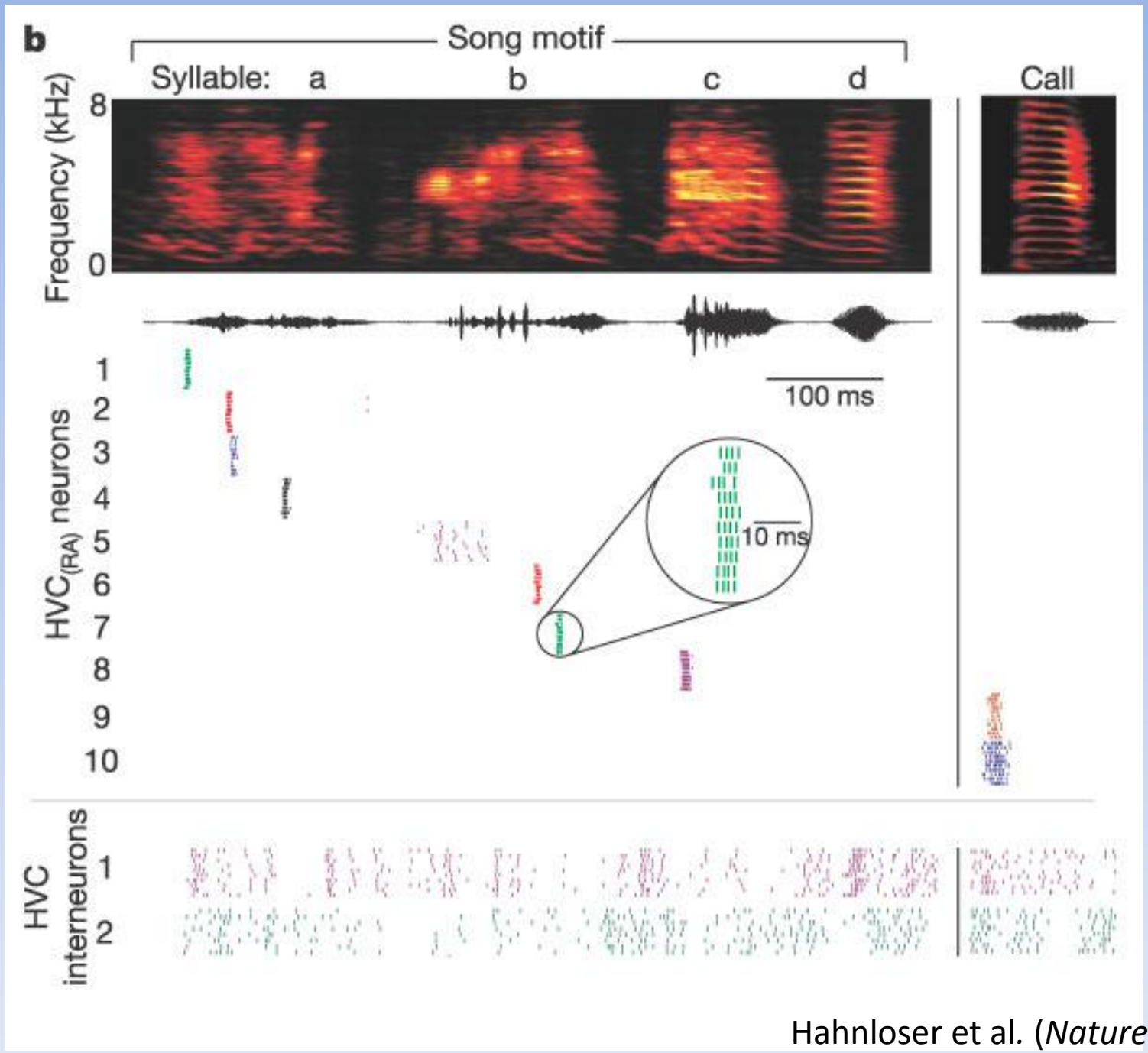
Hahnloser et al. (*Nature*, 2002)

Activity of HVC-RA neurons during singing



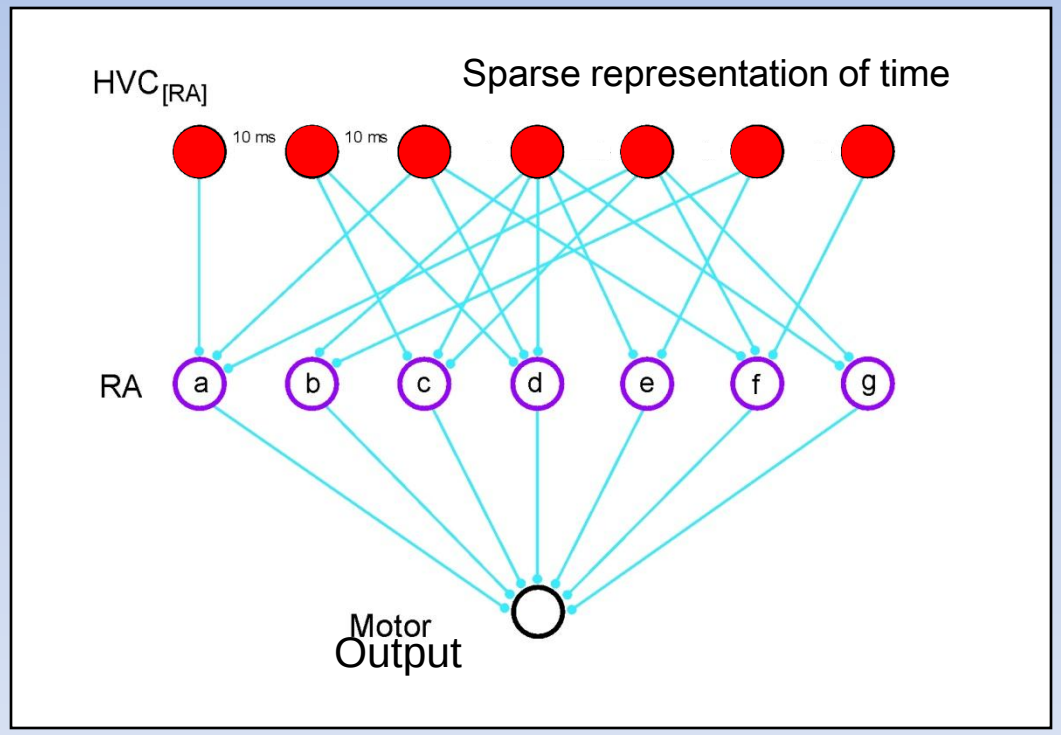


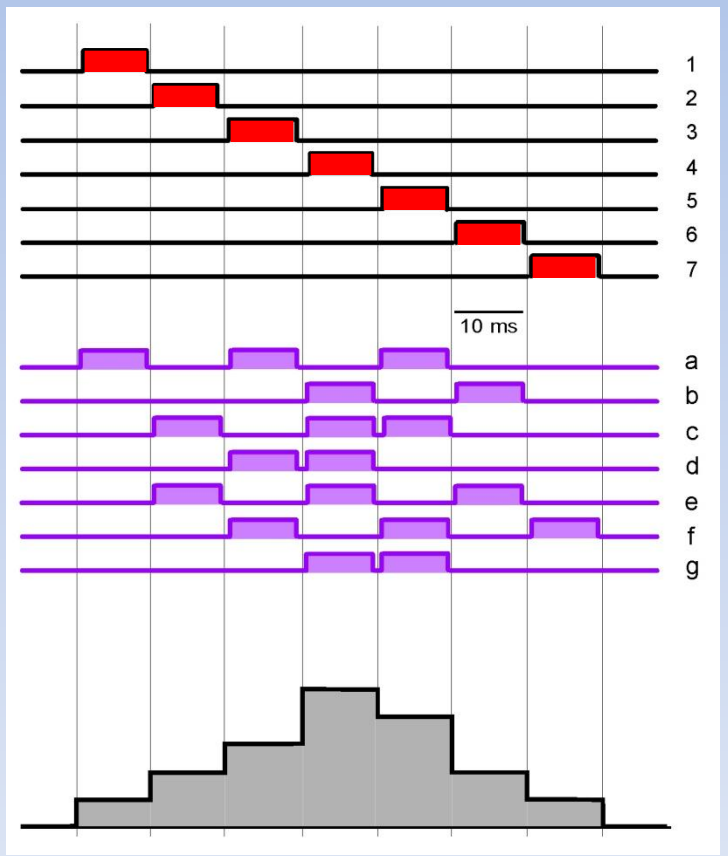
Hahnloser et al. (*Nature*, 2002)



Hahnloser et al. (*Nature*, 2002)

