Tame birds sing of freedom. Wild birds fly.

The unique research directions afforded by the complex behavior of songbirds

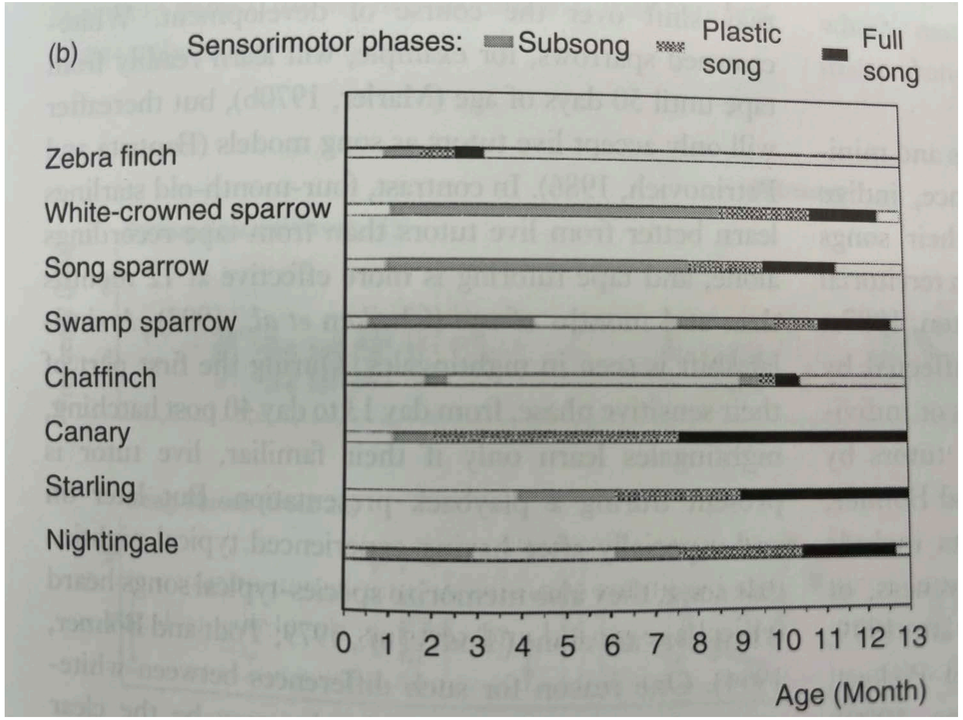
Motor skill —> Memory systems (Learning, decision, syntax)

What to learn? Store? Retrieve?

Time sensitivity (also depends on experience)

Specific selectivity

Gate attention



Outline

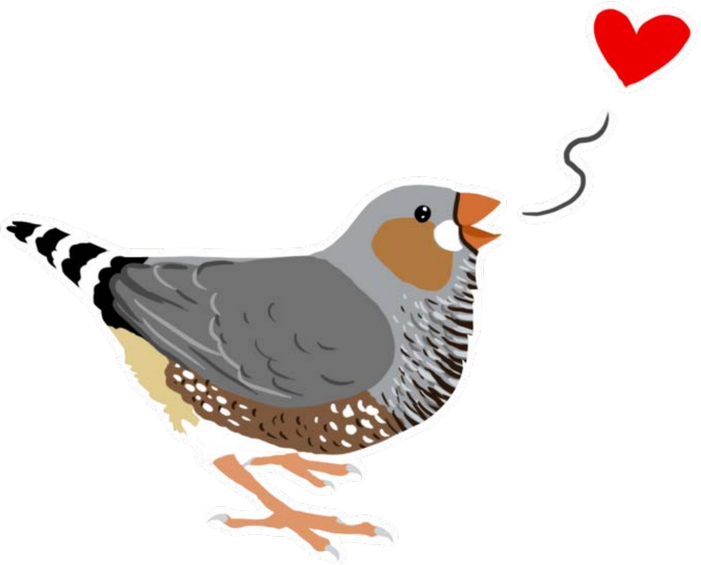
Species	Behavior	System / memory time scales	
	Stereotyped skill	Life time. Moment-to-moment (~10ms)	Close-ended learners
	Branching transitions	Production: 100-200 ms (Auditory: ~1 sec)	
	Hierarchical song Long-range syntax	Syllables: 8-500ms, Syntax rules: 1-7 sec, Seasonal plasticity: months, year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

