

Tame birds sing of freedom. Wild birds fly.

The unique research directions afforded by the complex behavior of songbirds

Motor skill \rightarrow Memory systems
(Learning,
decision,
syntax)



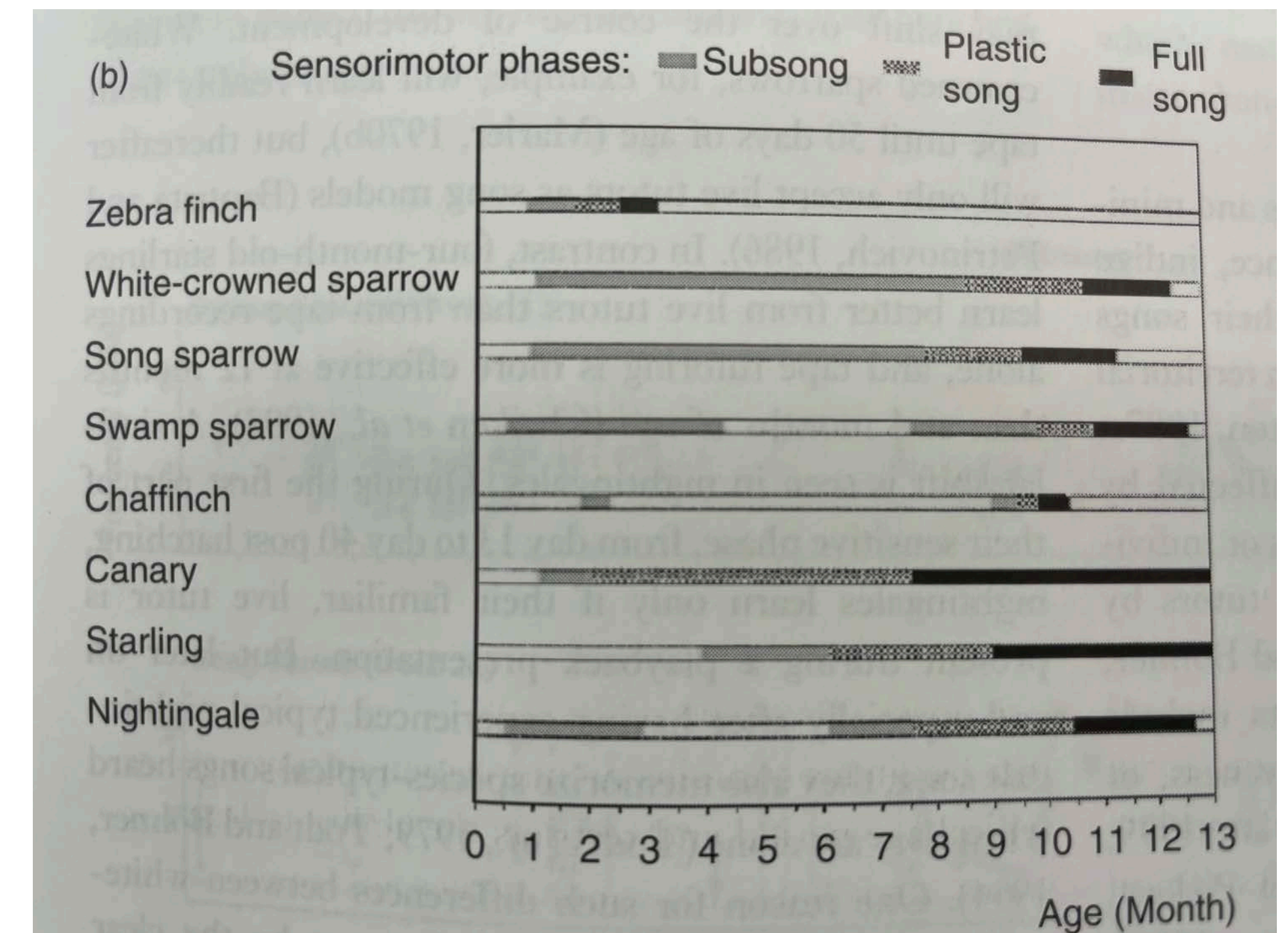
What to learn? Store? Retrieve?







Time sensitivity (Masking?)

Specific selectivity

Gate attention



Outline

Species	Behavior	System / memory time scales	
	Stereotyped skill	Life time. Moment-to-moment (~10ms)	Close-ended Learners
	Branching transitions	Production: 100-200 ms (Auditory: ~1 sec)	
	Hierarchical song Long-range syntax	Syllables: 8-500ms, Syntax rules: 1-7 sec, Seasonal plasticity: months, year	Open-ended Learners
	Extensive repertoire, Hierarchical memorization and retrieval, Acoustic matching	Acquisition: months, year Retrieval: 1 second	

Zebra Finches: masters of precision



Credit: Todd Roberts

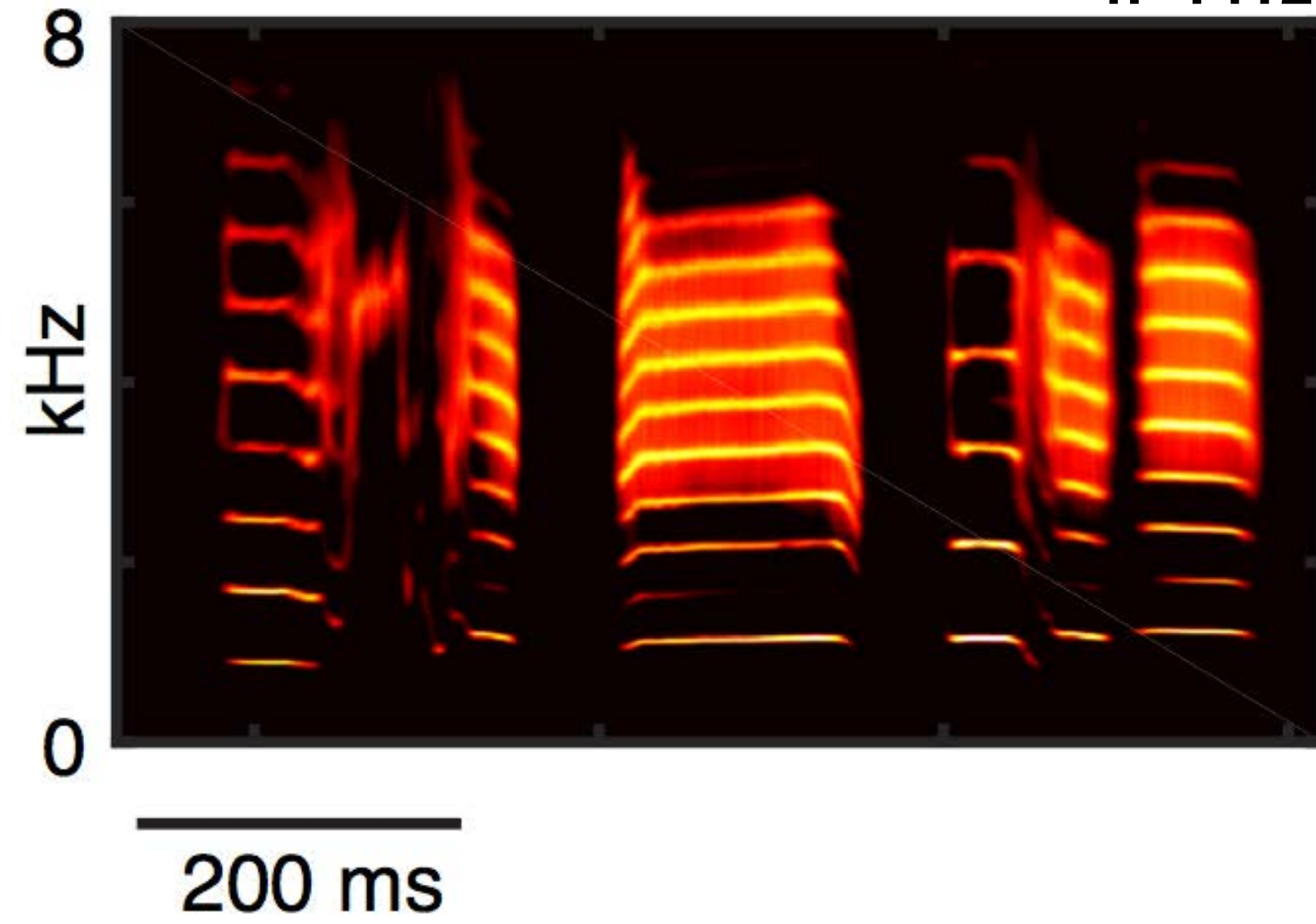
Zebra Finches: masters of precision



Dynamic Time Warping

Behavioral stability

n=1412



Song is a learned, complex, stereotyped motor behavior

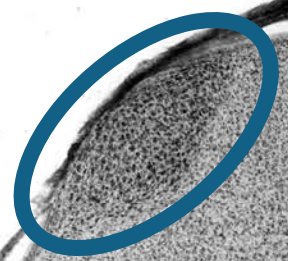
200 ms



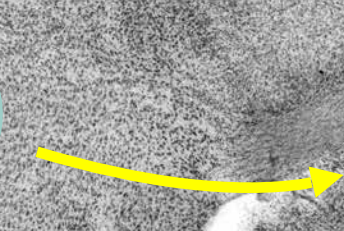
Reliable sequences of neurons drive song syllables



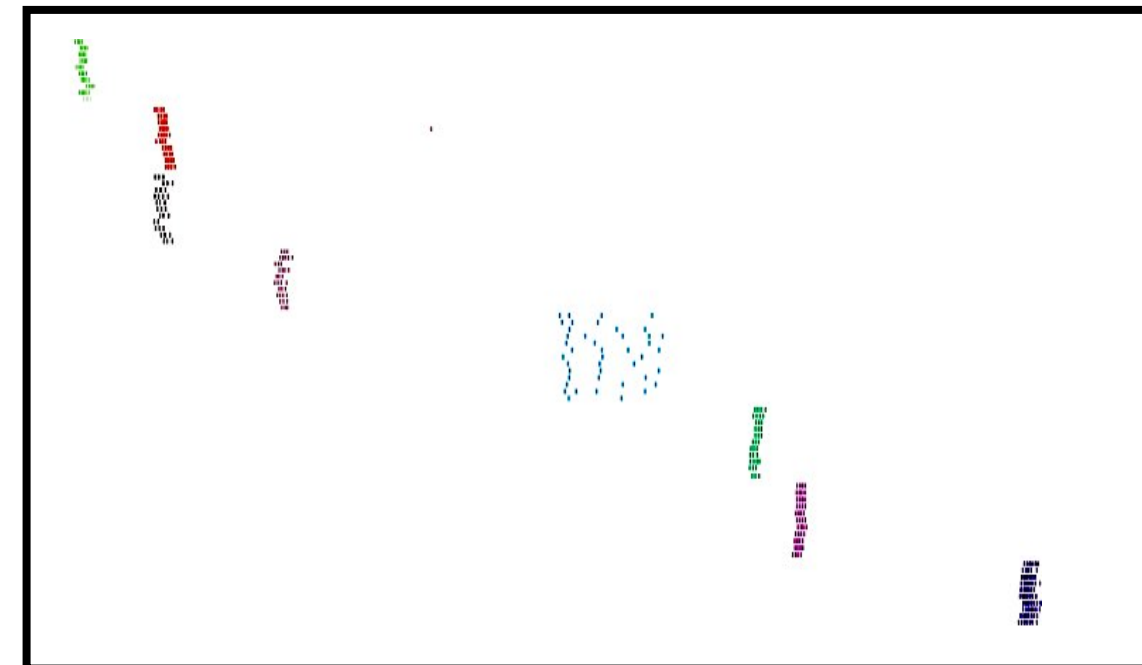
HVC



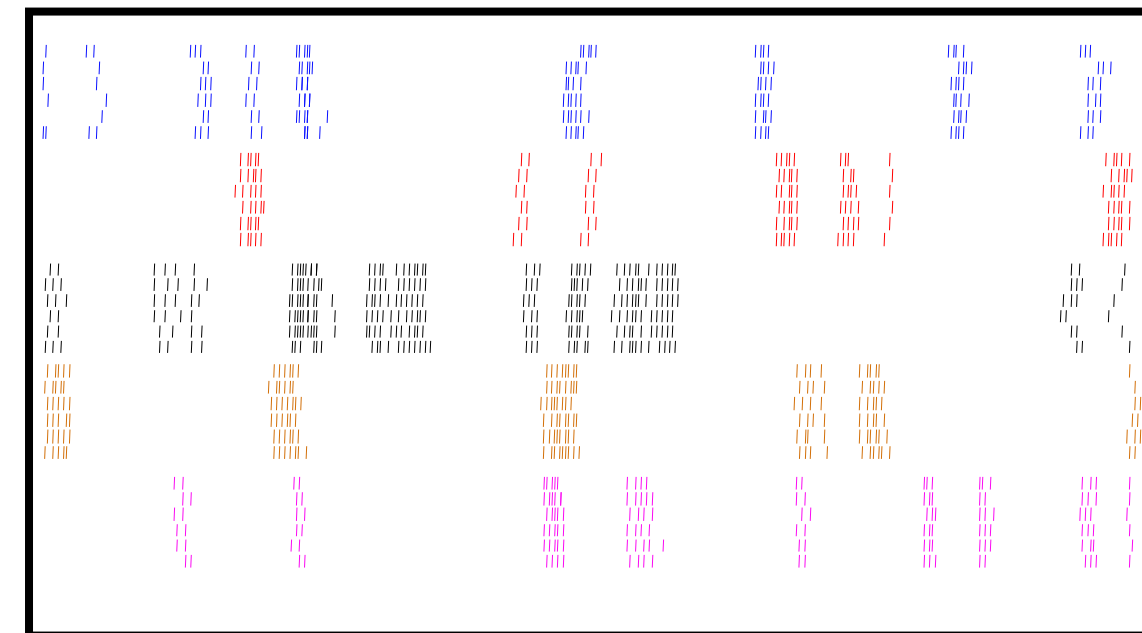
RA



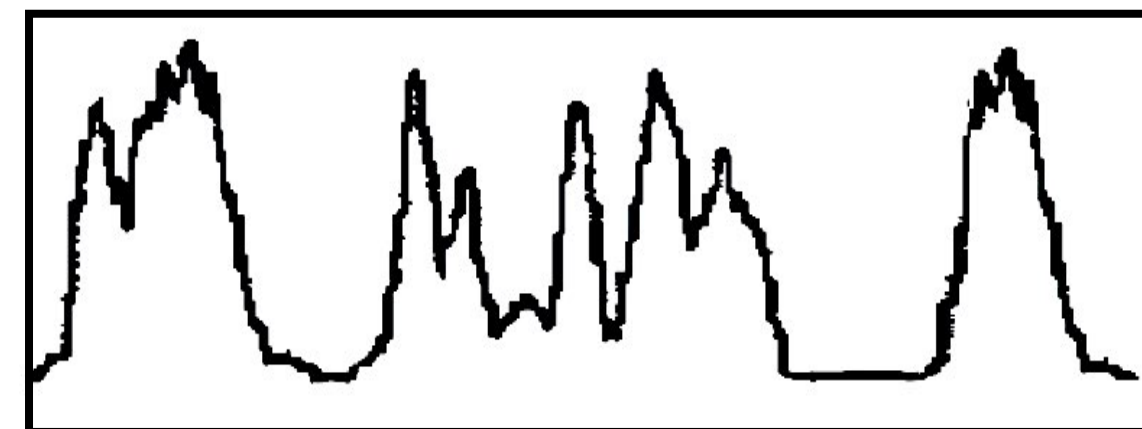
HVC neurons



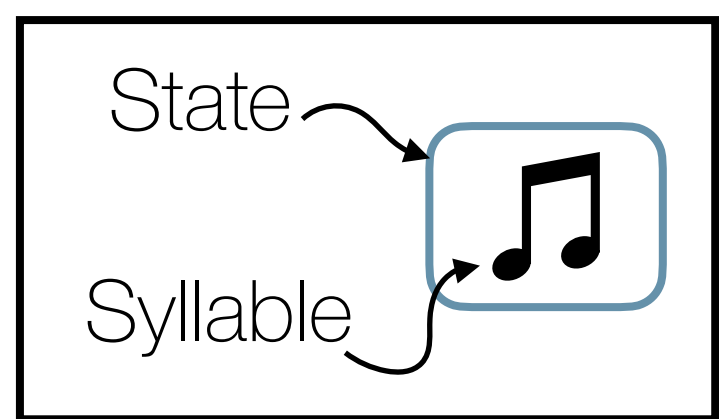
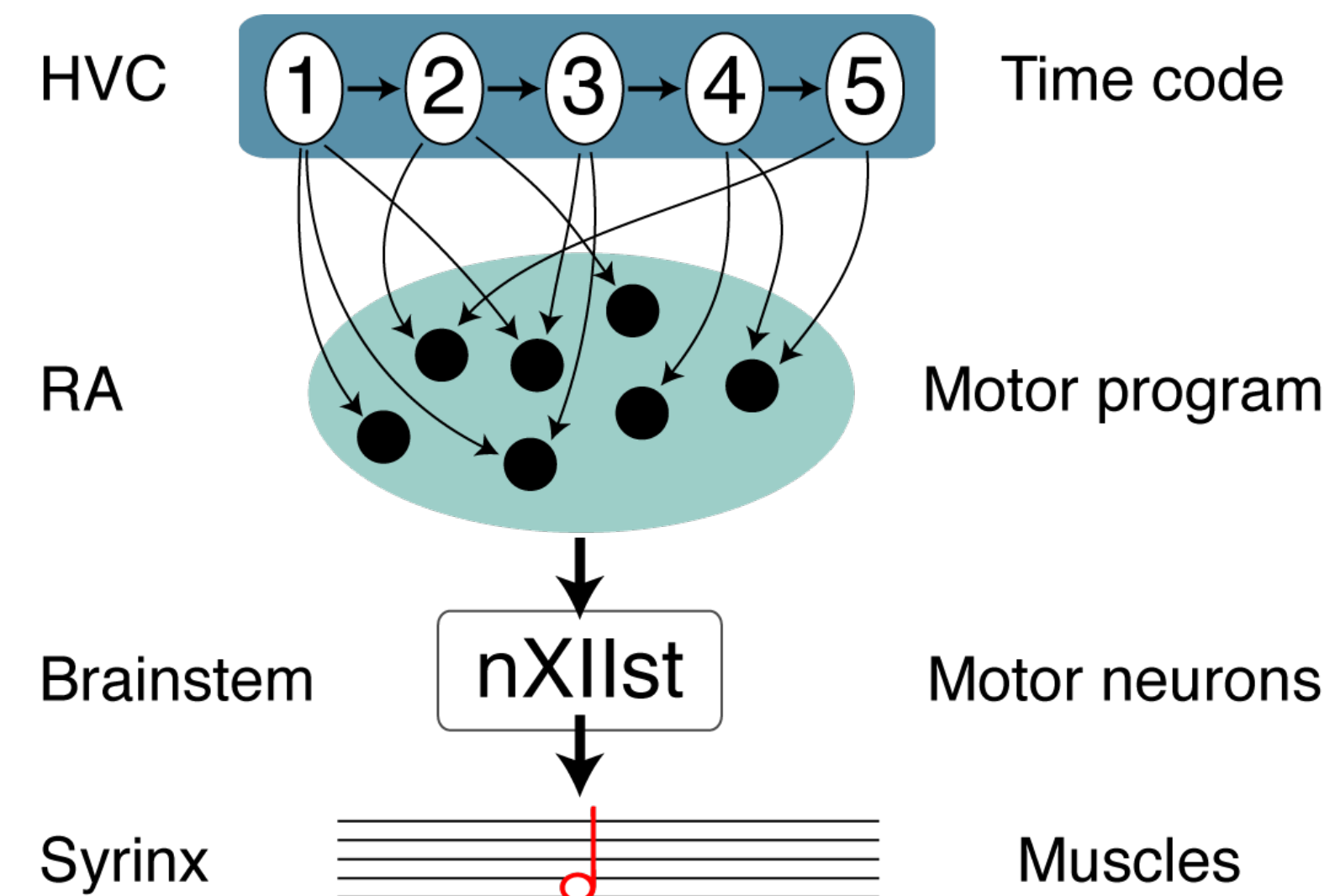
RA neurons



Muscles

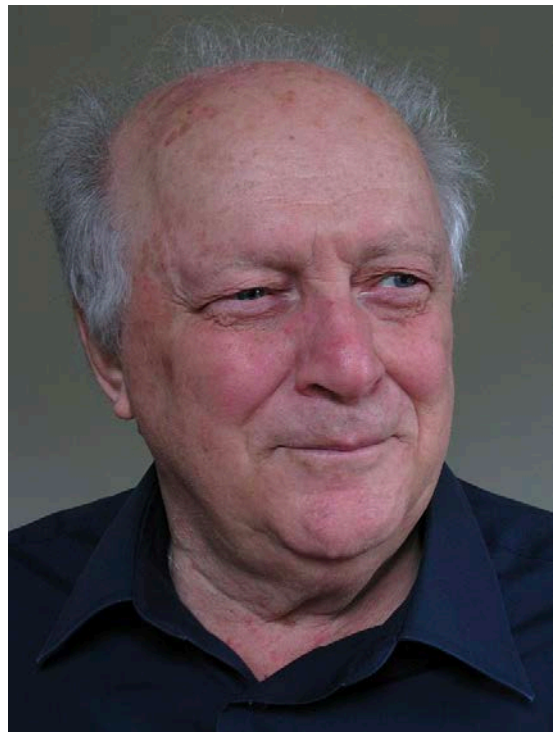


Neural state model

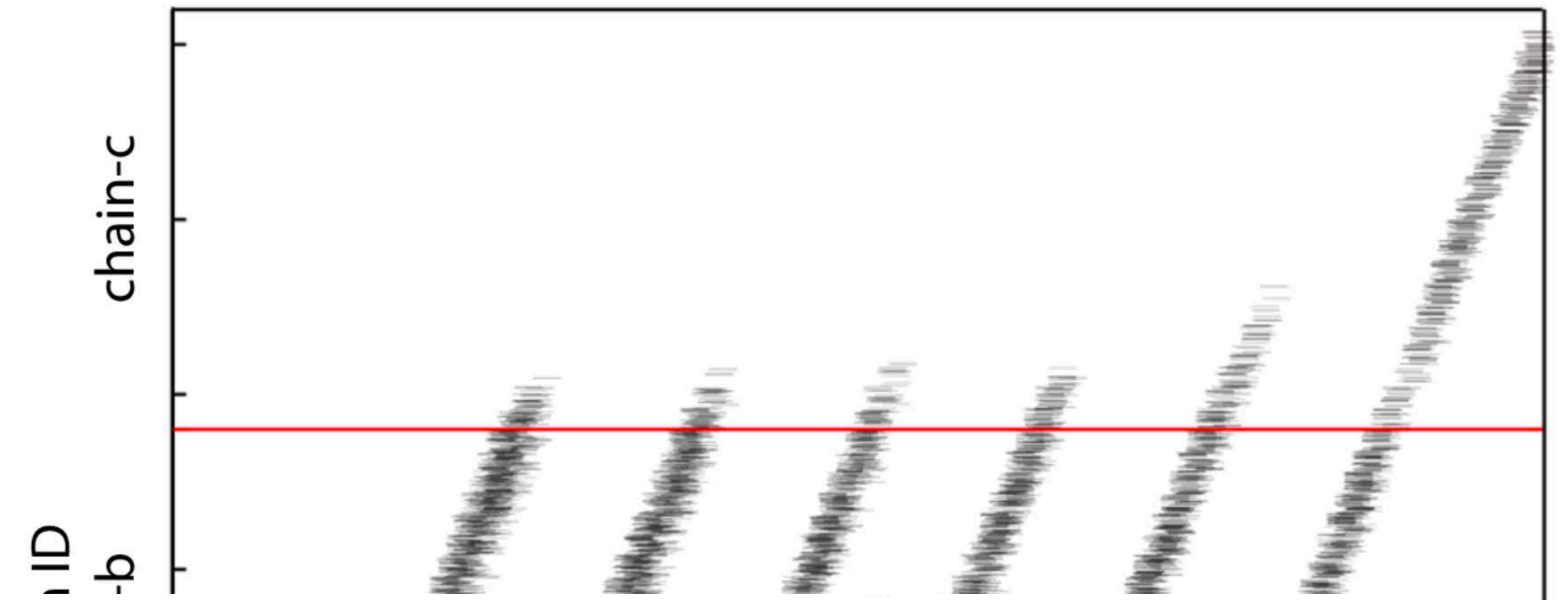
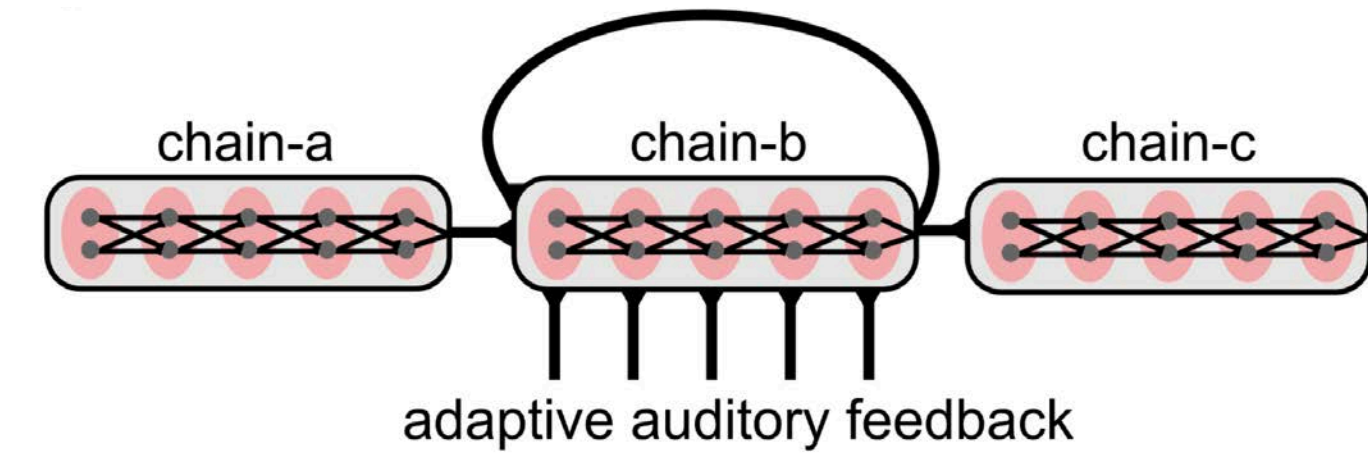
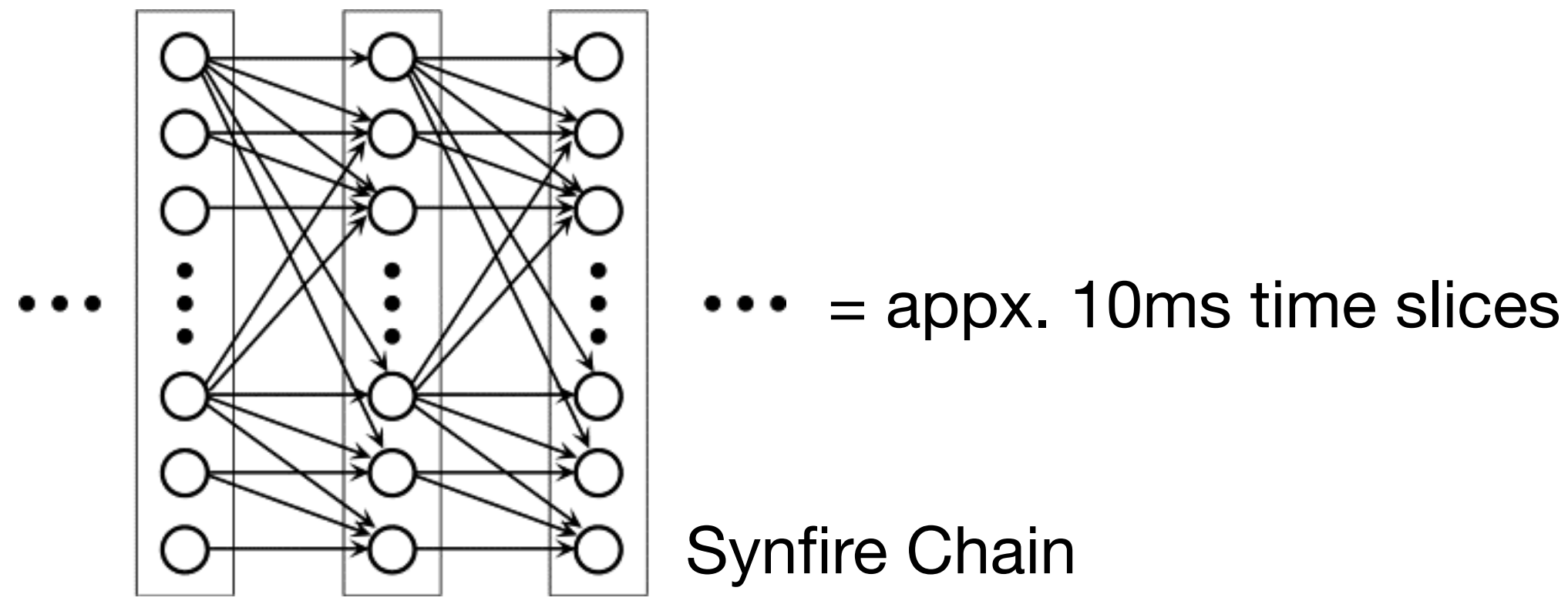


Tchernichovski 2001
Hahnloser et al 2002
Leonardo and Fee 2005
Kozhevnikov and Fee 2007

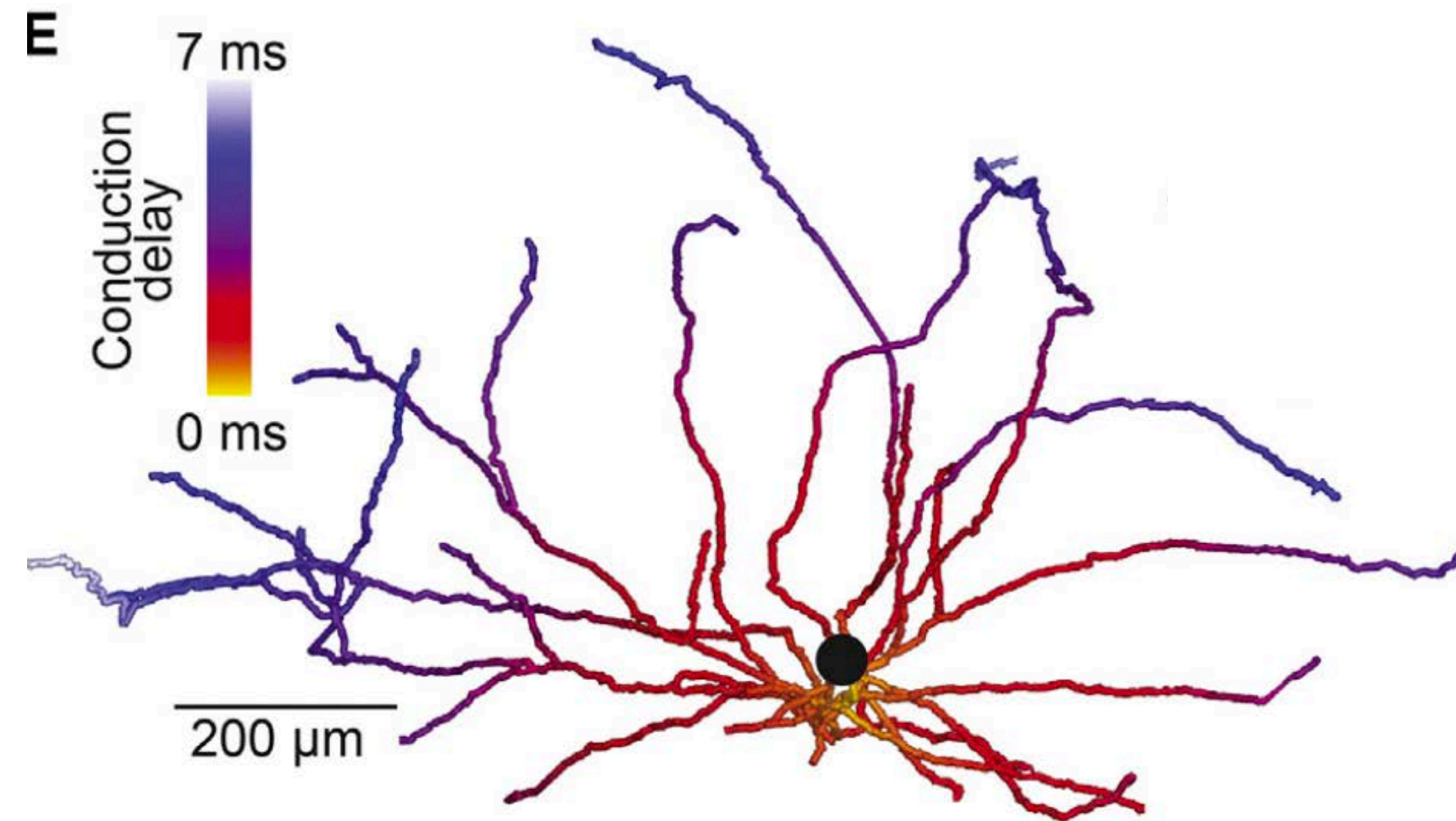
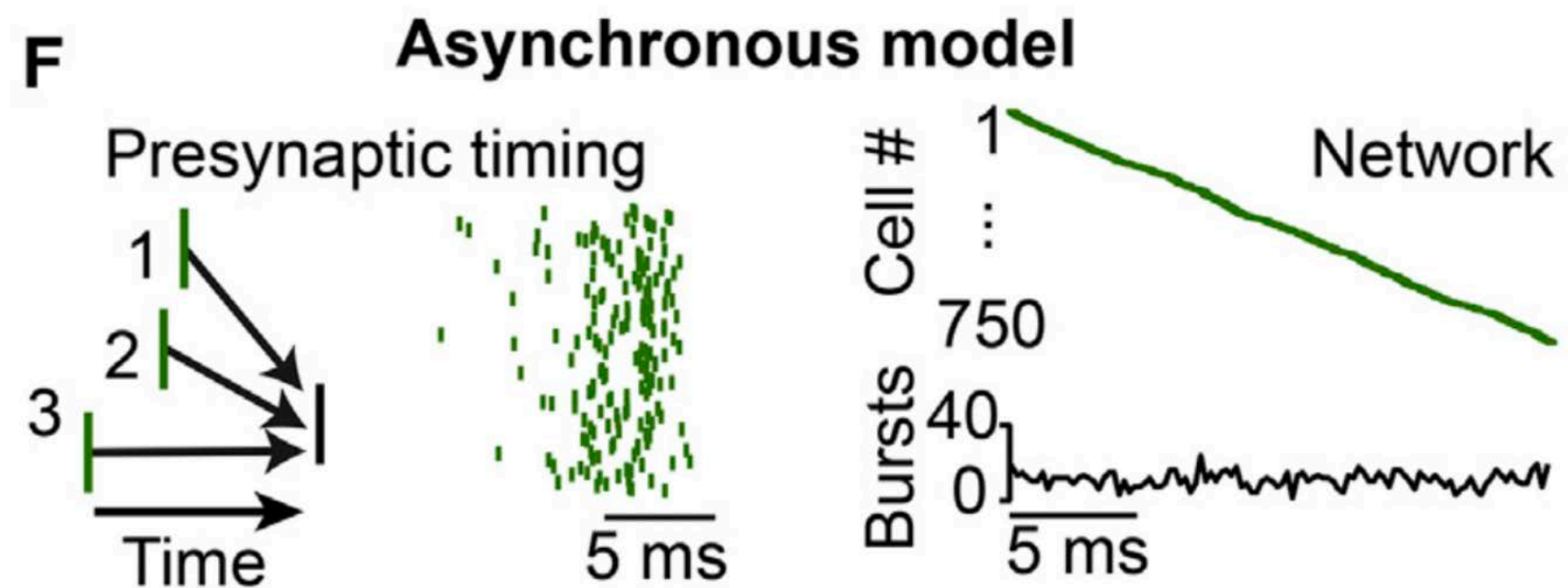
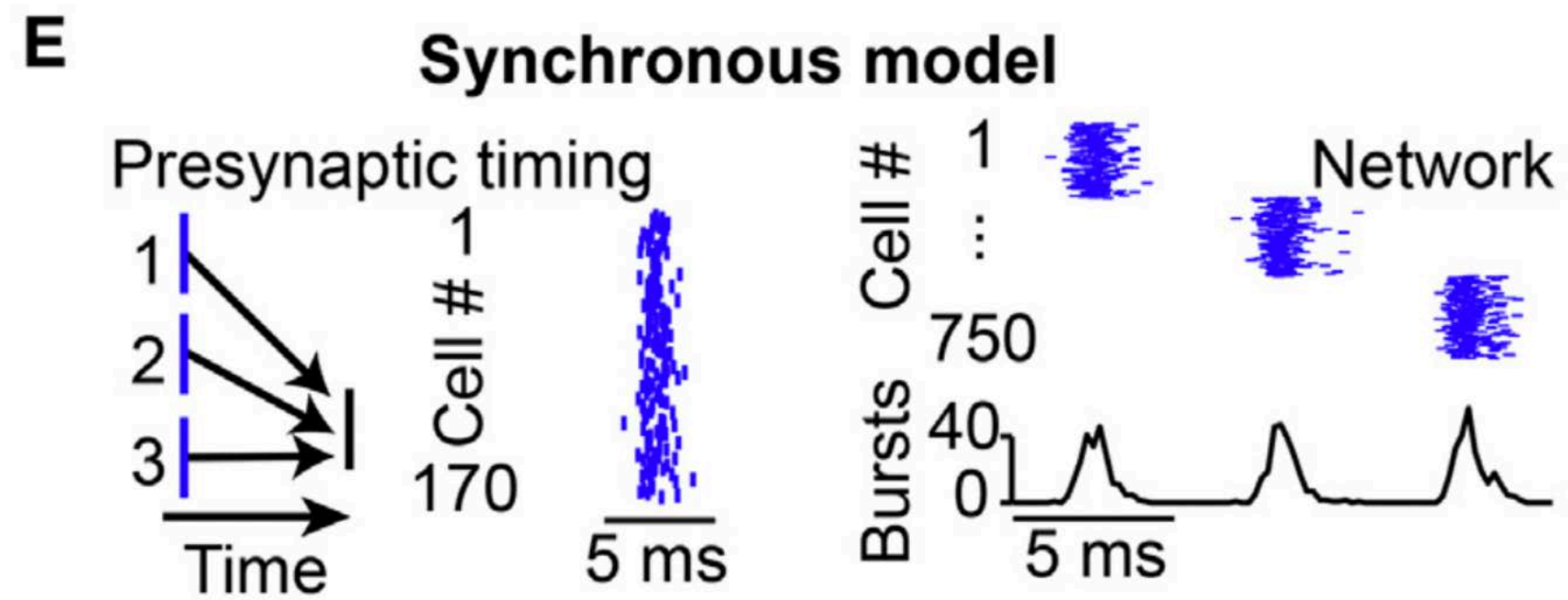
Models of robust neural sequences