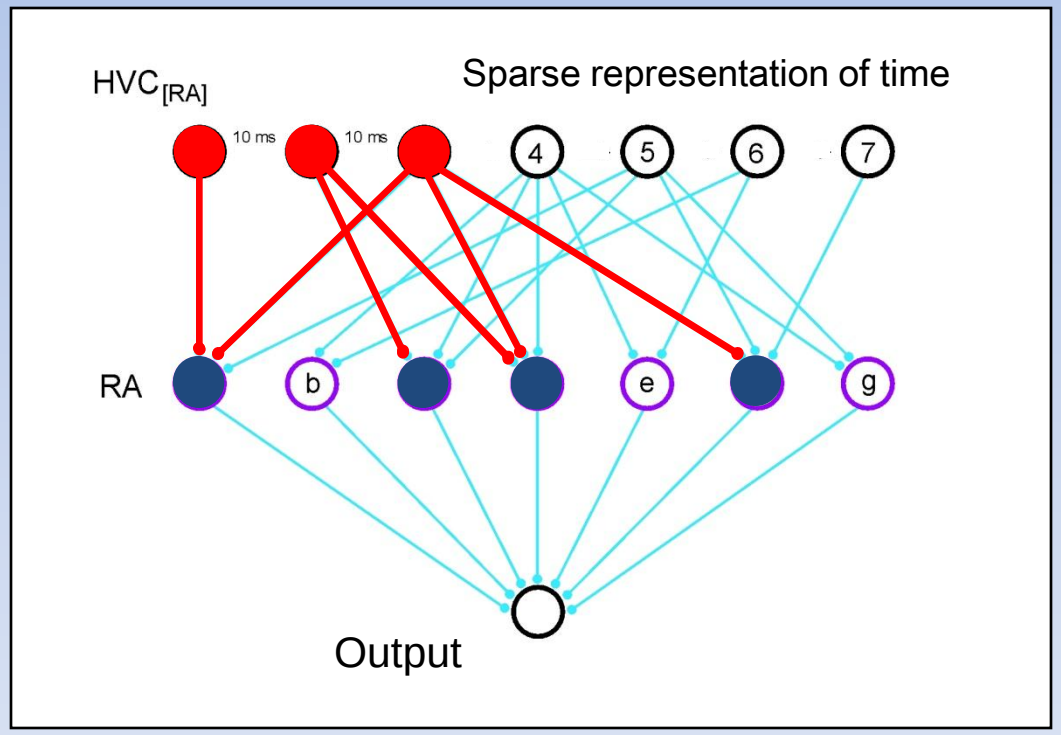
Simple sequence generation circuit

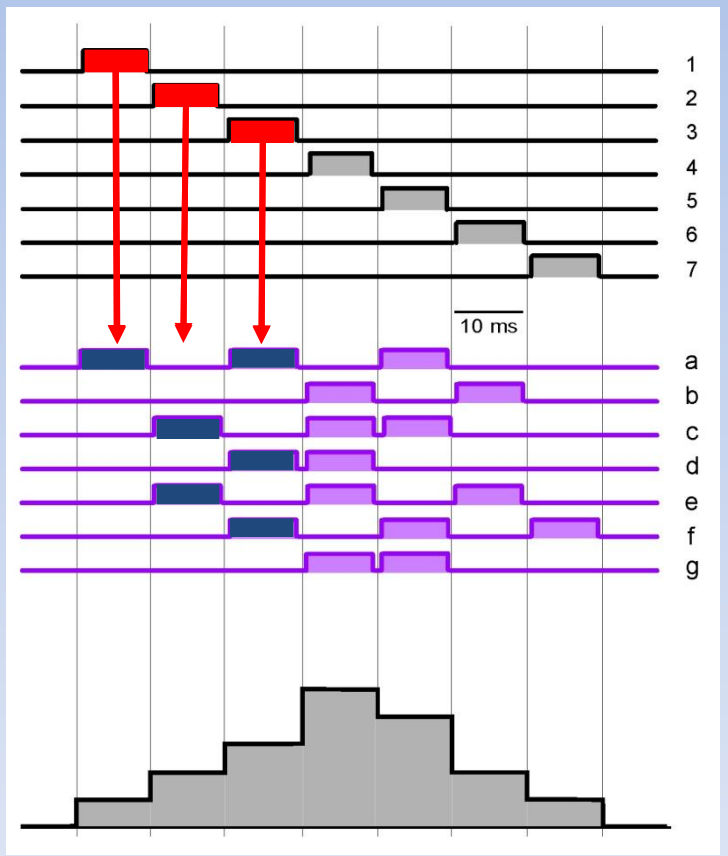




Leonardo and Fee, 2005

Simple sequence generation circuit

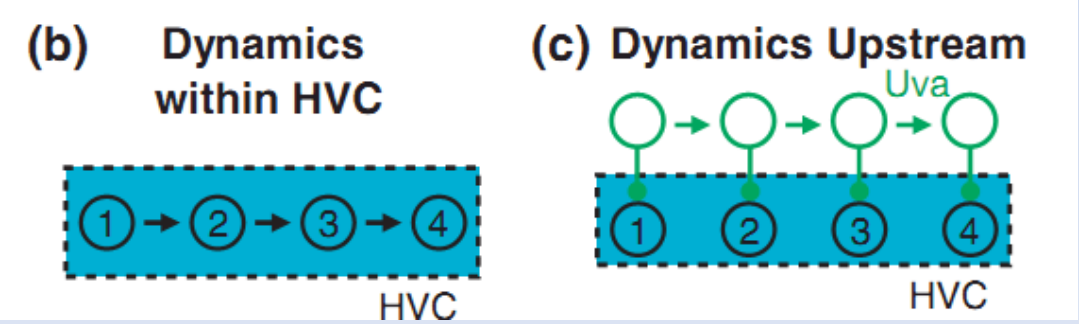




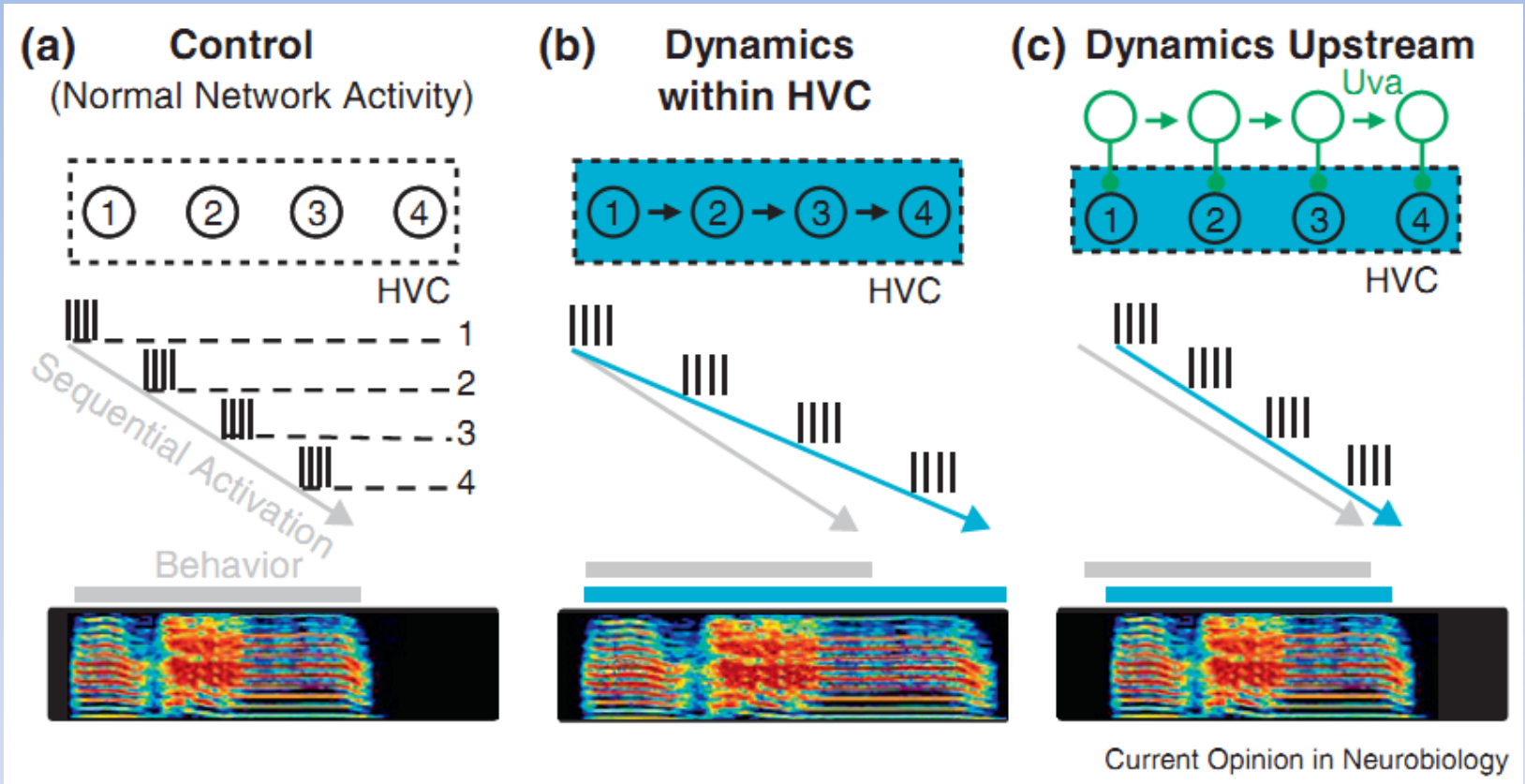
Leonardo and Fee, 2005

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?

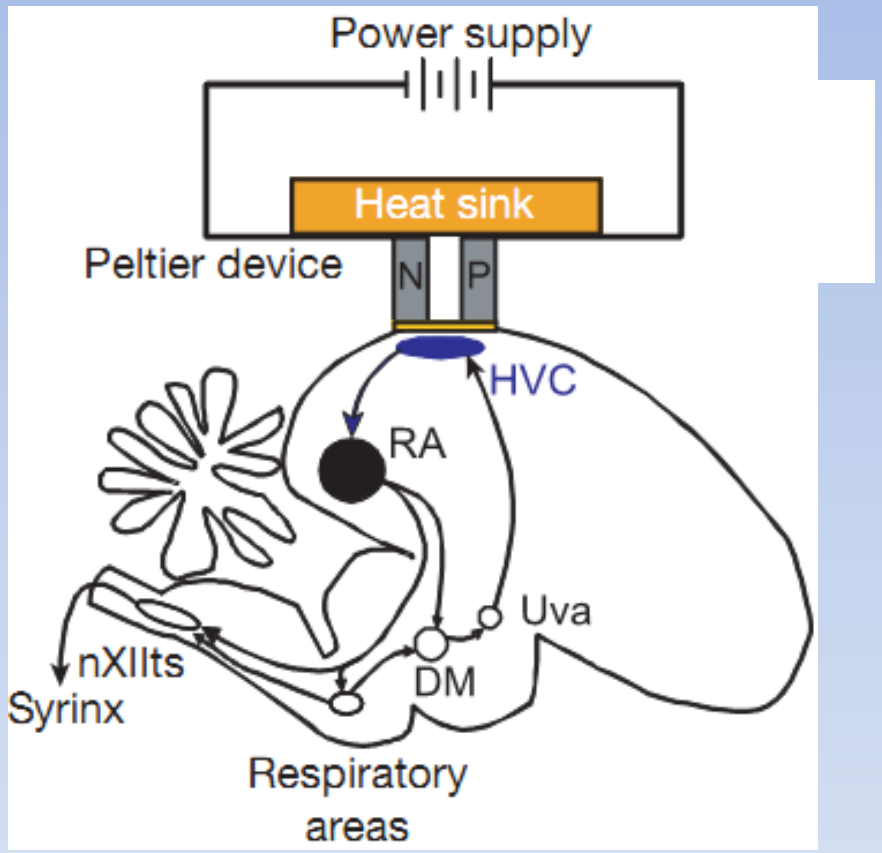


Are the dynamics generated within HVC?