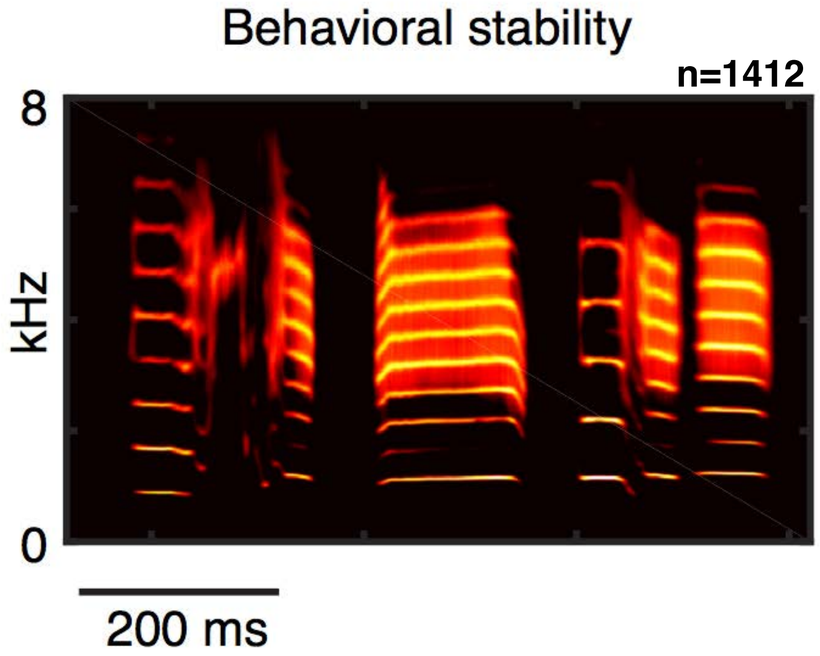
Zebra Finches: masters of precision

Credit: Todd Roberts

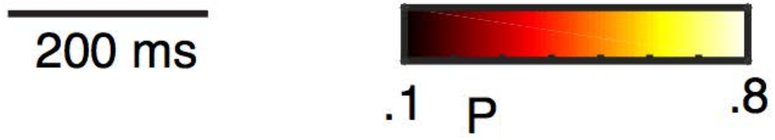
Zebra Finches: masters of precision

Dynamic Time Warping