Source: Wikipedia



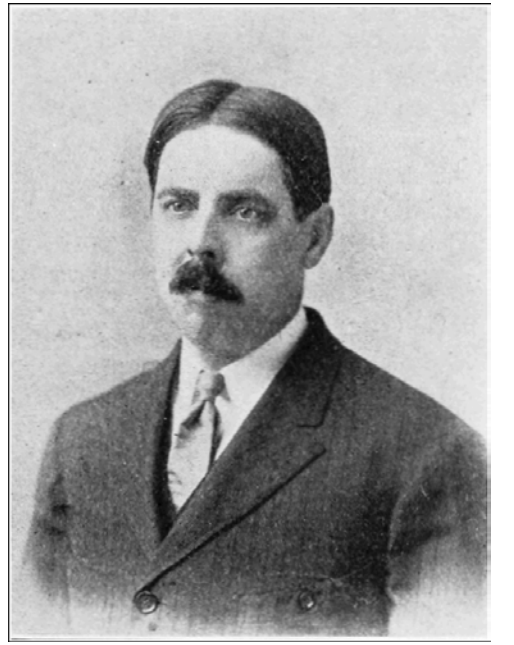
Alternative: Polychronous network



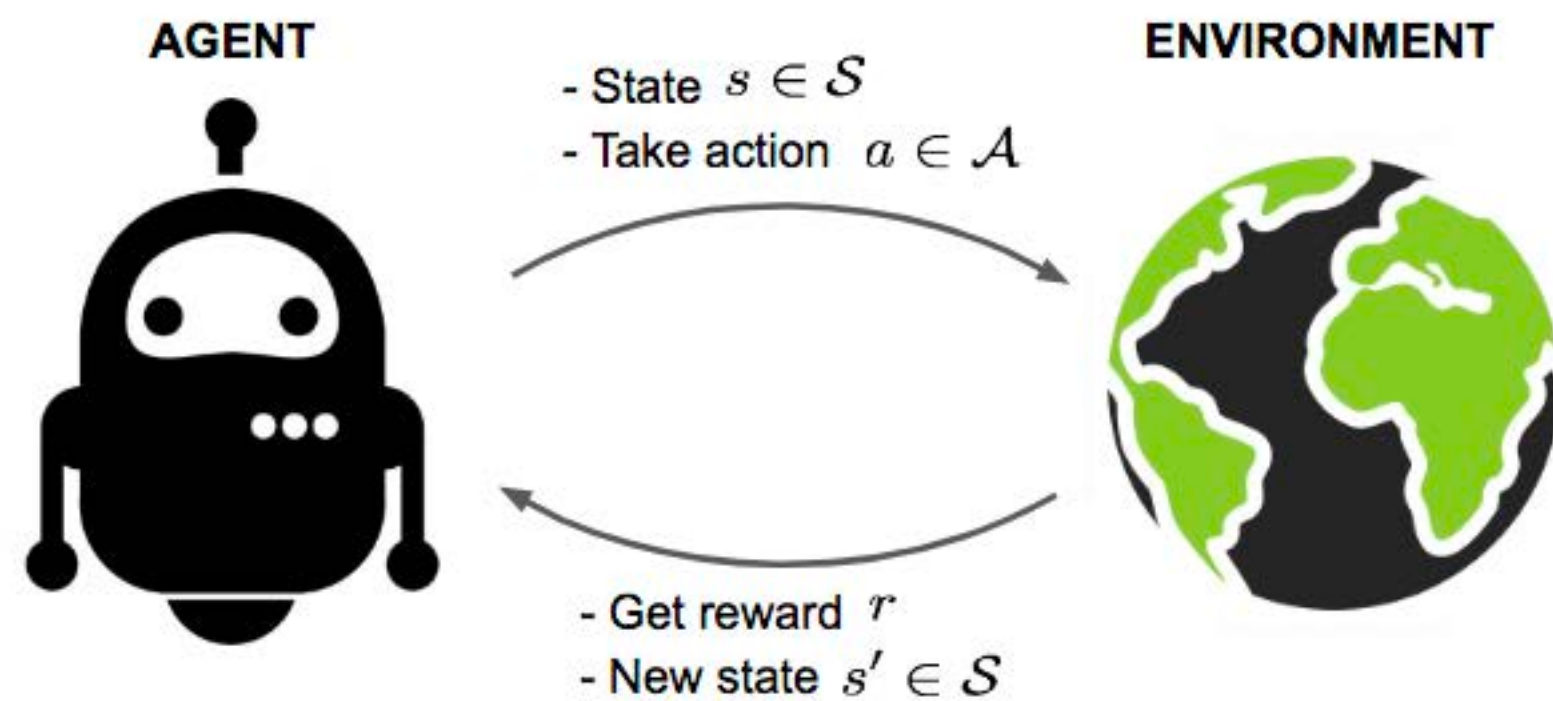
Principles of song evaluation and learning

"Responses that produce a satisfying effect in a particular situation become more likely to occur again in that situation, and responses that produce a discomforting effect become less likely to occur again in that situation"

(Edward) Thorndike's "Law of Effect", 1898 (source, Wikipedia)



Reinforcement Learning

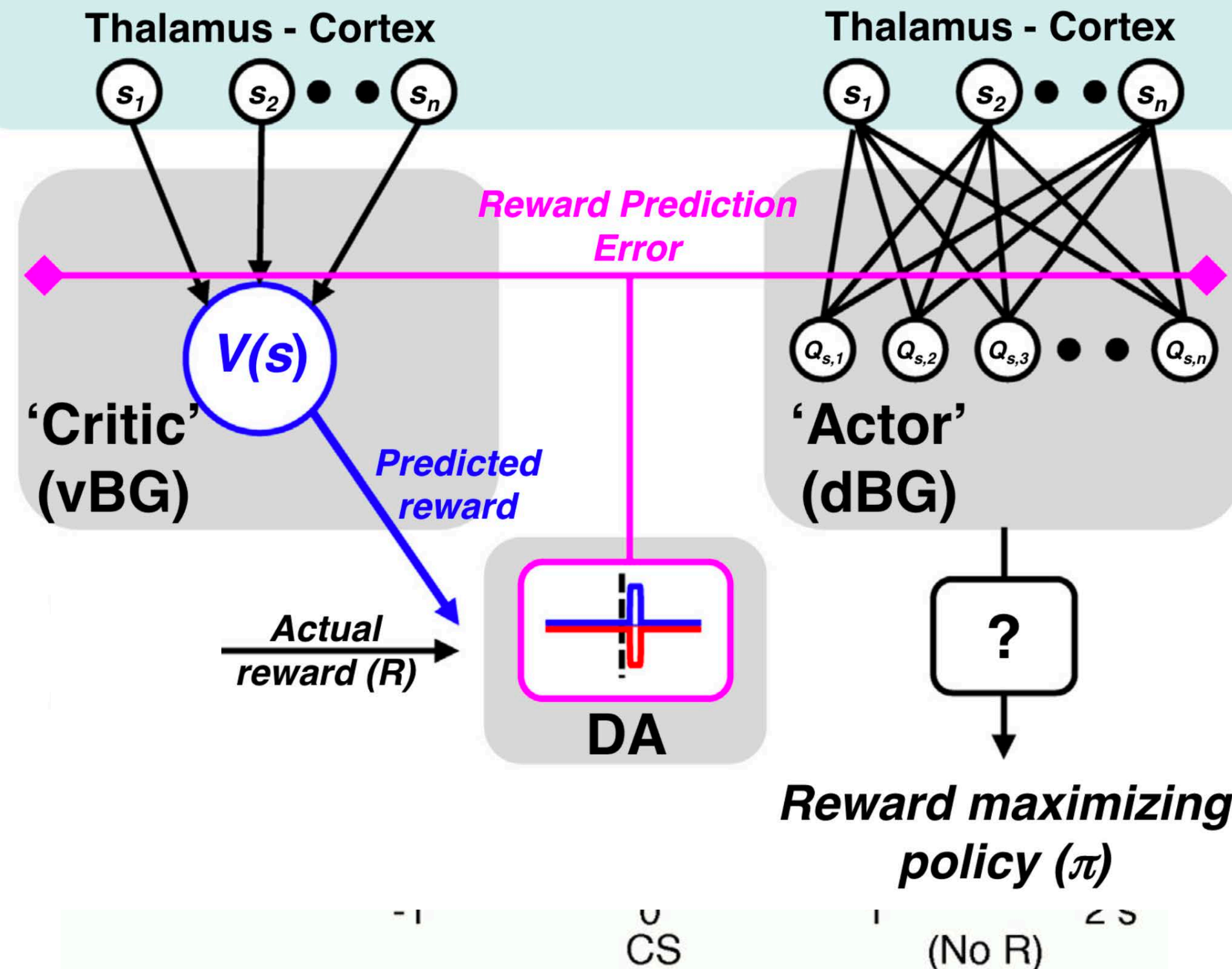


Dopamine Neurons in VTA signal RPE

No prediction

RL for reward

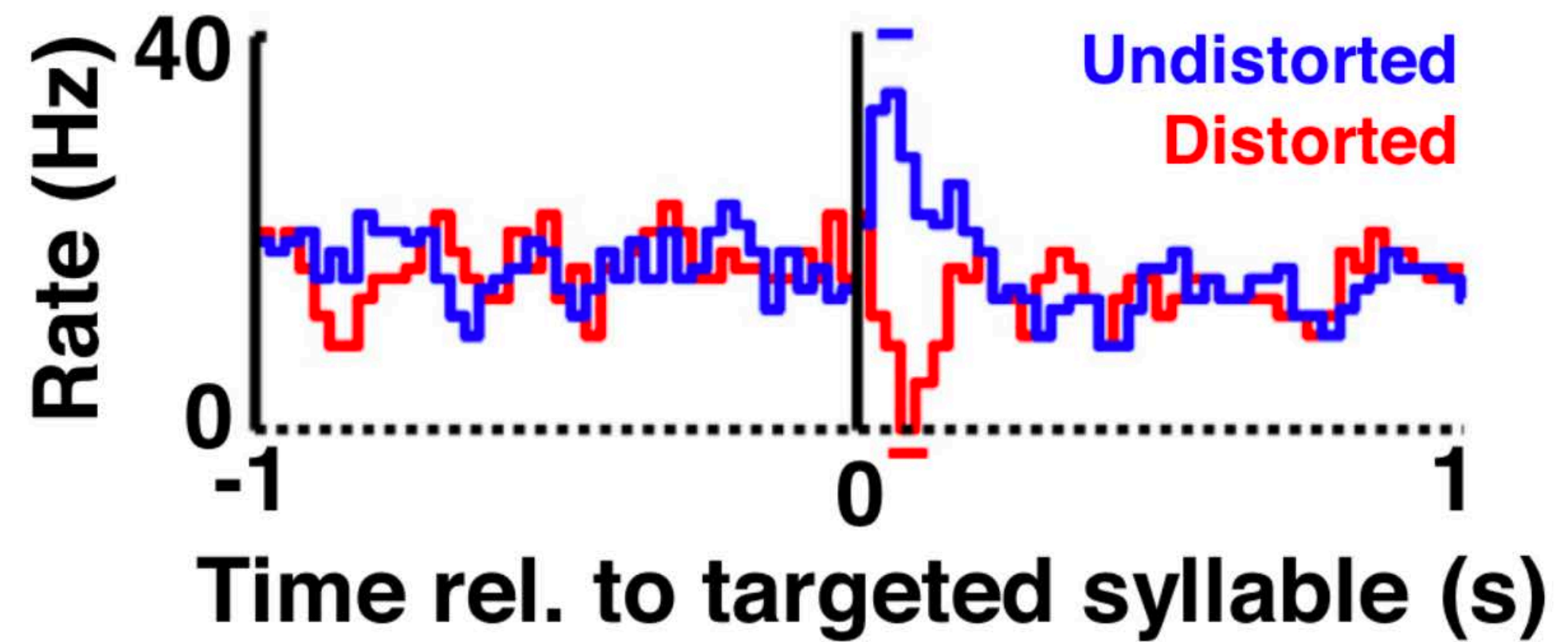
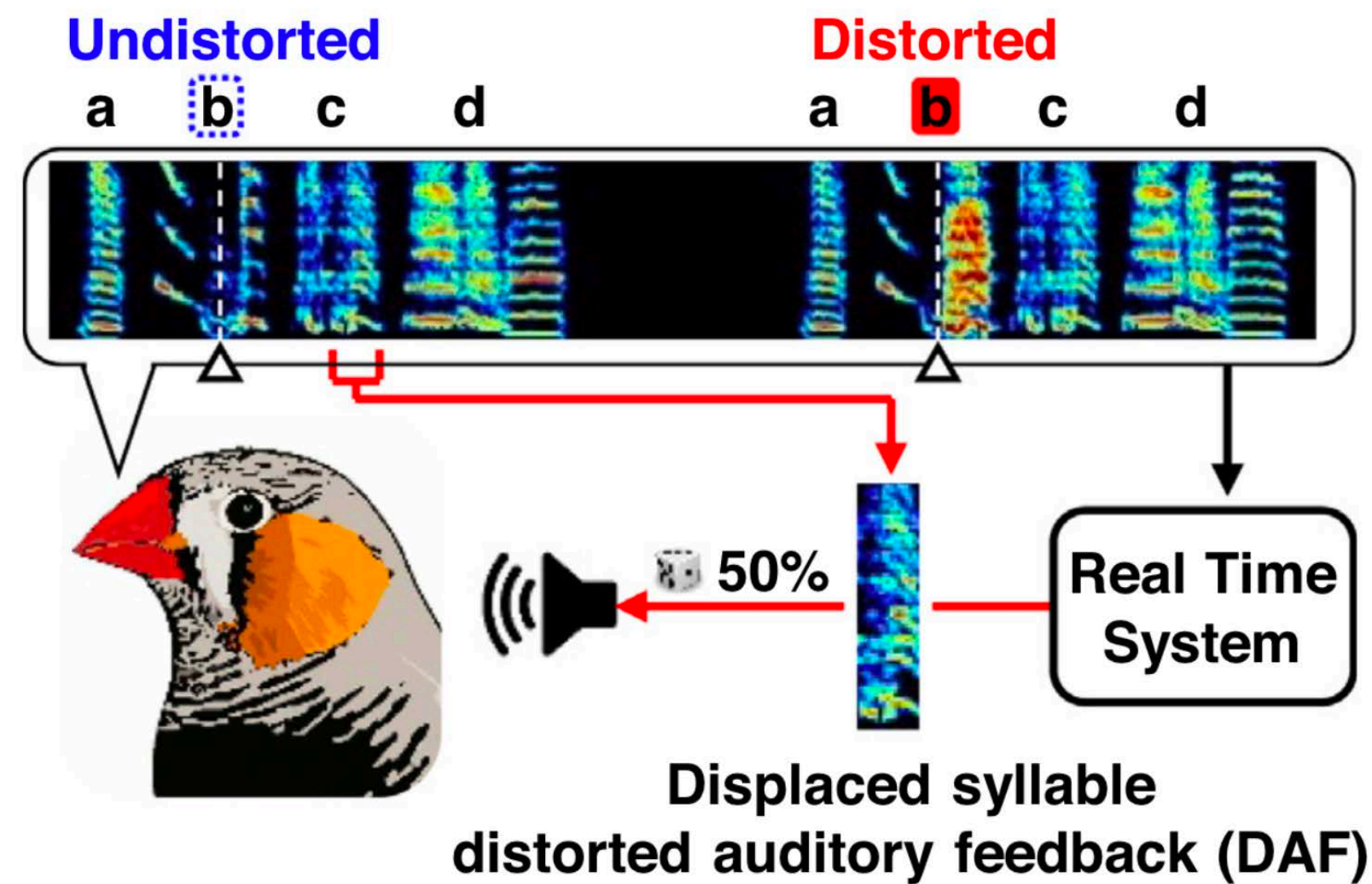
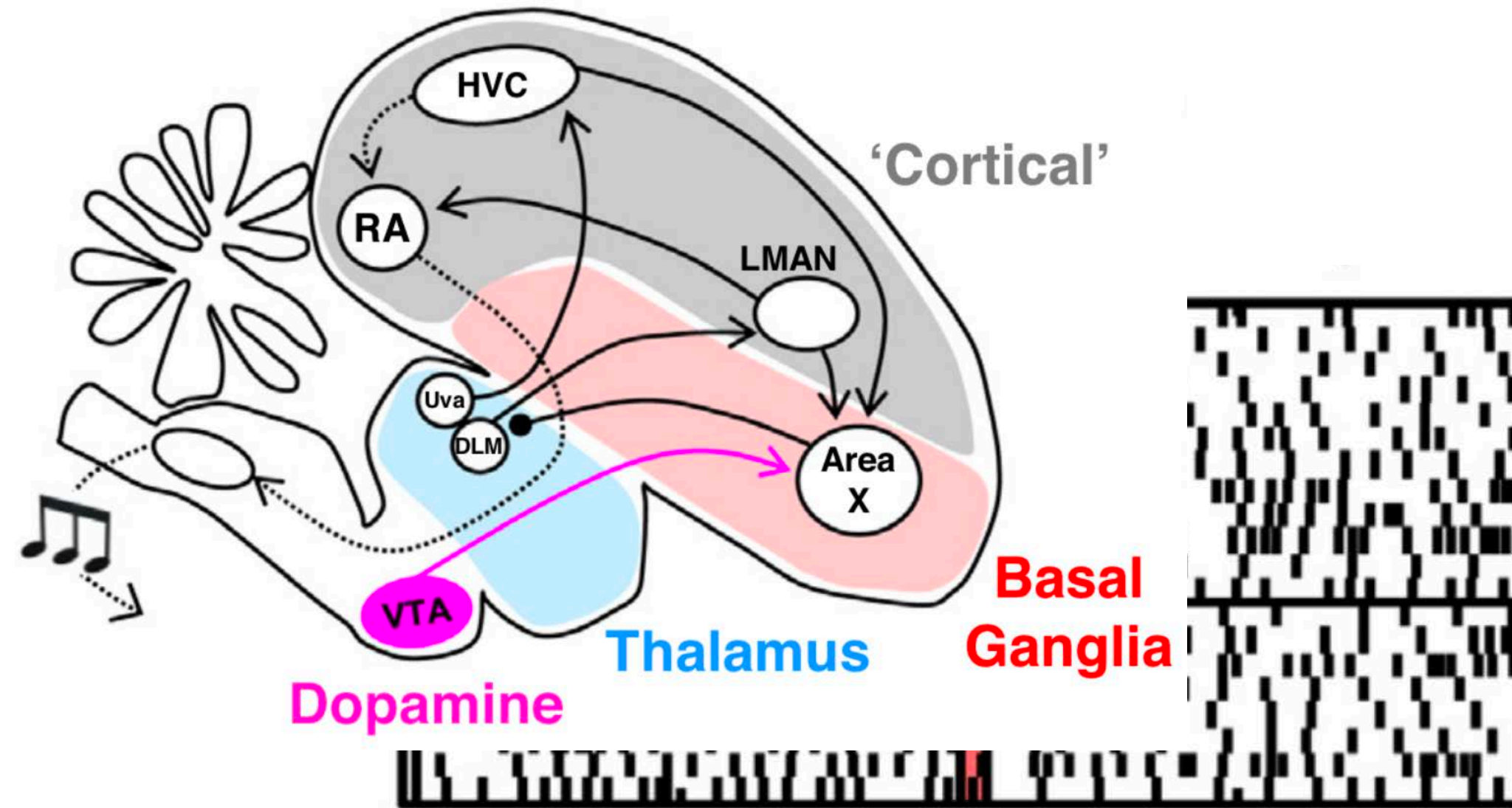
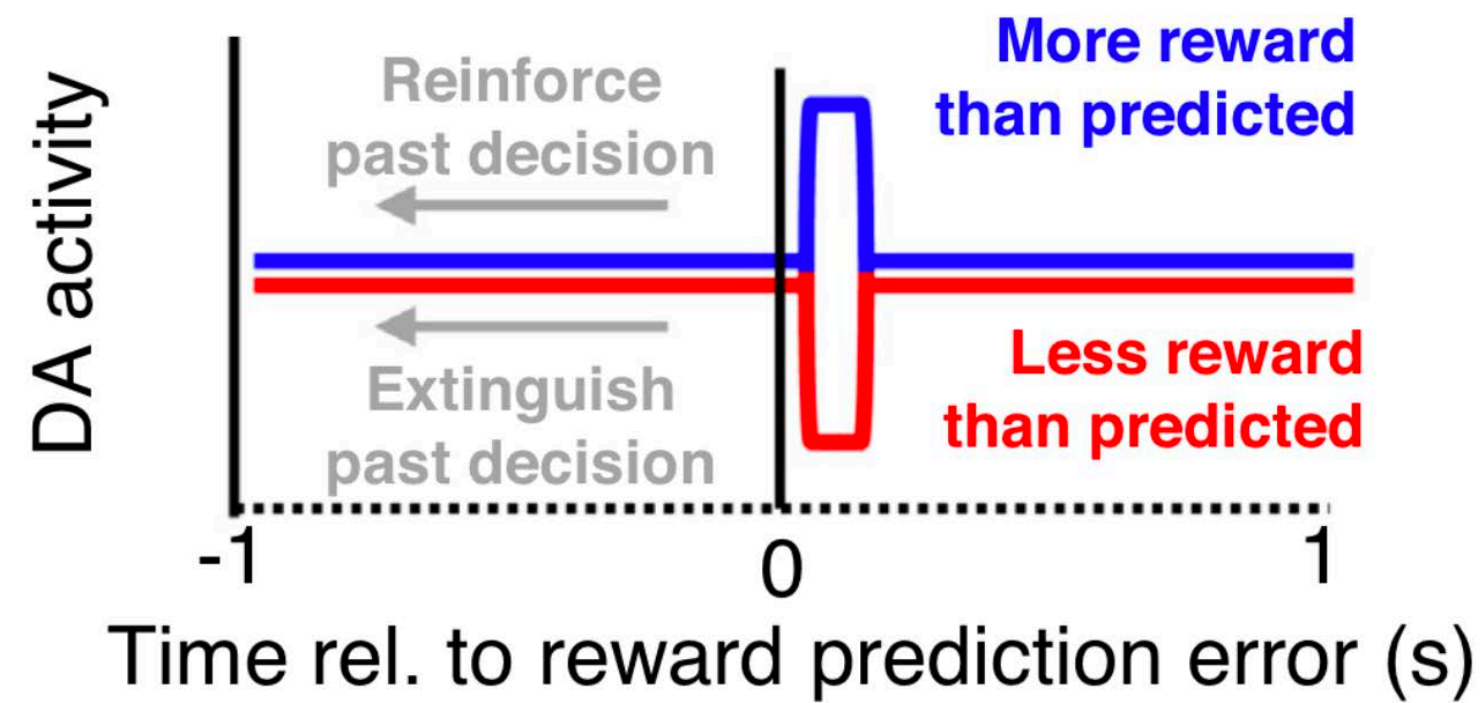
'STATE' = (e.g. cue, place, situation, percept)



$Q(s,a)$ = 'quality' of taking action 'a' in state 's'

Principles of song evaluation and learning

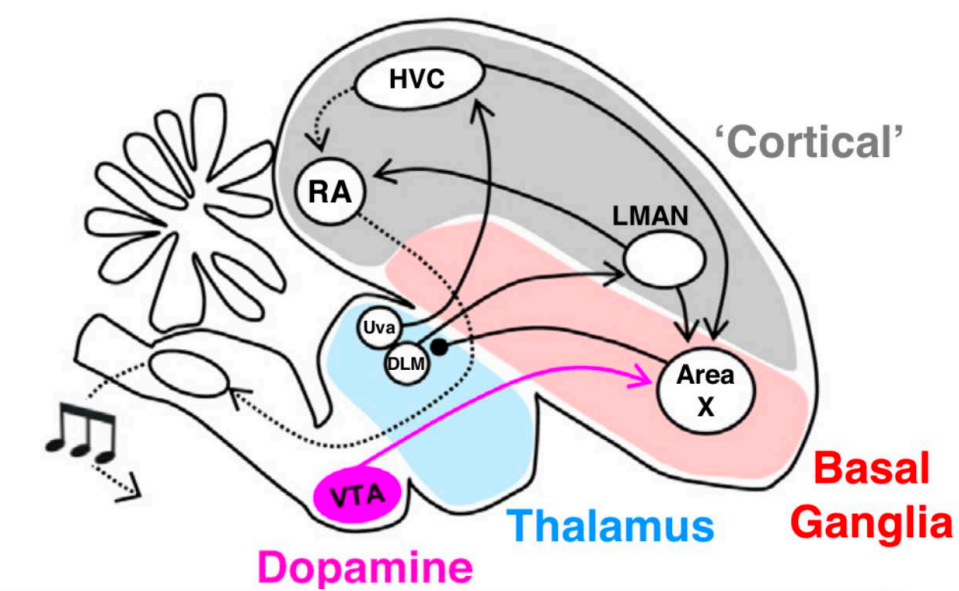
Dopamine Neurons in VTA signal RPE



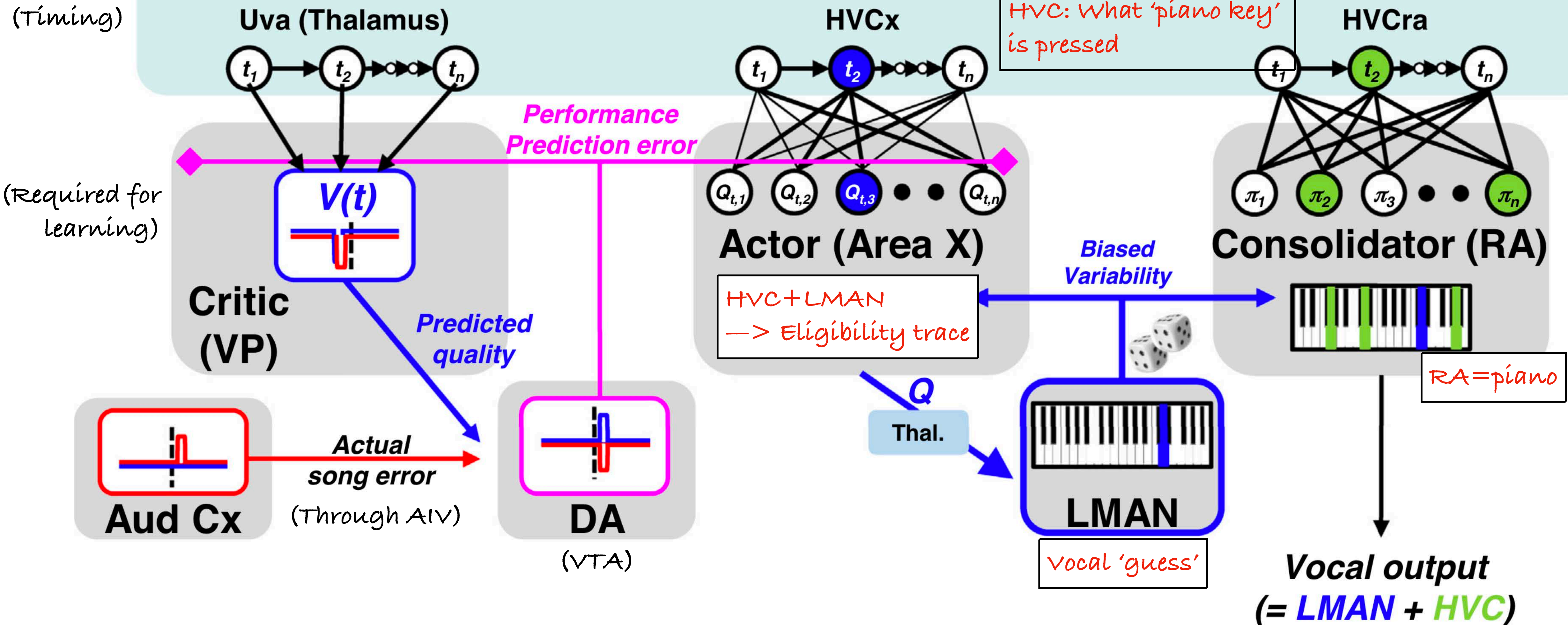
How does VTA compute song RPE?

Principles of song evaluation and learning (Actor-Critic model)

Works for 10-50 ms time bins



'STATE' = Current time-step of the song

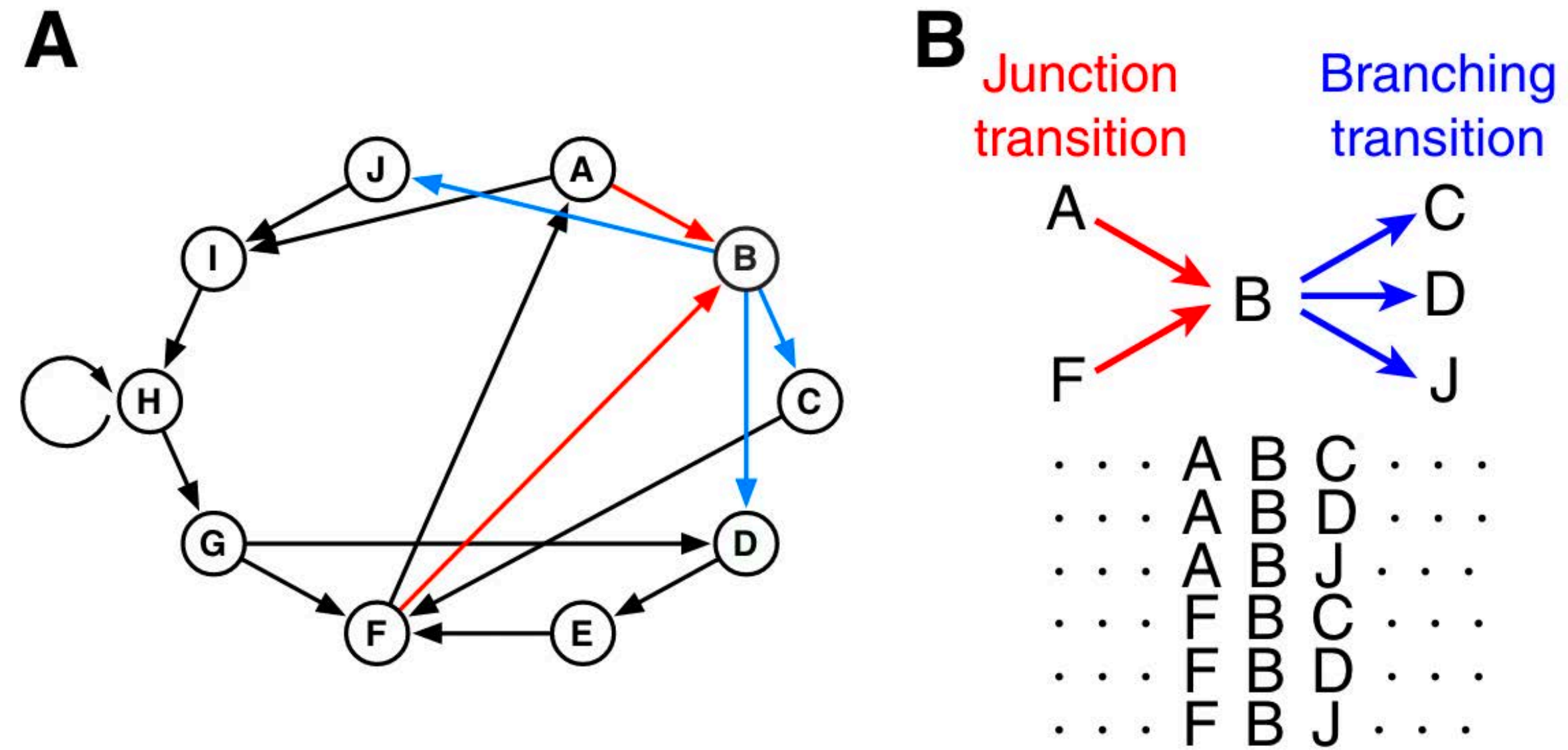


Bengalese Finches: branching transitions





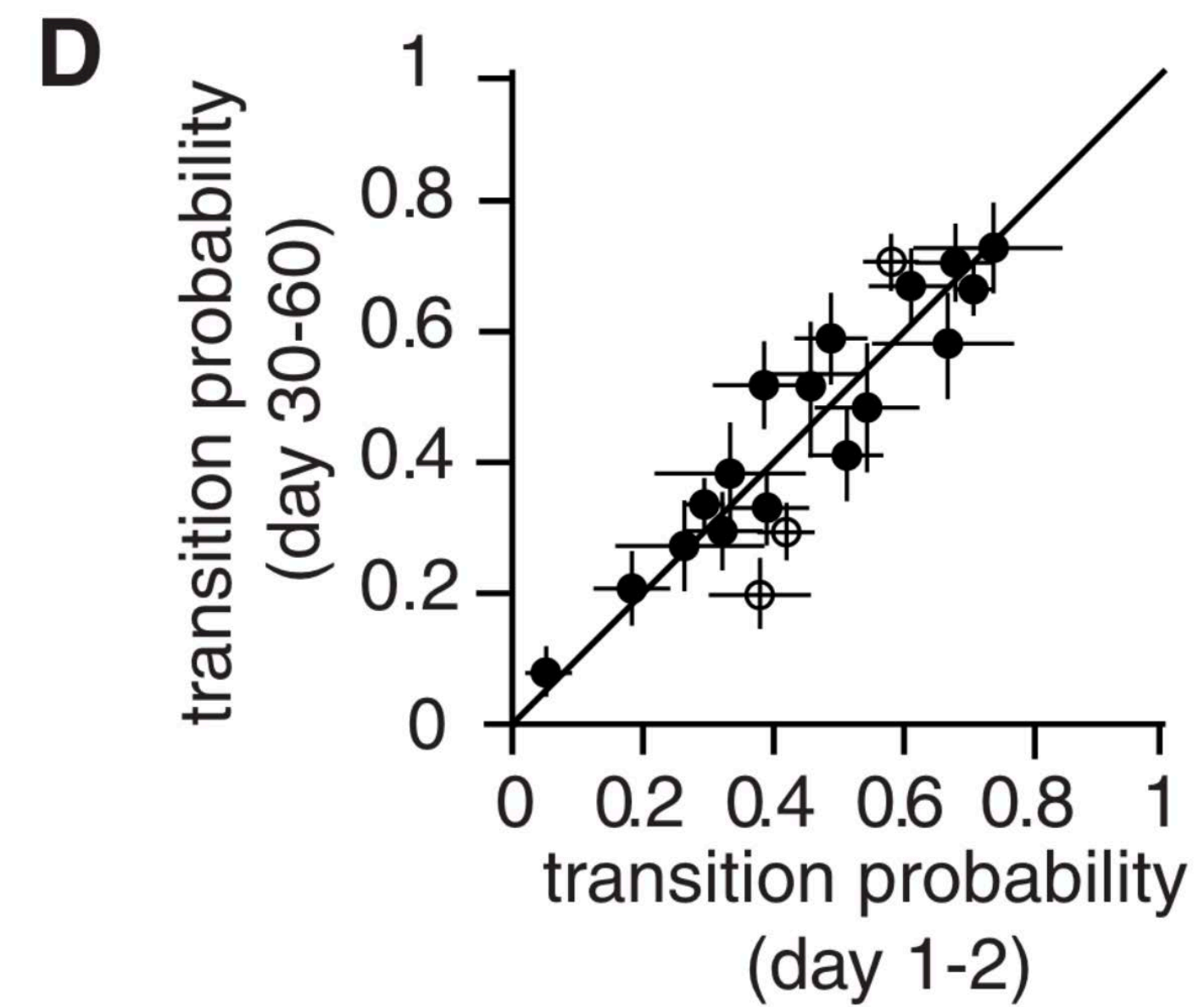
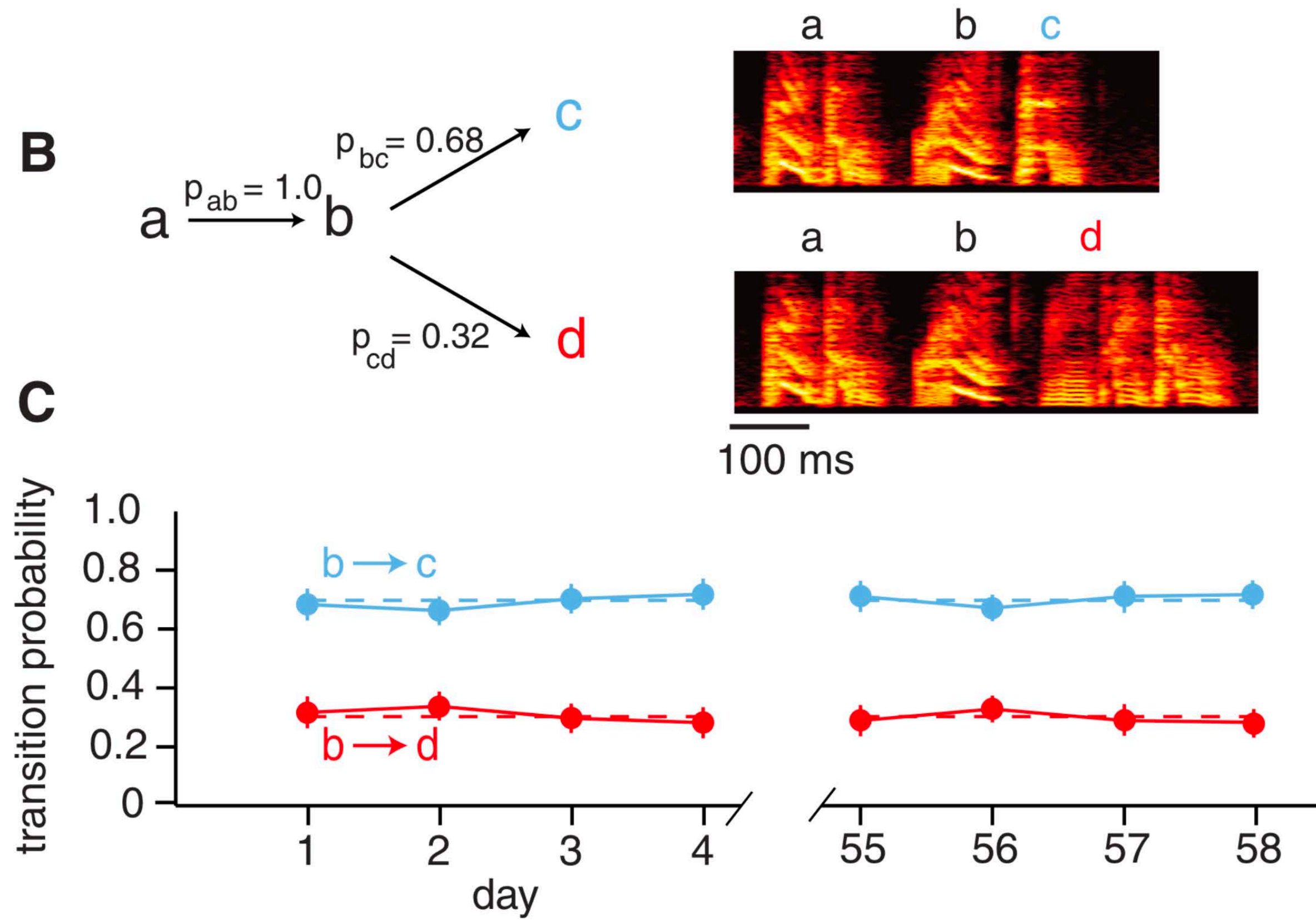
Bengalese Finches: branching transitions

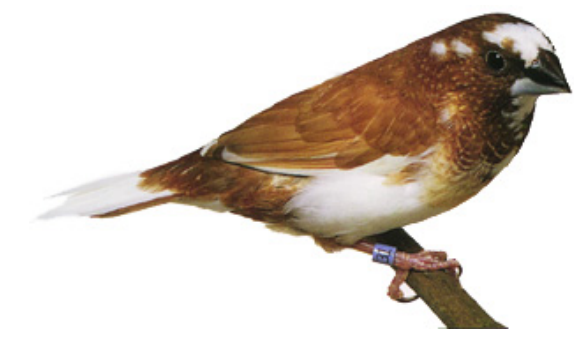


Compared to Zebra Finches:
 What is similar? What is different?