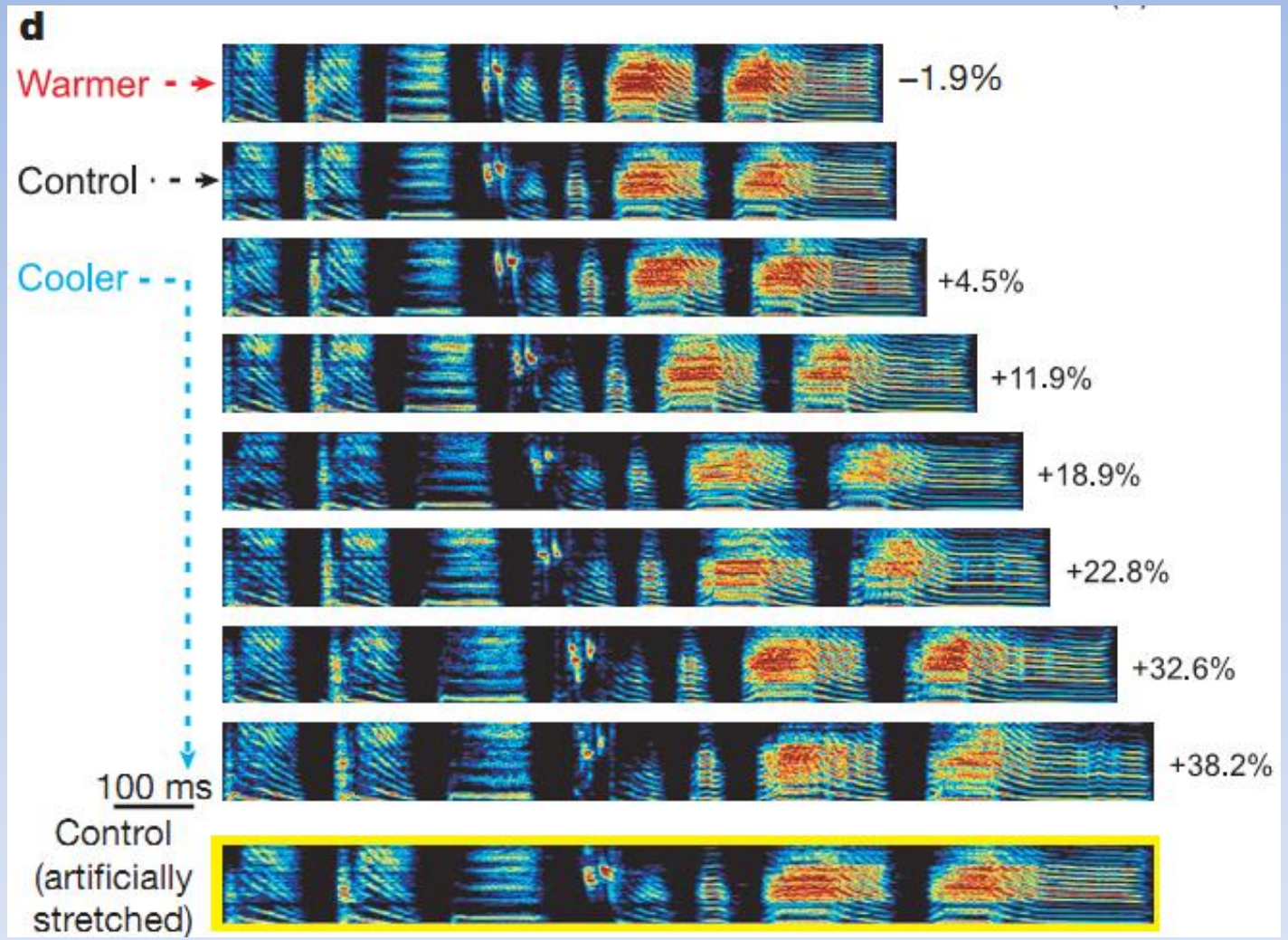
Fee & Long (*Curr Opin Neurobiol*, 2011)

Local manipulation of brain temperature



Long & Fee (*Nature*, 2008)

Cooling of HVC- 3% per 1 degree



Long & Fee (*Nature*, 2008)

Part 1: Summary

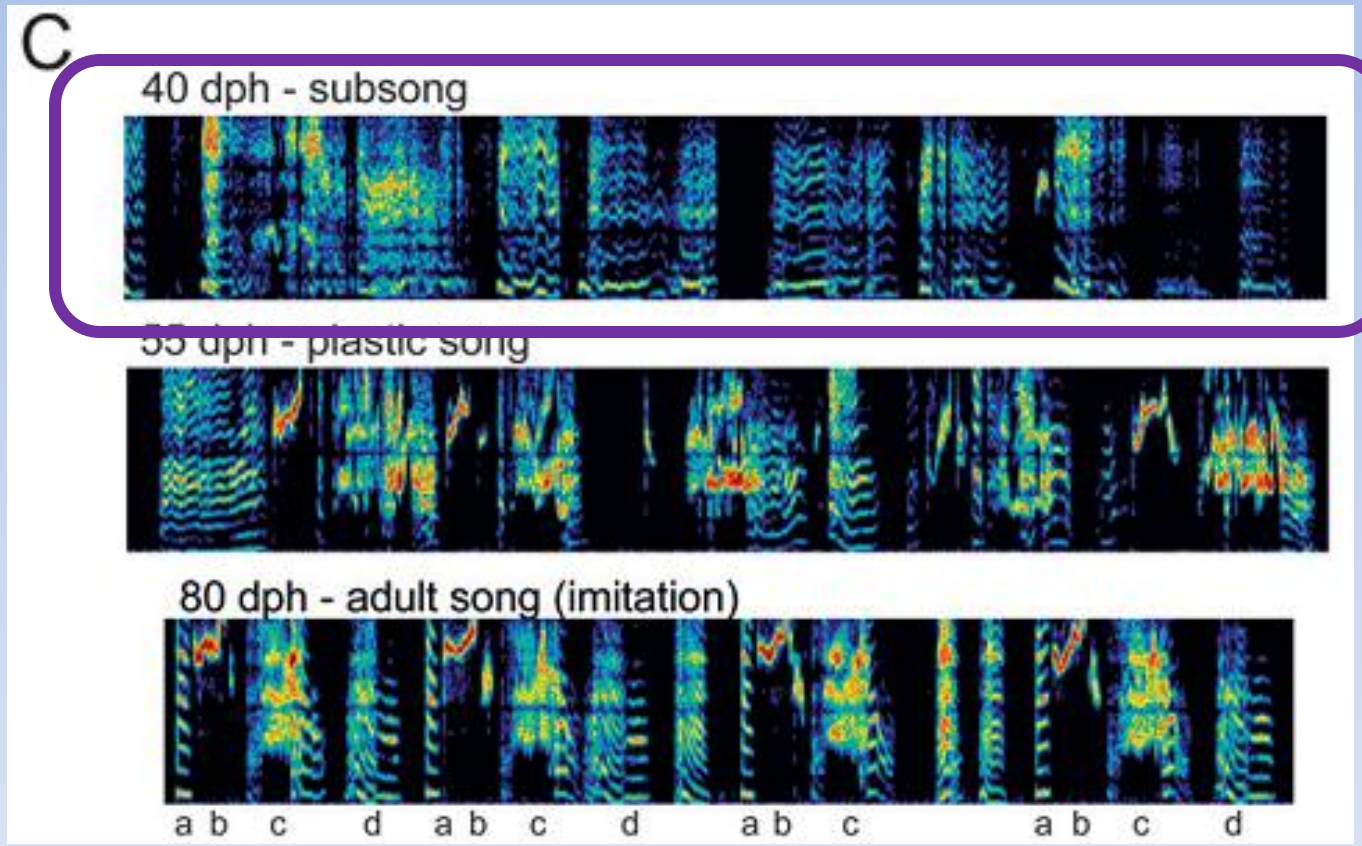
HVC:

- 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.

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



Fee & Scharff (*ILAR*, 2010)

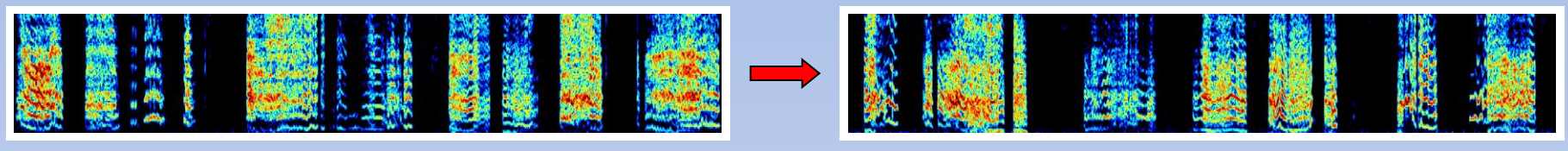
- **Question**:

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

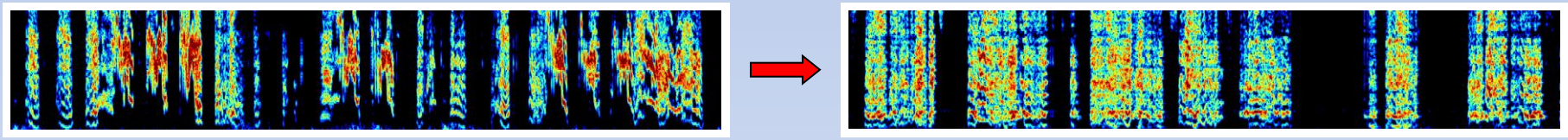
HVC-lesioned birds could still produce subsong!

Control **no HVC**

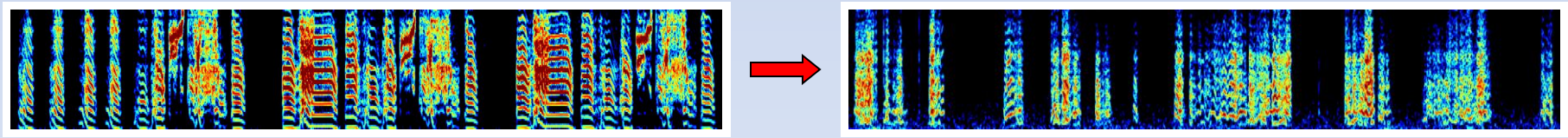
Subsong stage (37 dph)



Plastic song stage (50 dph)