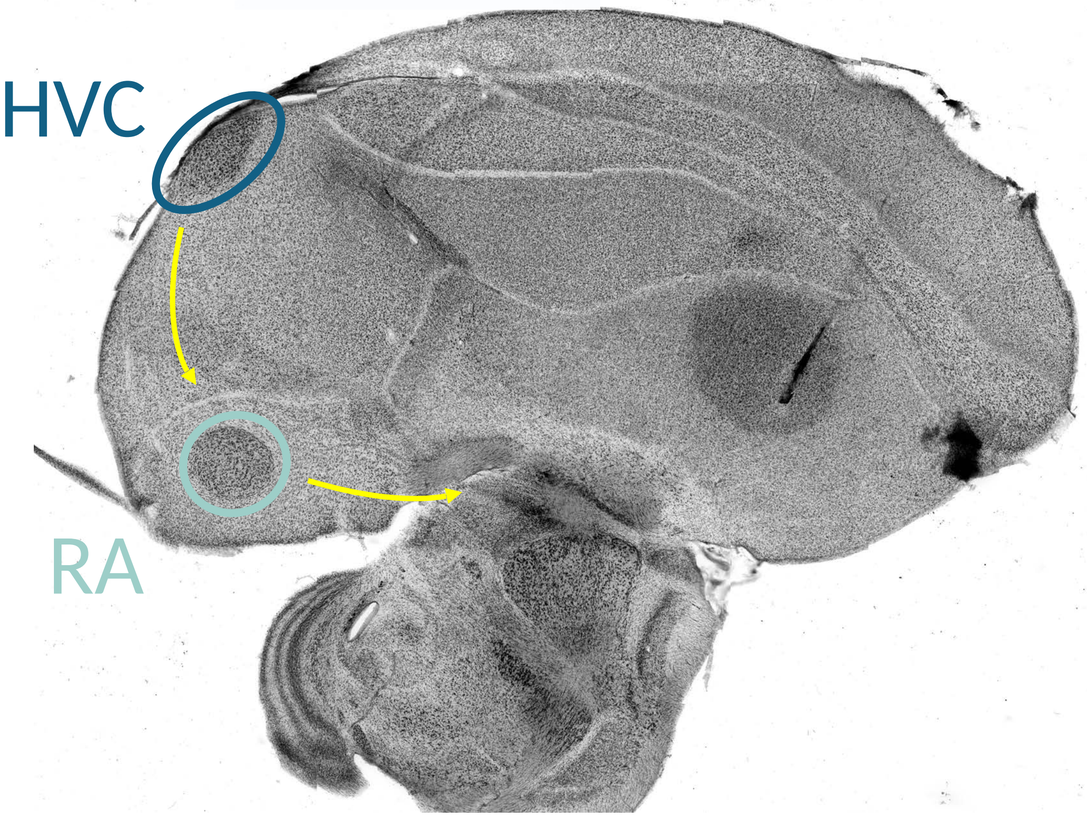


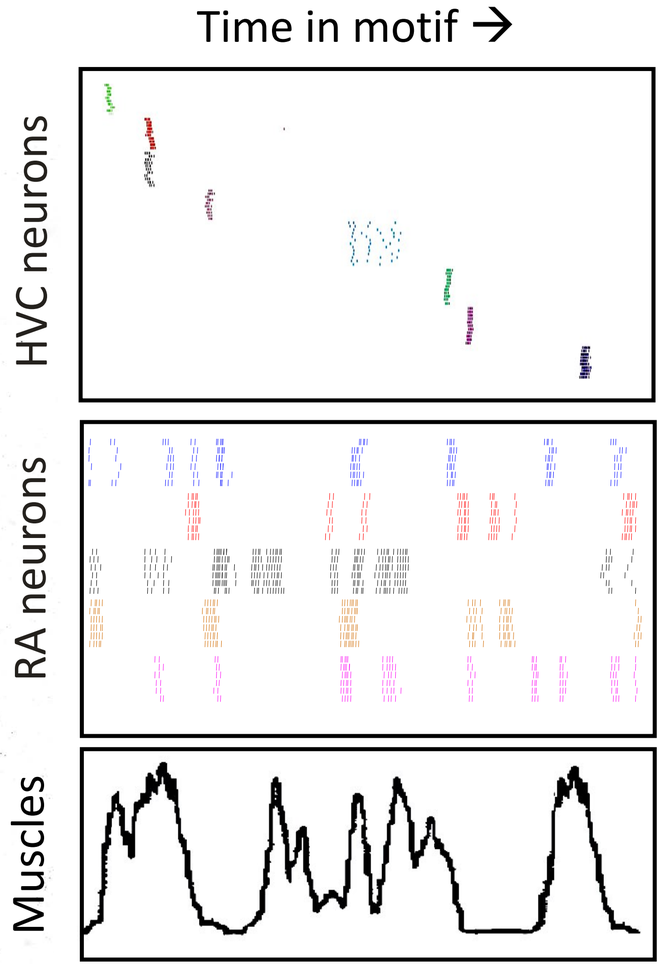


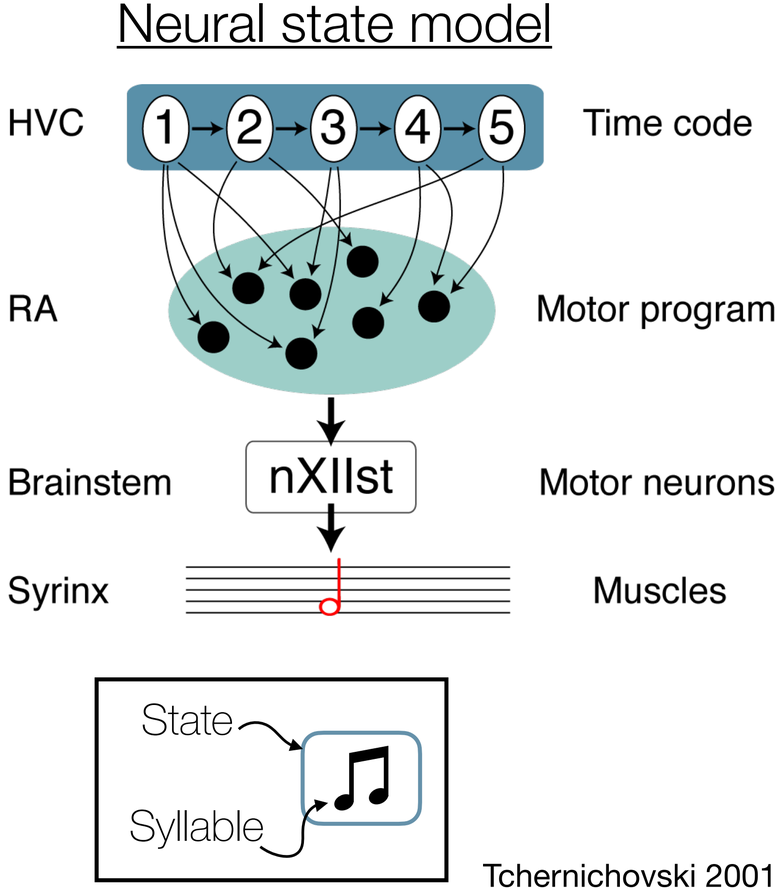
Song is a learned, complex, stereotyped motor behavior