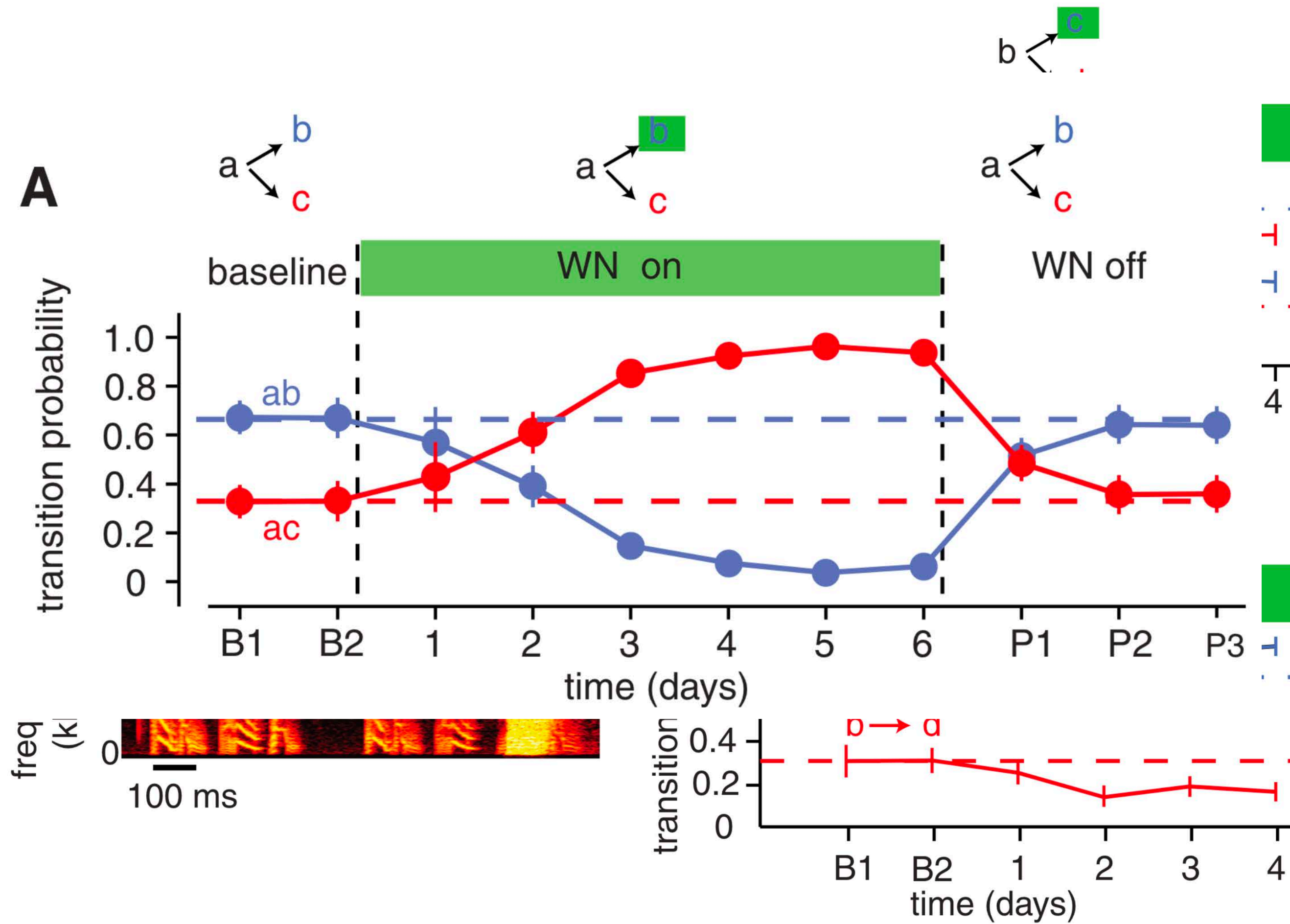


Bengalese finches crystallize transitions





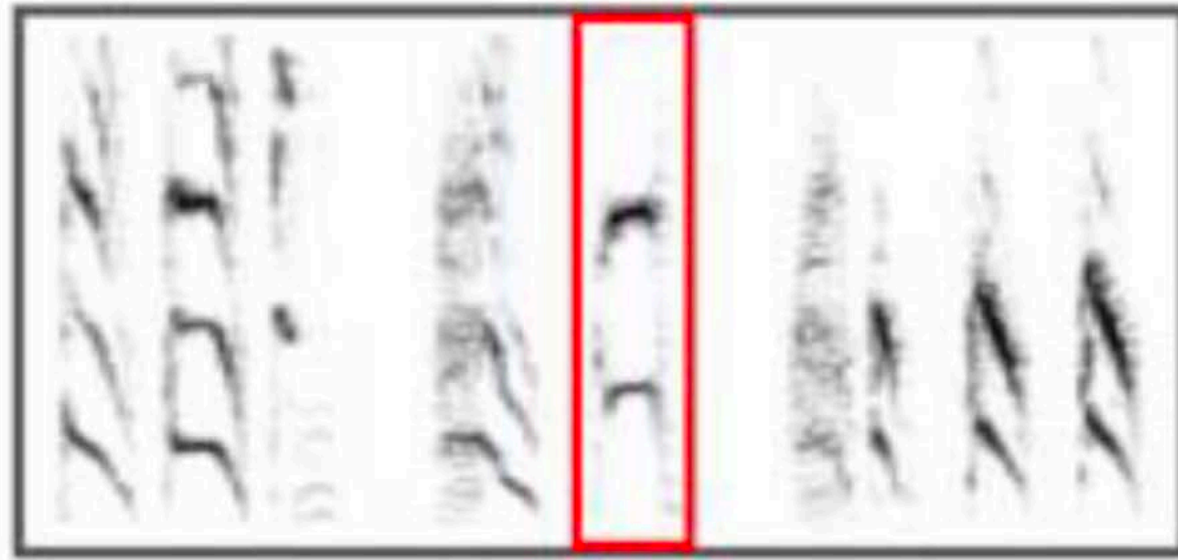
Bengalese finches crystallize transitions





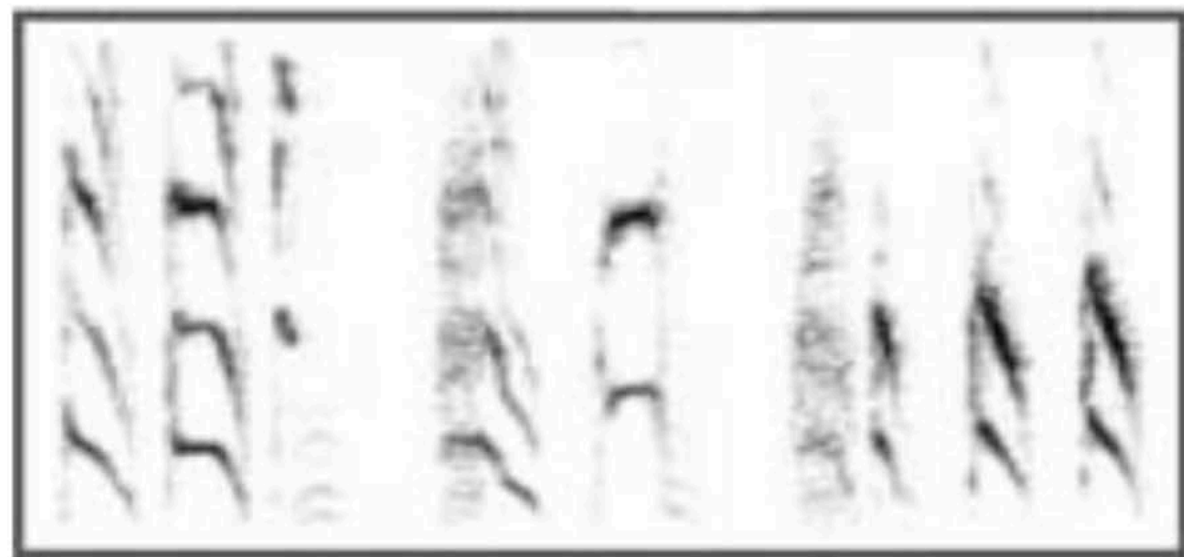
Branching transitions involve auditory feedback

1. bird sings

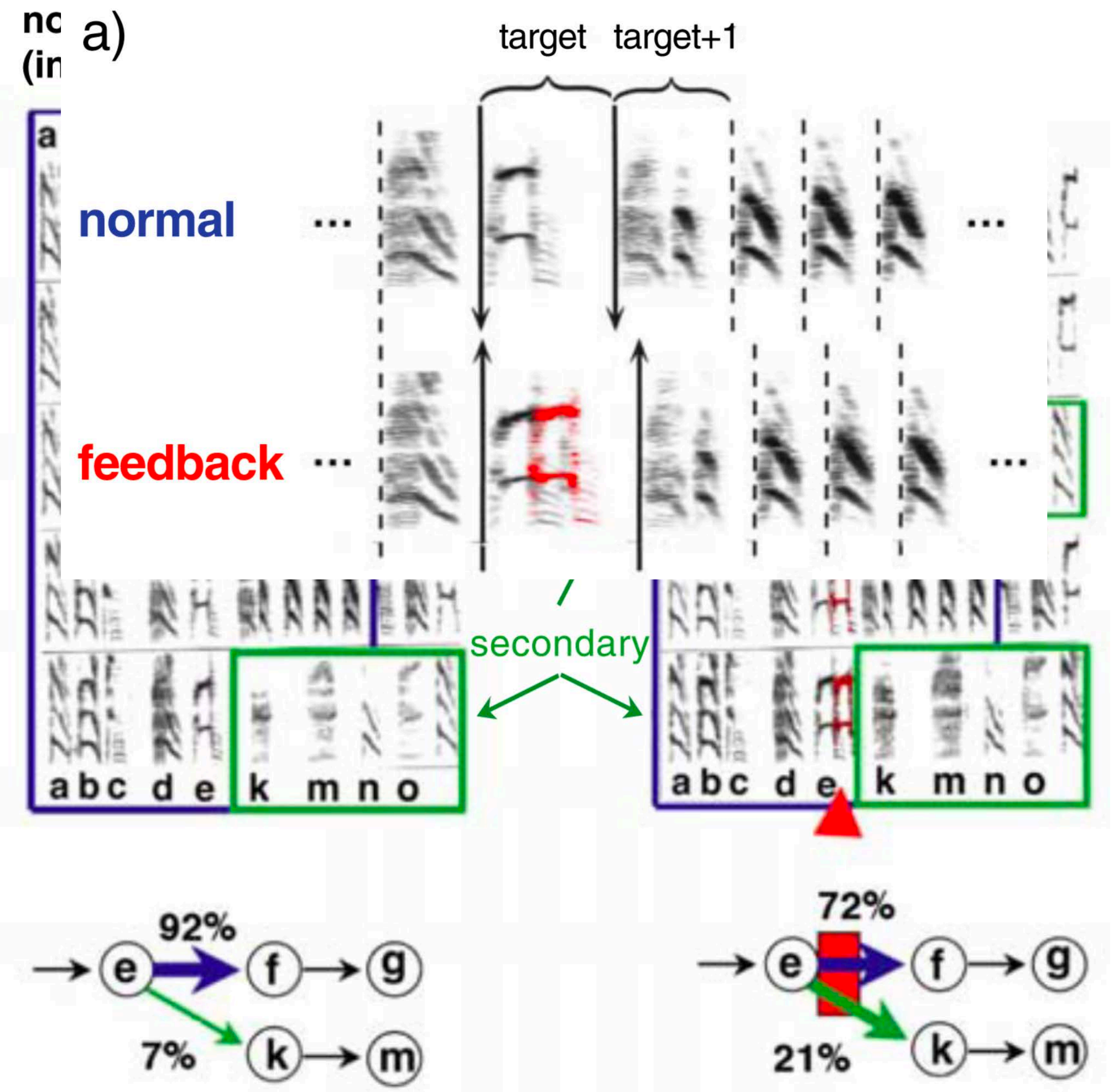
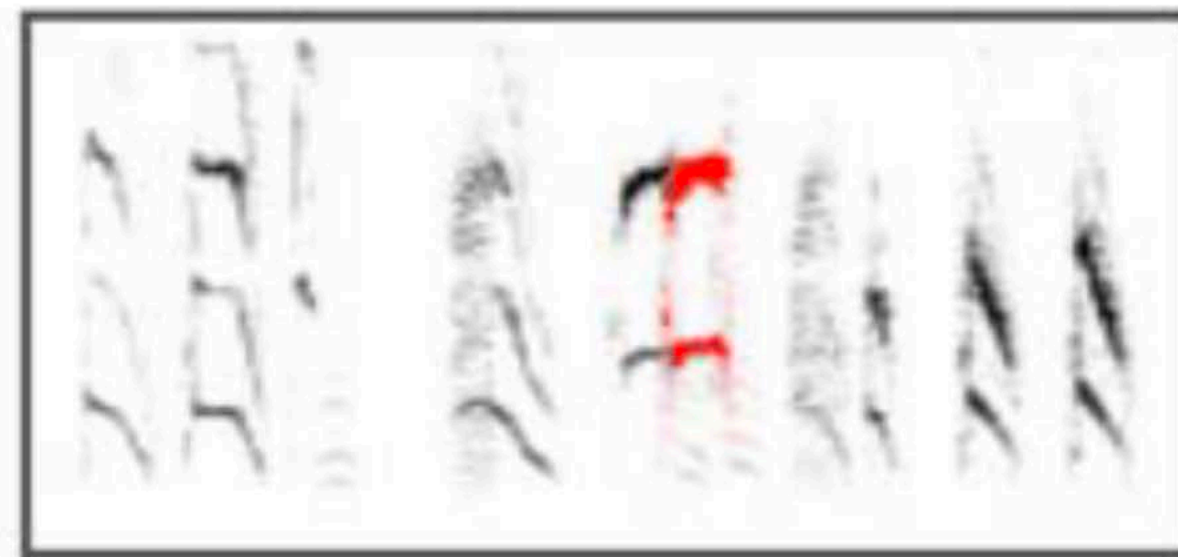


2. computer detects pre-targeted syllable

catch trial

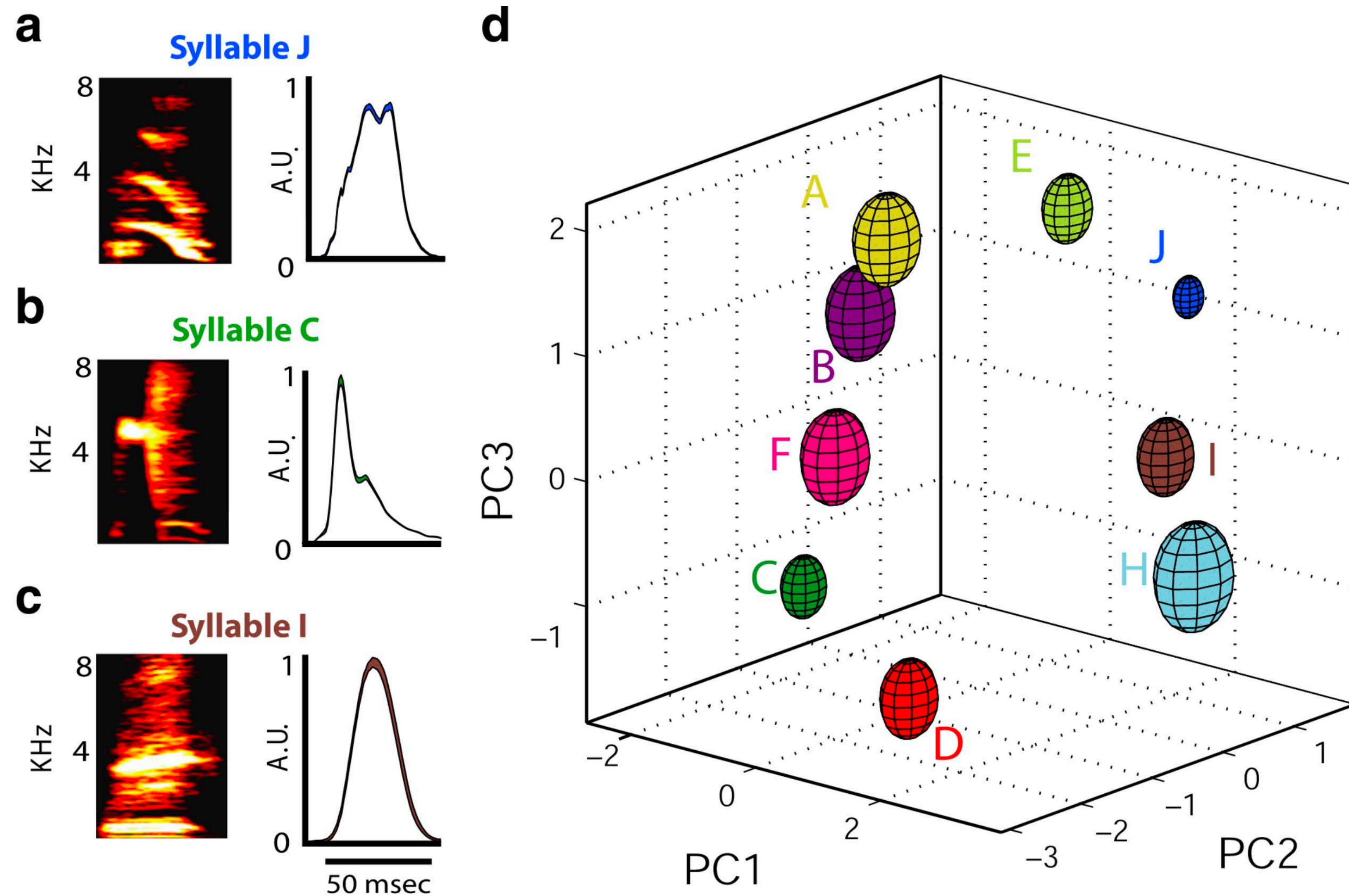


feedback trial





Are sequence and phonology related?

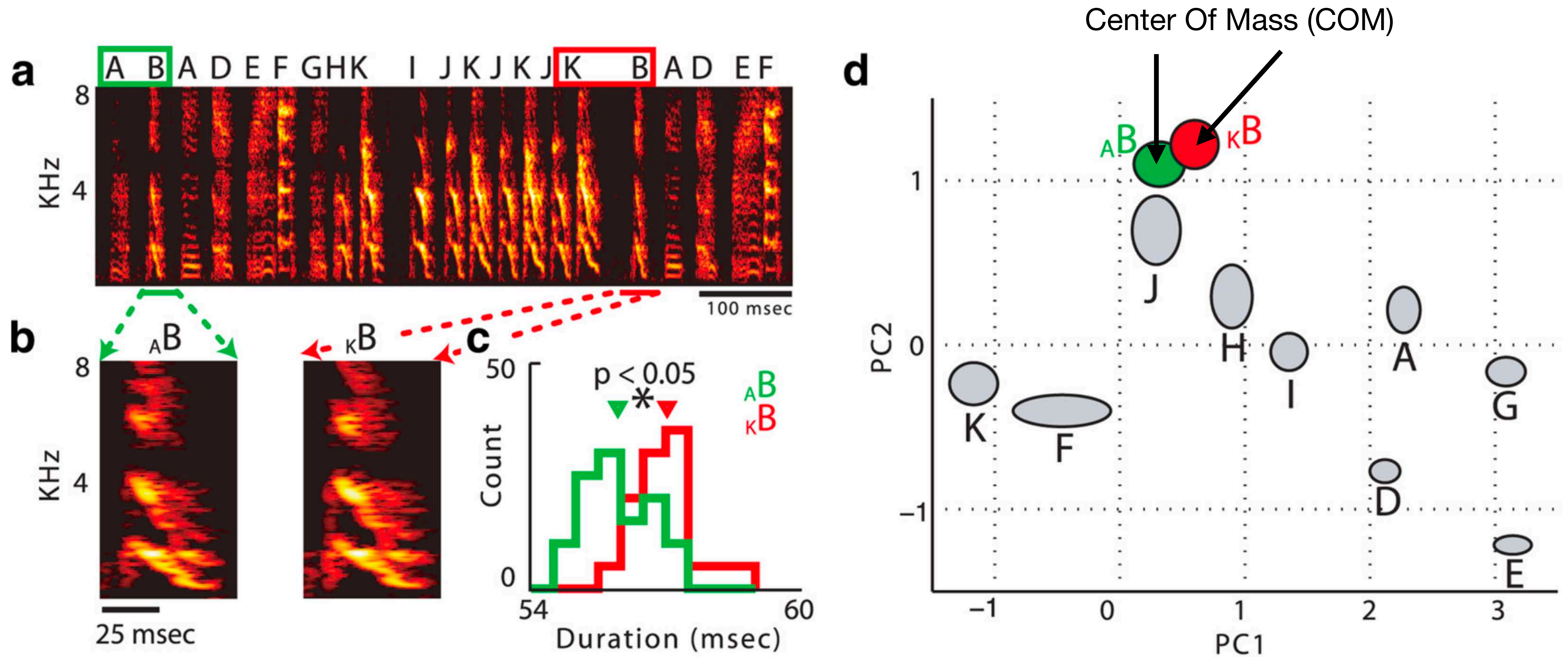


Syllable phonological metrics:

- duration,
- fundamental frequency,
- time to half-peak amplitude,
- frequency slope,
- amplitude slope,
- spectral entropy,
- temporal entropy,
- spectrotemporal entropy

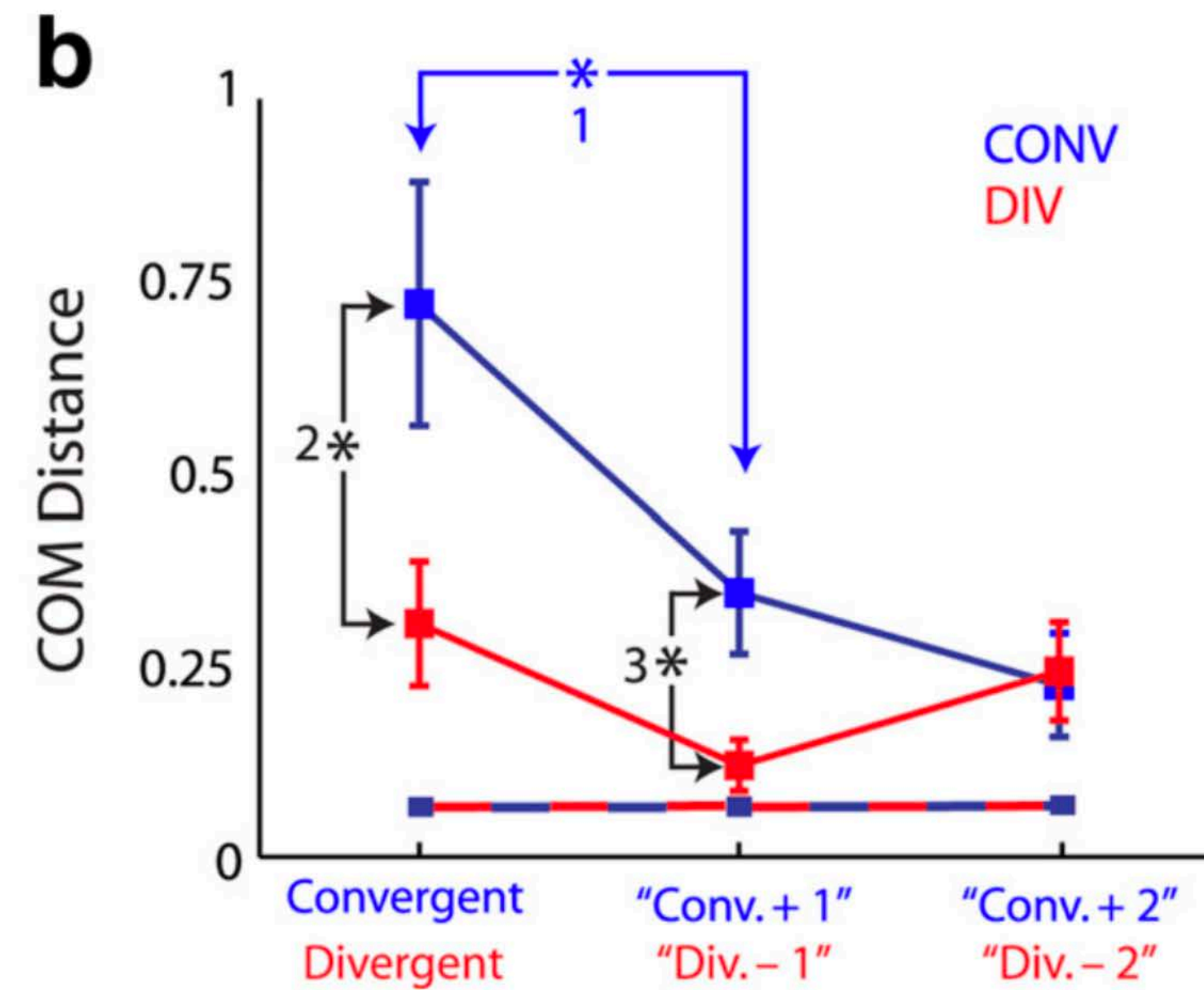
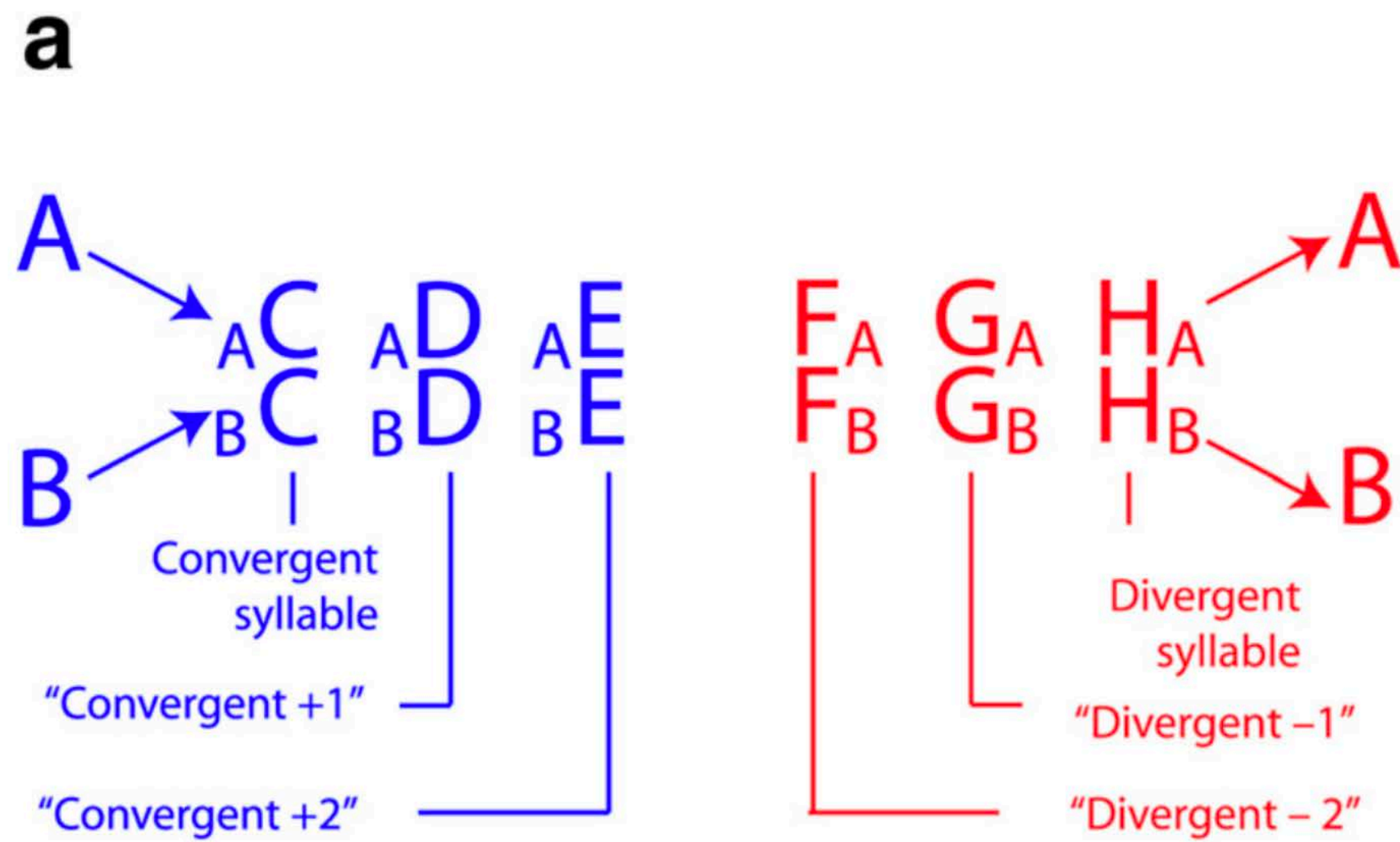
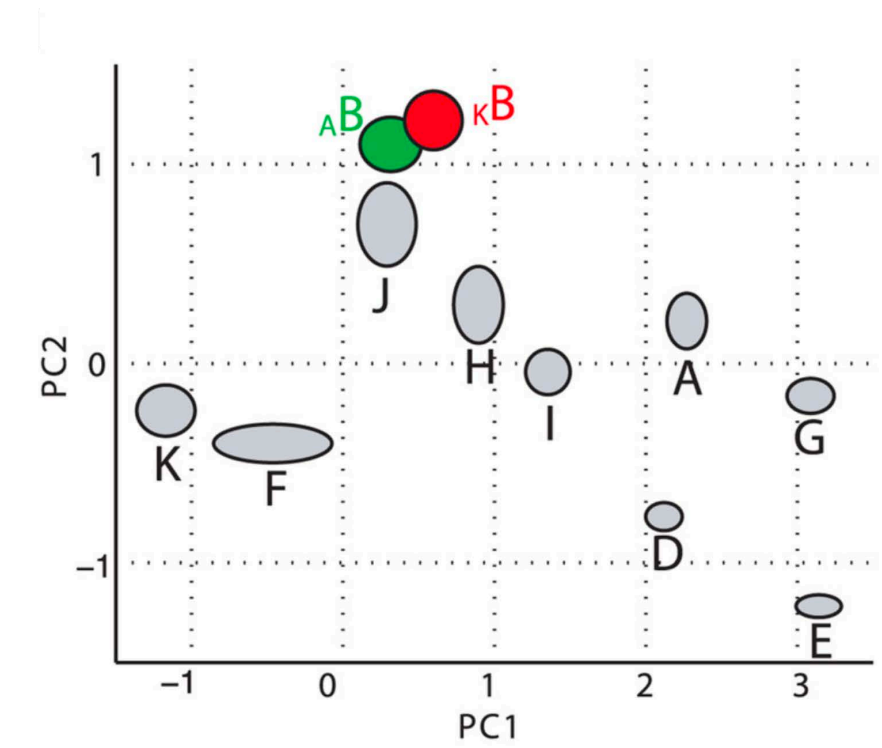


Are sequence and phonology related?



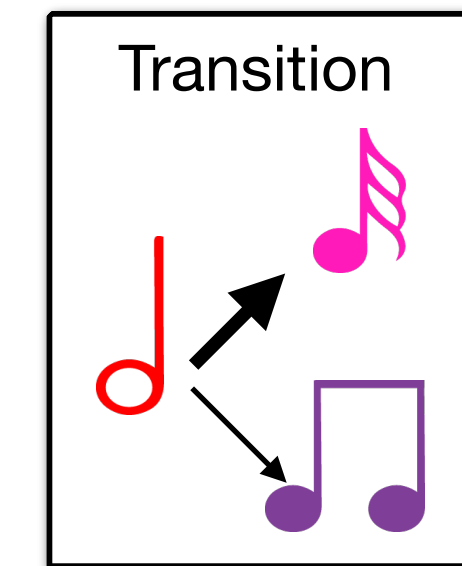
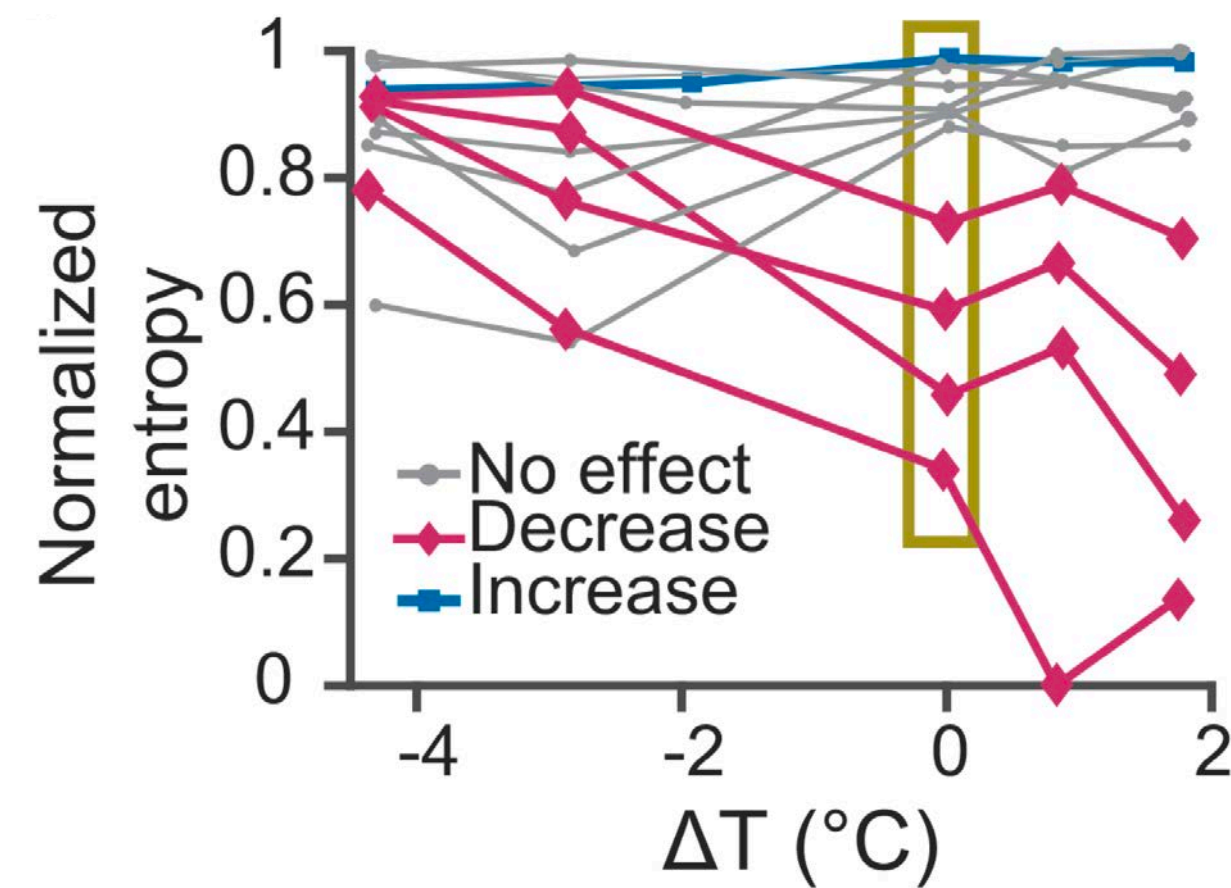
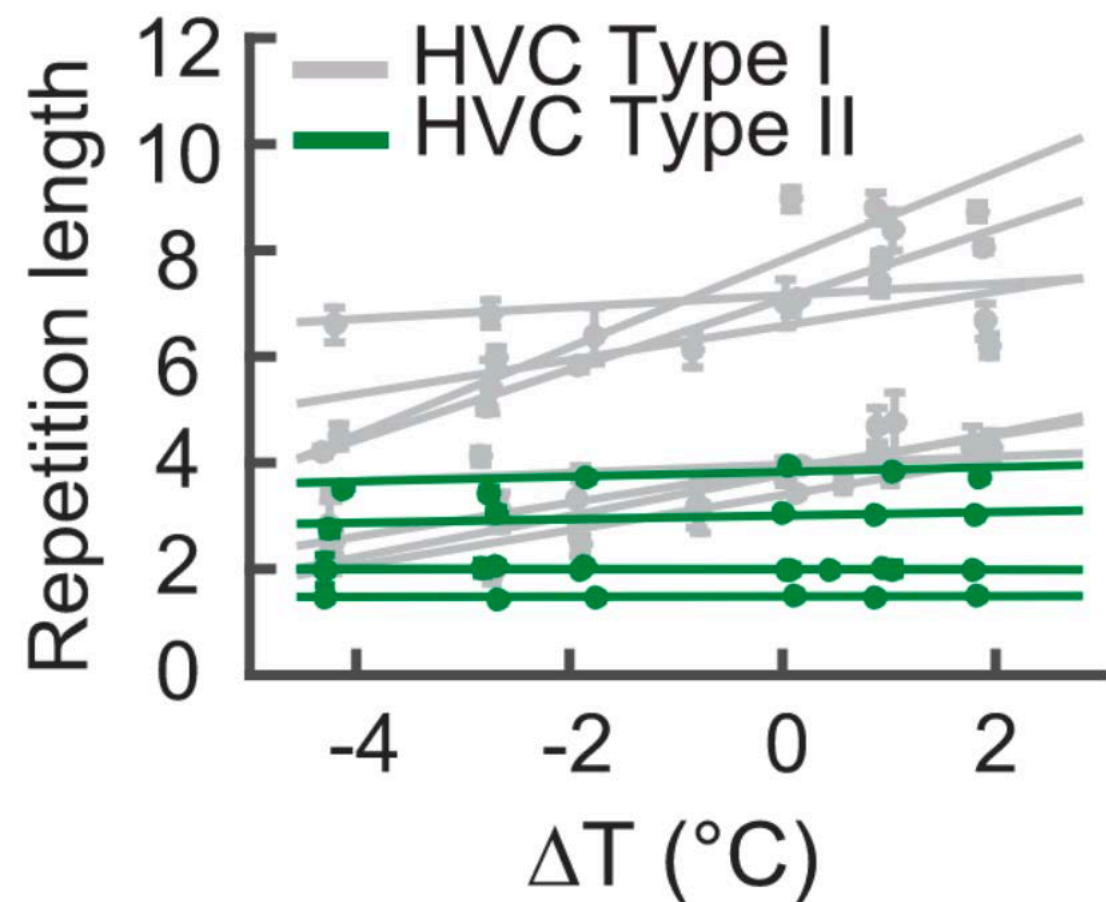
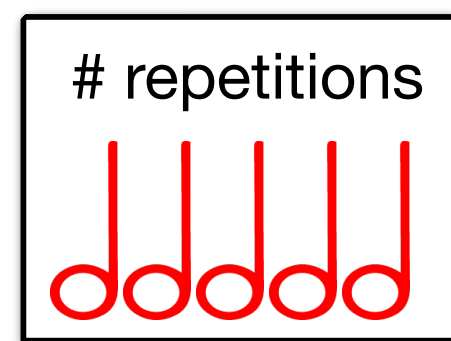
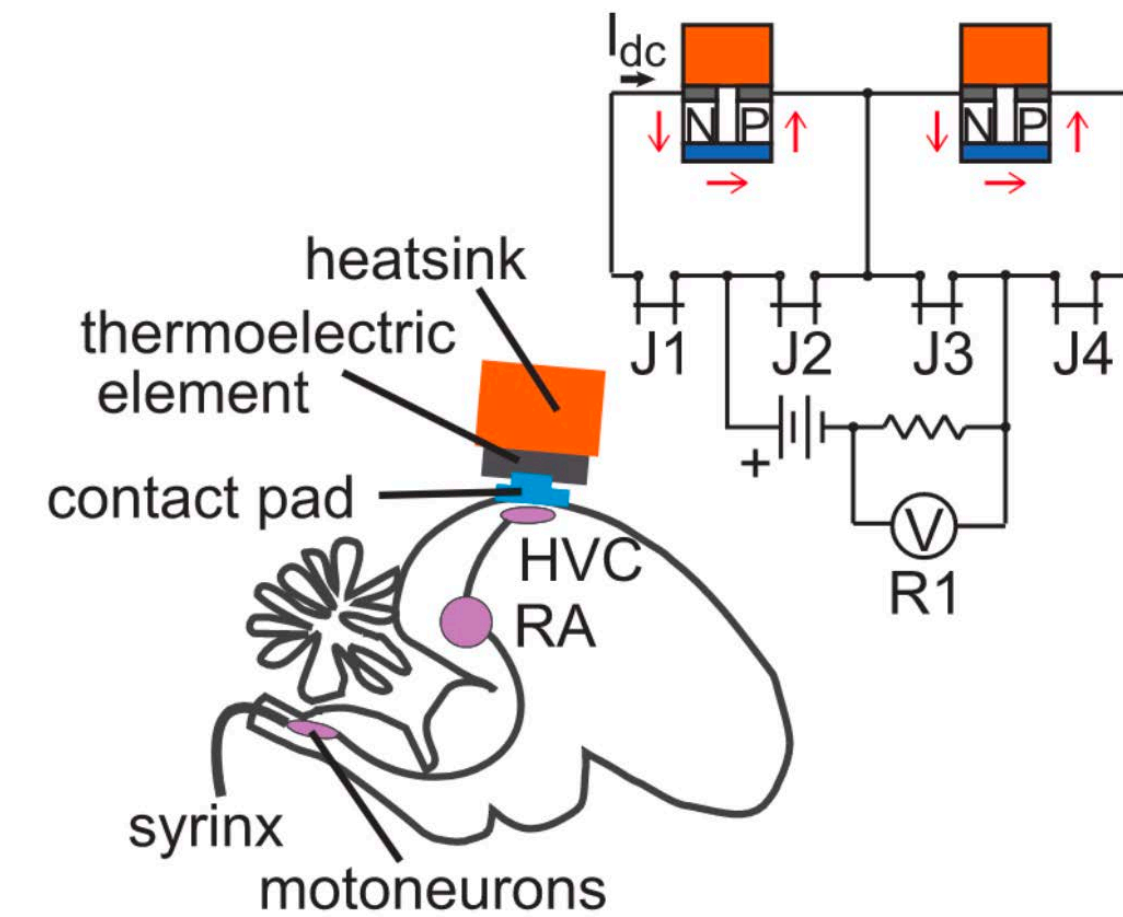
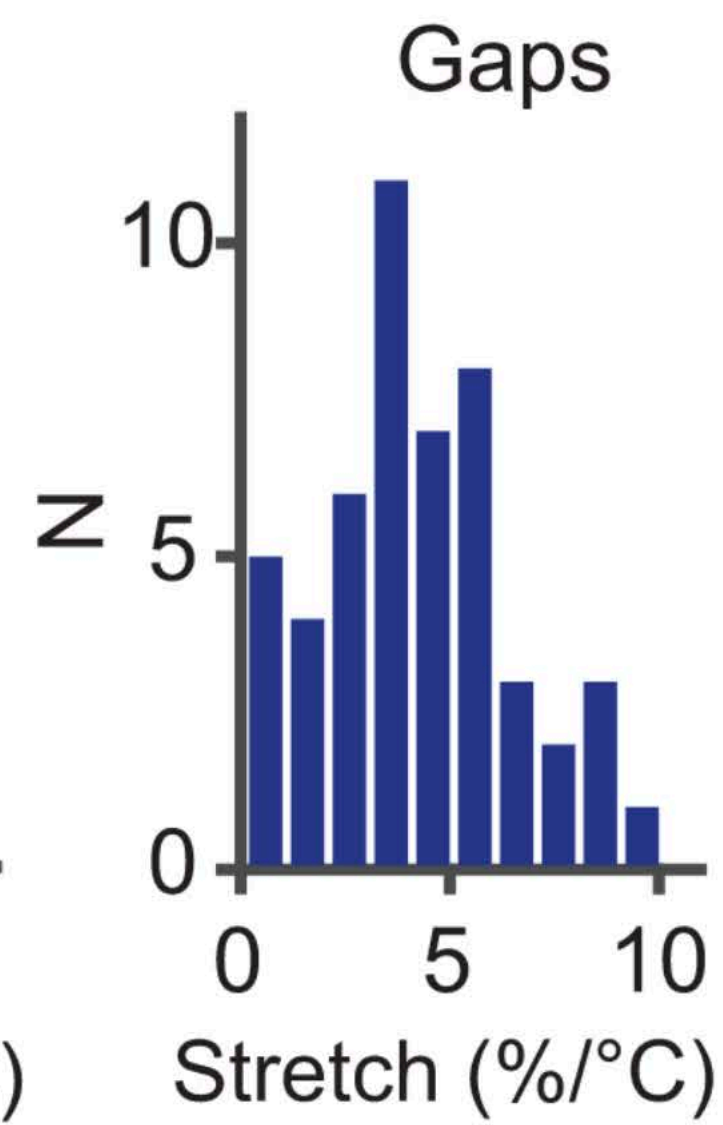
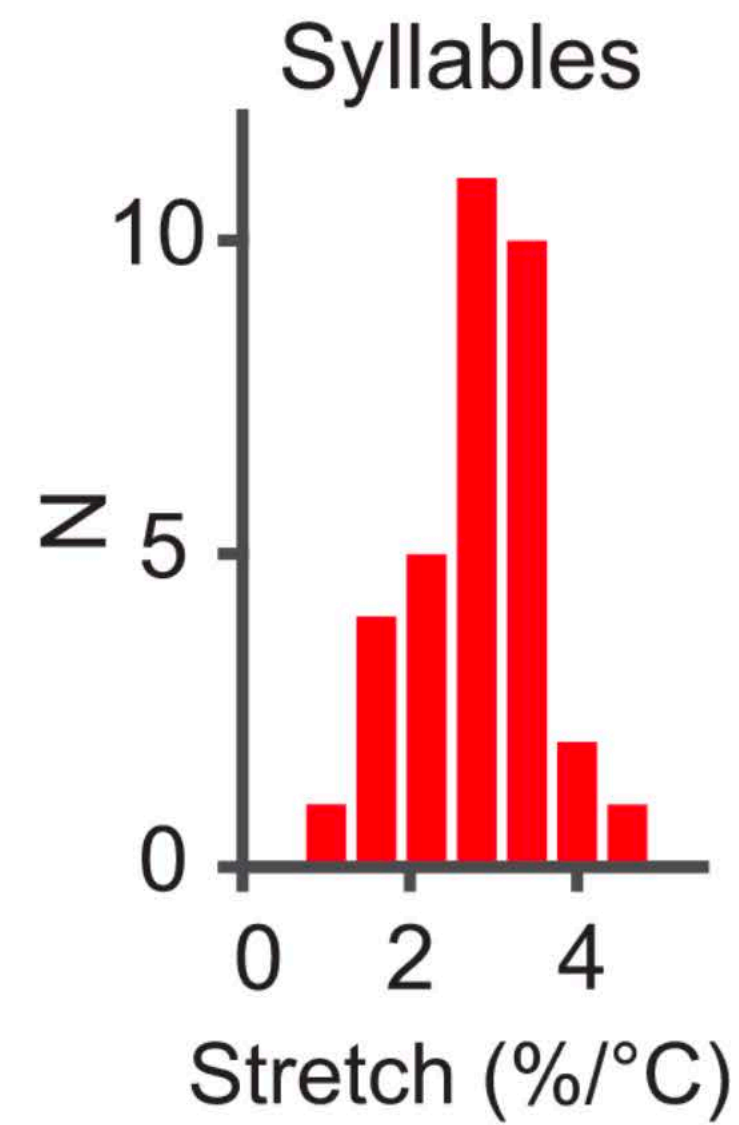
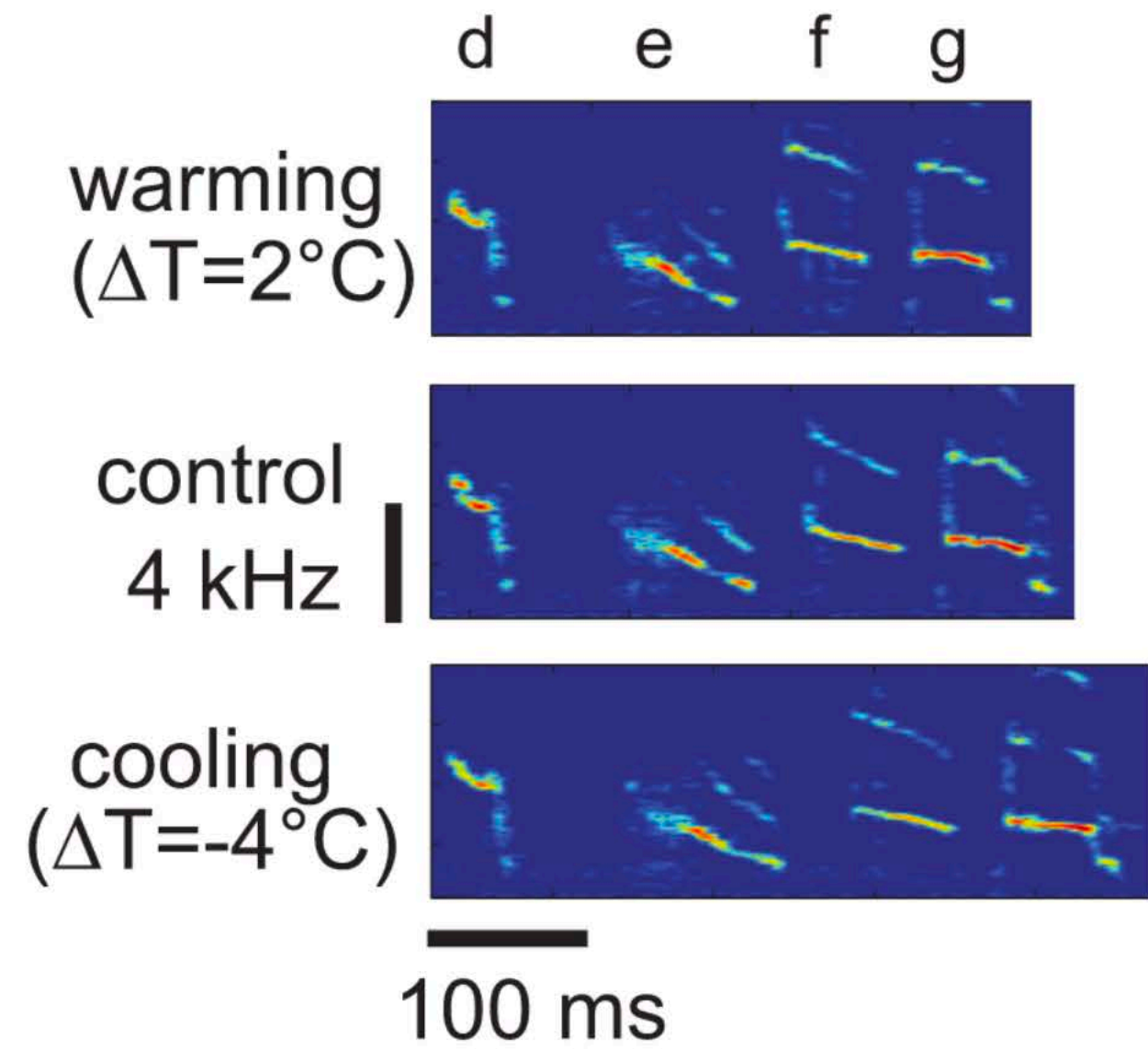