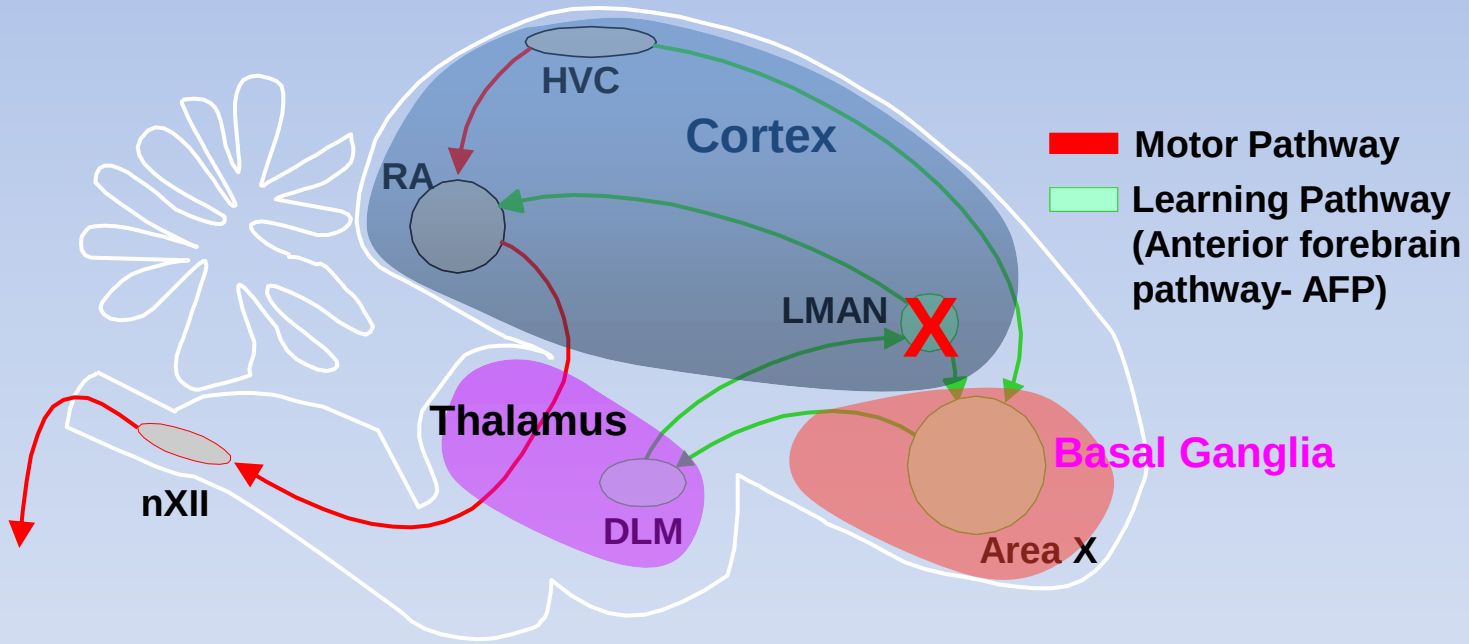


Adult



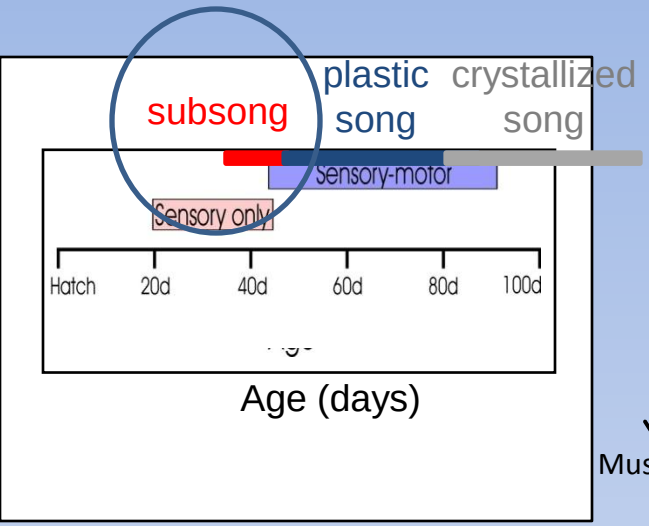
250 ms

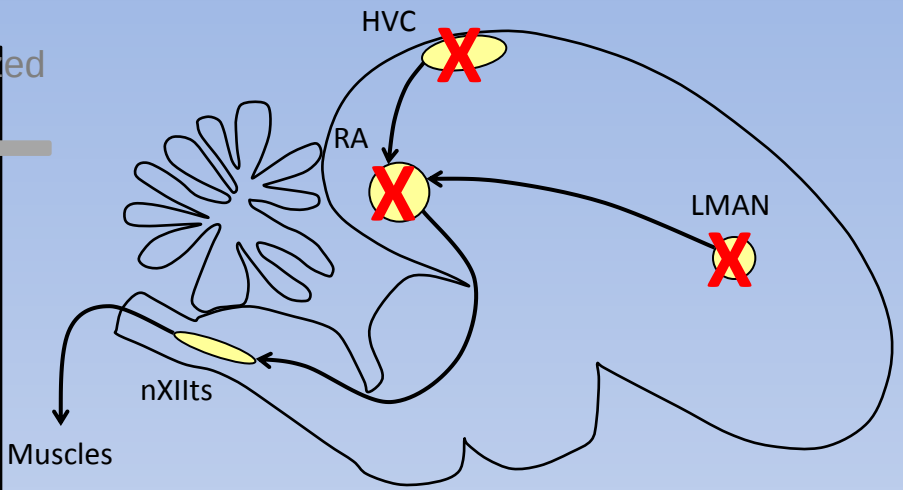
Aronov et.al. (2008) *Science*

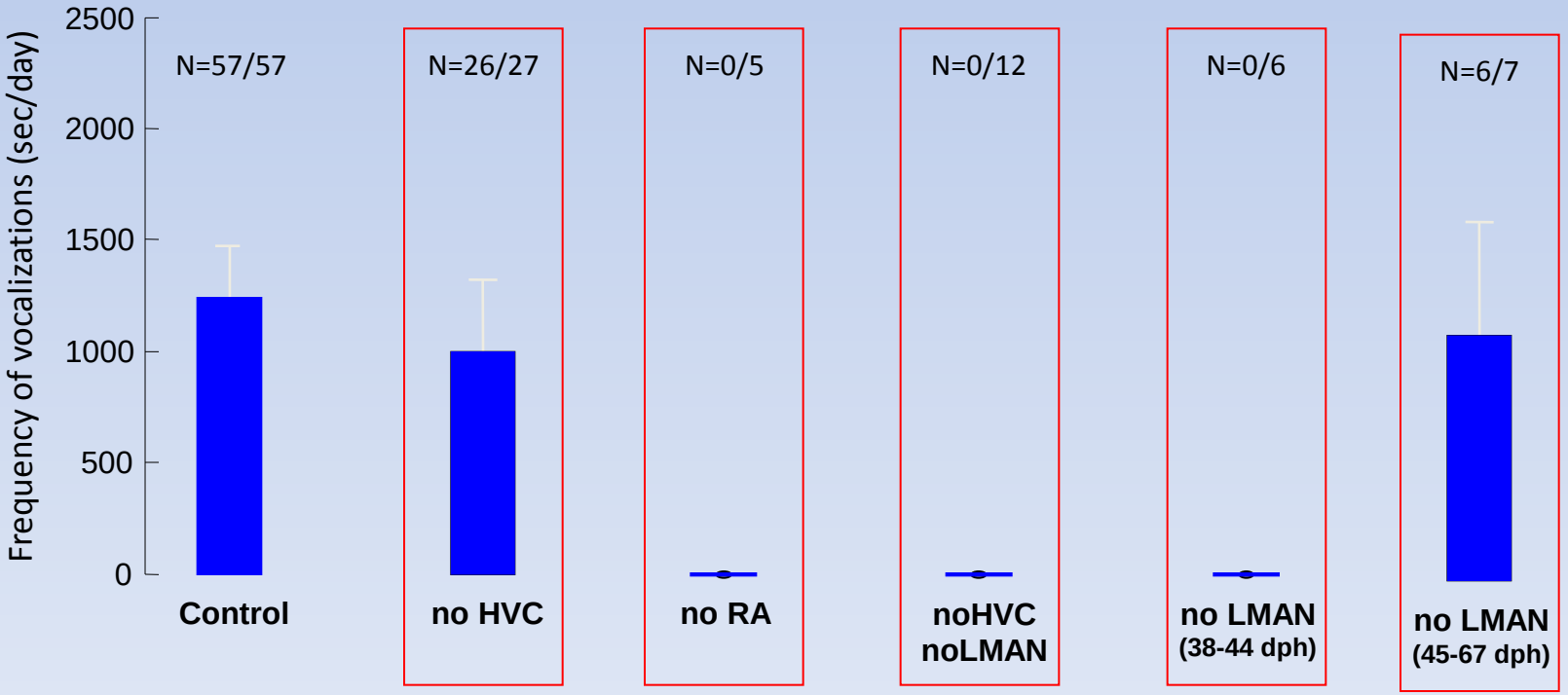


•The learning pathway is not necessary for adult song production, but is required for learning (Bottjer, 1984, Scharff and Nottebohm, 1991)

What drives subsong production?