Reliable sequences of neurons drive song syllables

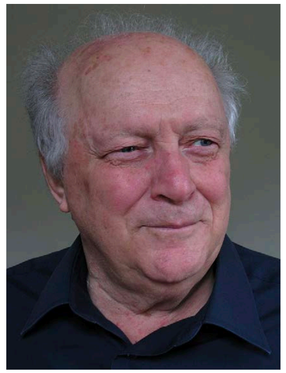




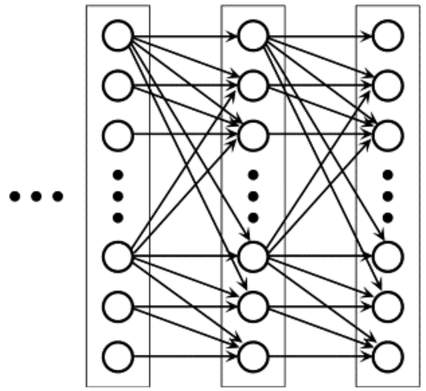


Tchernichovski 2001
Hahnloser et al 2002
Leonardo and Fee 2005
Kozhevnikov and Fee 2007

Models of robust neural sequences

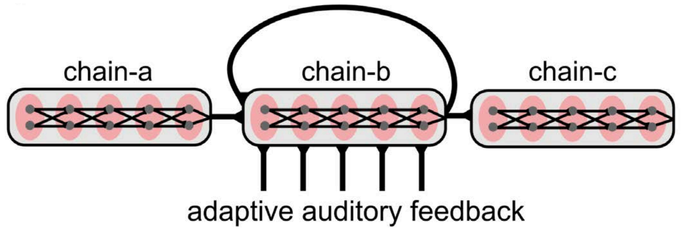


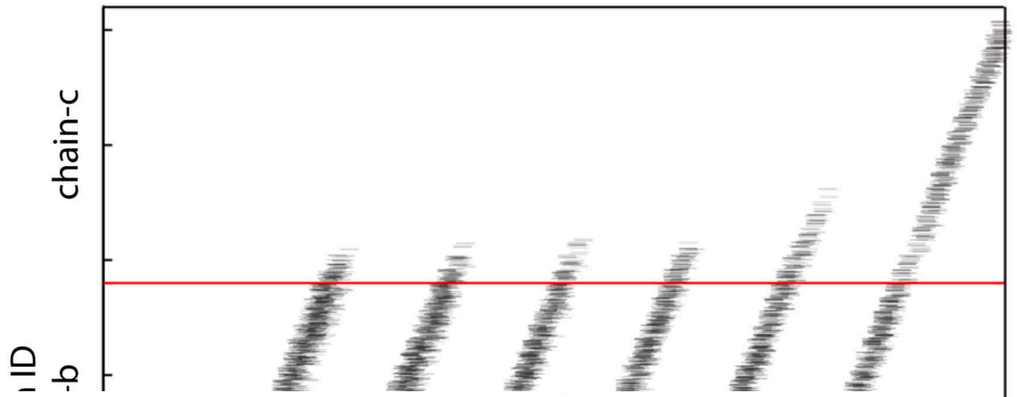