Are sequence and phonology related?





HVC cooling changes Bengalese finch syntax

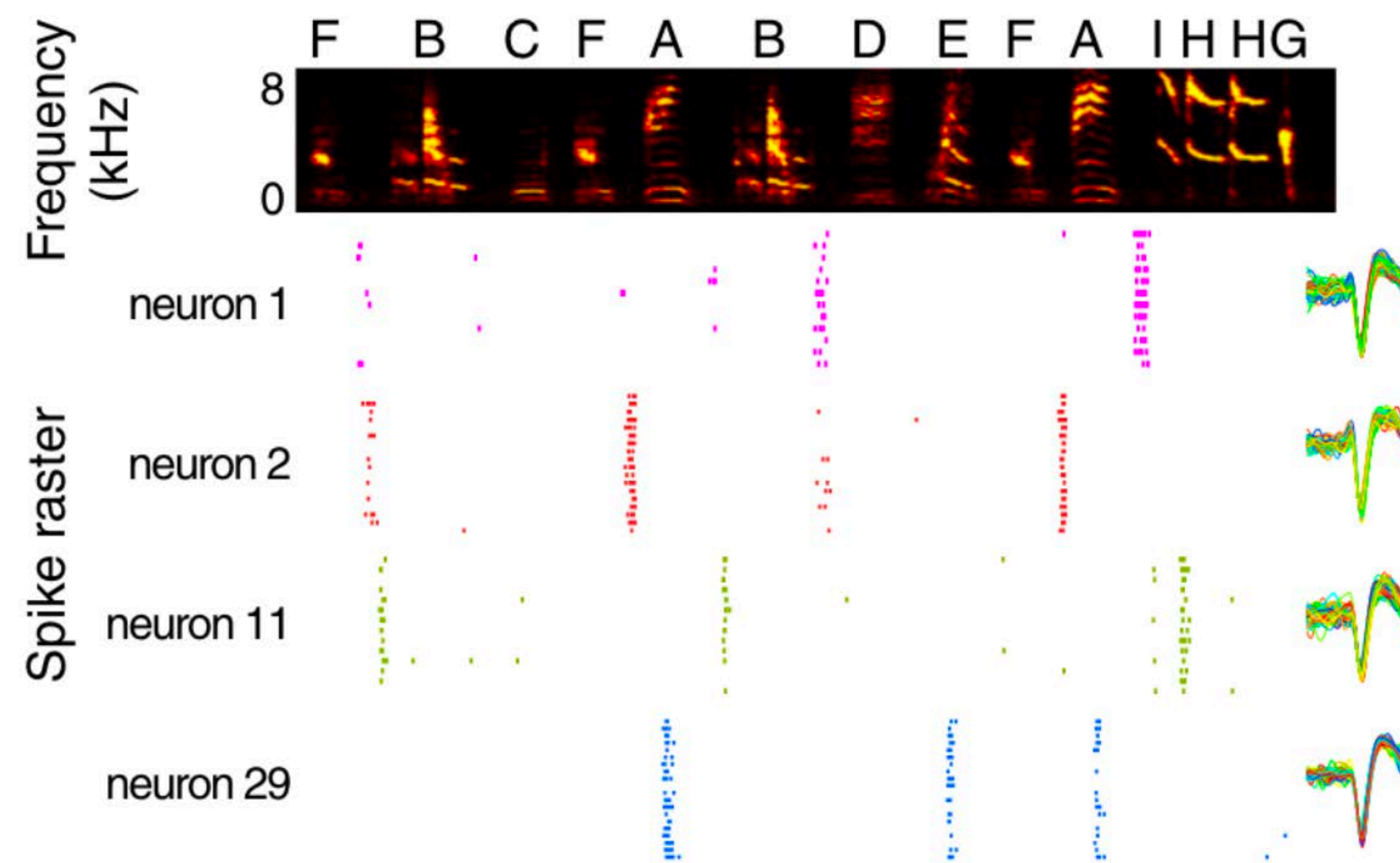
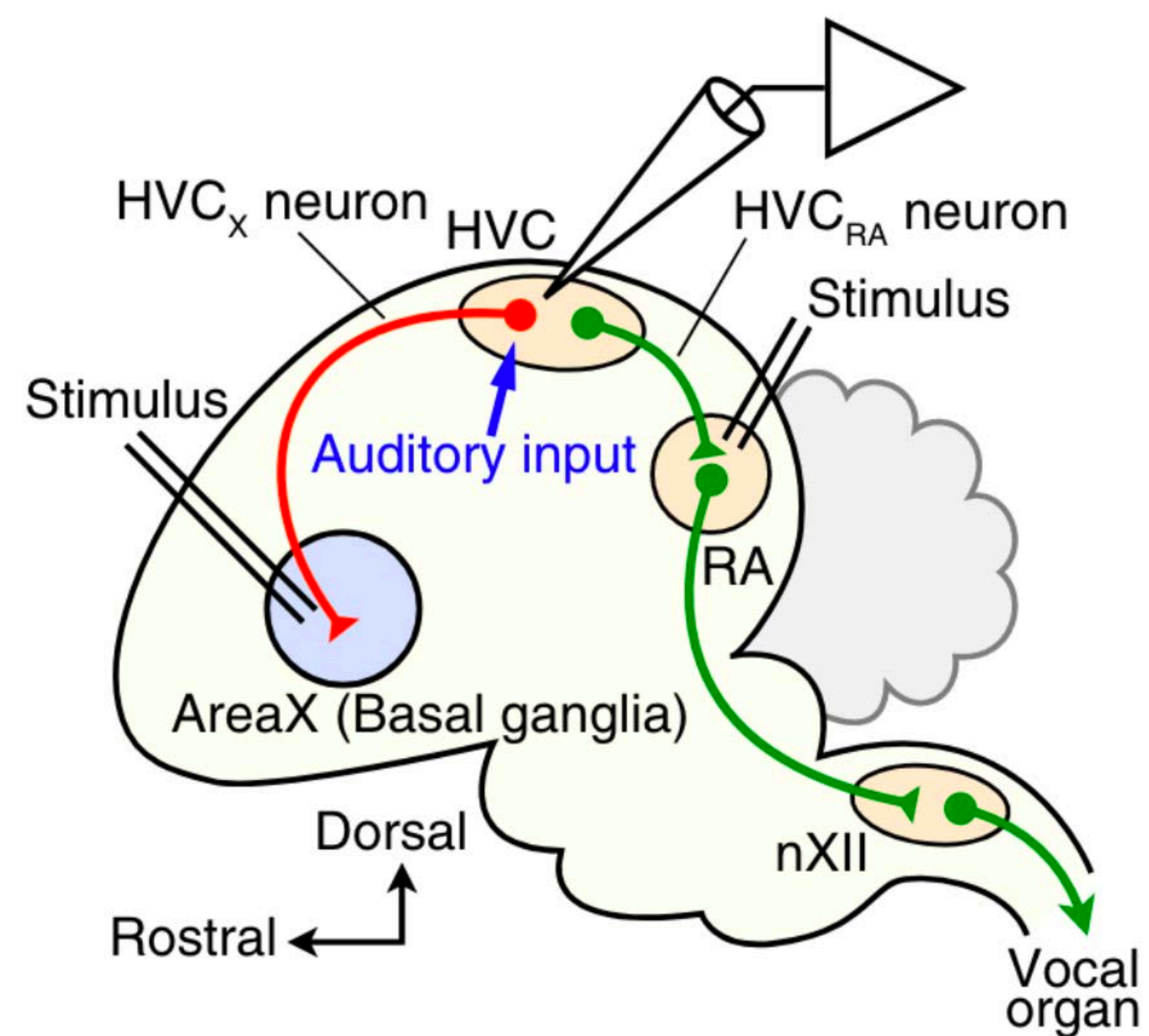


What syntax properties are reflected in HVC activity?



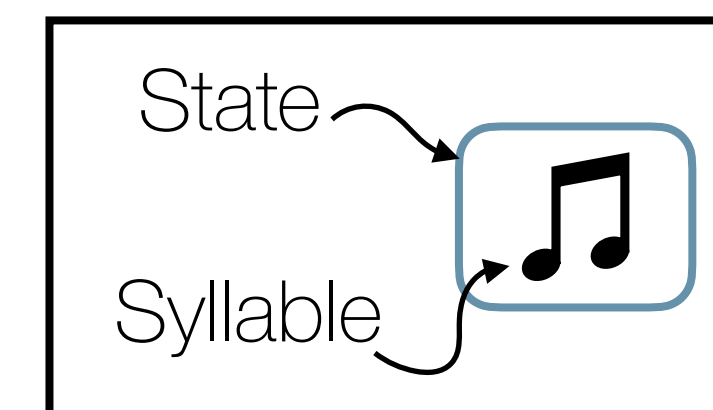
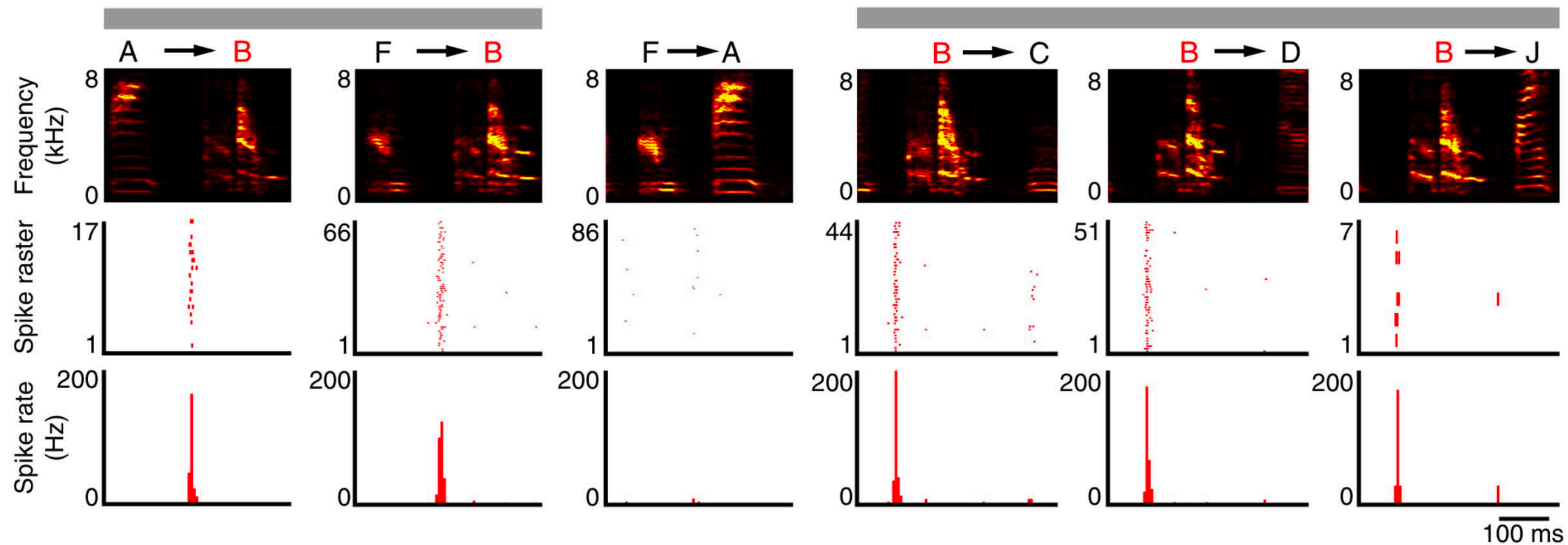
Neural encoding of Bengalese finch syntax

Fujimoto 2011



Junction transition including syllable "B"

Branching transition including syllable "B"

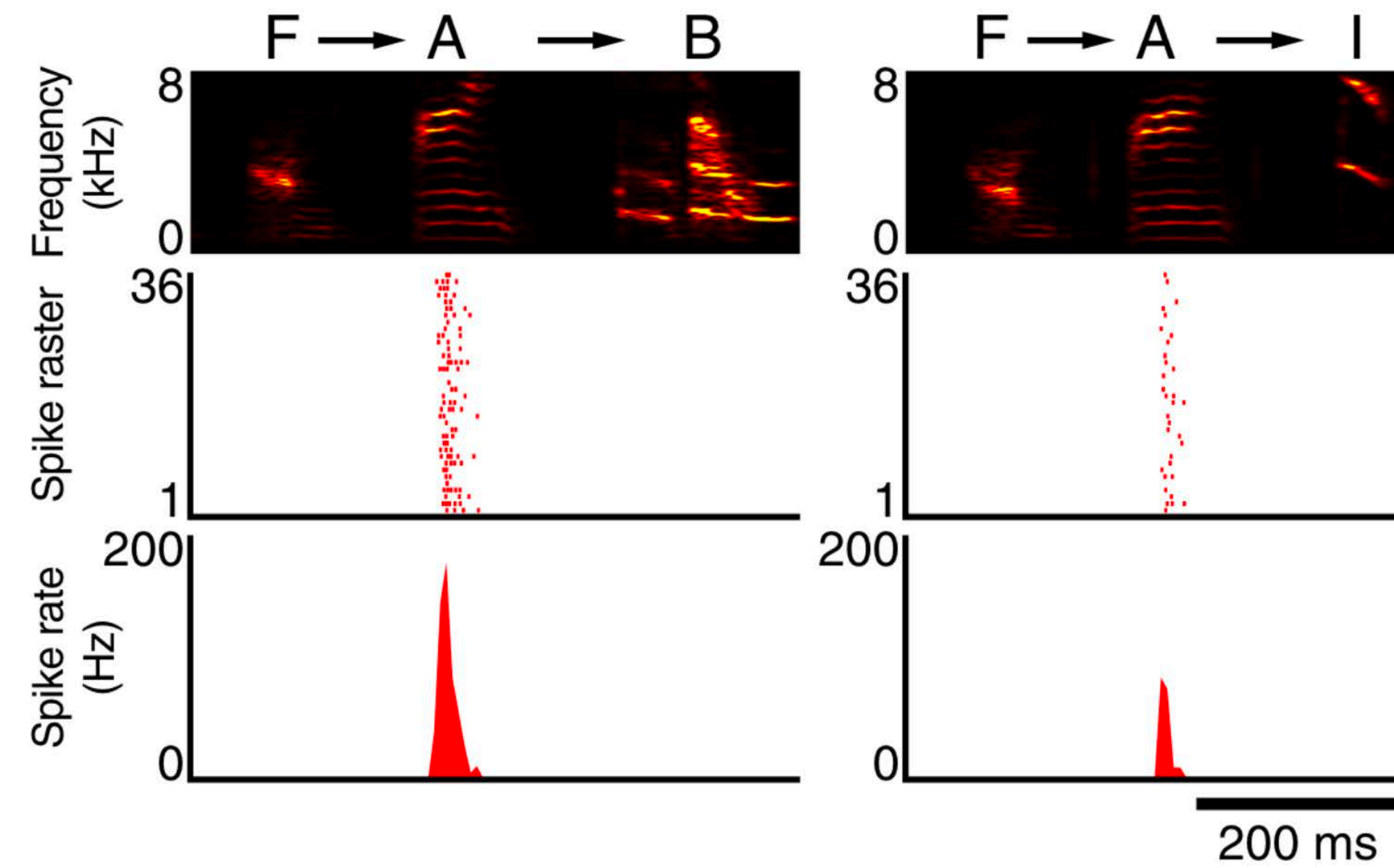
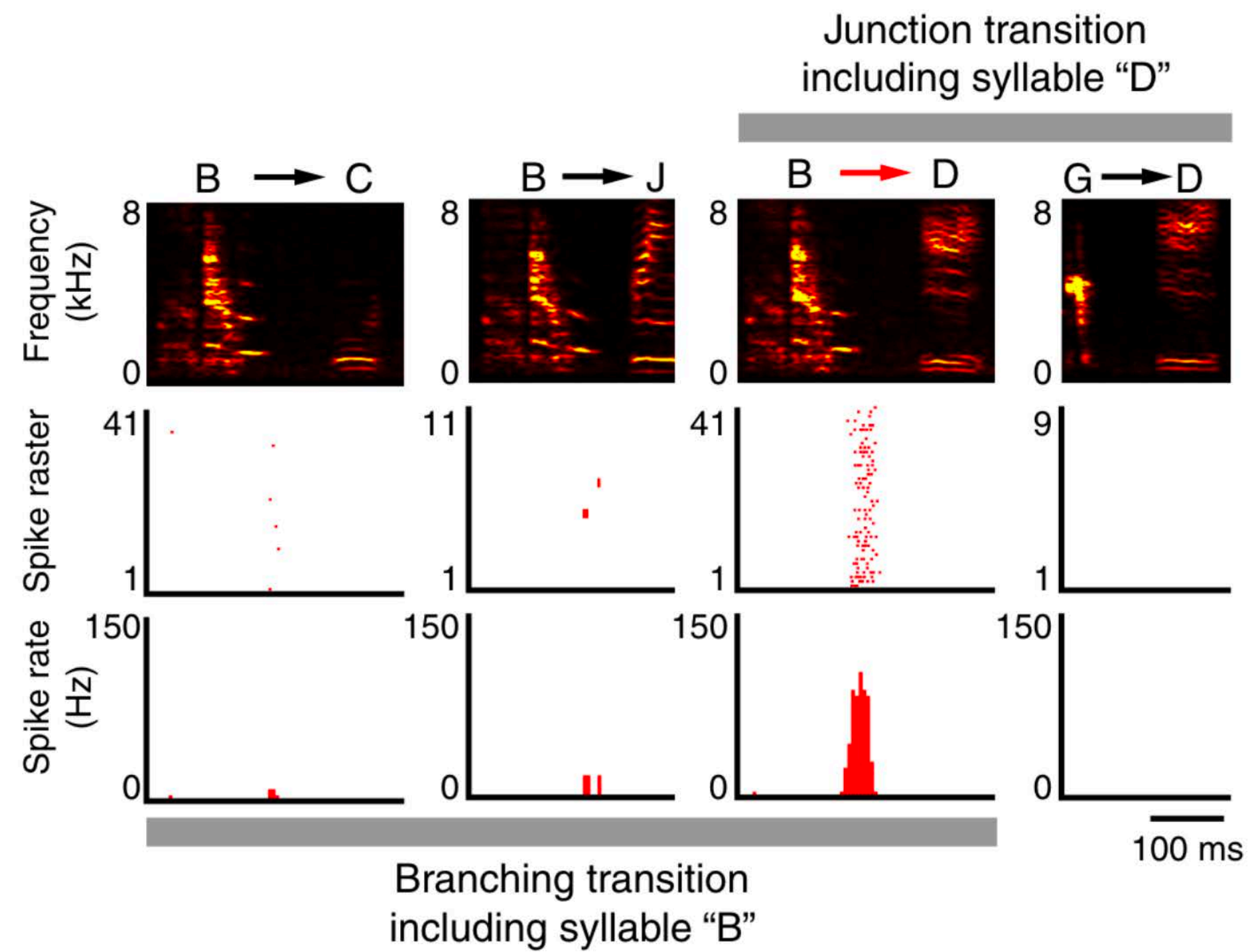




Neural encoding of Bengalese finch syntax

Fujimoto 2011

Transition specific activity

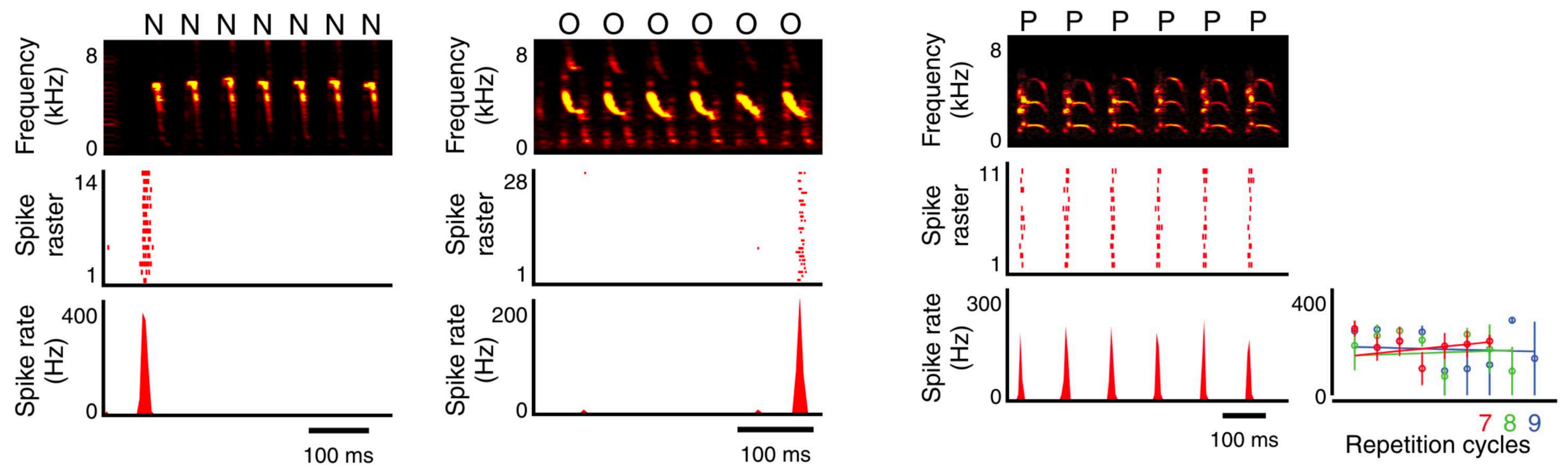




Neural encoding of Bengalese finch syntax

Fujimoto 2011

Repetition specific activity

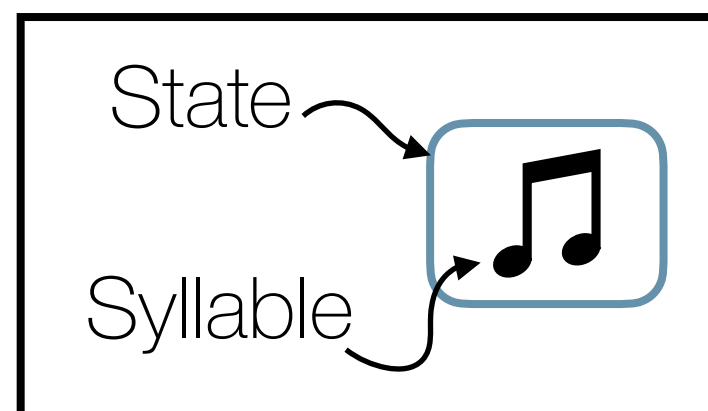
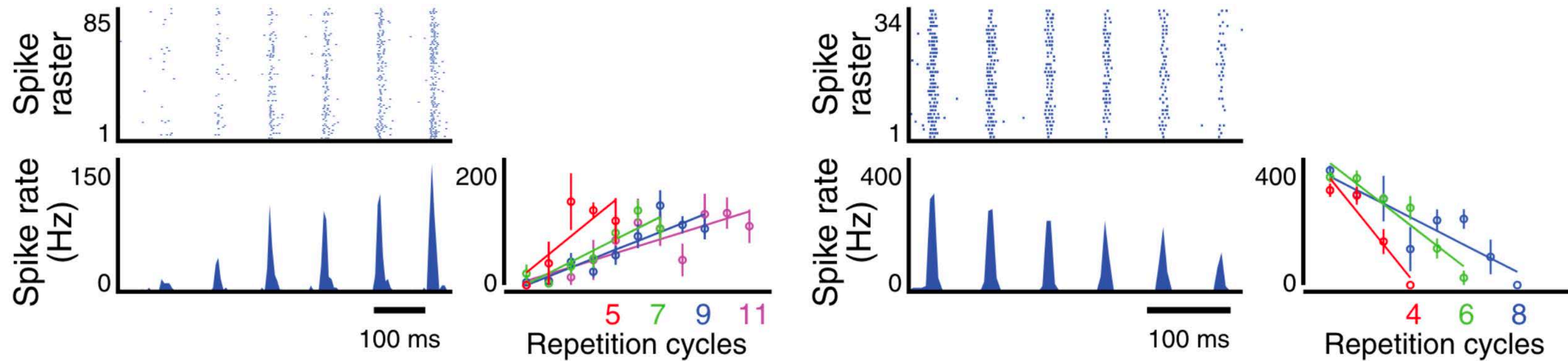




Neural encoding of Bengalese finch syntax

Fujimoto 2011

Repetition specific activity



Do we abandon the neural state model?
Or, change it somehow?

Interim summary - extending a stereotyped behavior



Konrad Lorenz and Nikolaas Tinbergen

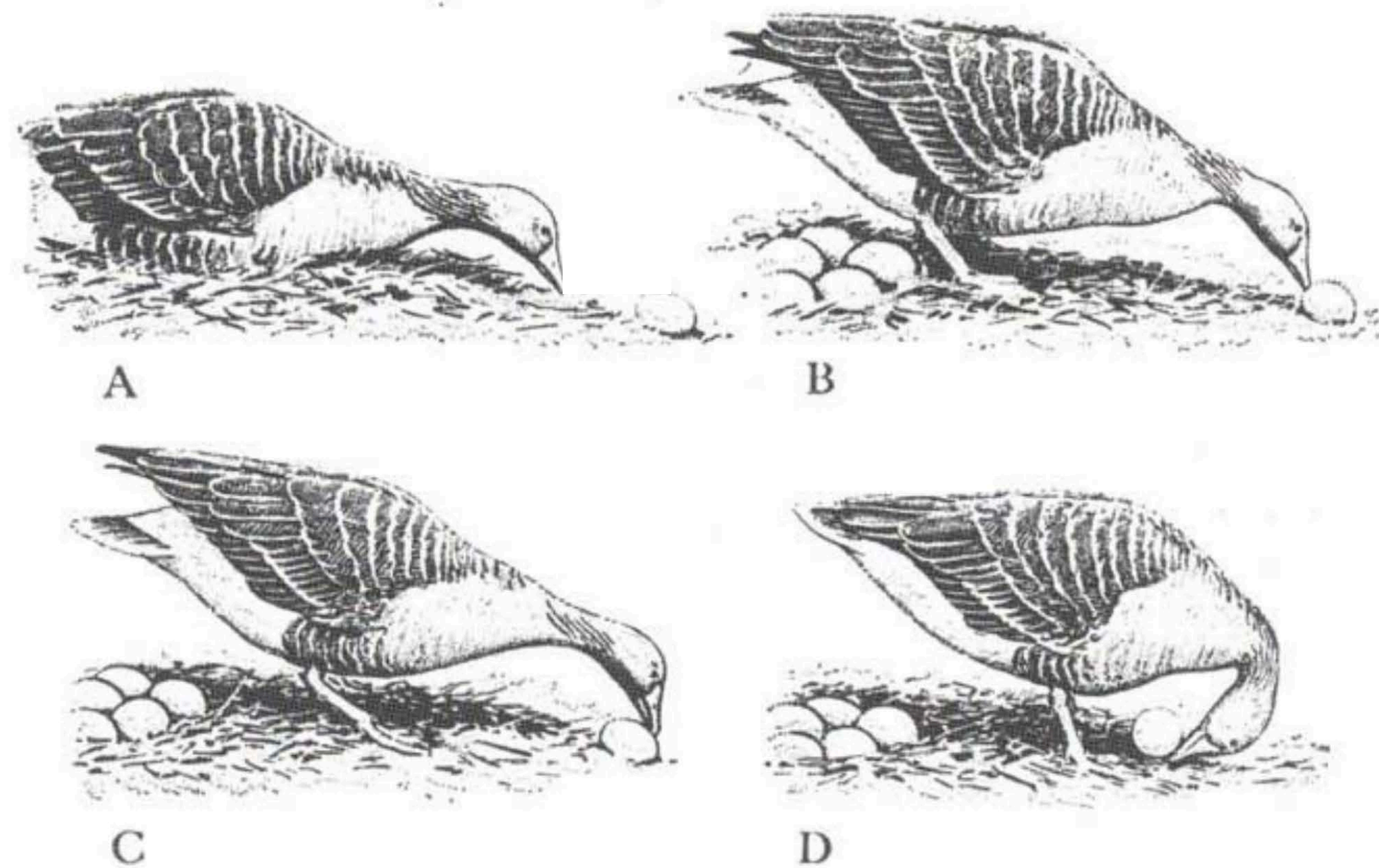
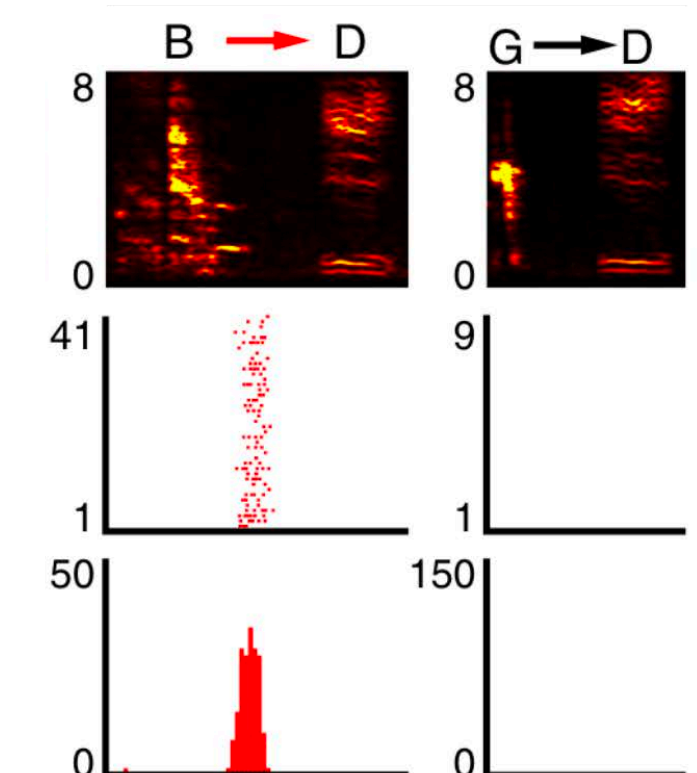
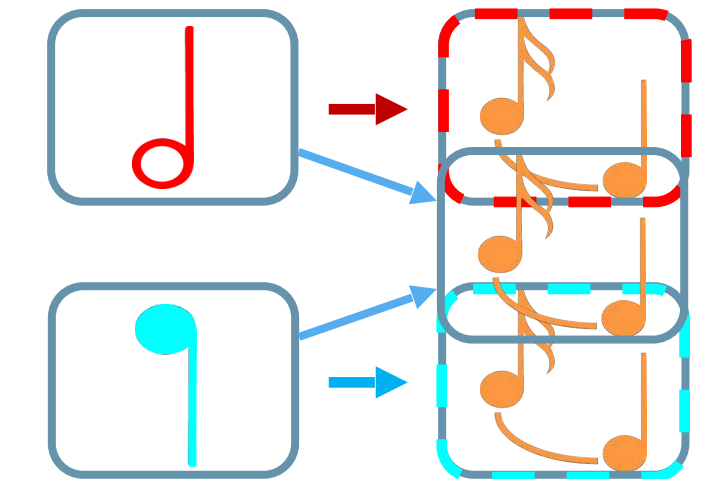
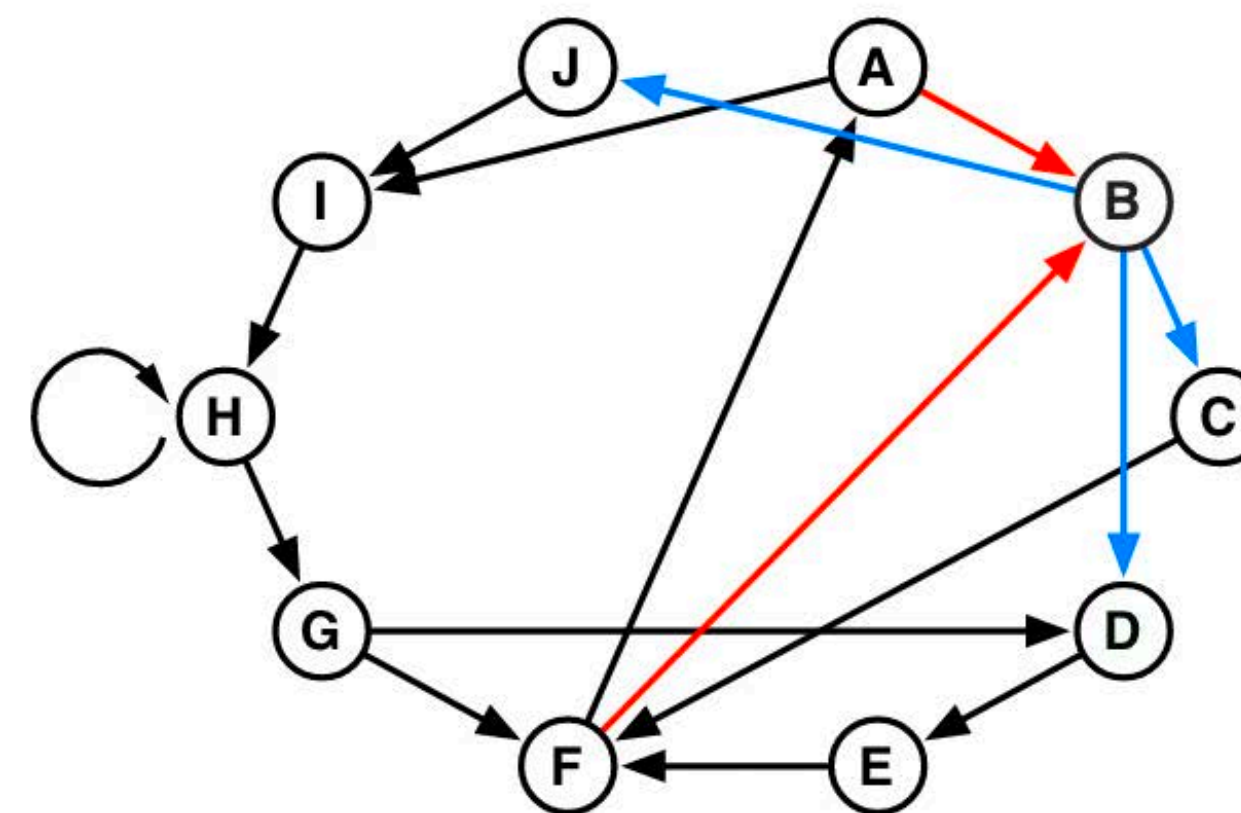
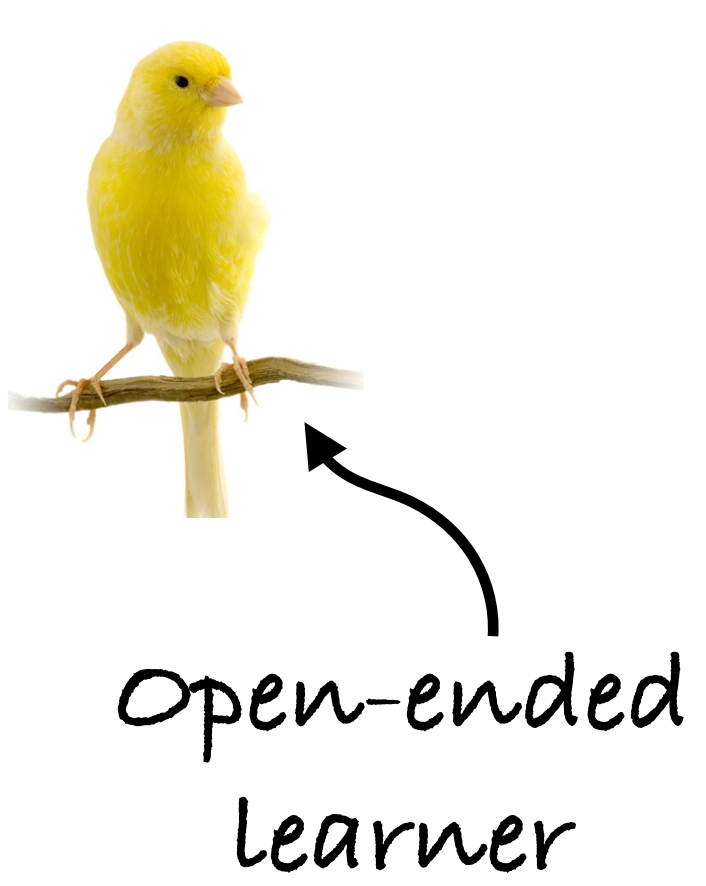