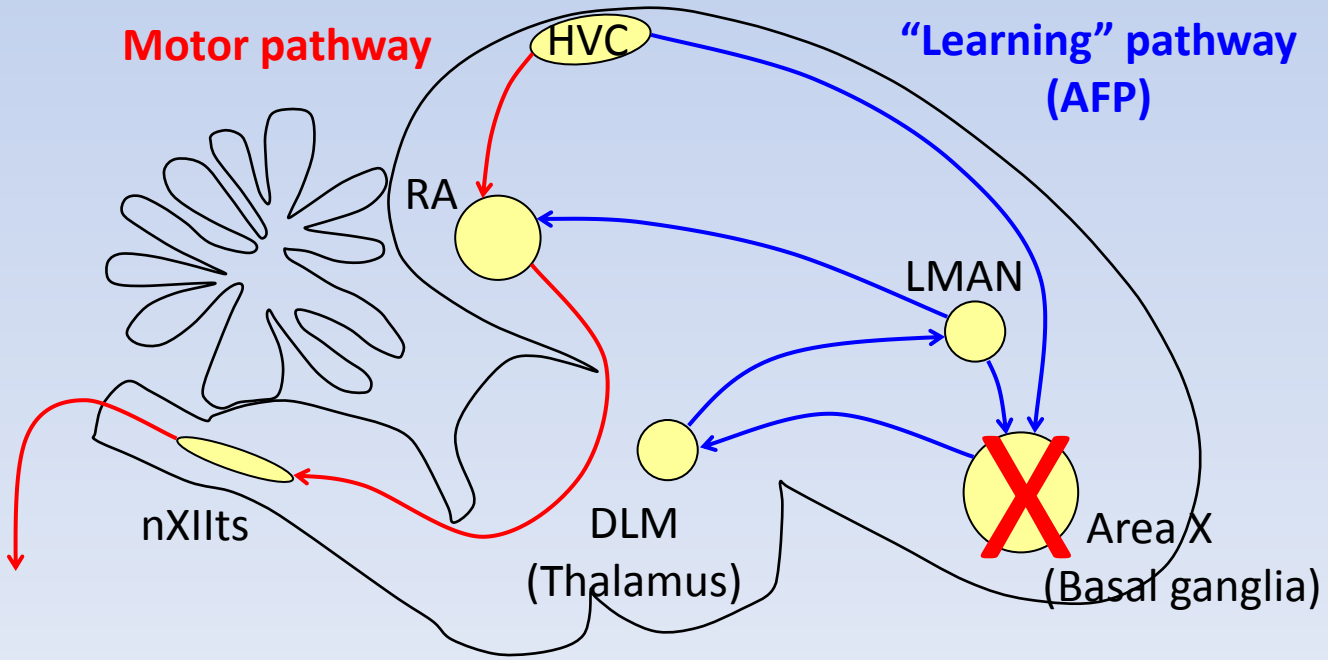




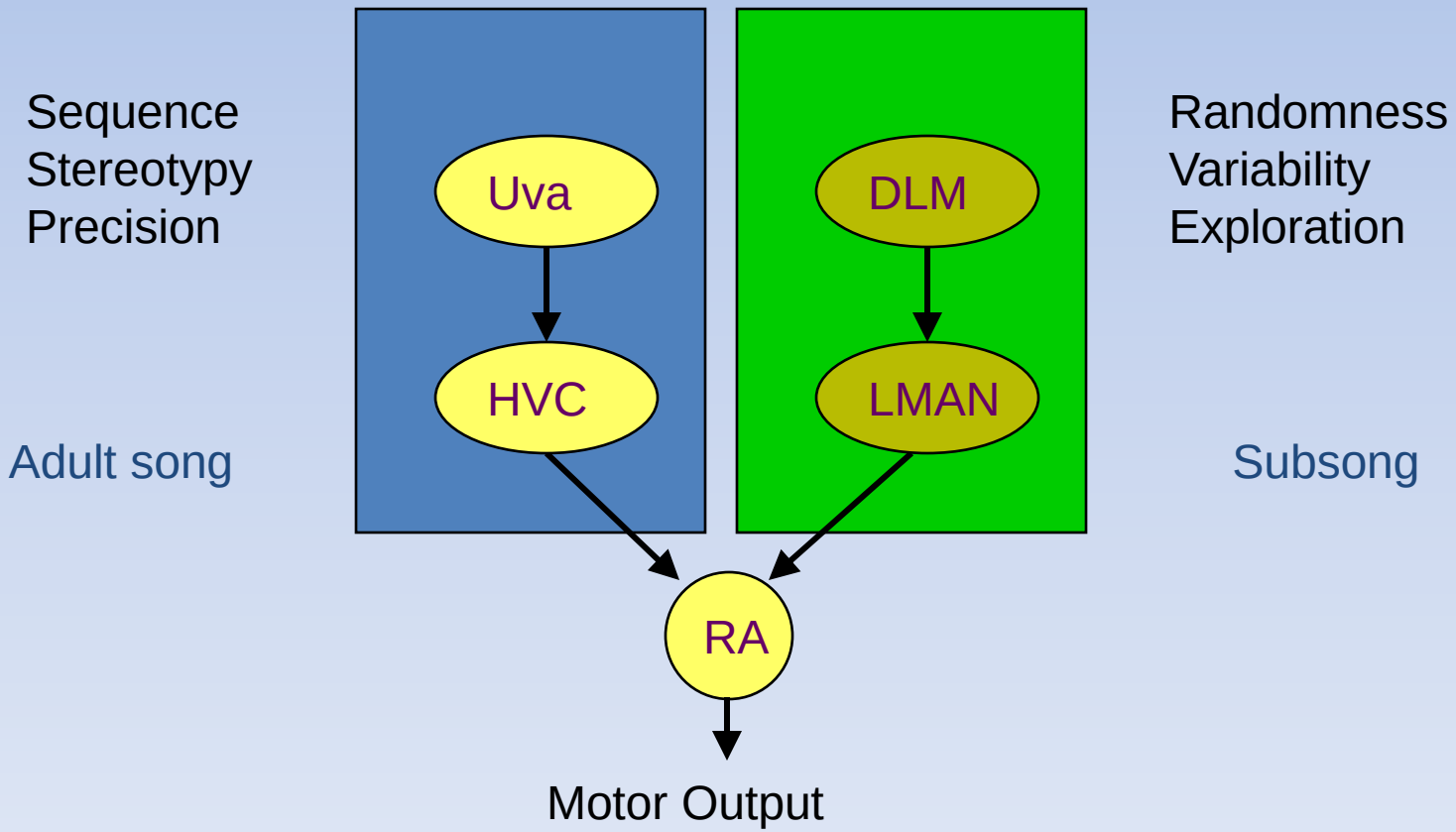
Aronov et.al. (2008) *Science*

- 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.



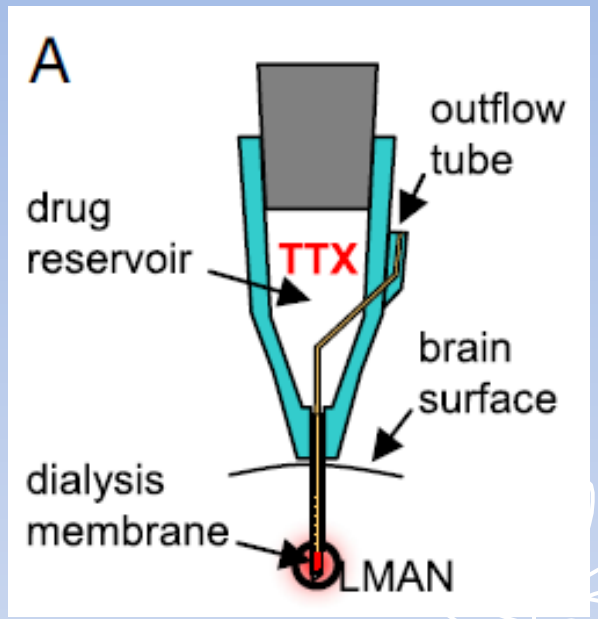
Separate premotor pathways for stereotyped song and babbling

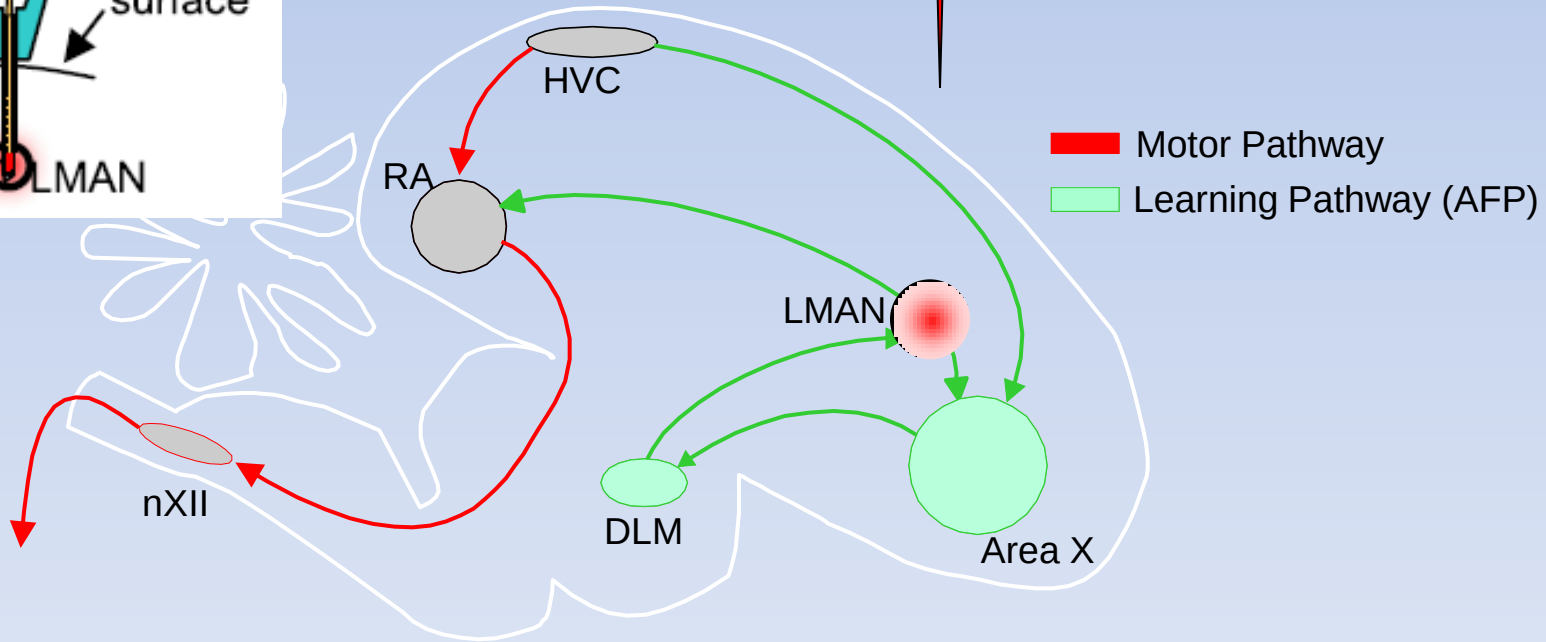


- **Question**:

  What is the role of LMAN in older juveniles?