Source: Wikipedia



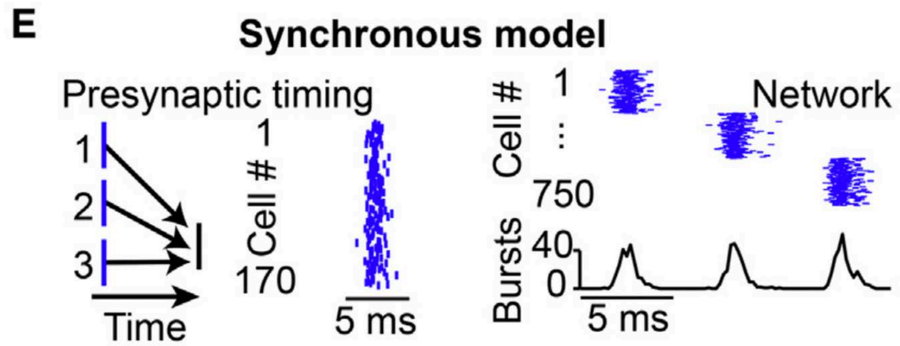
• • • = appx. 10ms time slices

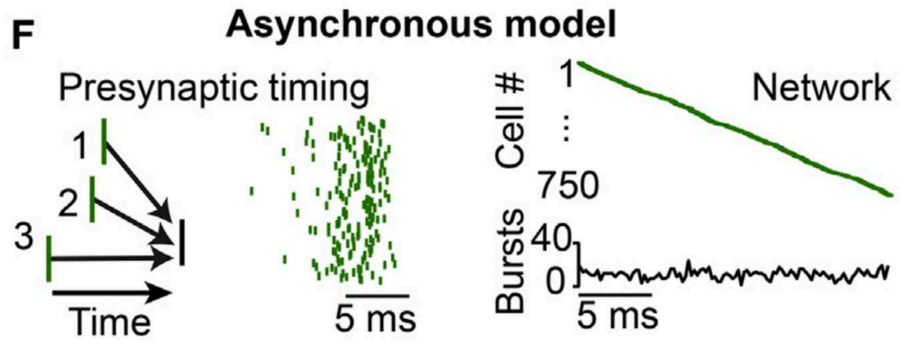
Synfire Chain

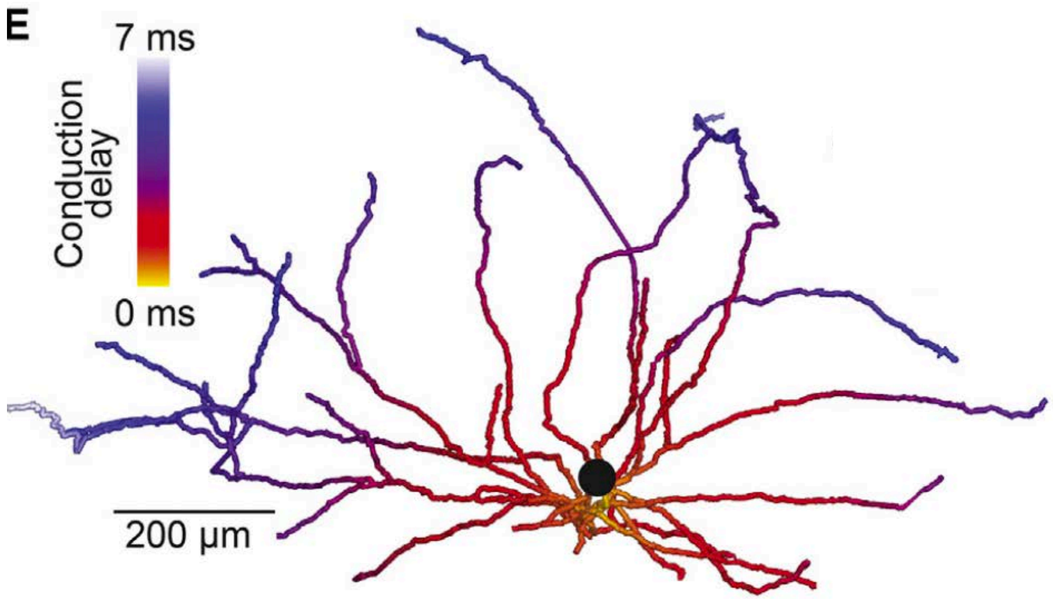




Alternative: Polychronous network







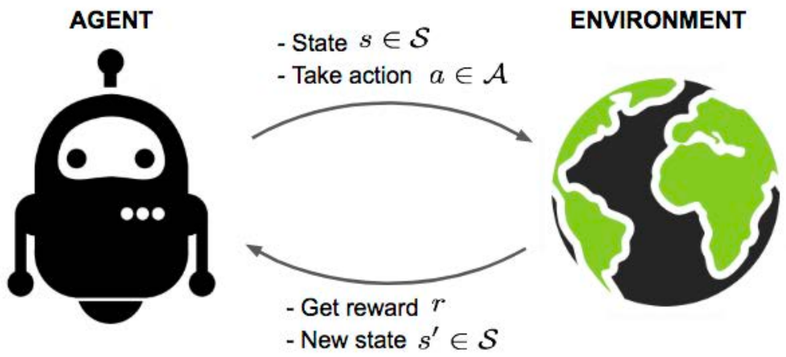
Abeles 1982
Long 2010
Wittenbach 2015
Egger 2020