Fig. 1. Normal performance of the egg-rolling movement

Lorenz and Tinbergen 1938

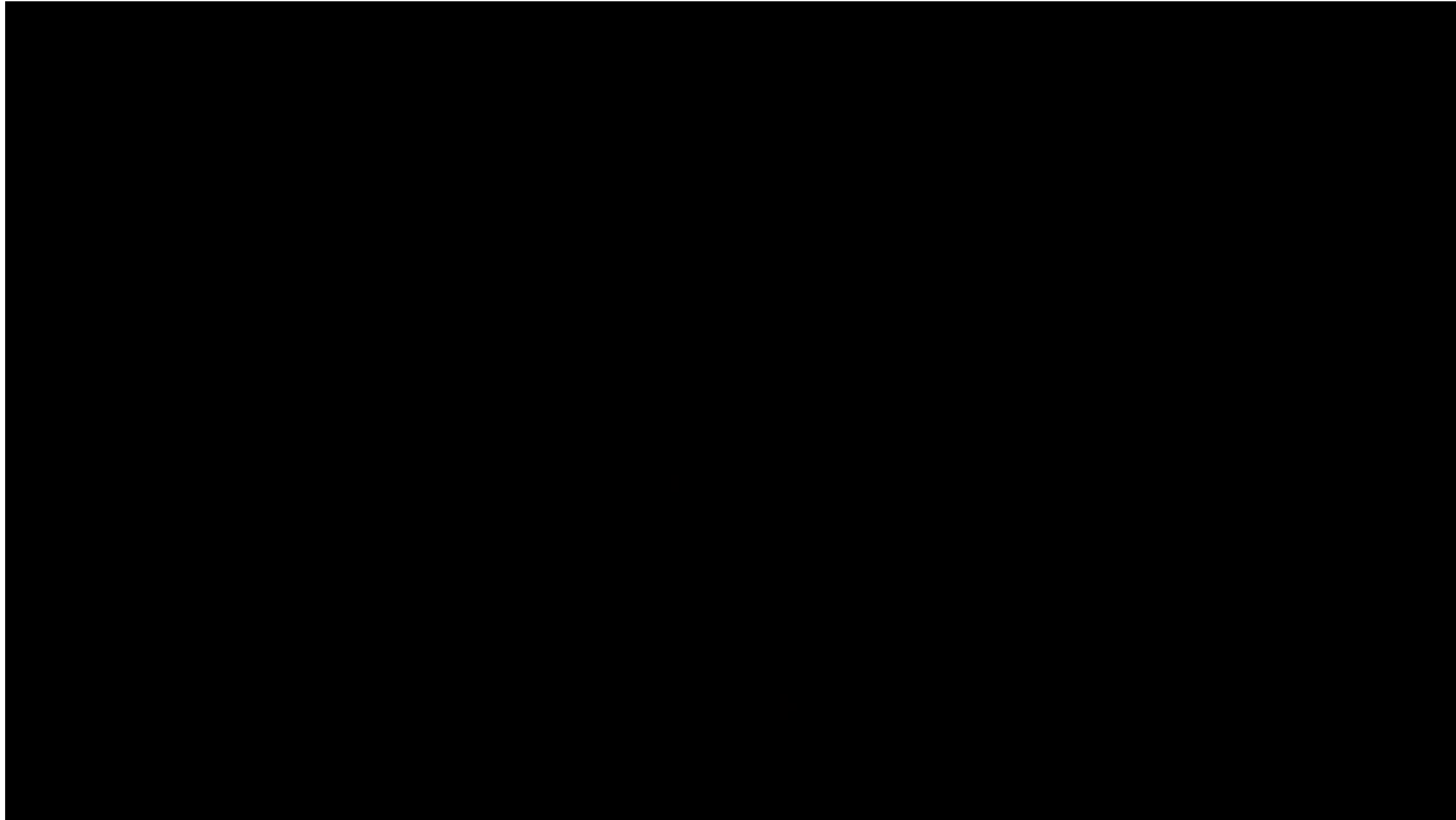
Flexible syntax





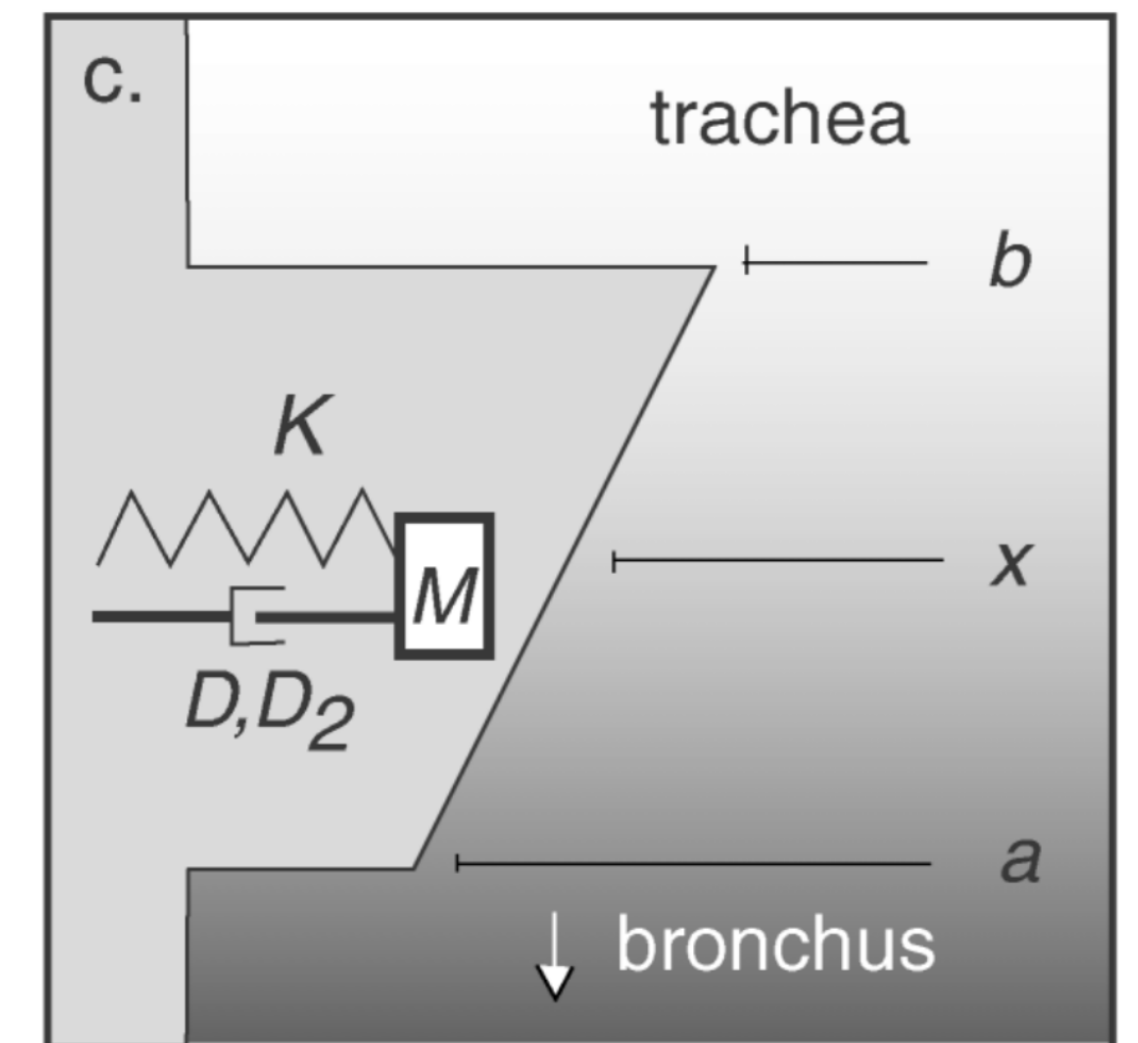
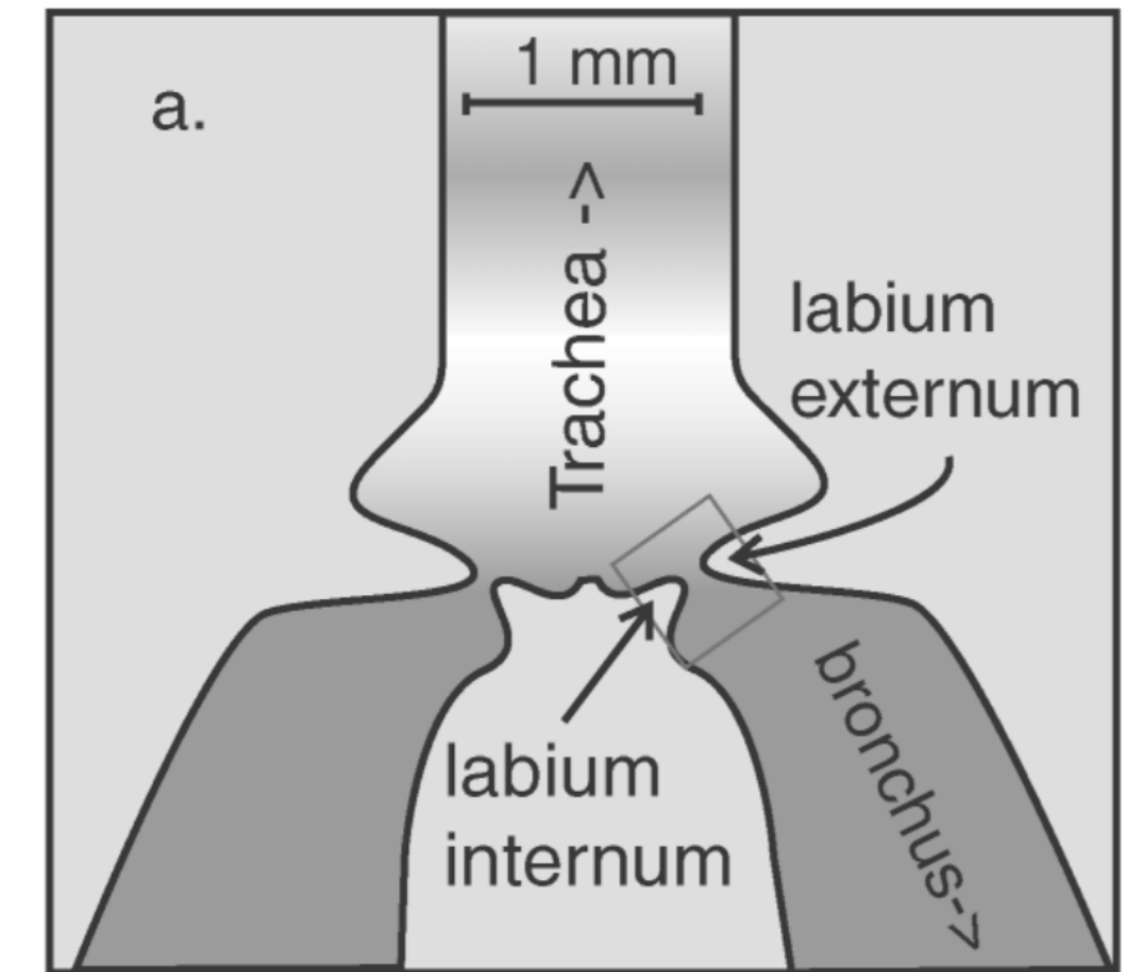
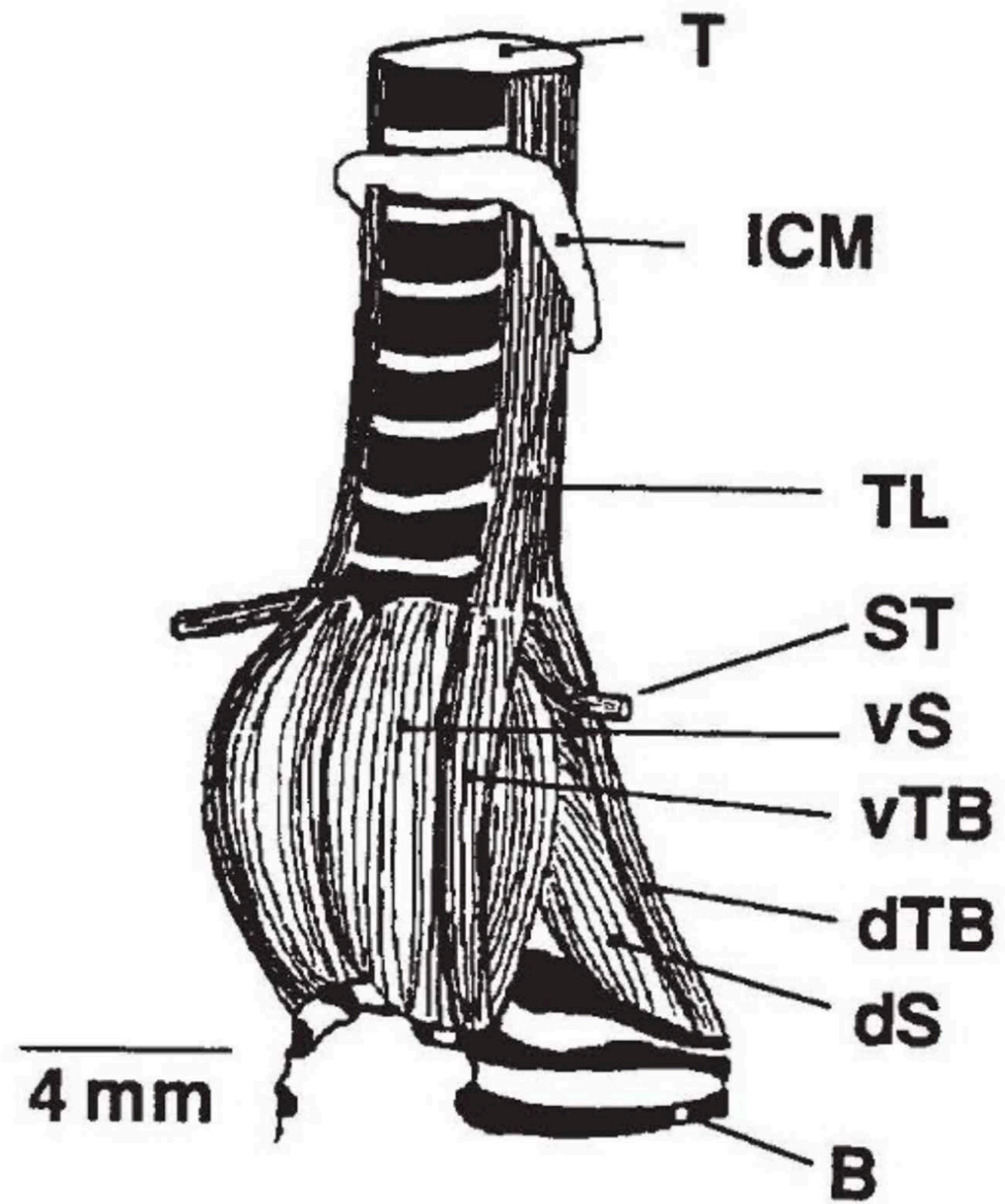
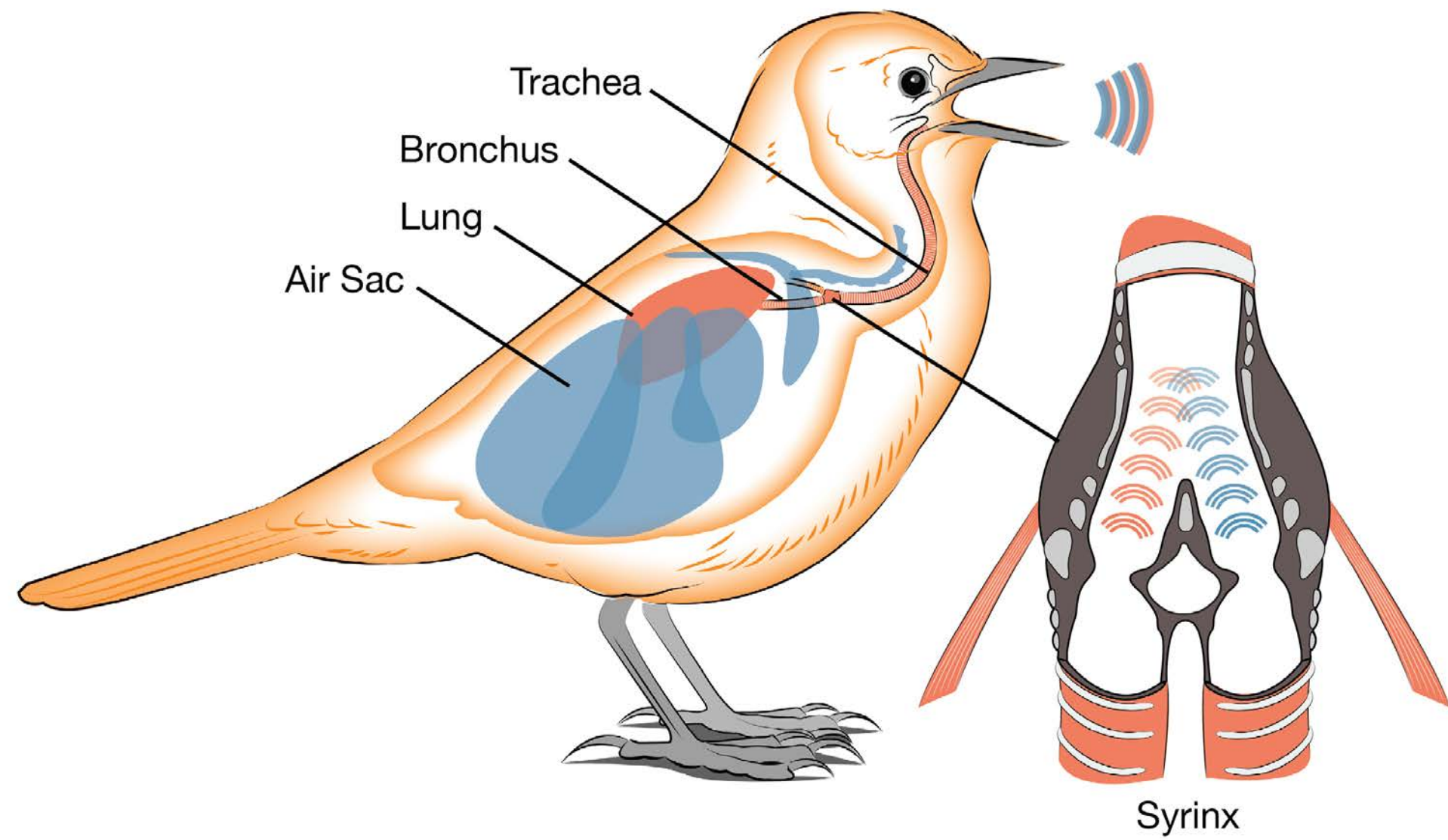
Canaries: Long-range, hierarchical, syntax rules

(Motor syntax and working memory)



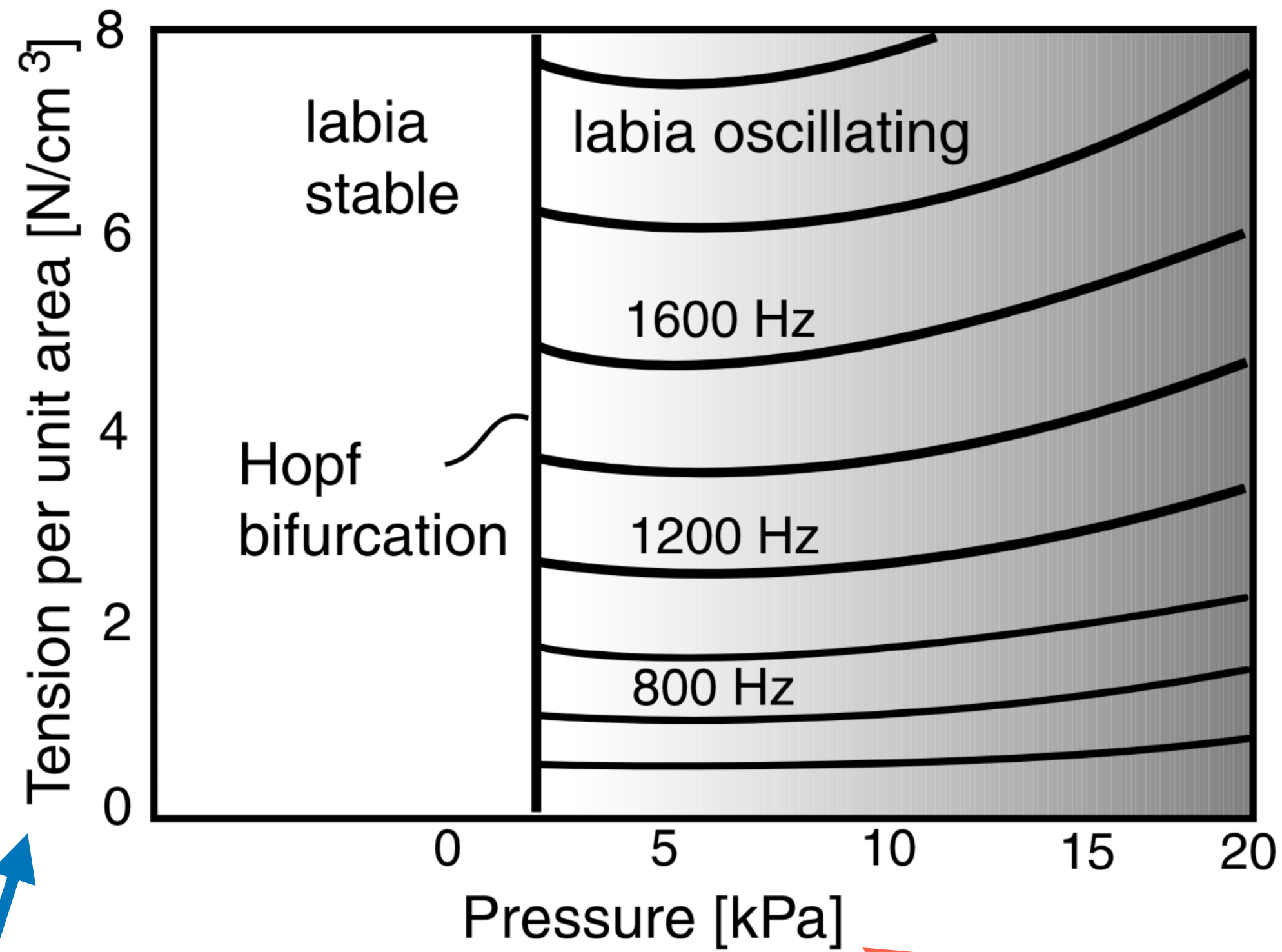


Interlude: Physics of song





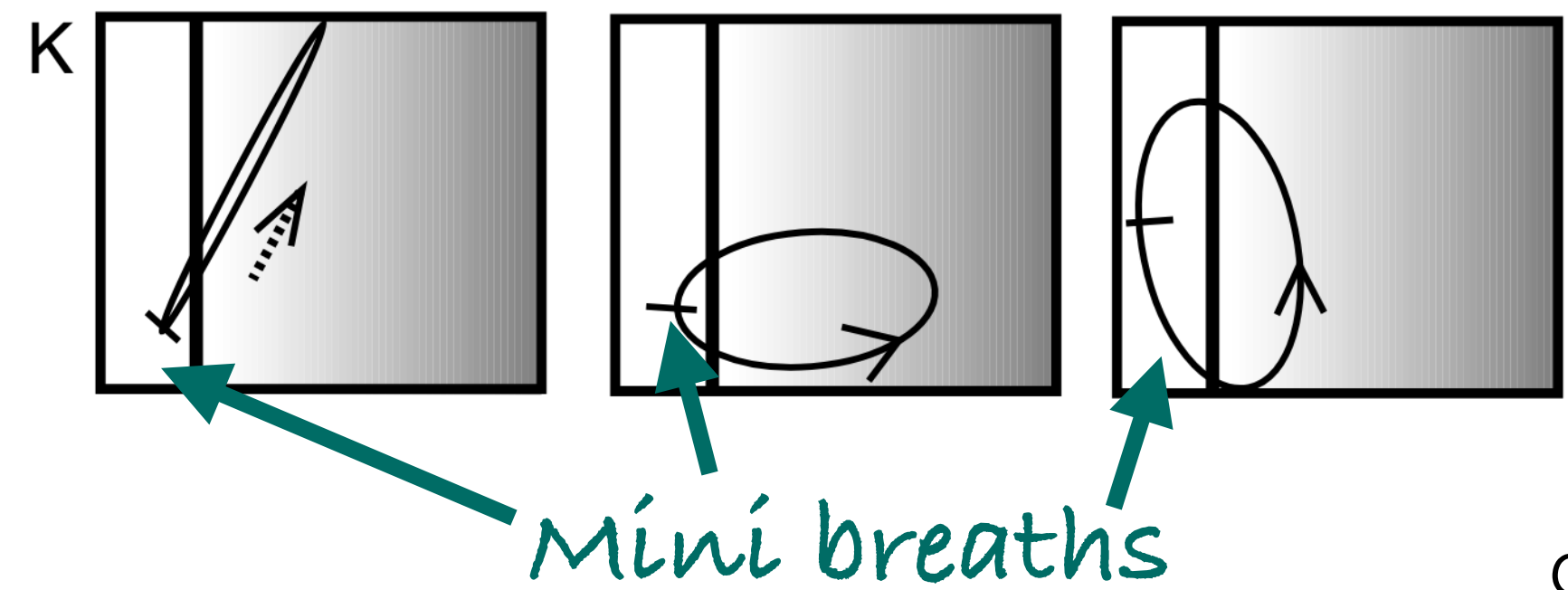
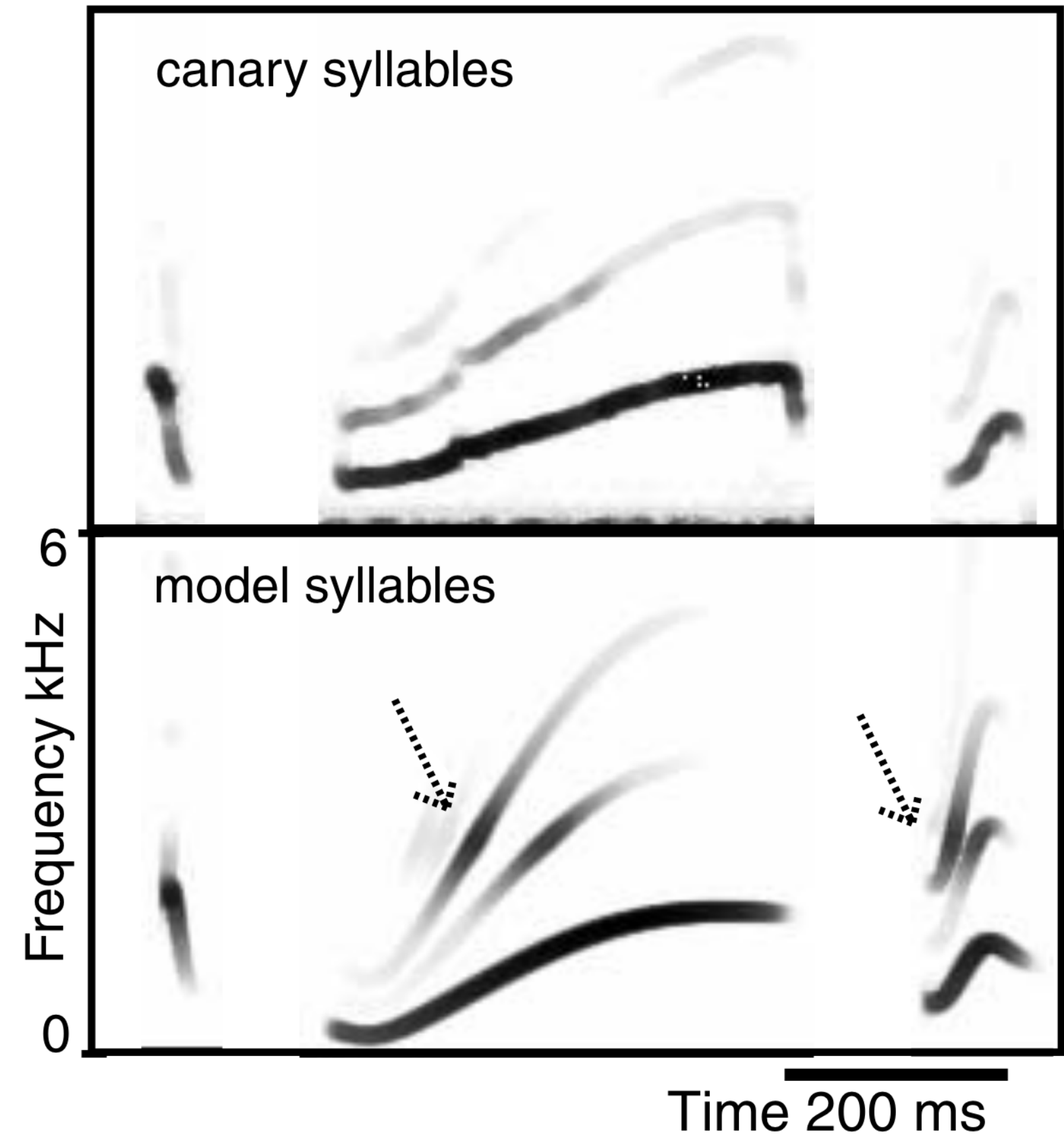
Oscillatory solutions of the labia equations of motion



Muscles

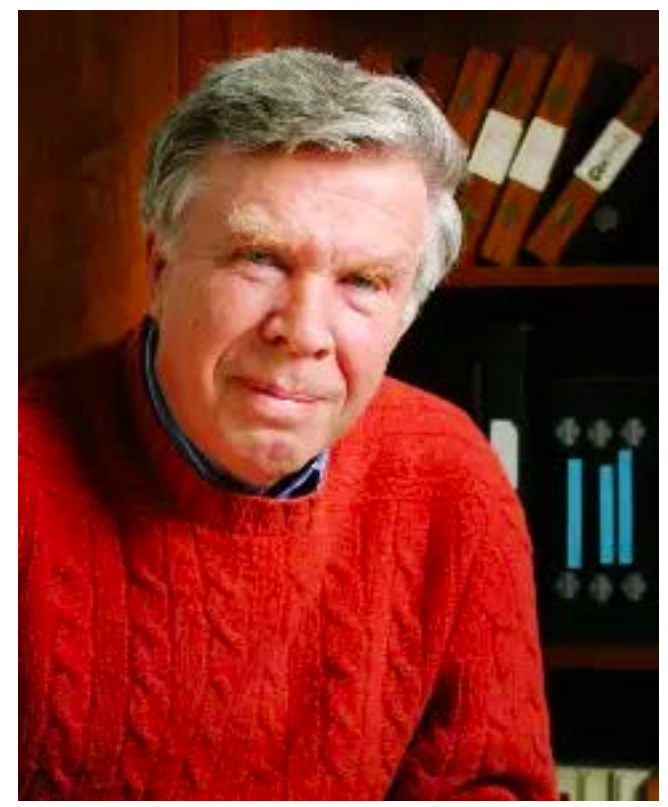
Also:
Beak and trachea filter
Beak clicks

Bronchi
air pressure

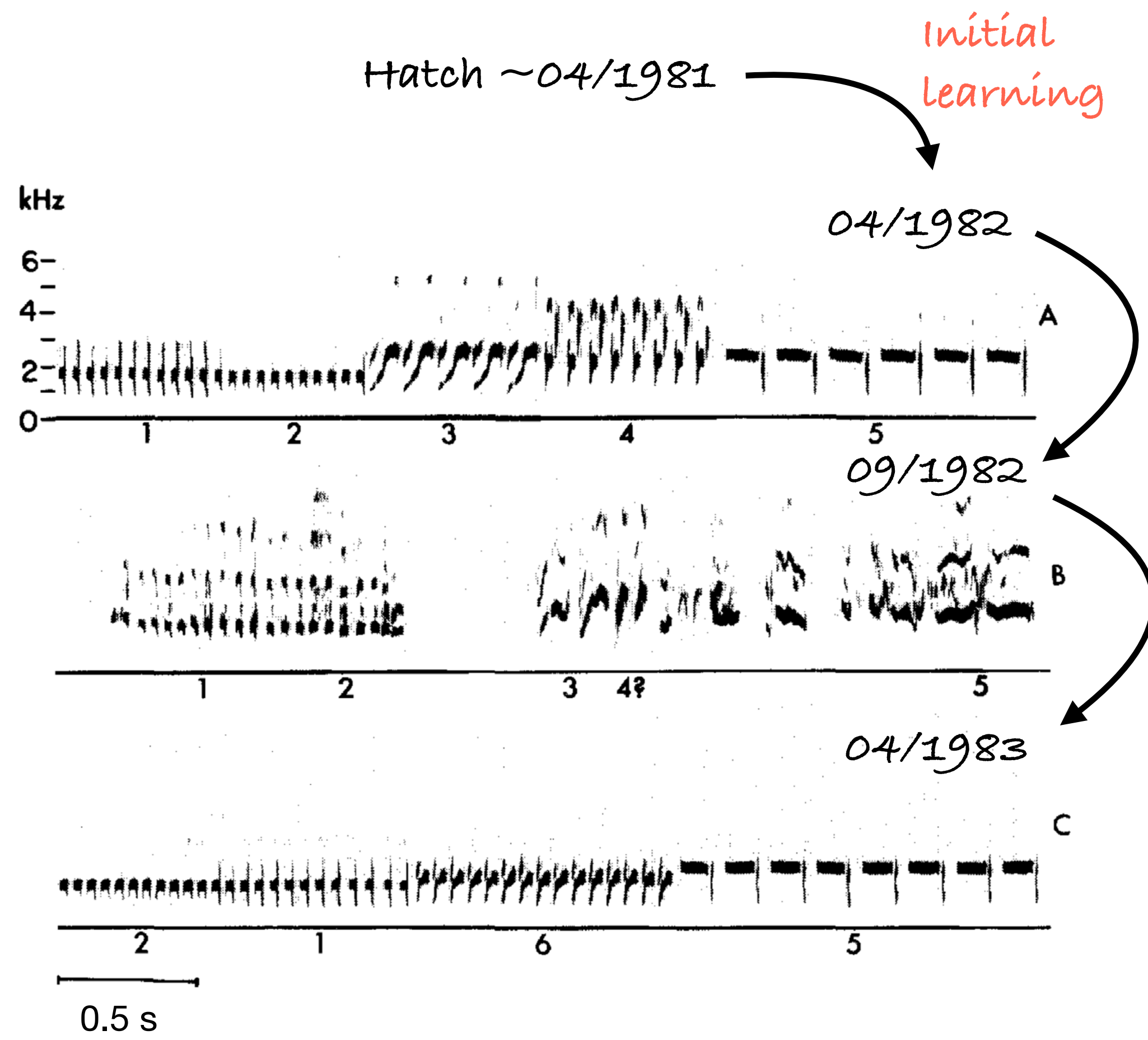




Canary song syntax: Syllable repertoire

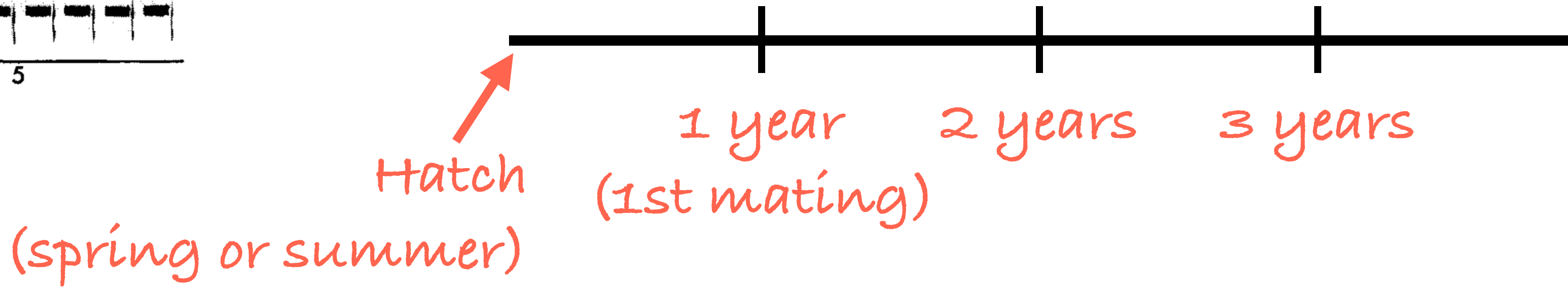


Fernando Nottebohm



~38 ●

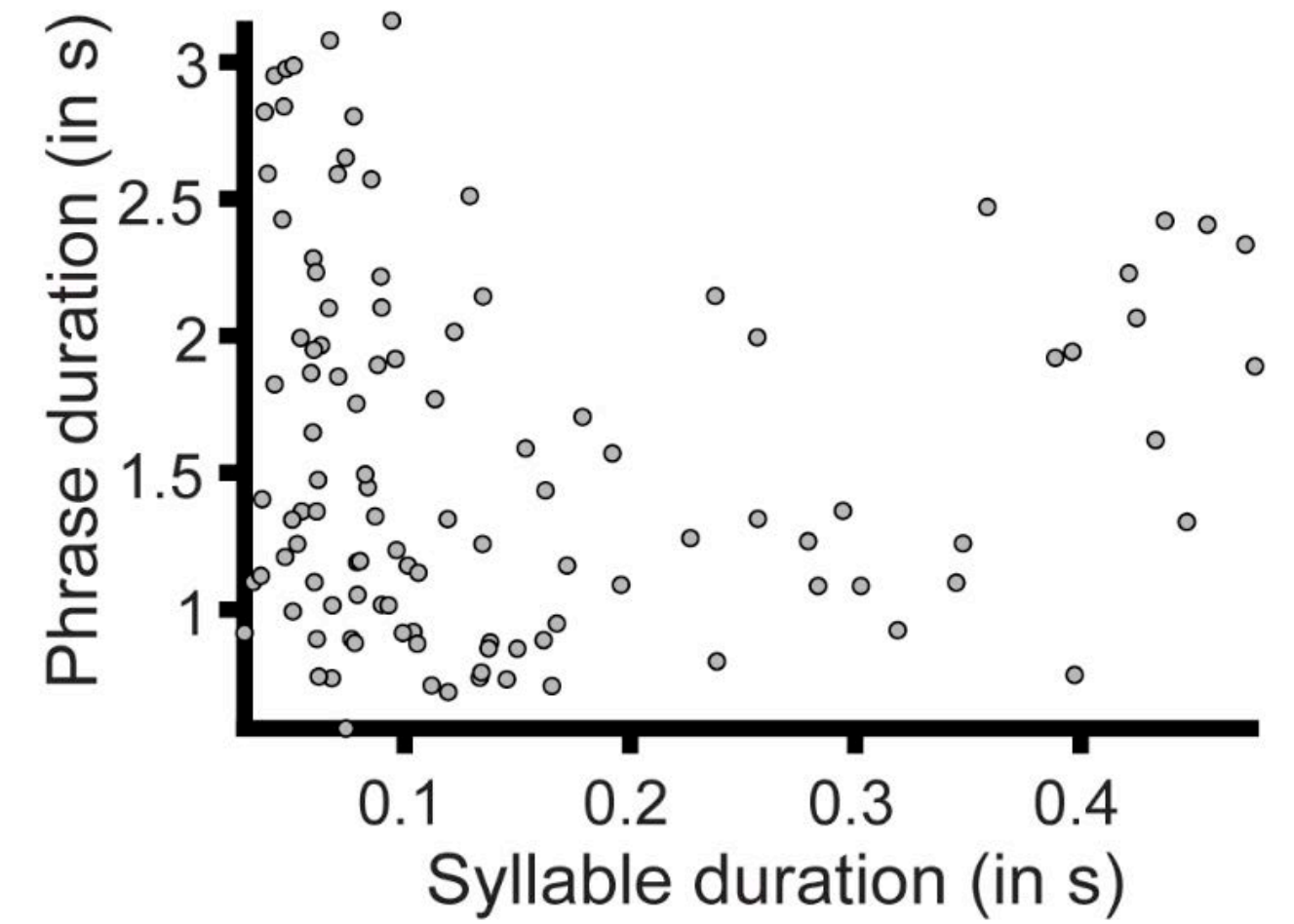
~25 ●
syllables





Canary song syntax: Hierarchical sequences

Syllables compose phrases:



Waterslager canaries
(Markowitz 2013)



Canary phrases are an innate syntactic structure



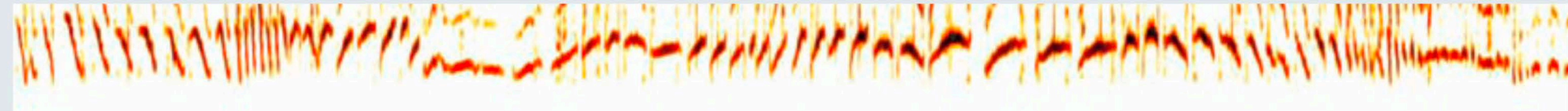
Noam Chomsky

A



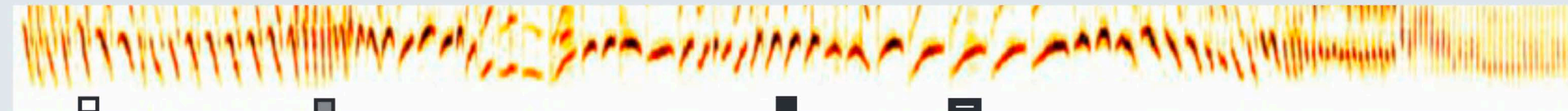
'Tutor'

B



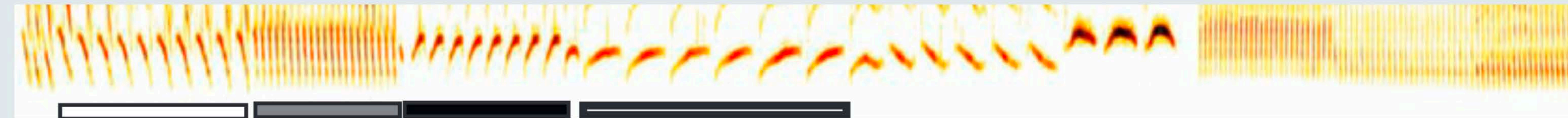
200dph

C



250dph

D

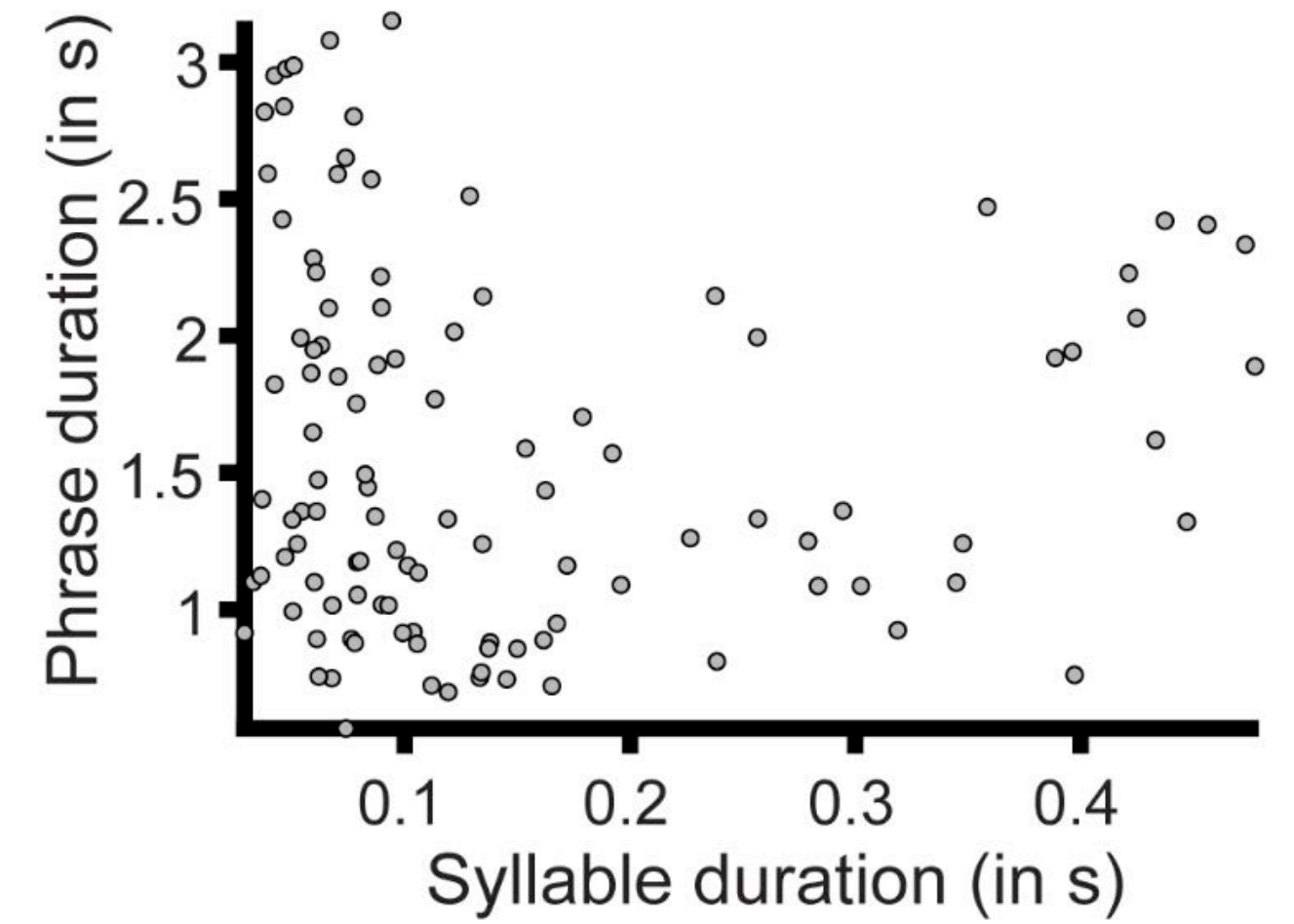


300dph

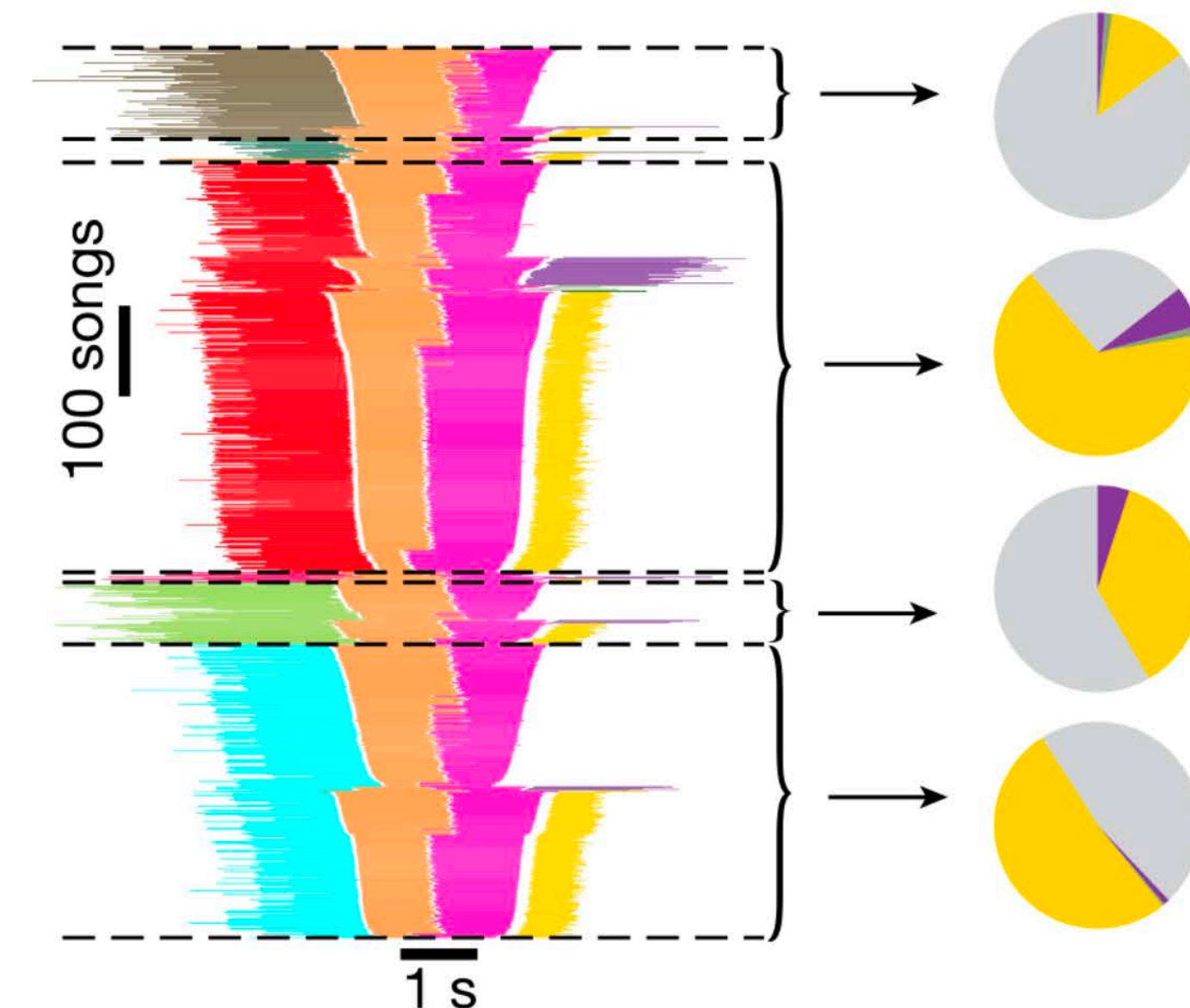
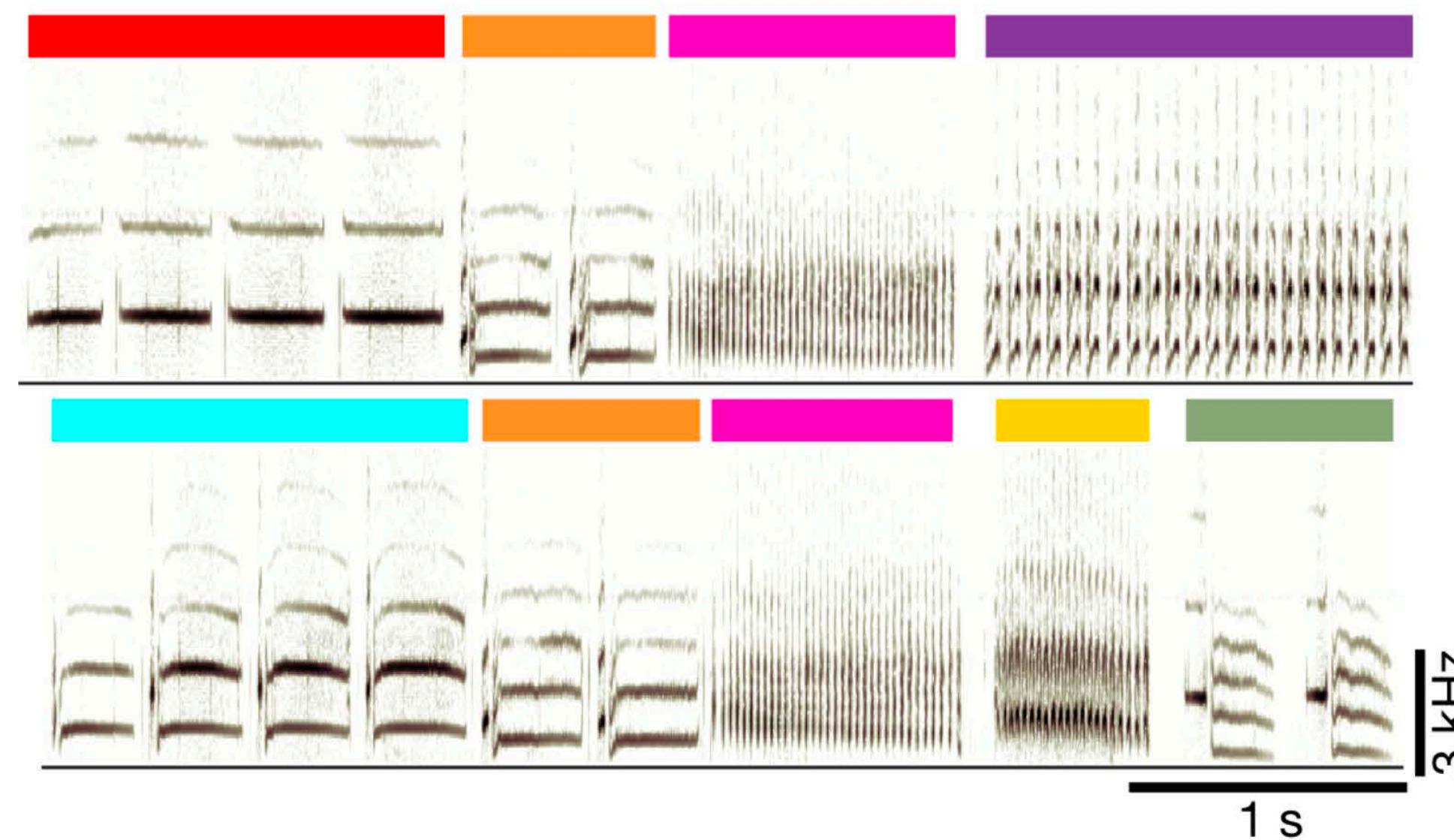
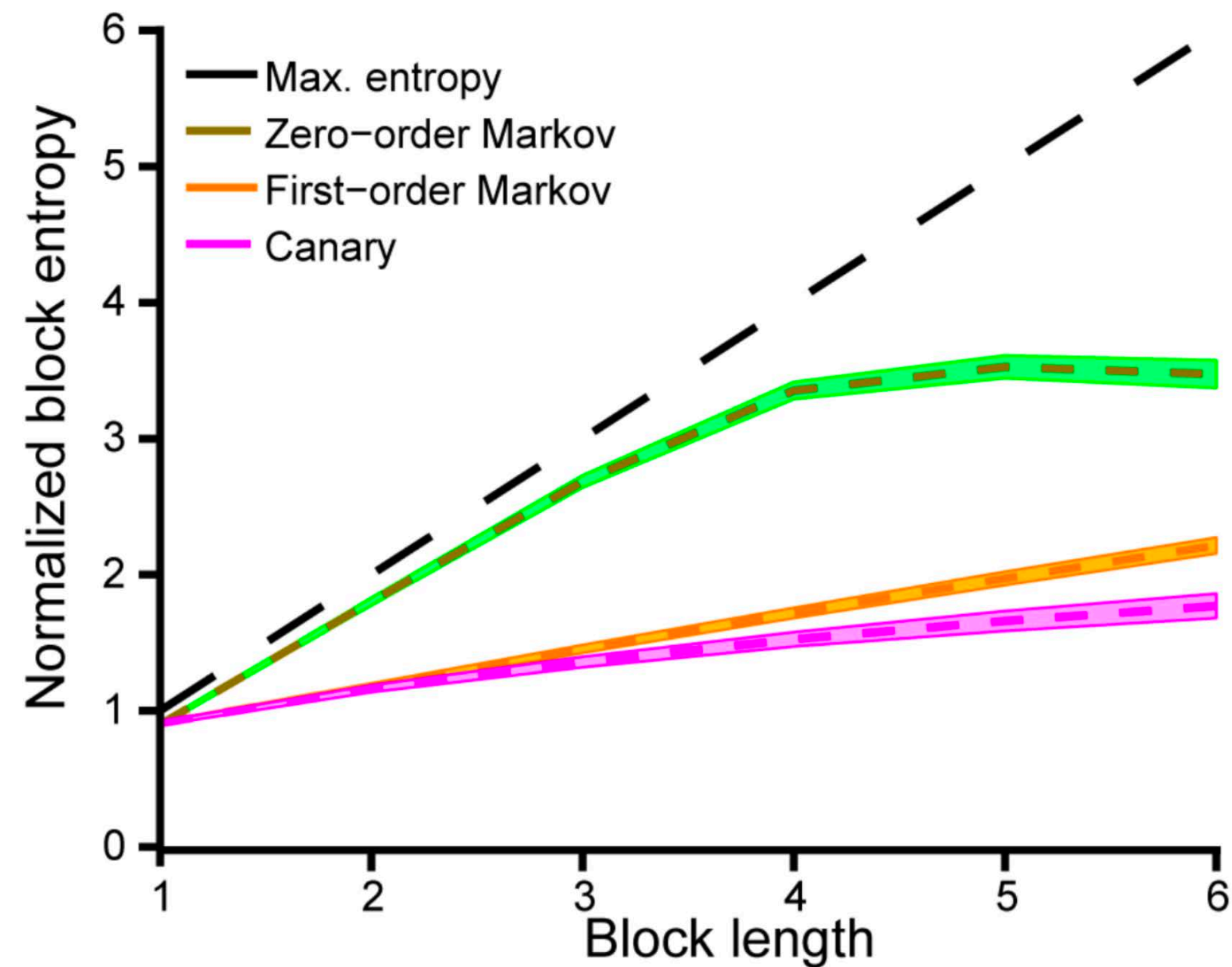


Canary song syntax: Hierarchical sequences

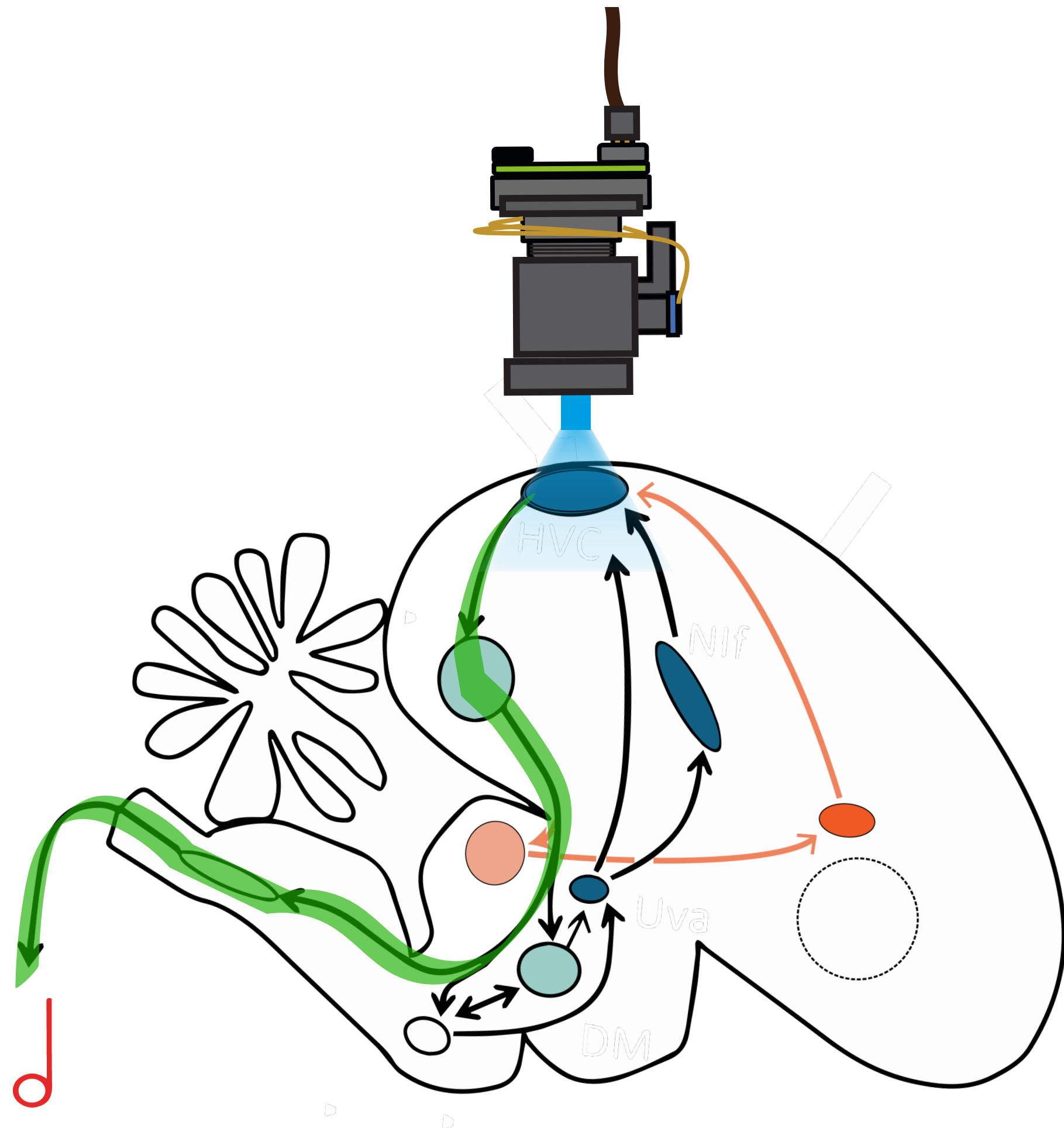
Syllables compose phrases:



Phrase sequences obey long-range syntax rules

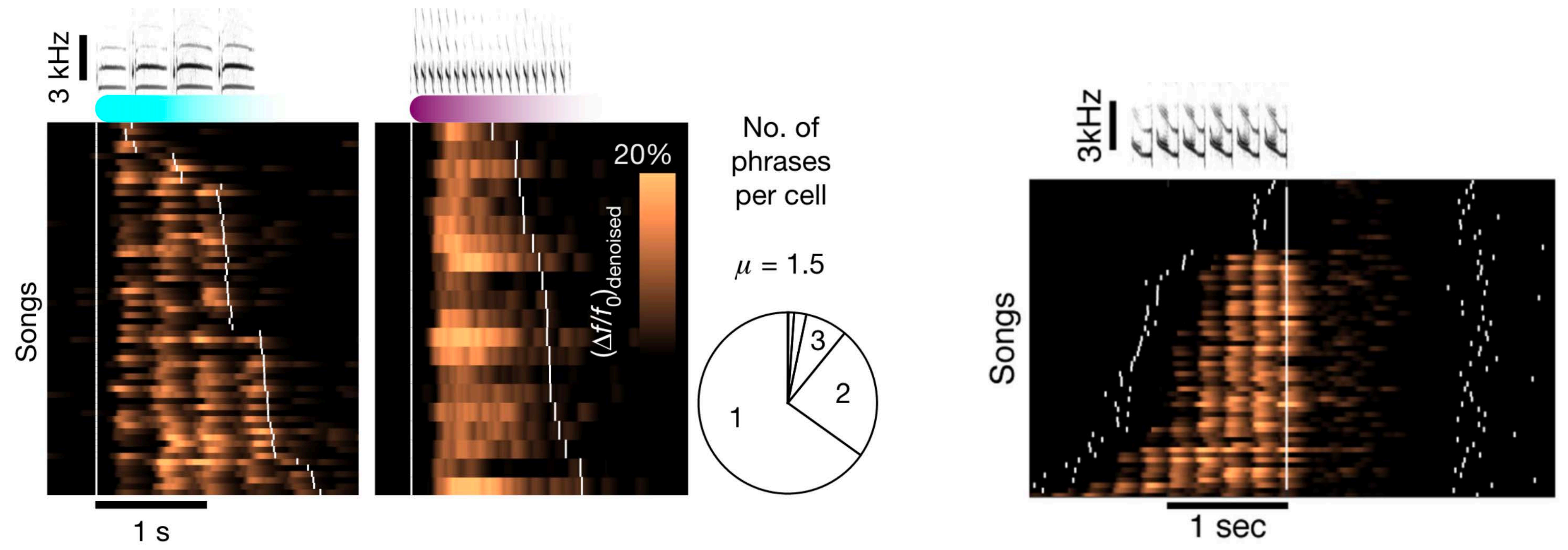


Song-locked canary premotor activity is syllable specific

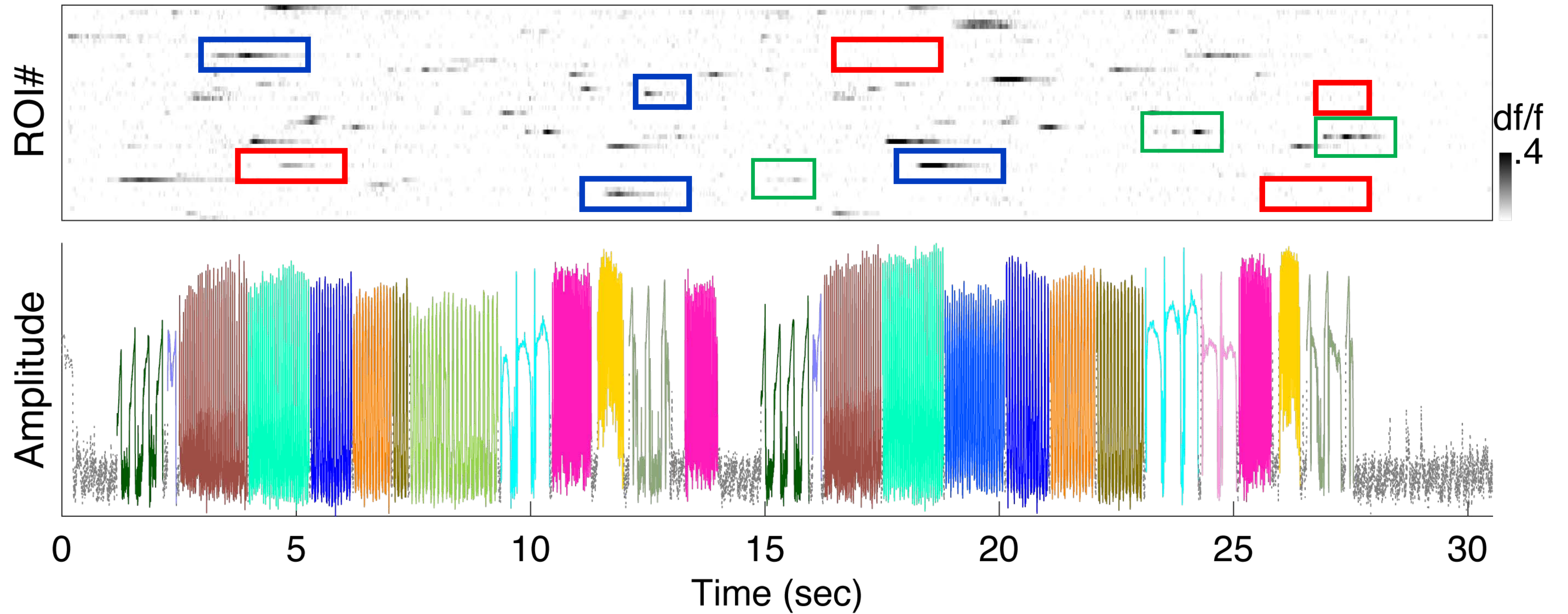


The premotor song circuit

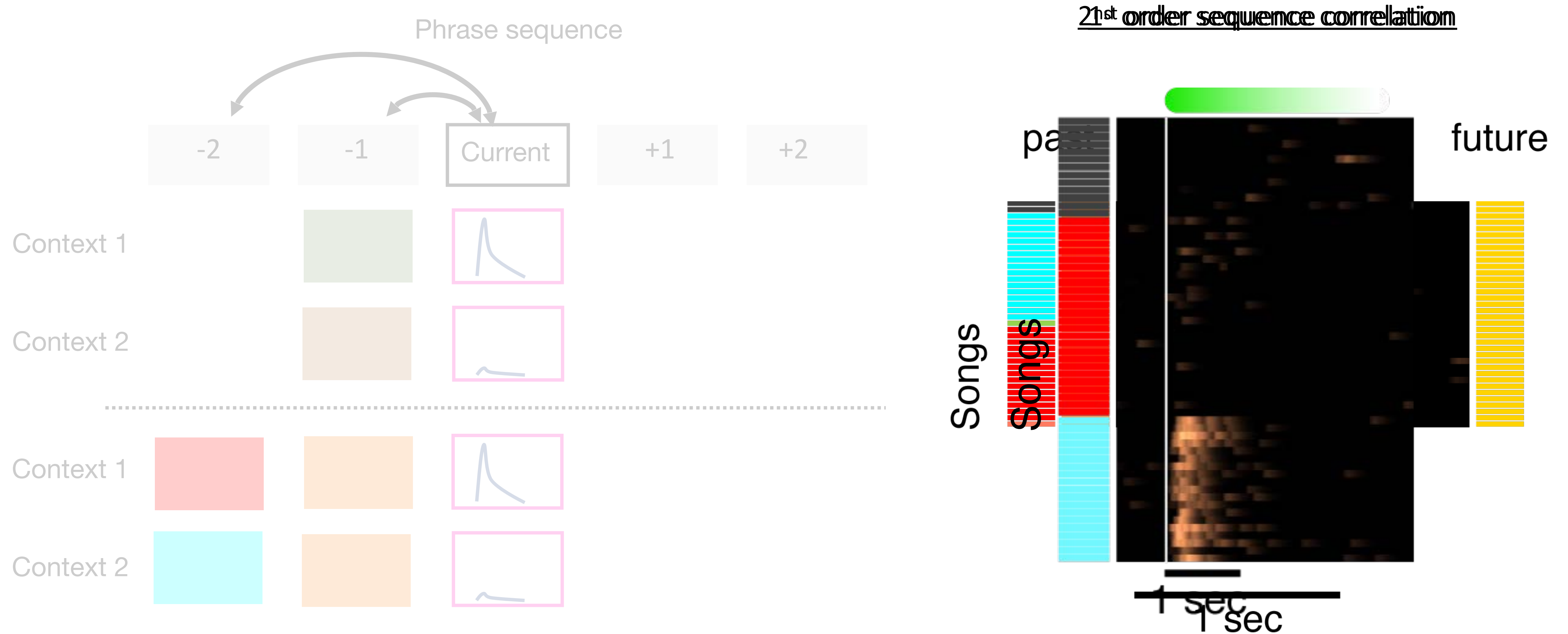
HVC activity is locked to behavior



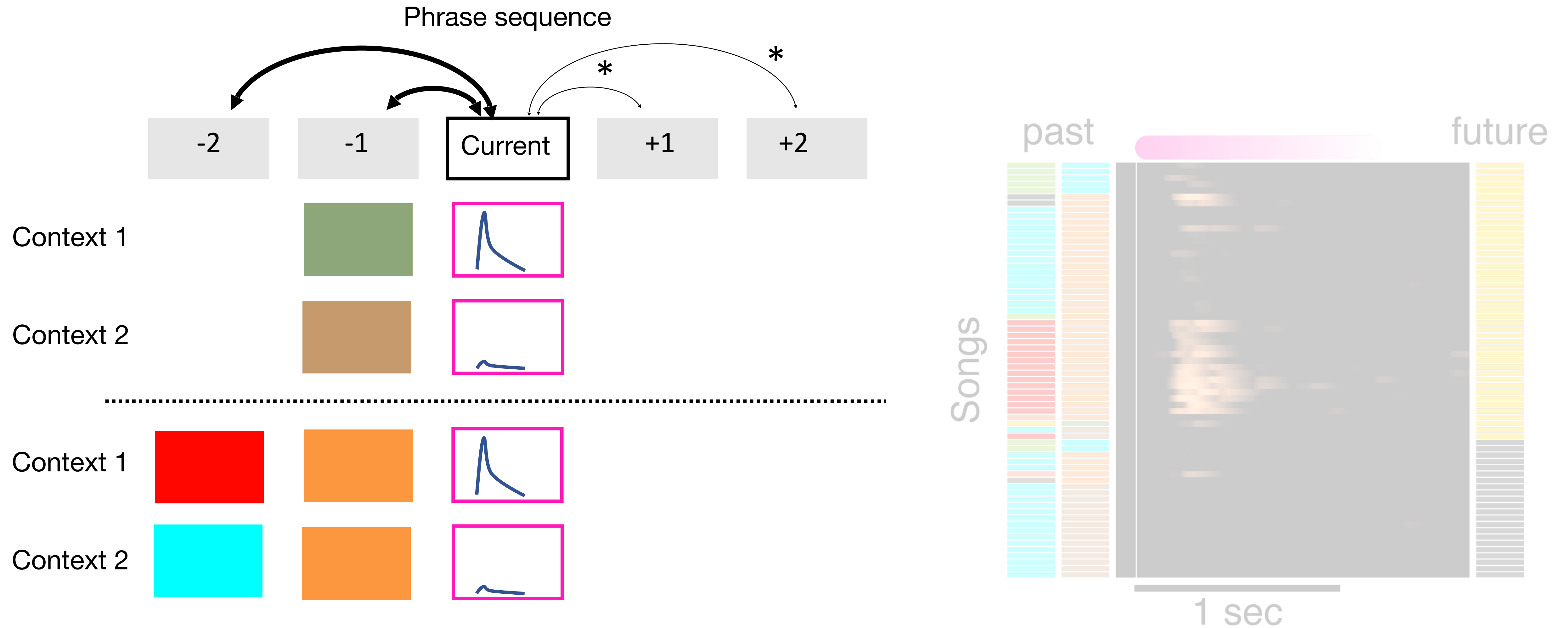
HVC activity is context dependent



HVC neurons reflect long-range sequence information



HVC neurons reflect long-range sequence information

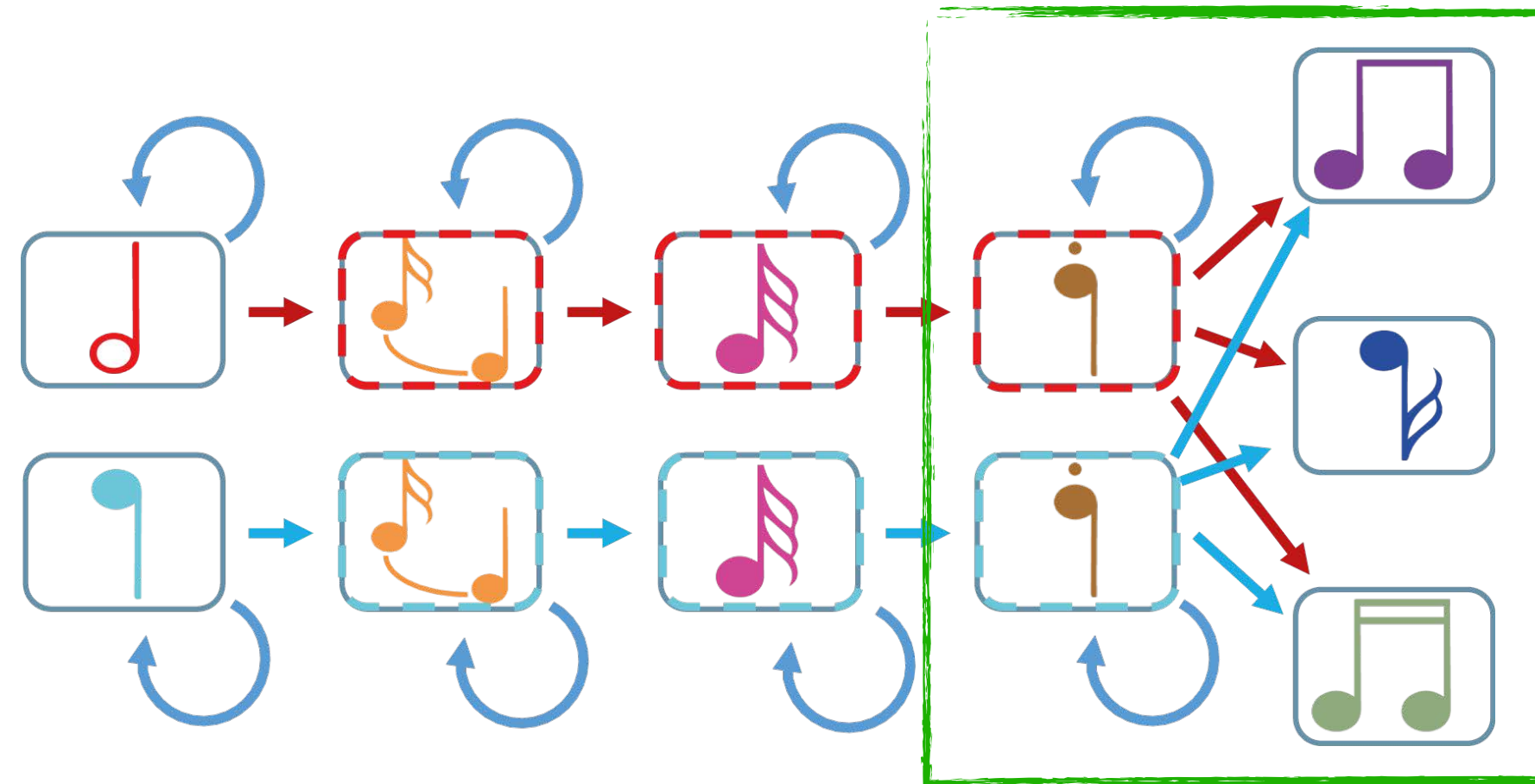


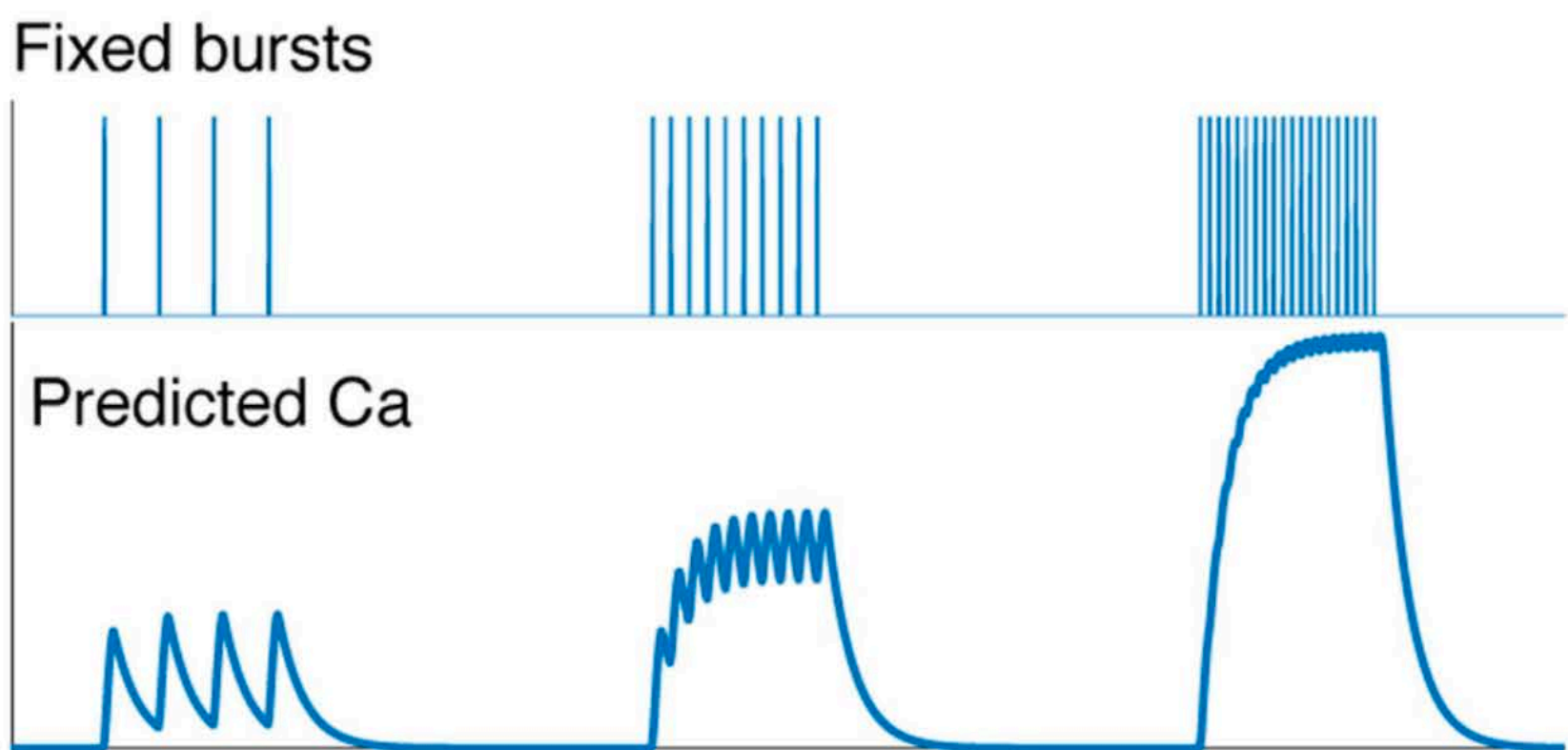
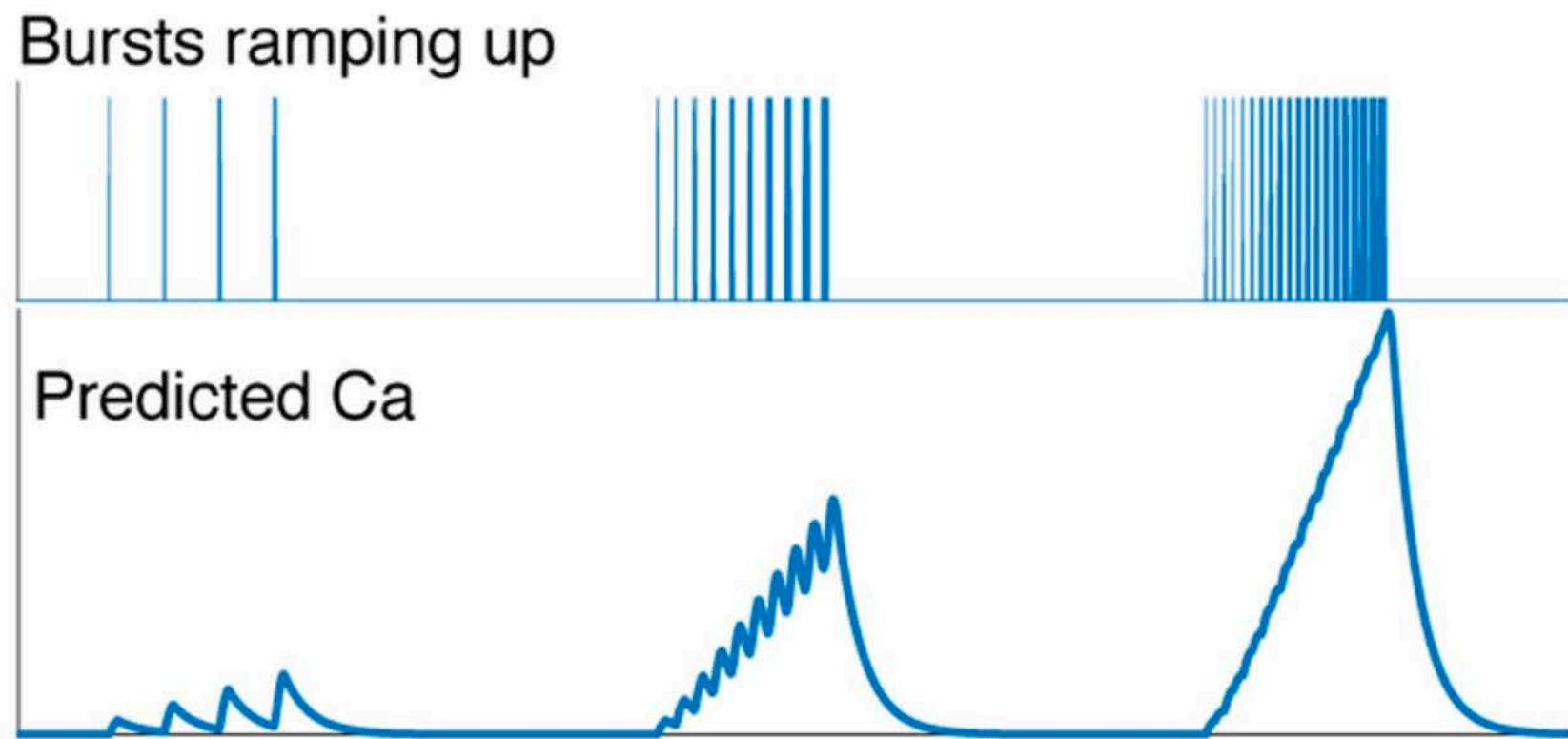
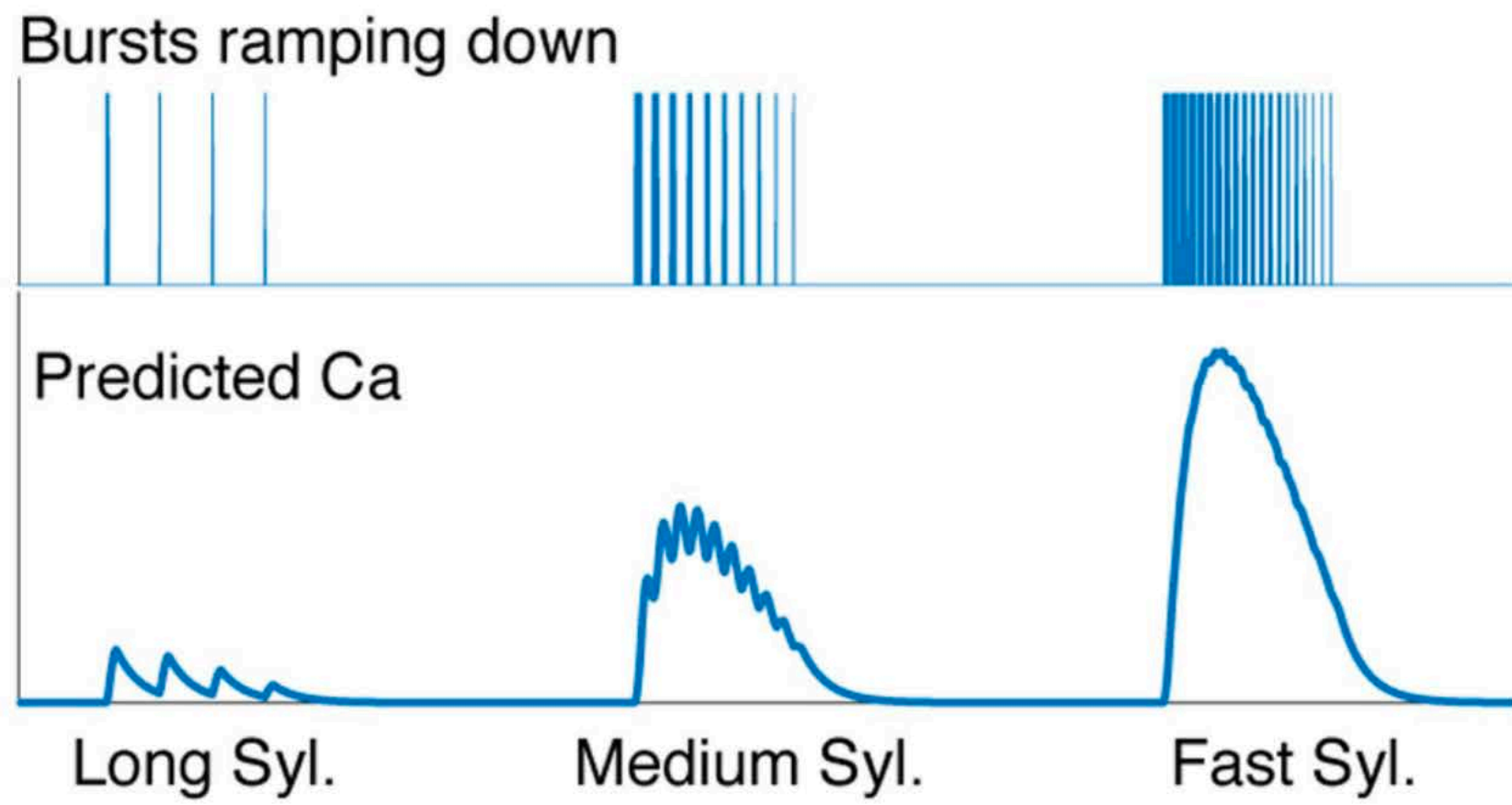
* : $p < 10^{-6}$

The hidden neural states underlying canary syntax

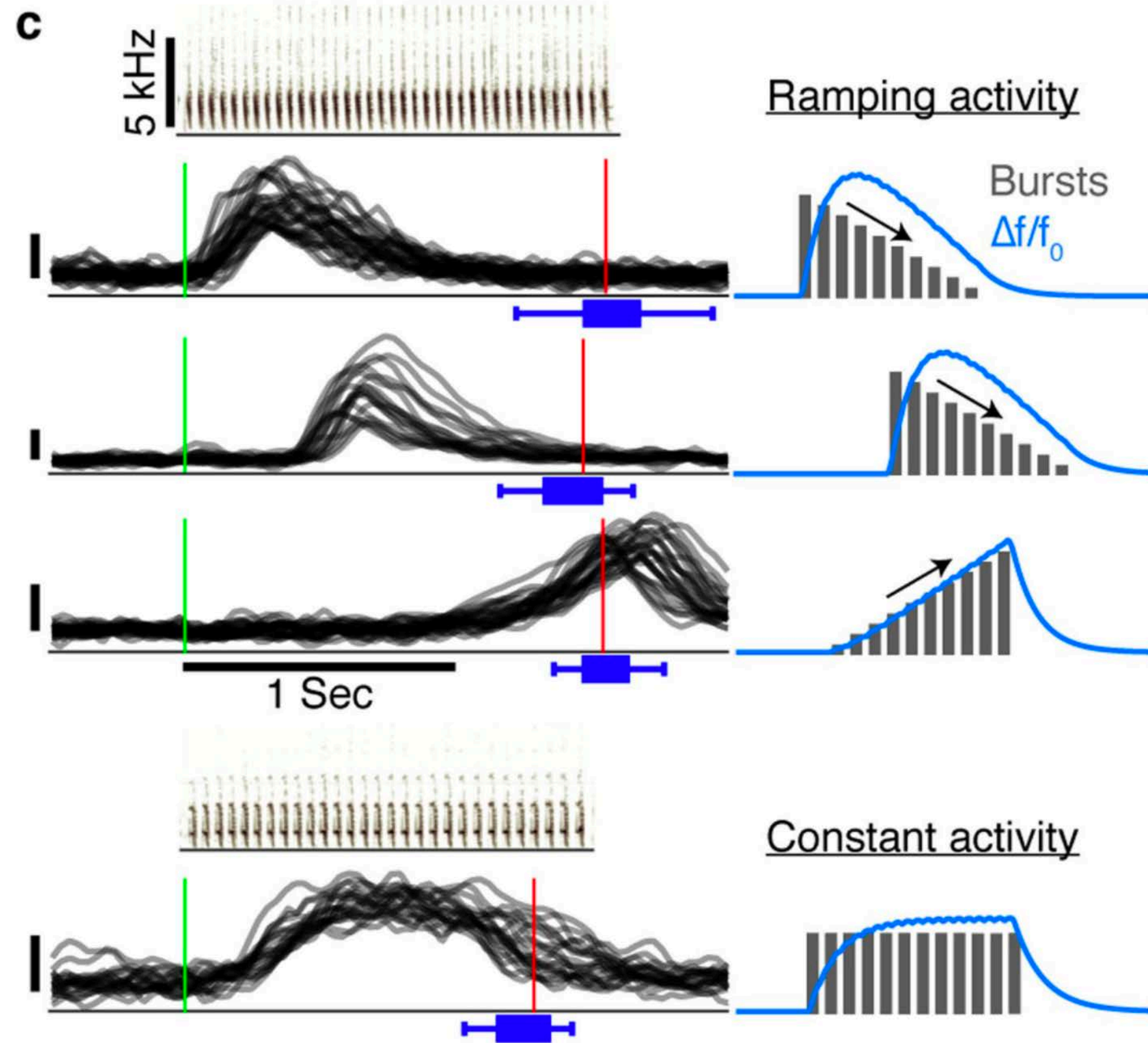


—> Phrase sequence —>

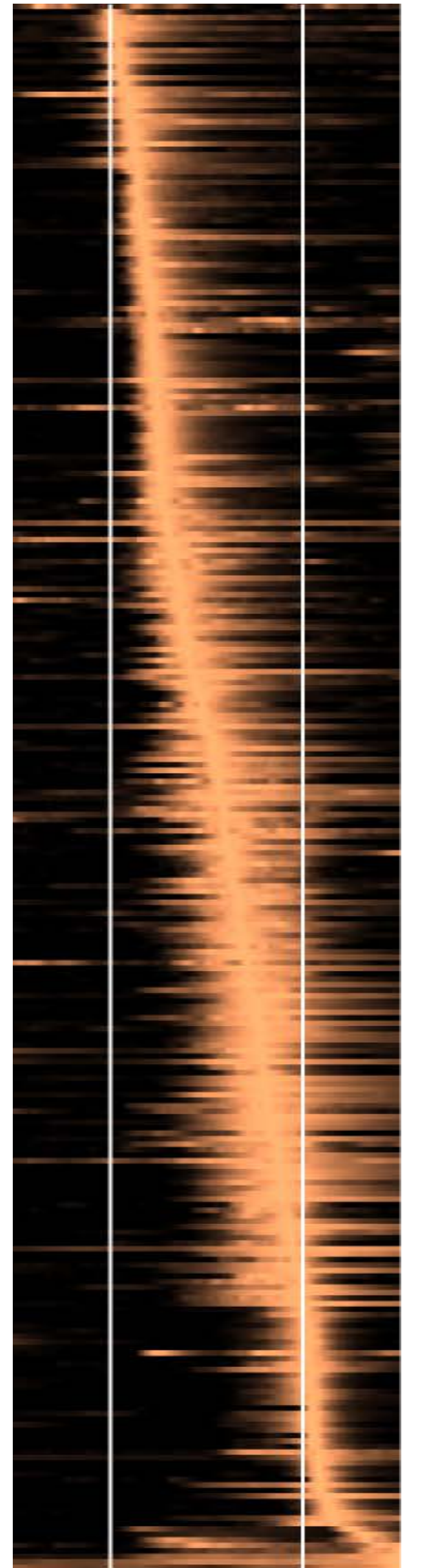




HVC neurons also reflect timing information



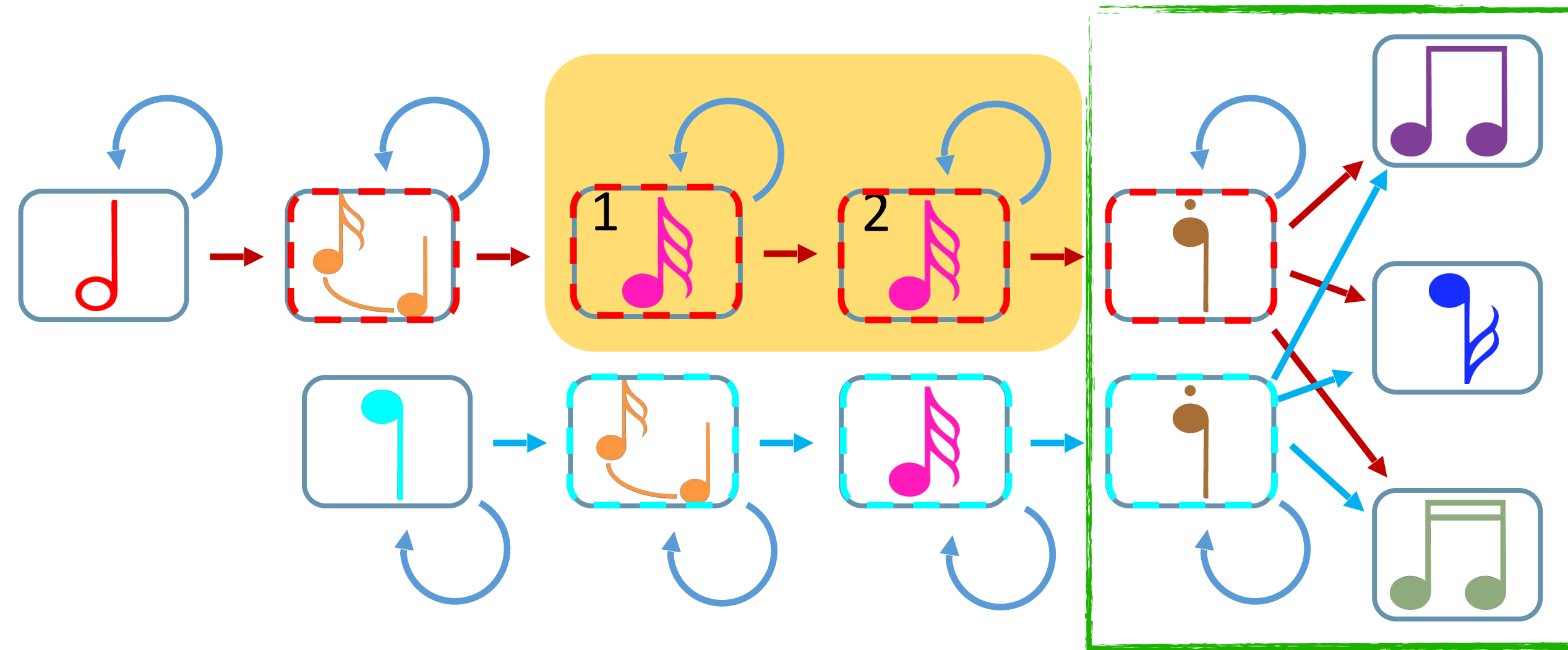
Cells



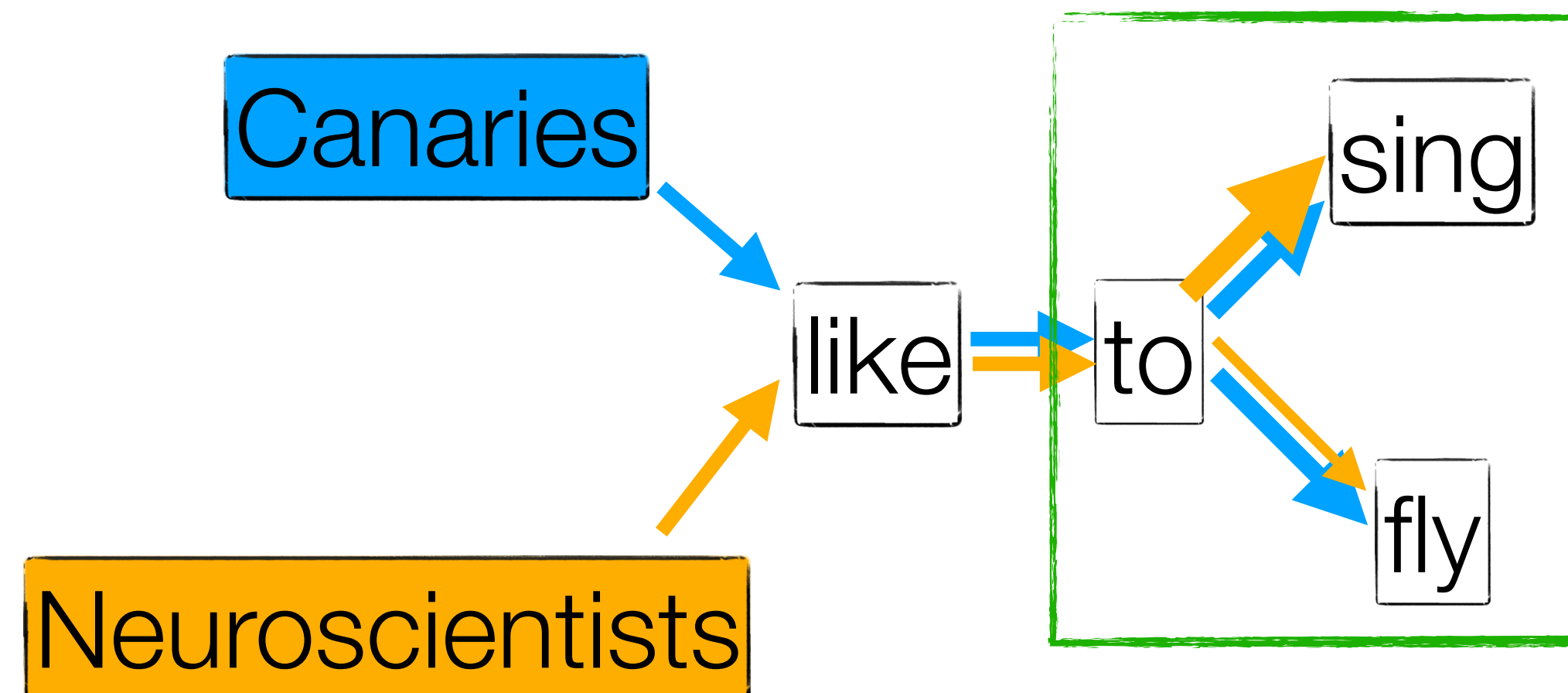
Norm. Time

Interim summary -

Motor working memory model - time scale of 1-7 sec



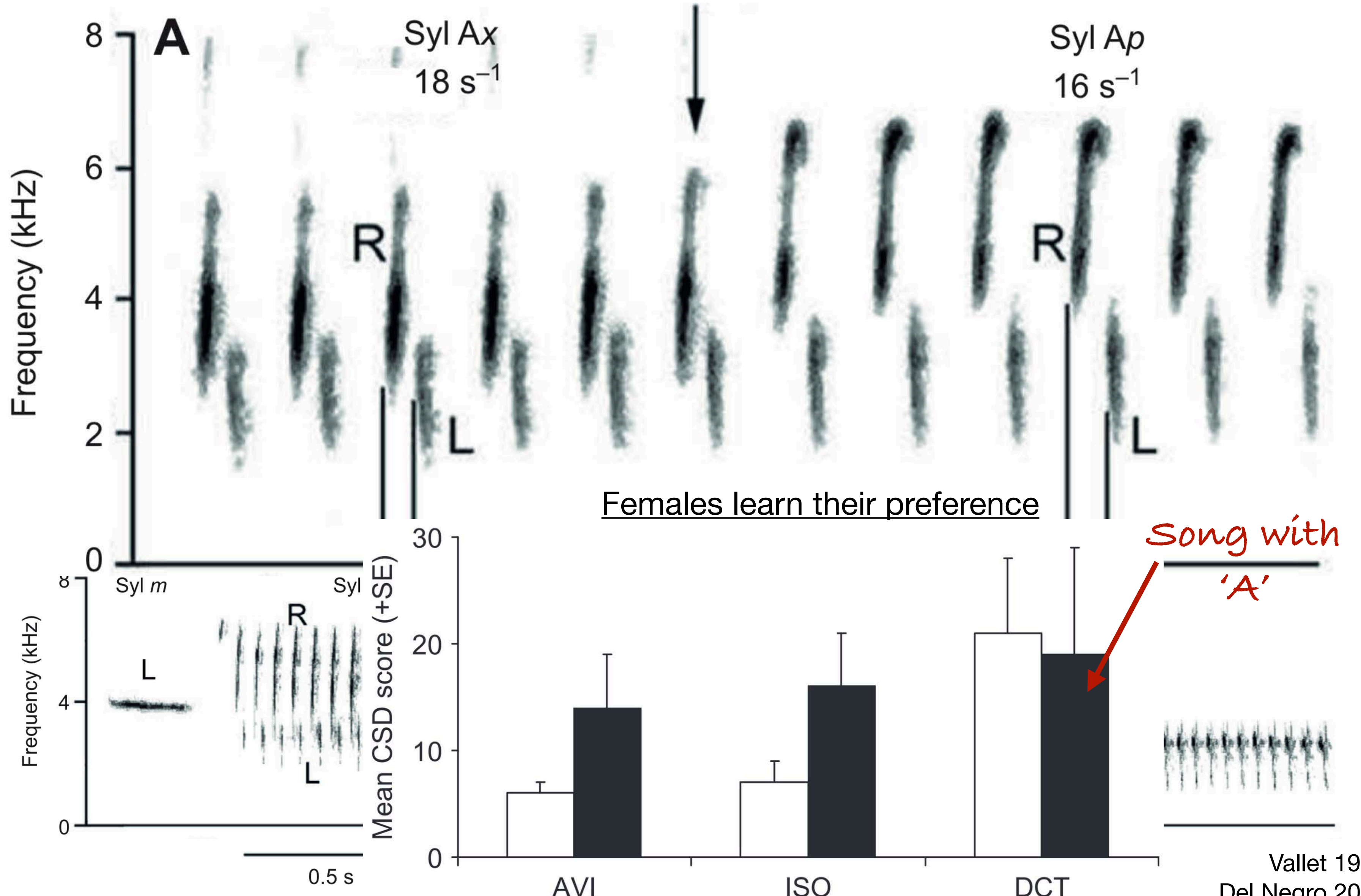
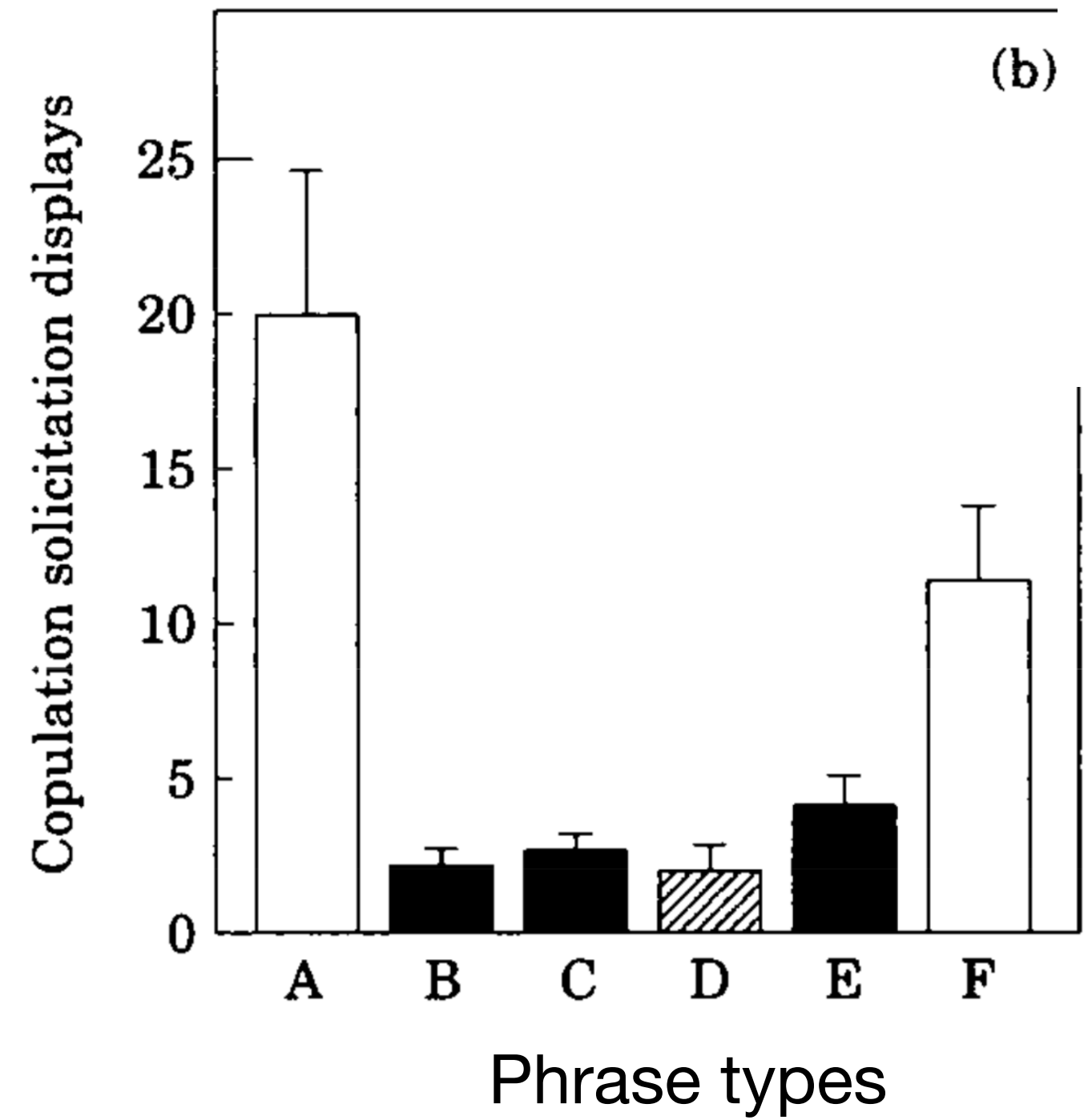
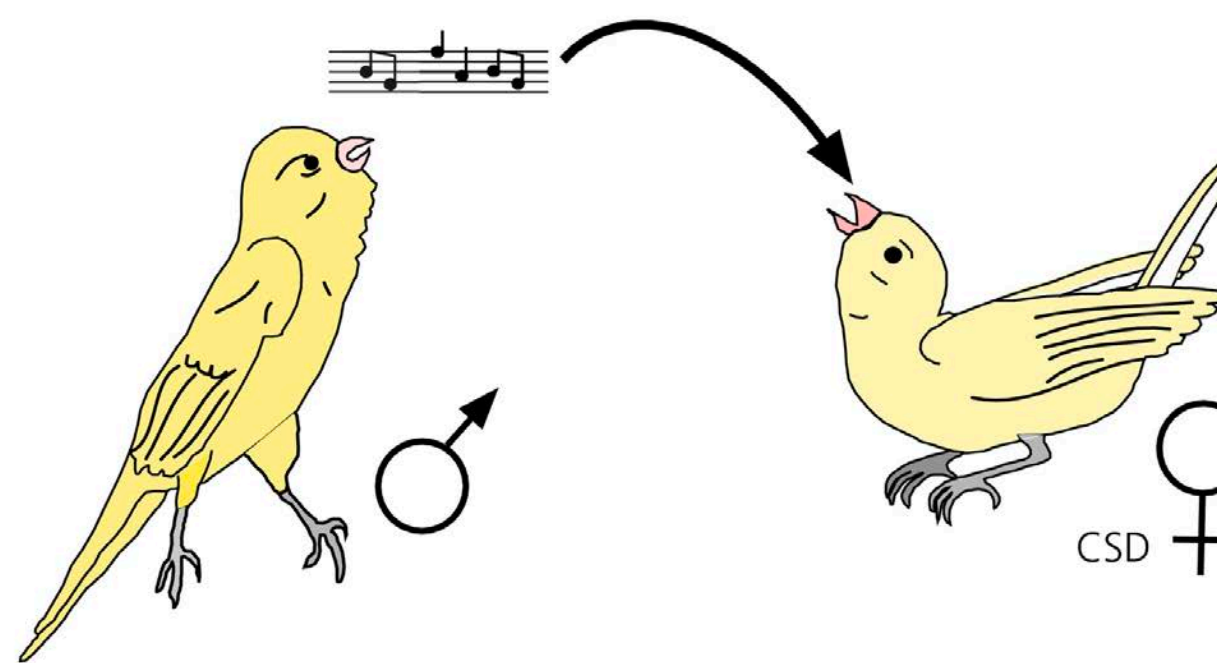
High order syntax rules





Canary song preferences

Rapid inter-hemispheric coordination



T = Tutored



Canaries: Neurogenesis and adult plasticity

Neurogenesis: In mammals, HPC and OB. In birds, most of the telencephalon.

Table 1. Ratio of spring to fall measures of brain variables.

Variable	Mean \pm standard deviation		<i>P</i>	Spring: fall ratio
	Spring	Fall		
HVc* (mm ³)	0.884 \pm 0.243	0.444 \pm 0.105	< .001	1.99
RA* (mm ³)	0.519 \pm 0.114	0.293 \pm 0.058	< .001	1.77
Rt† (mm ³)	0.572 \pm 0.056	0.481 \pm 0.039	< .001	1.19
SpM† (mm ³)	0.111 \pm 0.015	0.099 \pm 0.013	> .05	1.12
Caudal forebrain* (mm ³)	7.93 \pm 0.120	6.47 \pm 0.440	< .001	1.23
Brain weight (g)	0.754 \pm 0.065	0.655 \pm 0.041	< .001	1.15
HVc:Rt	0.764 \pm 0.186	0.463 \pm 0.118	< .001	1.65
RA:Rt	0.608 \pm 0.213	0.385 \pm 0.122	< .001	1.58

*Corresponds to volume reconstruction of left and right structures.
†Corresponds to volume reconstruction of left structures.

†Corresponds to volume reconstruction of left structures.

Seasonal anatomical changes

Neurogenesis and neuronal recruitment

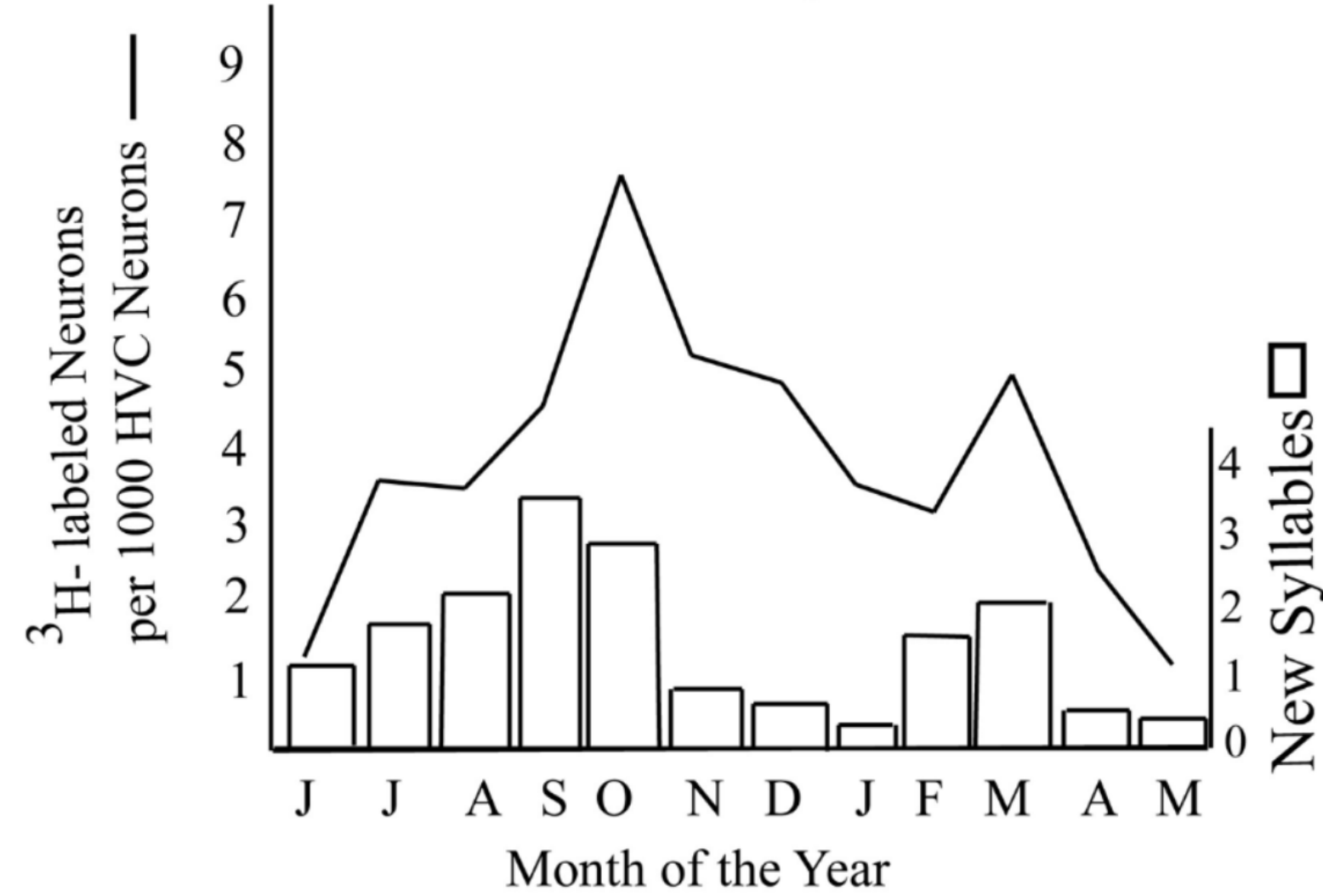
Hormones, circuit, and song interaction

What are the potential benefits?

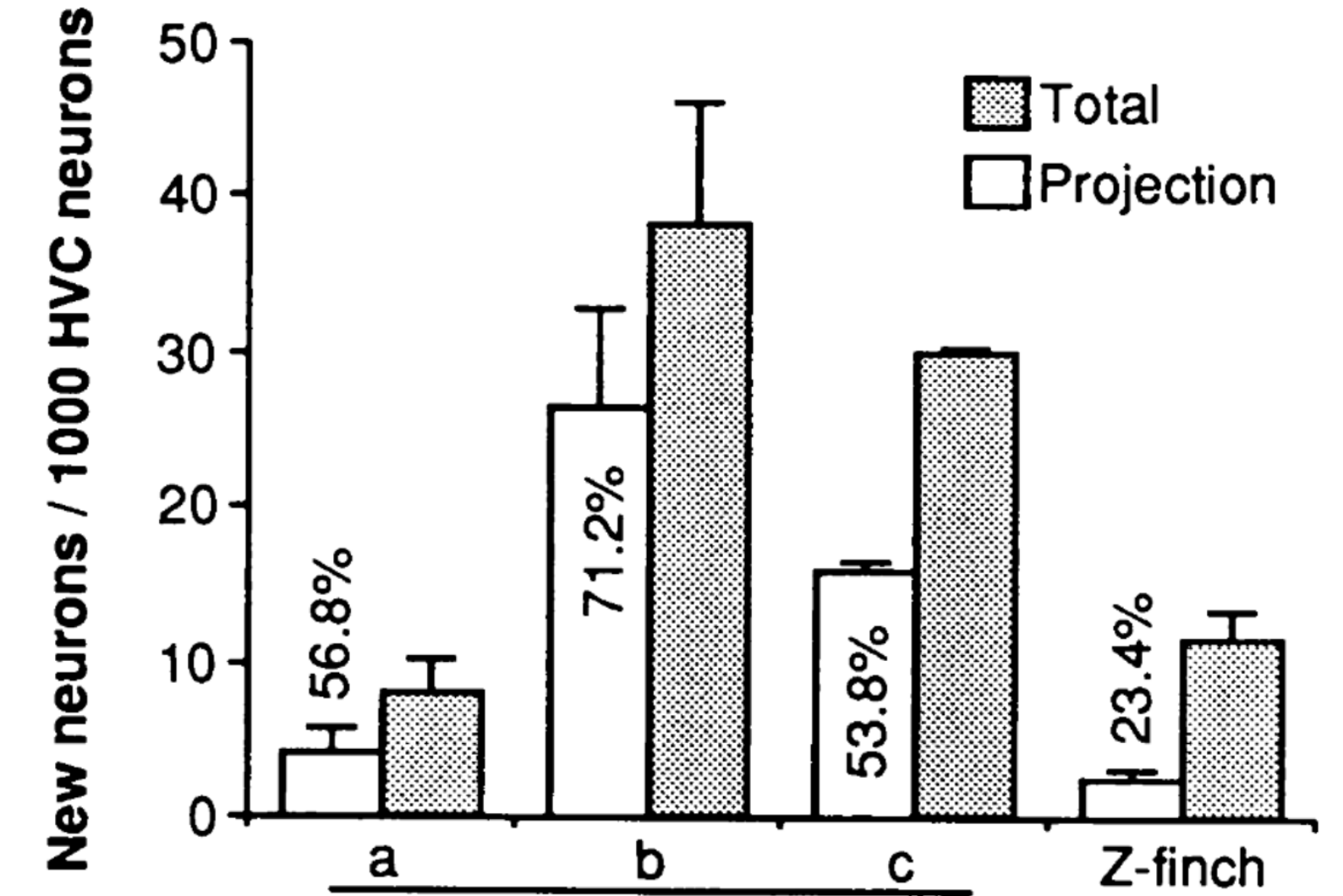
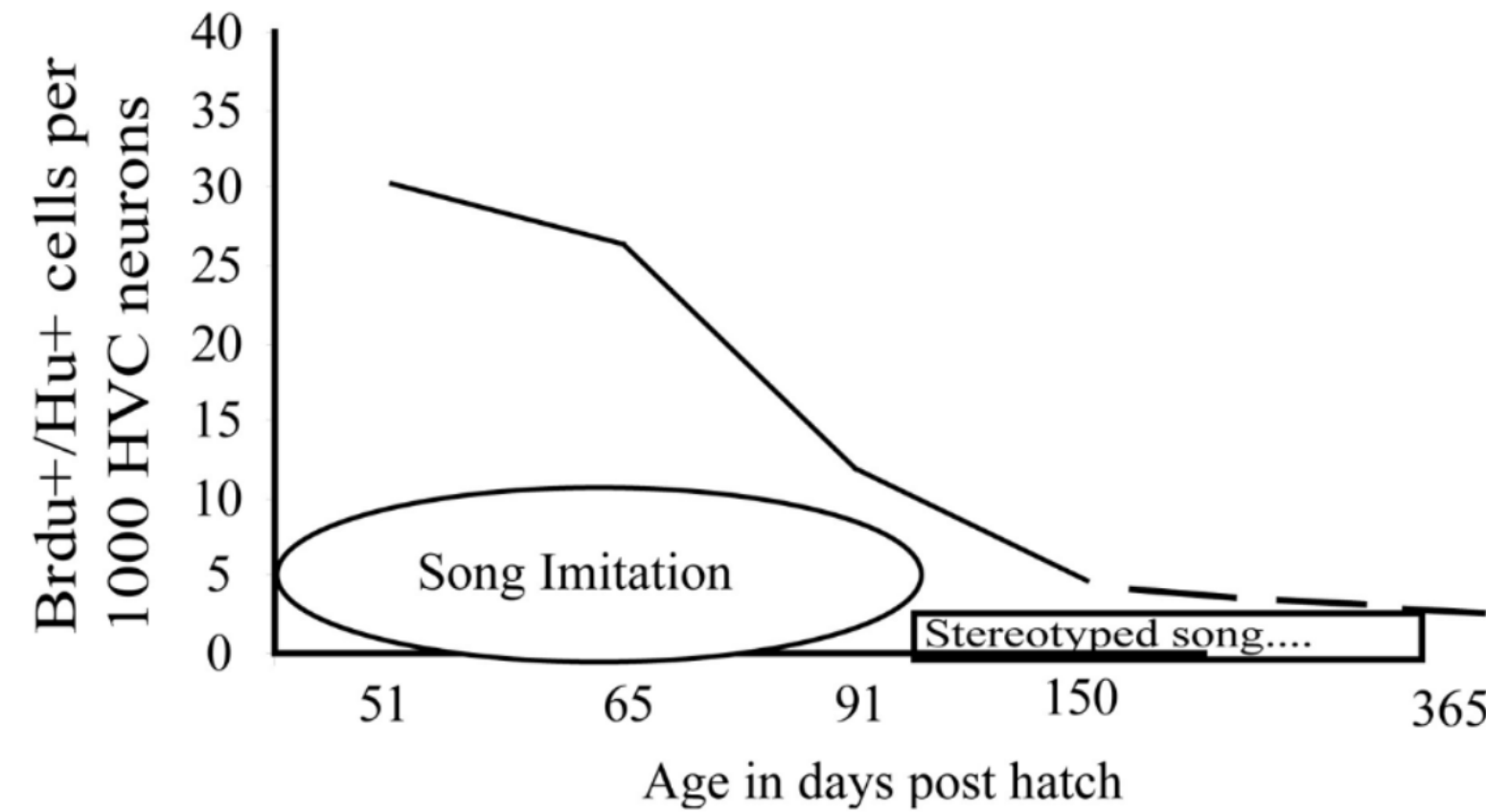


Canaries: Neurogenesis and adult plasticity

Canary



Zebra Finch



1yr, spring
1yr, 4yr, fall fall

SEASONAL CHANGES IN THE EXPRESSION OF THE ANDROGEN RECEPTOR (AR)- AND ESTROGEN RECEPTOR (ER)-mRNA IN THE HVC (MEAN ± SE)

Silvergrains/Cell in HVC	ARmRNA	ERmRNA
Autumnal singing period	14.5 ± 2.3	12.1 ± 4.2
Early breeding season	17.3 ± 4.1	14.2 ± 2.9
Late breeding season	10.2 ± 3.7	2.1 ± 1.0
Moult	4.2 ± 2.2	2.5 ± 1.2

Which neurons get replaced?