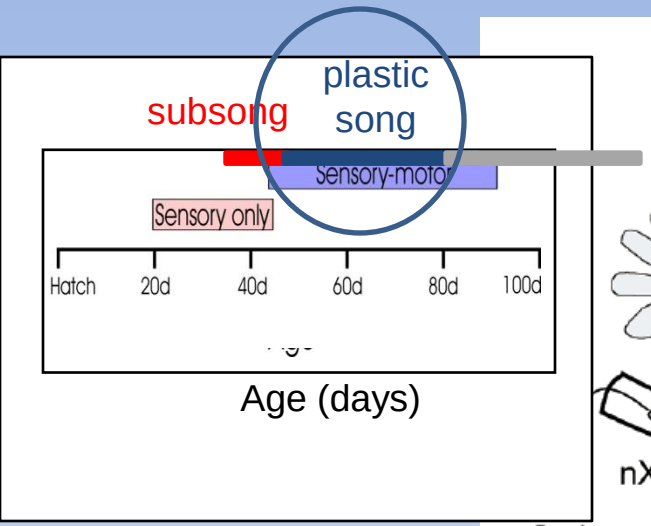
Role of LMAN in older juveniles

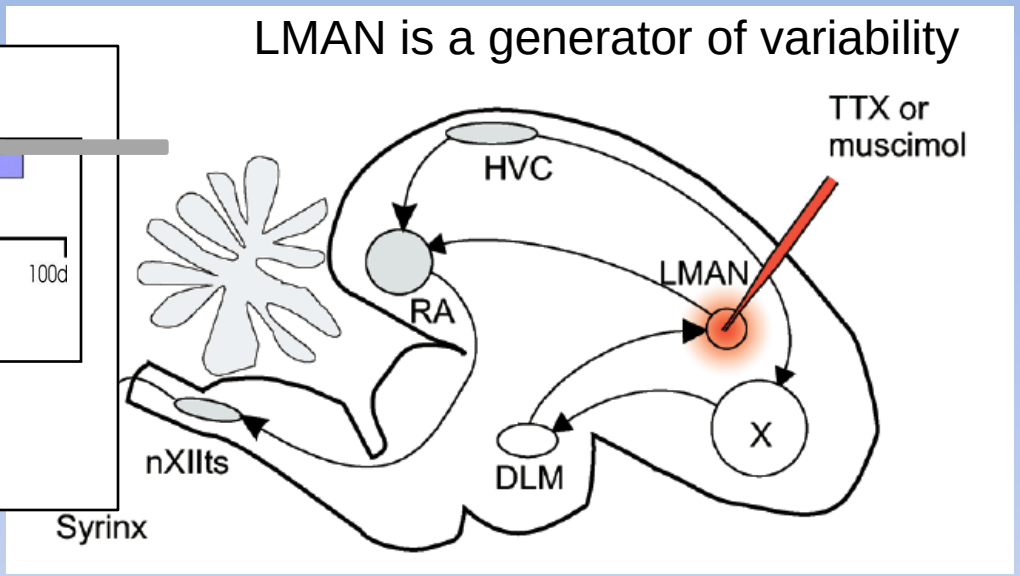


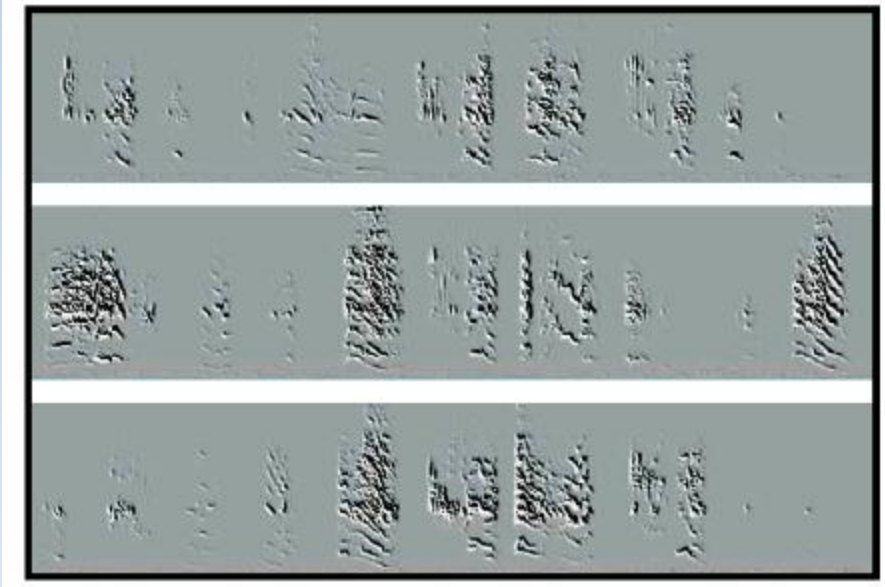


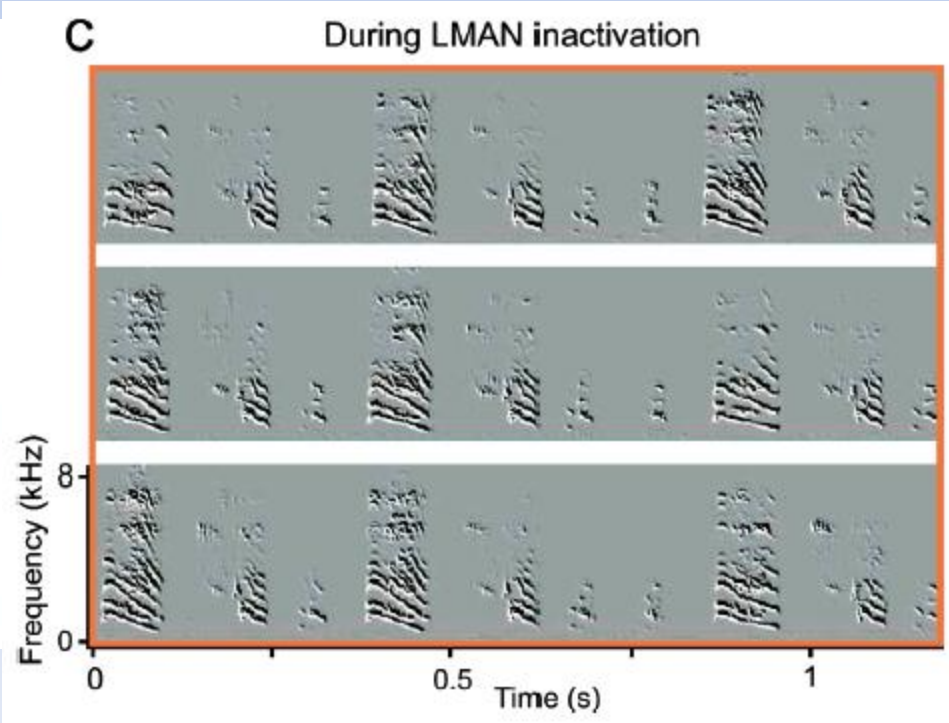
Andalman & Fee (2009)