In X, interneurons

In HVC, mostly HVCRA, some interneurons

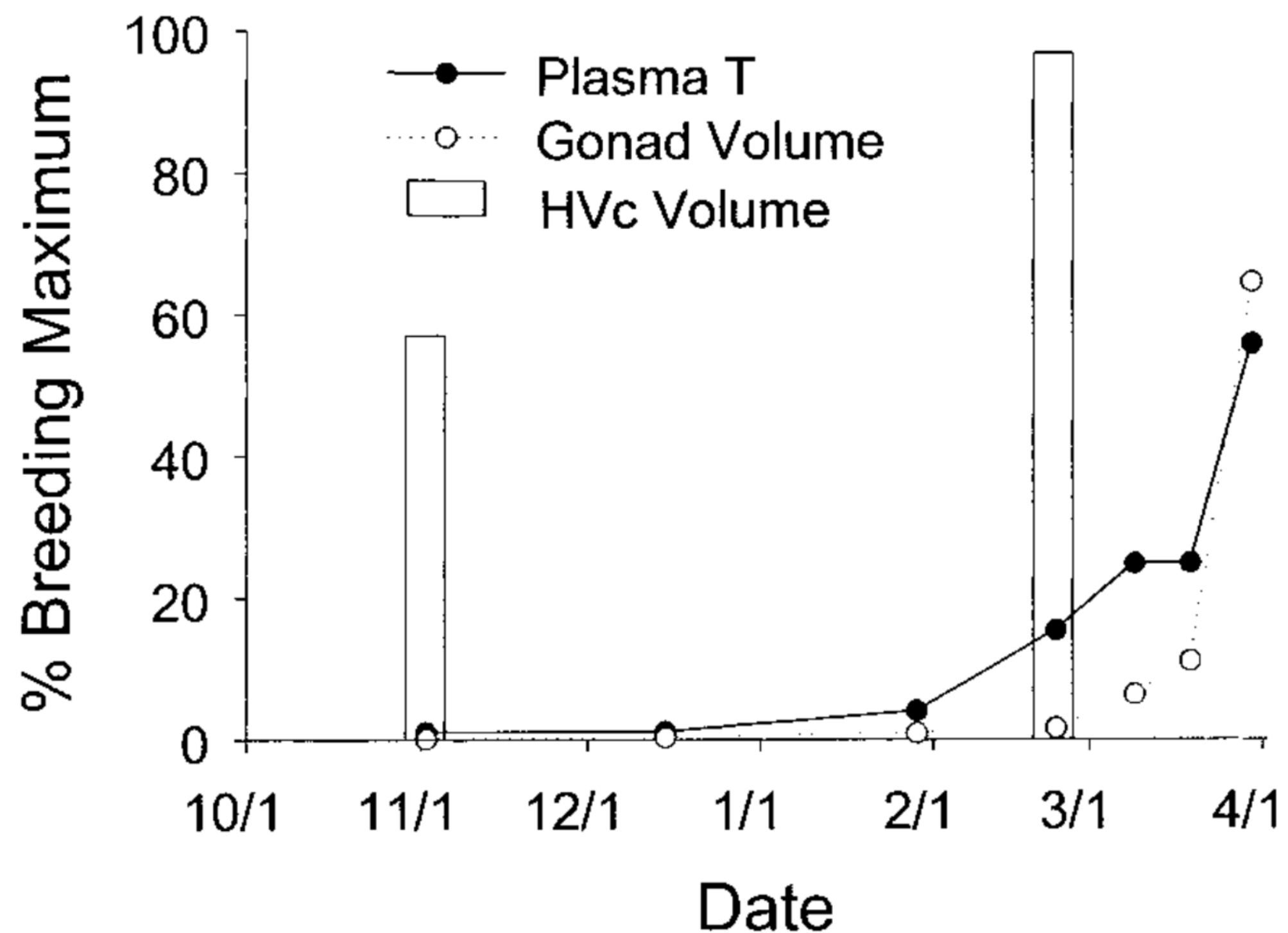
About 50% replaced every year

Which contributes more to HVC growth, hormones? Or singing?



Testosterone and adult plasticity

HVC growth precedes reproductive development



Tramontin 2001, In sparrows

Experiment in Gambel's white-crowned sparrows:
Jump from short to long photoperiod + Testosterone.

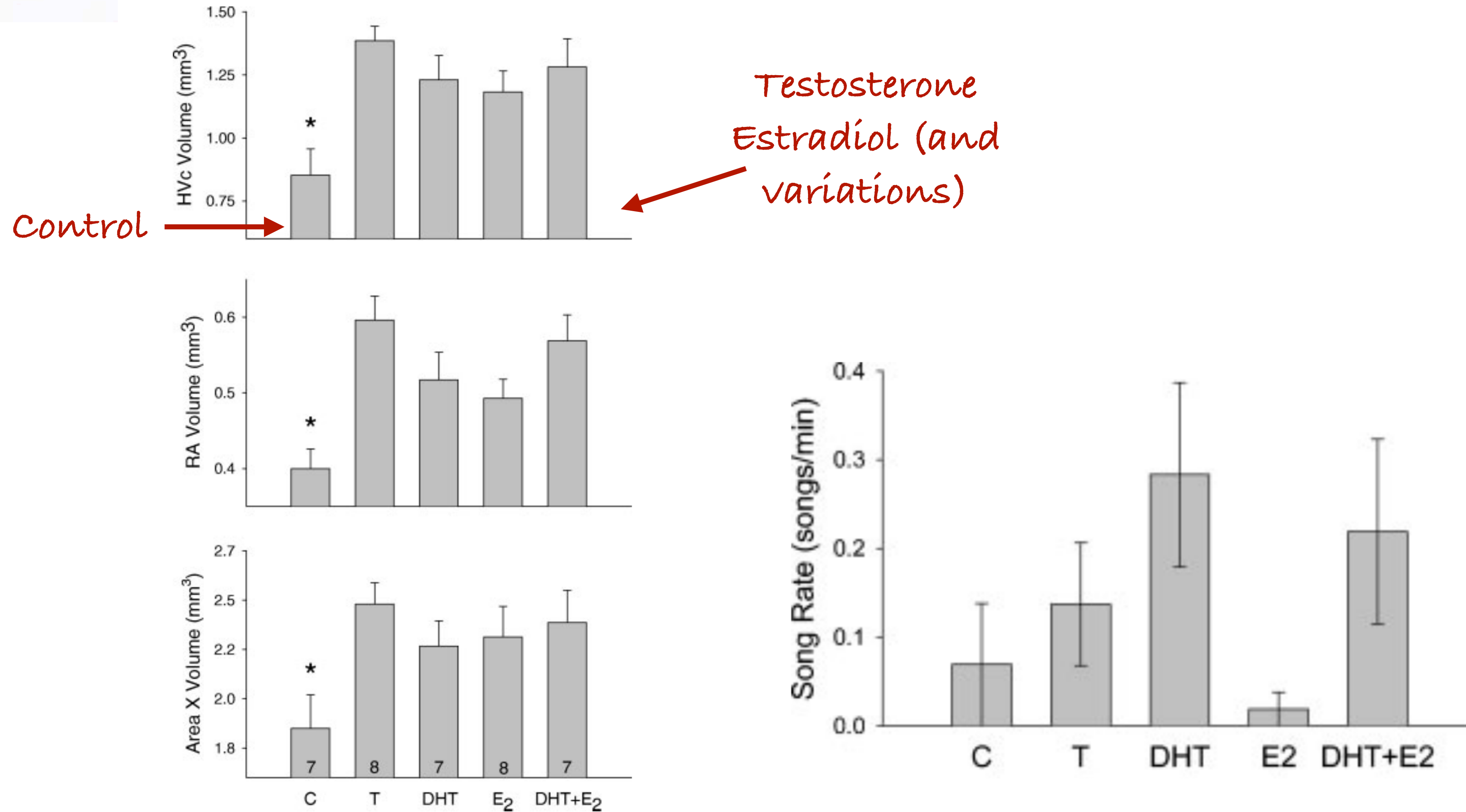
Result: HVC grow from 90k to 140k neurons in 7 days.
Song stereotypy is, still, delayed to 20 days
.. the circuit needs to wire

HVC grows (and decays) faster than RA and X
Further studies show that growth in RA,X needs Testosterone
affecting HVC first

Mass of syrinx (also has androgen receptors) shrinks in non-breeding season.



Testosterone and adult plasticity



And back: Singing → increase expression of the gene for BDNF → neuronal recruitment in HVC

What is the adaptive value of neurogenesis and of seasonal plasticity? (Speculative)

A substrate for adult learning (re-open the sensitive period).

Performance-related hypertrophy. Regression in off-season.

New substrates (in HVC, NCM) for creating perceptual memories.

Replace damaged, overworked, premotor neurons.

(evidence, rate of singing is proportionate to new neuron recruitment.. but this is not true in seasonal singers)

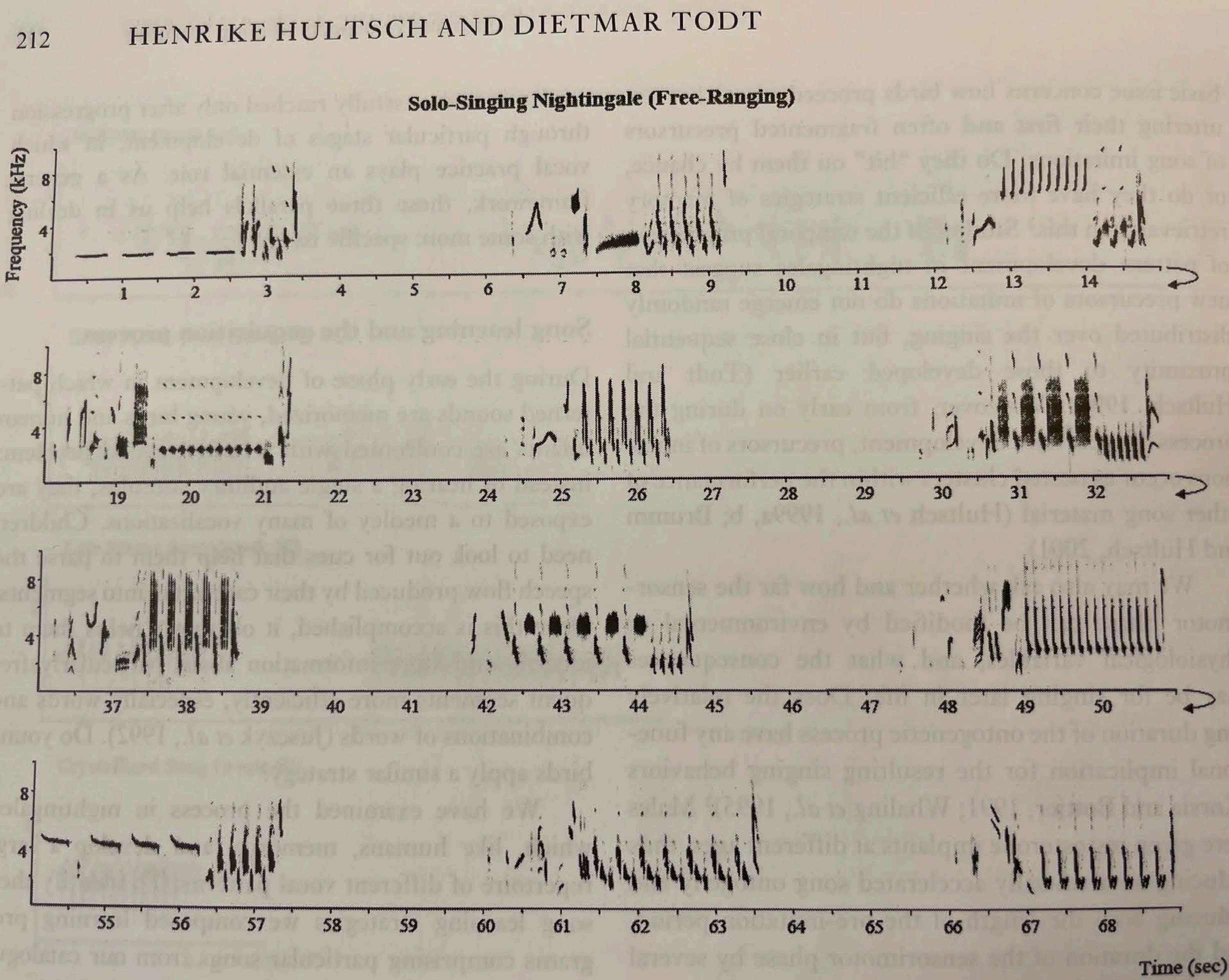
Multi-year process of pruning and keeping expert neurons.

Nightingales: Acquisition, storage, and retrieval of large repertoires





Nightingales: Acquisition, storage, and retrieval of large repertoires



Interactions between neighbors - what to sing next?

Play nice or overlap

Acoustic matching

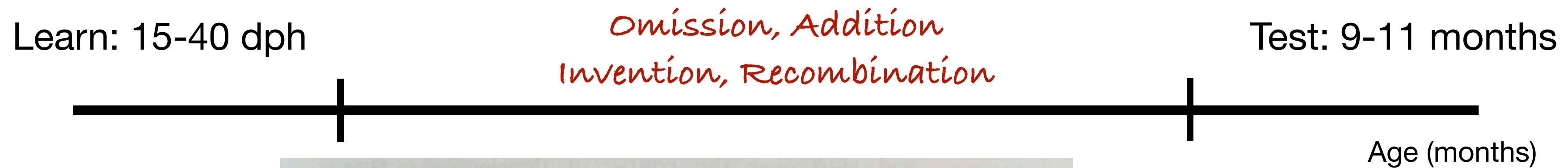
Learning: how much exposure is needed for a large repertoire (200 song types)?

Hierarchical memorization and retrieval

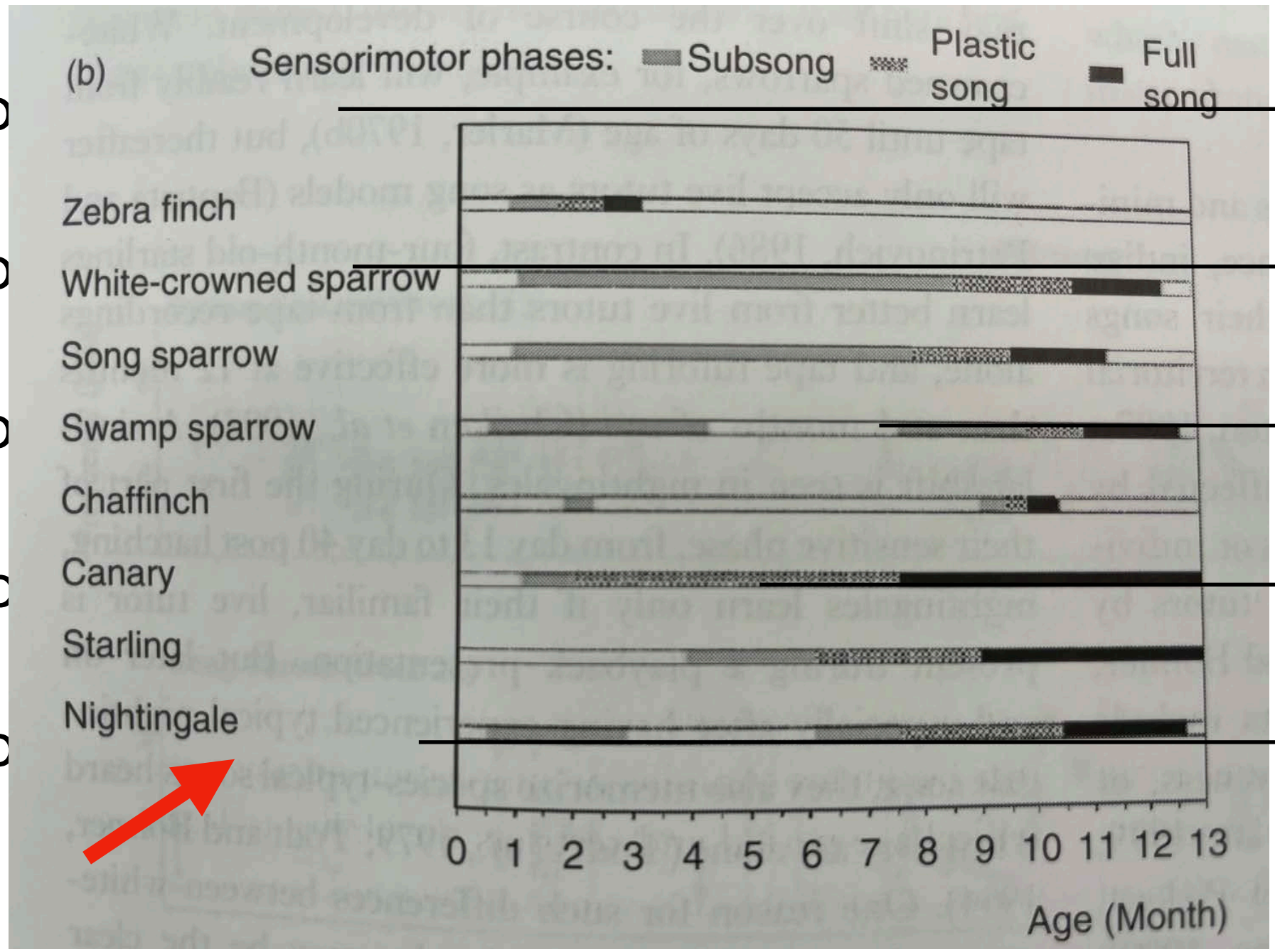
Figure 17.6 A sequence of twelve songs of a nightingale, taken from a longer bout of solo singing.



What processes occur between initial acquisition and adult production?

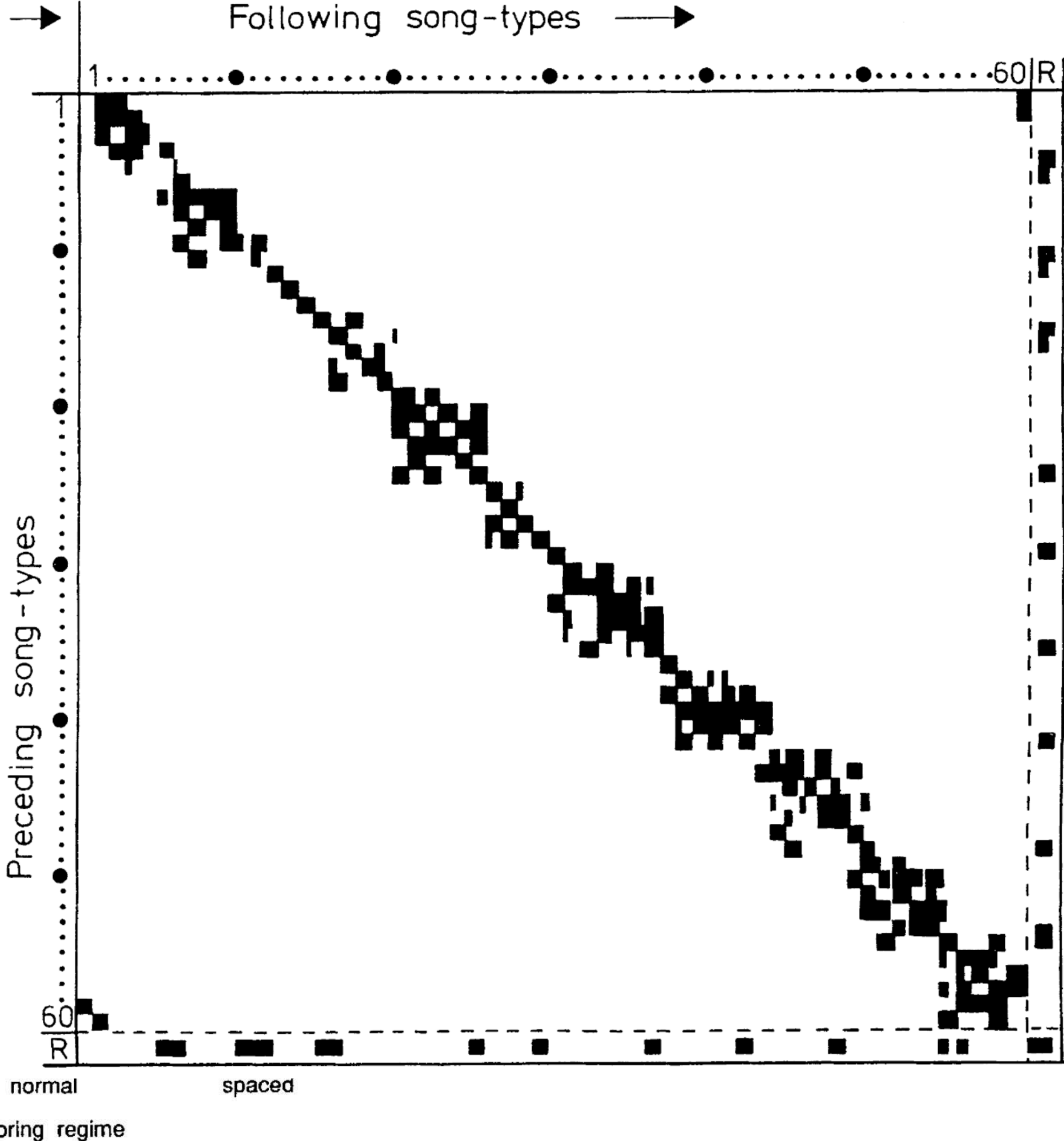


- Experiment: play so → Result: 30% songs learned
- Experiment: play so → Result: 75% songs learned
Similar with 20 or 60 songs
- Experiment: play so → Result: A live tutor is needed at 13-40 dph
Playback learning works in later stages
- Experiment: Play so → Result: Improve learning
- Experiment: play co → Result: segmented song



Nightingales: Evidence for hierarchical

memorization and (or) retrieval



Learn: 15-40

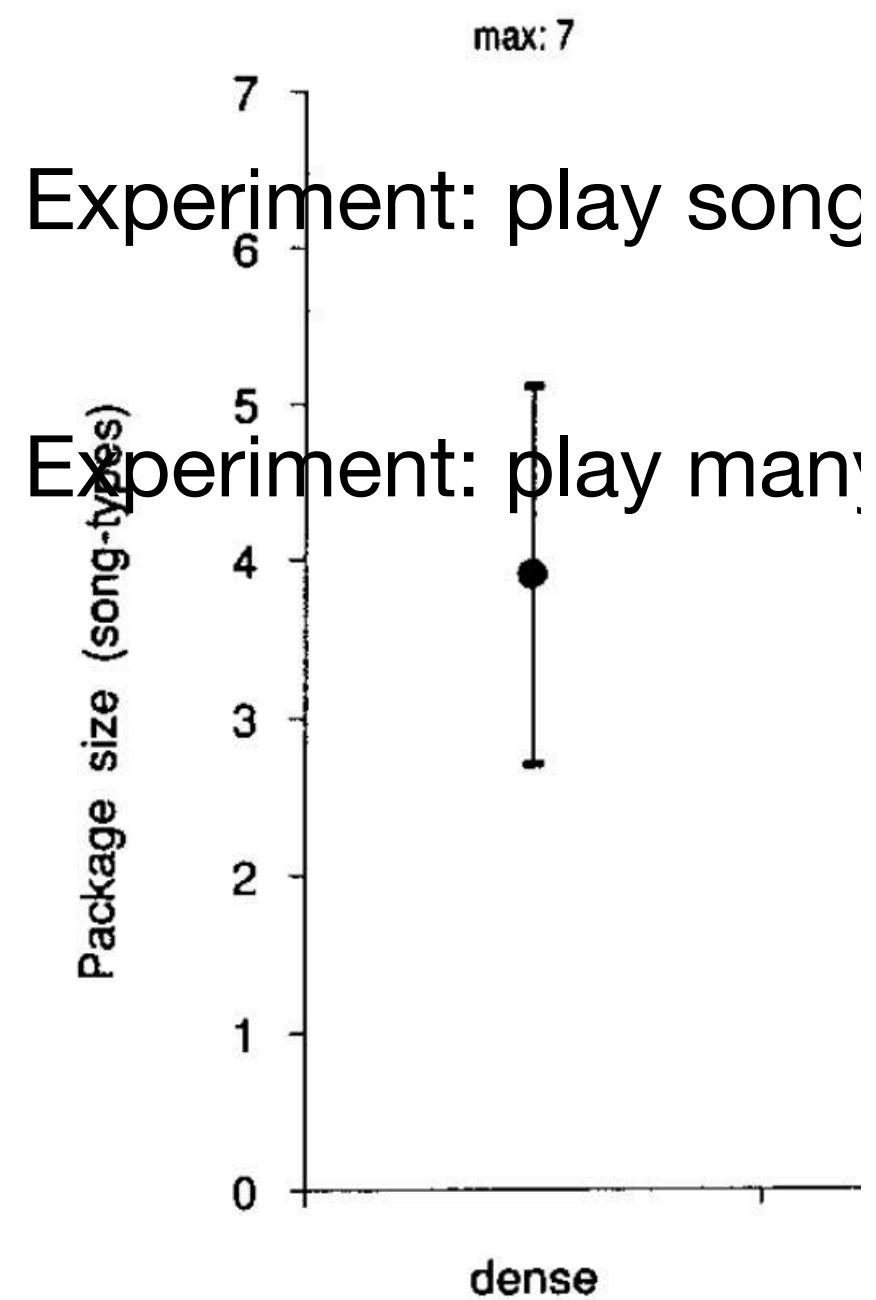
Age: 9-11 months

Experiment: play large

Experiment: play dense

Experiment: play song

Experiment: play many



packages of 3-4 songs
of short term memory

packages have typical size

packages are normal and
in the order of the first playback

memorization of entire sequence,
begins first.
indicating a hierarchical process



Interaction effects on song retrieval

What to expect from vocal interaction?
Nightingale songs = sentences?

Nightingale #1

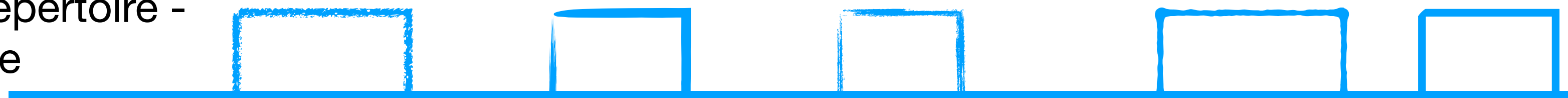


Stimulus out of repertoire



Nightingale #2

Stimulus included in repertoire -
Retrieve from the same
group / package

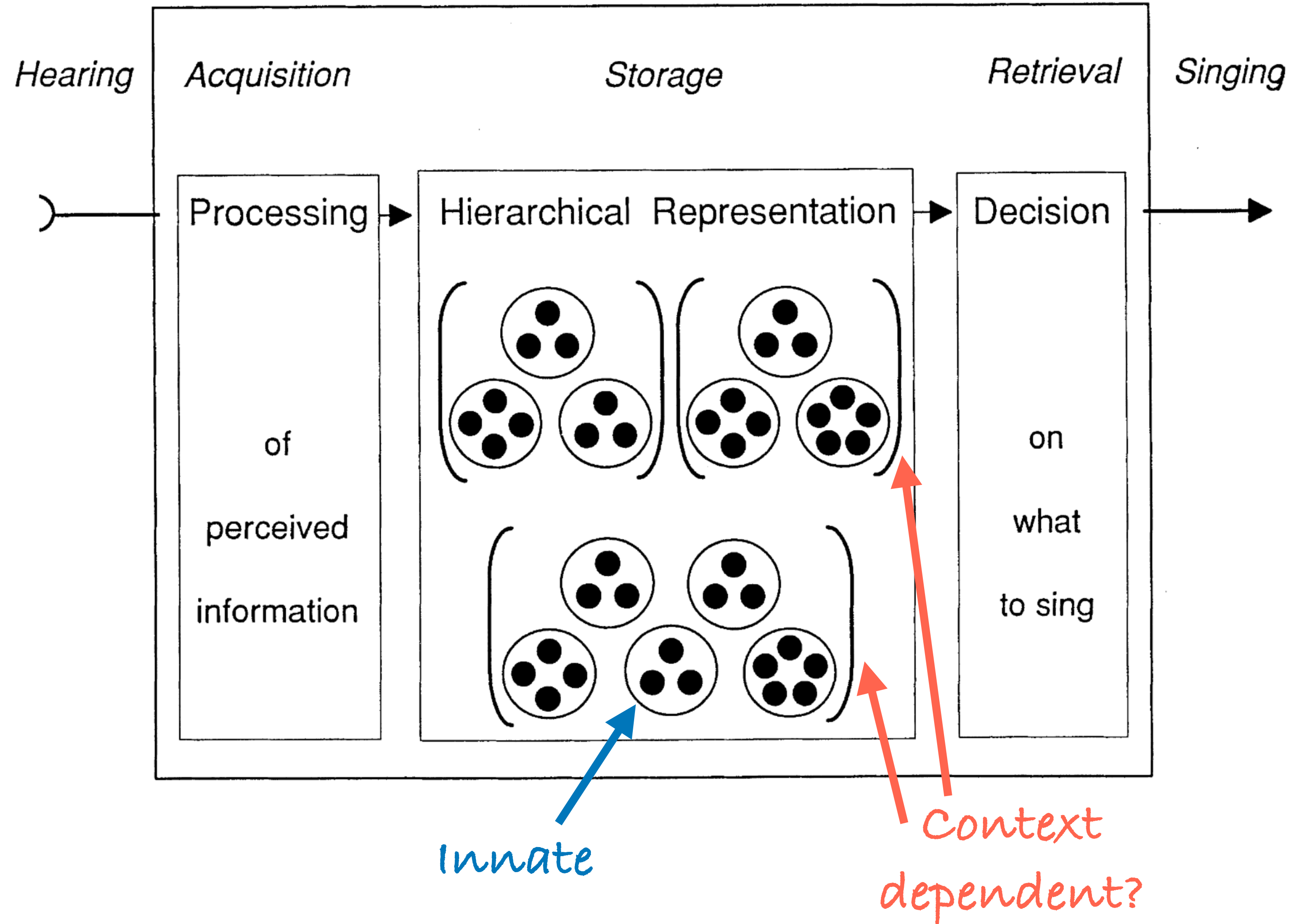


Stimulus is a reply to a previous song -
Aggressive or friendly? Determined by overlap.

Songs can be dormant (not used) but elicited later in song matching.



Model: Hierarchical memory system



Summary

Species

Behavior

System / memory time scales

Models

Close-ended learners

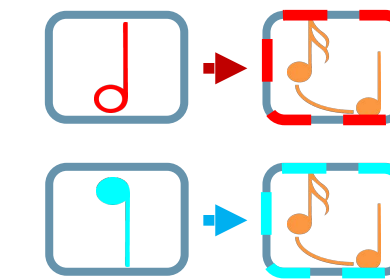
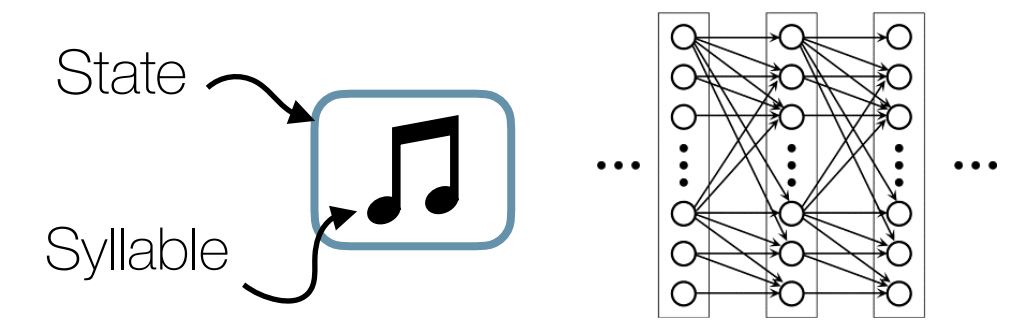


Stereotyped skill

Branching transitions

Life time.
Moment-to-moment (~10ms)

Production: 100-200 ms
(Auditory: ~1 sec)



Open-ended learners

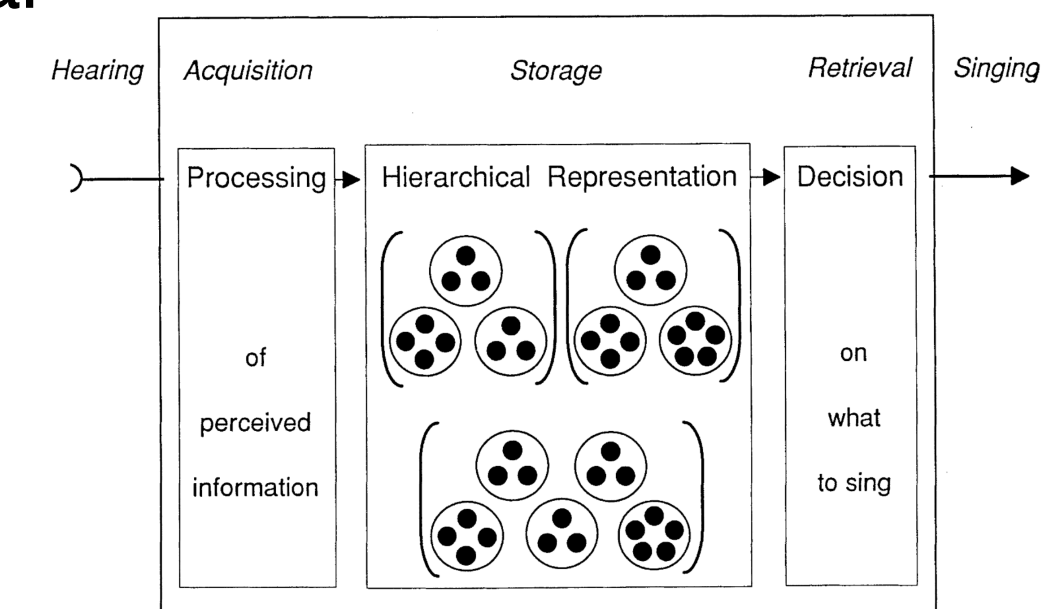
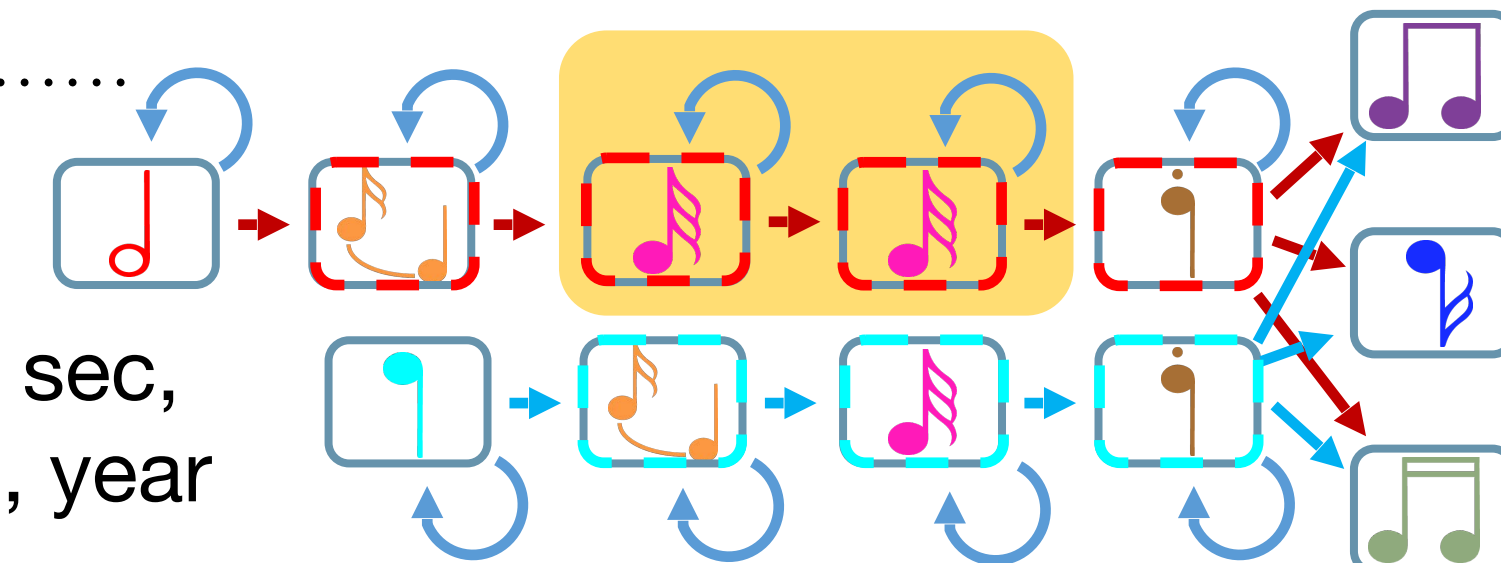


Hierarchical song
Long-range syntax

Extensive repertoire,
Hierarchical memorization and retrieval,
Acoustic matching

Syllables: 8-500ms,
Phrase sequence rules: 1-7 sec,
Seasonal plasticity: months, year

Acquisition: months, year
Retrieval: 1 second



The Lyrebird

(From the BBC's "The Life of Birds")