Role of LMAN in older juveniles

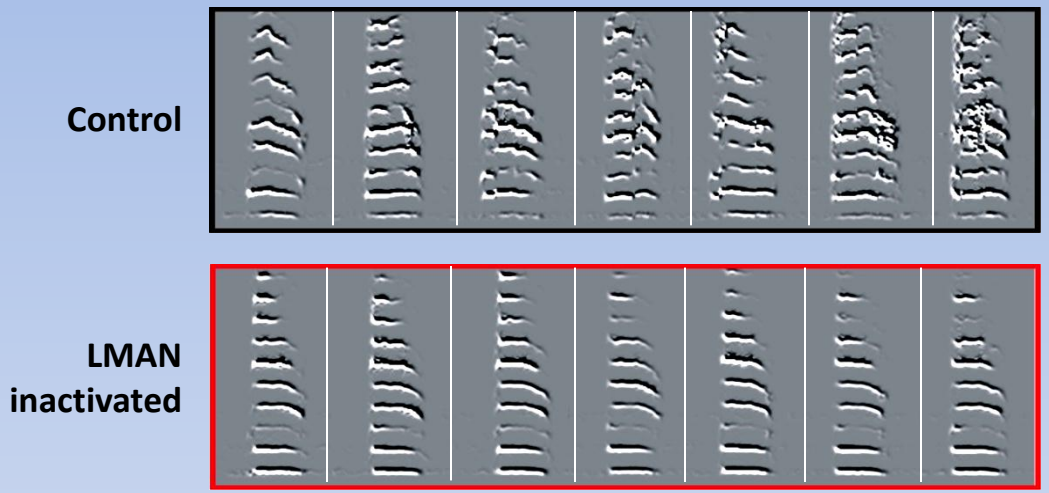


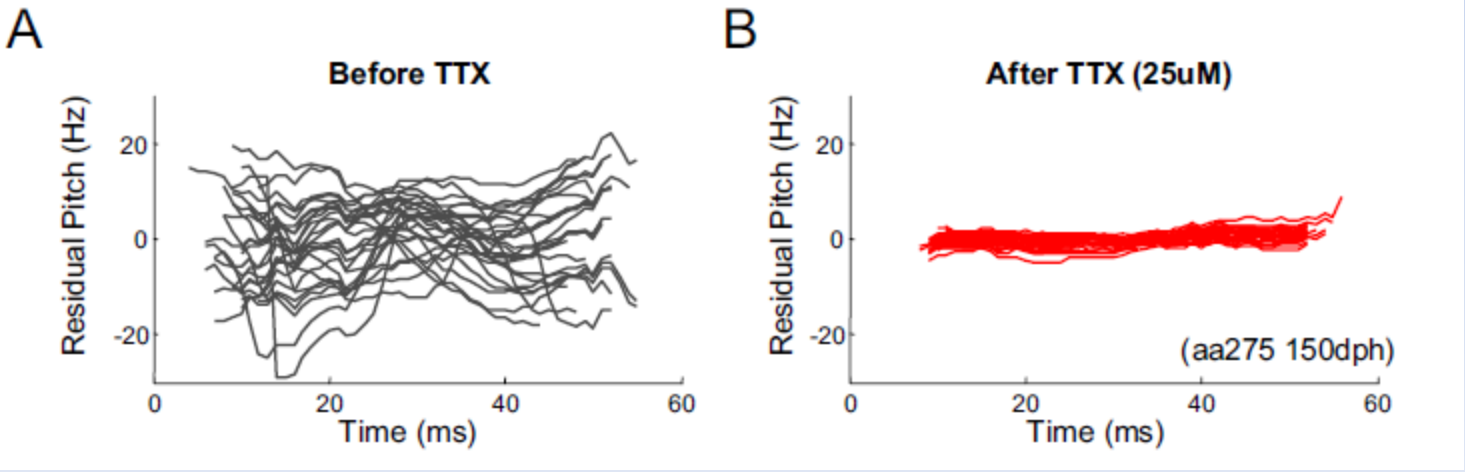




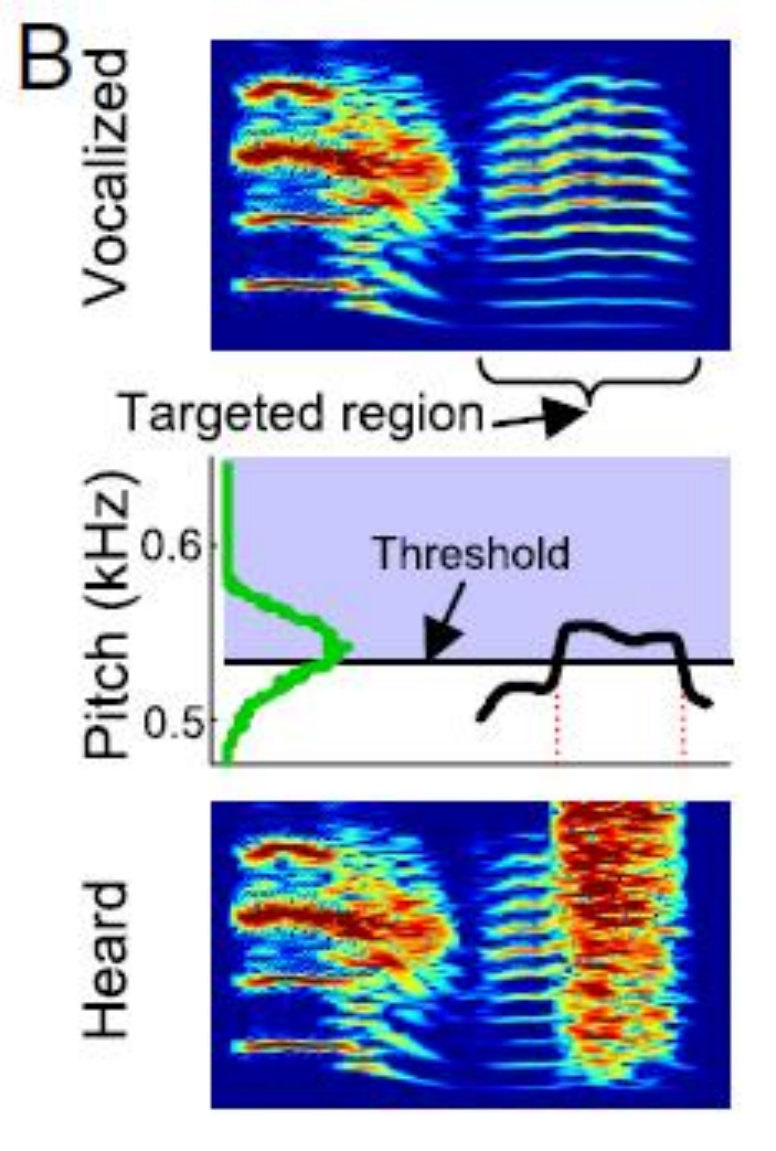


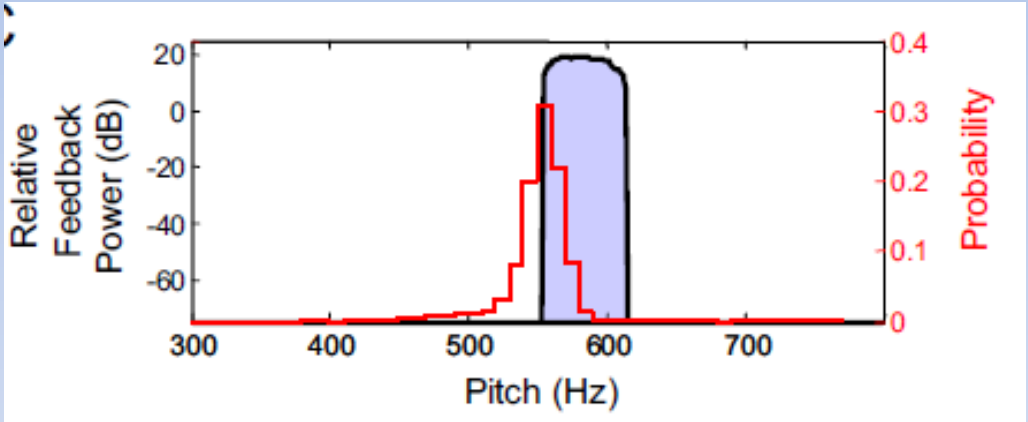
Reduced variability in pitch after LMAN inactivation during crystalized song





Conditional auditory feedback





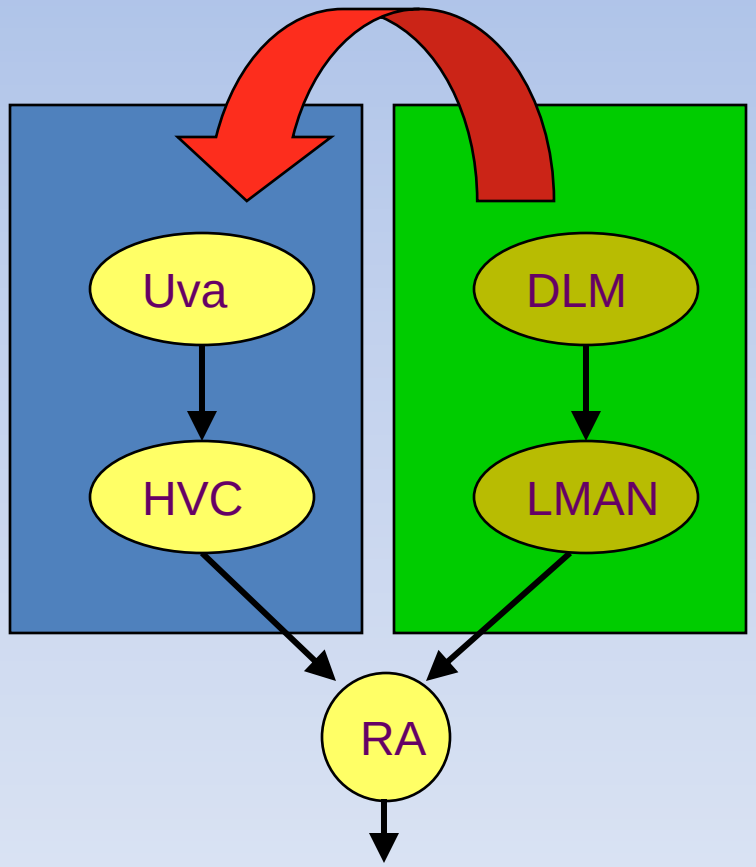
Andalman & Fee (PNAS, 2009)

LMAN is a generator of variability

- LMAN is the essential premotor nucleus for the earliest ‘babbling’ vocalizations (Aronov and Fee, 2008).
- LMAN adds variability to enable exploration.
- 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).

Separate premotor pathways for stereotyped song and babbling

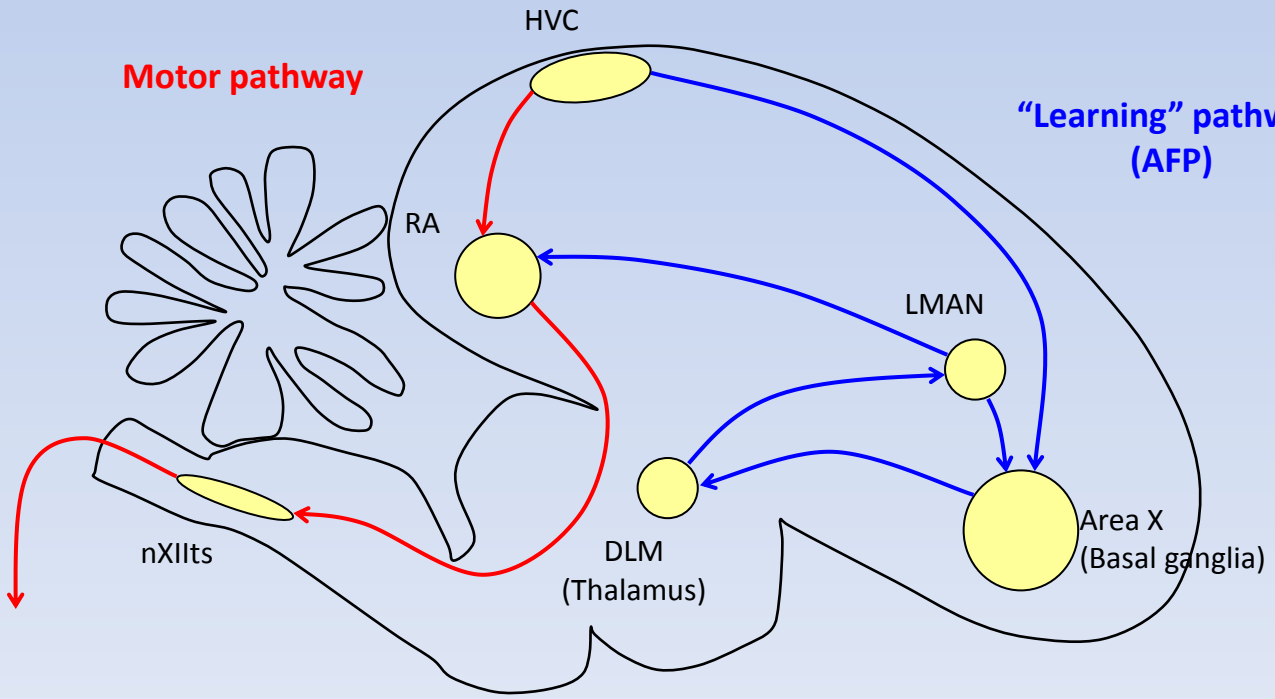
Sequence
Stereotypy
Precision



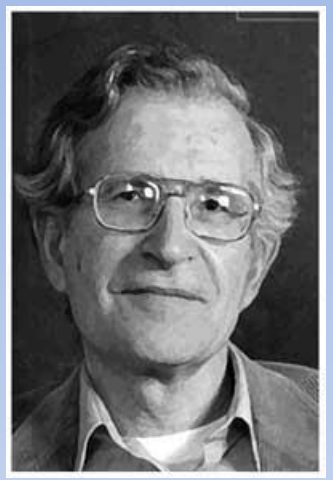
Randomness
Variability
Exploration

Summary

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



Chomsky: Universal grammar constraints syntactic diversity in humans.



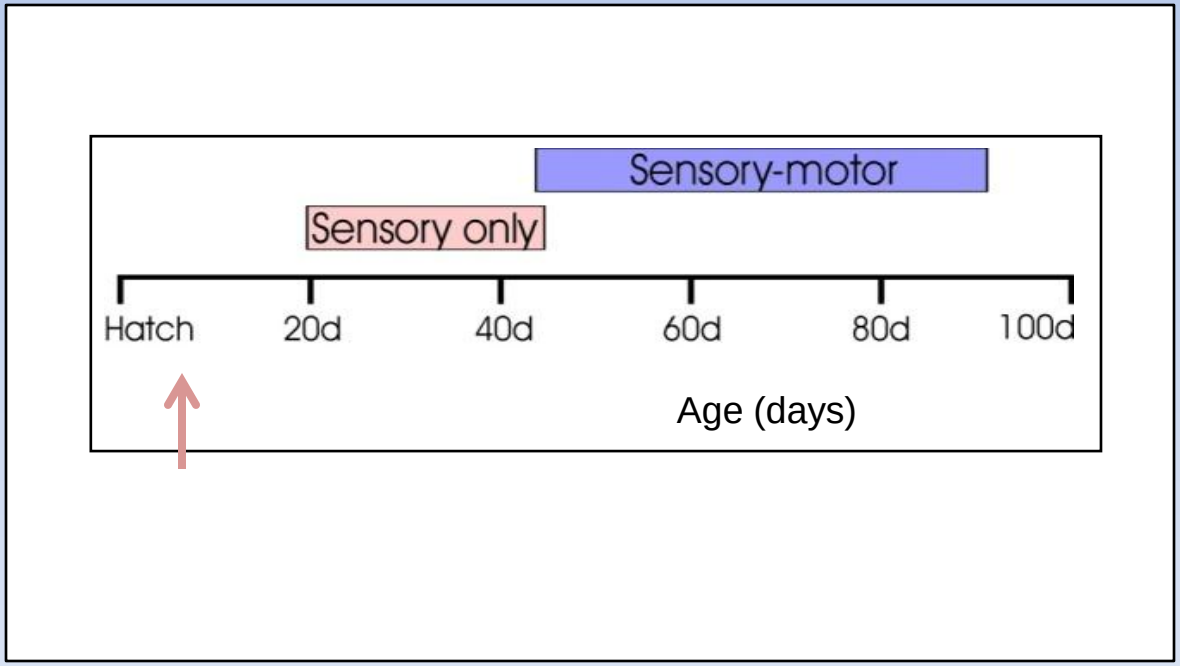
In other words: genes constrain language diversity.

Ofer Tchernichovski:
Do genes constrain song diversity?

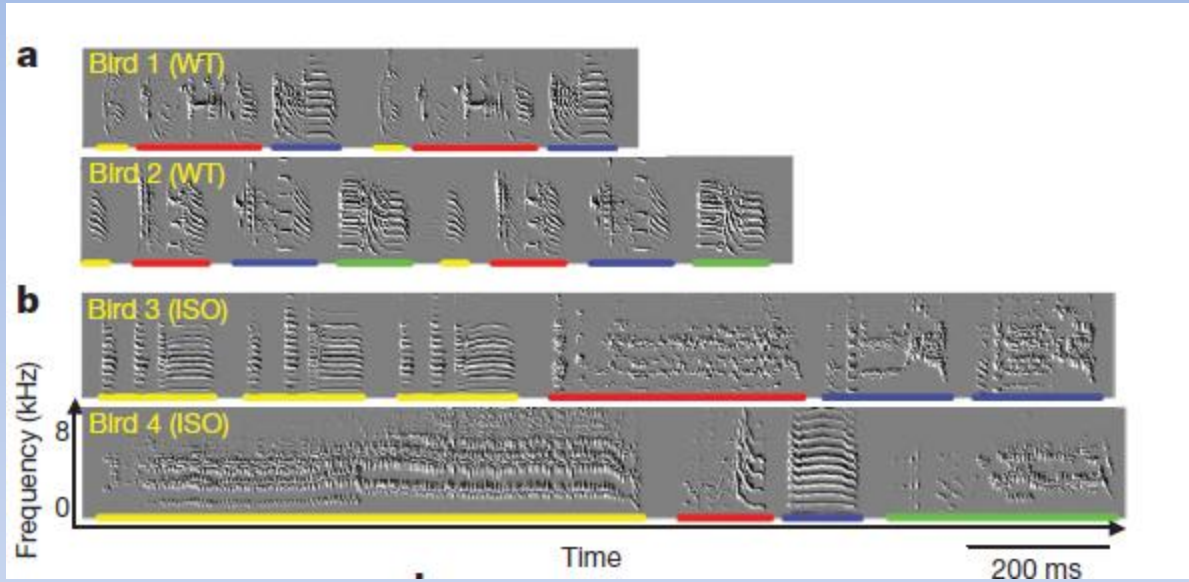
Song culture in birds

- Some songbirds provide biologically tractable models of culture: some members of species show individual variation in singing, and geographically separated groups have local song dialects.
- 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?



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



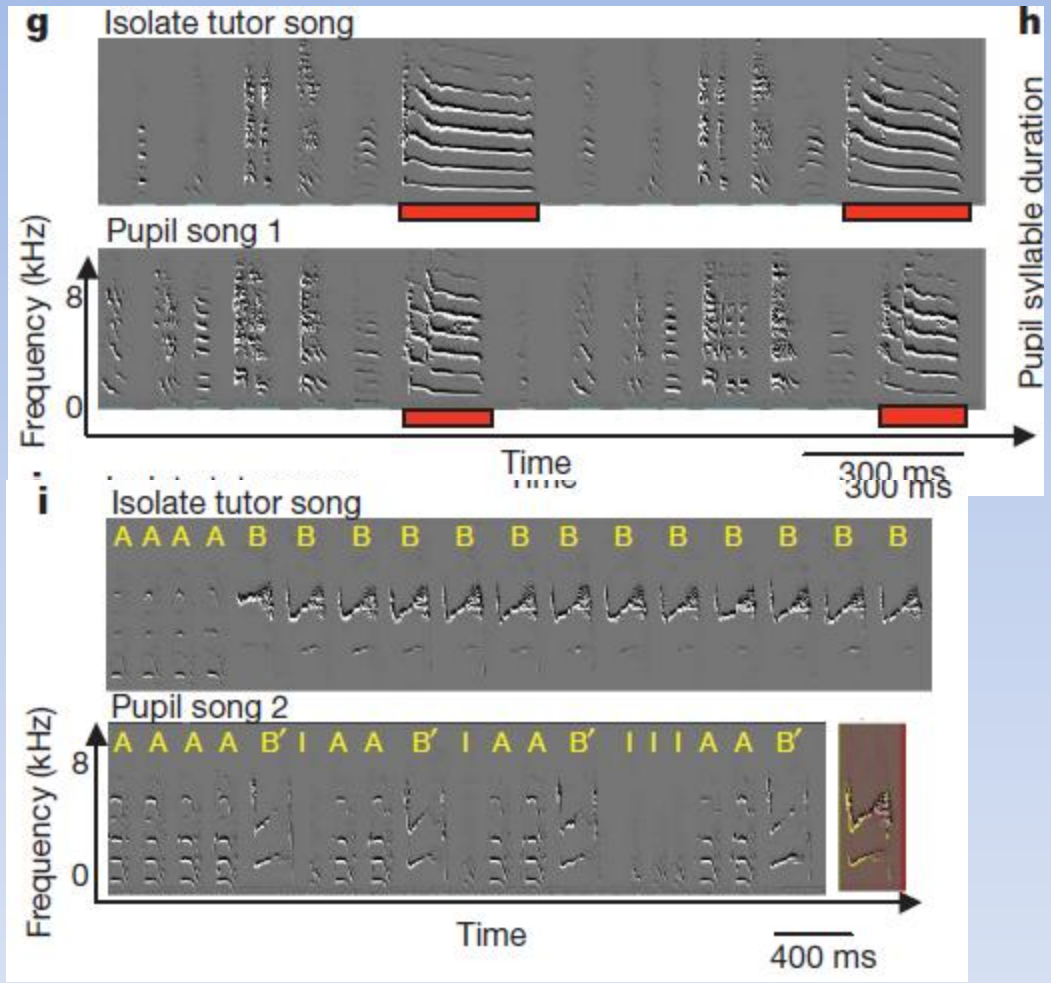
Birds are establishing the ‘song template’ very early, during the sensory period.

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

Konishi 1965; Marler 1970

Fehe´r et al. Nature 2009
The lab of Ofer Tchernichovski

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



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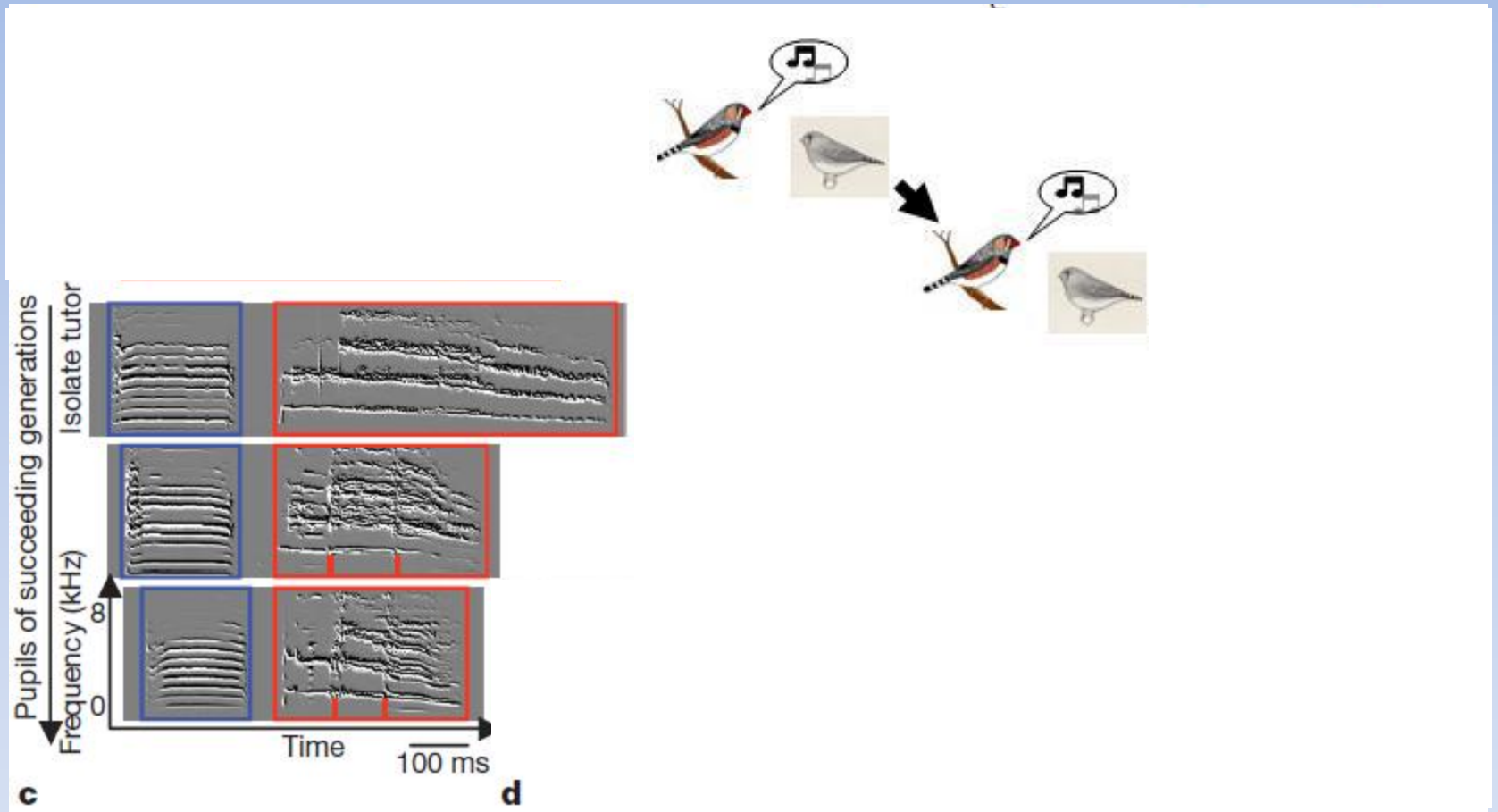

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Song evolved towards the wild-type in three to four generations. Thus, species-typical song culture can appear de novo.