Principles of song evaluation

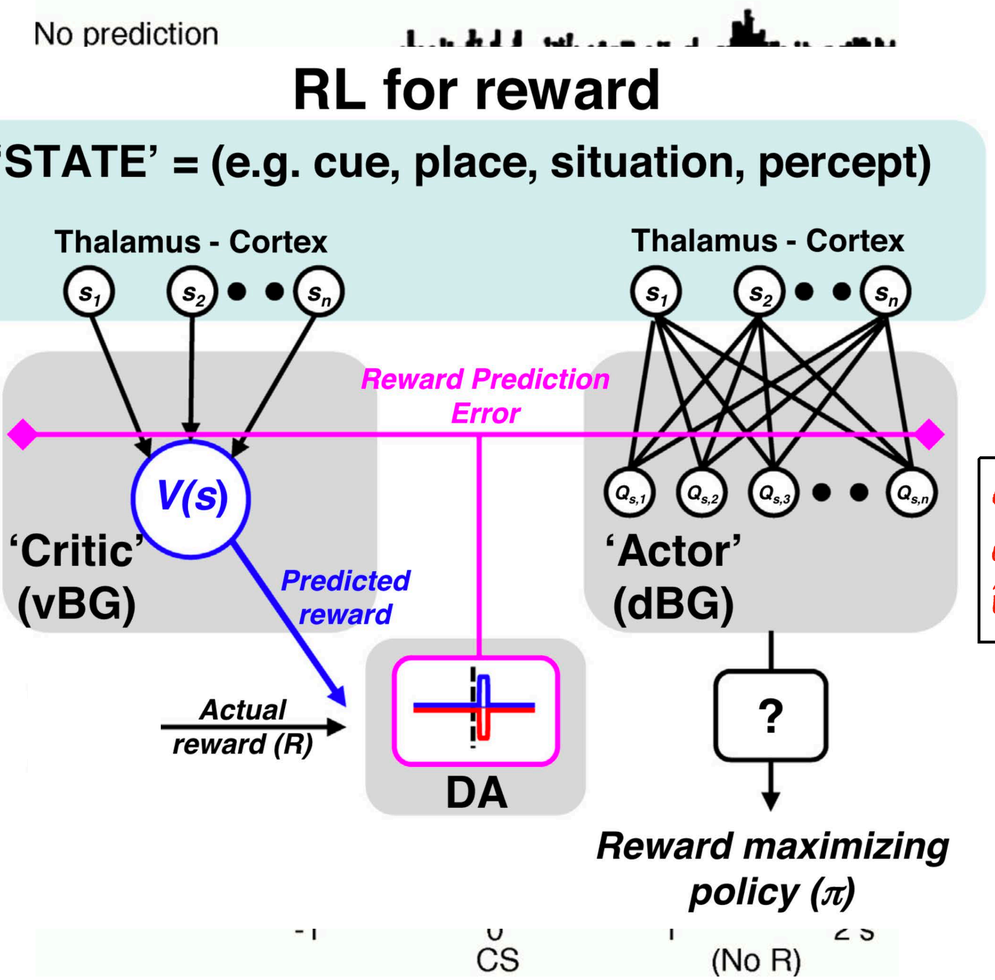
"Responses that produce a satisfying effect in a particular situation become more likely to occur again in that situation, and responses that produce a discomforting effect become less likely to occur again in that situation"

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

Reinforcement Learning



Dopamine Neurons in VTA signal RPE

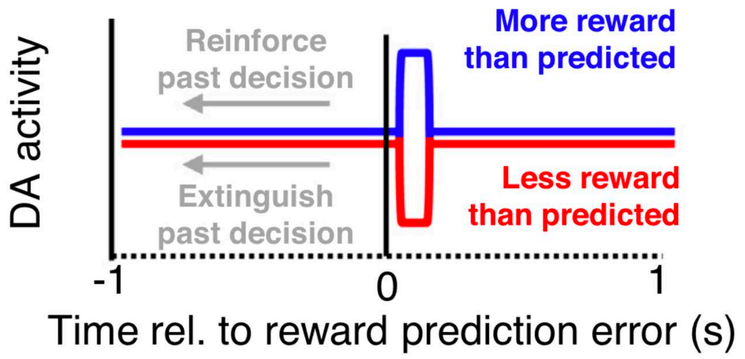


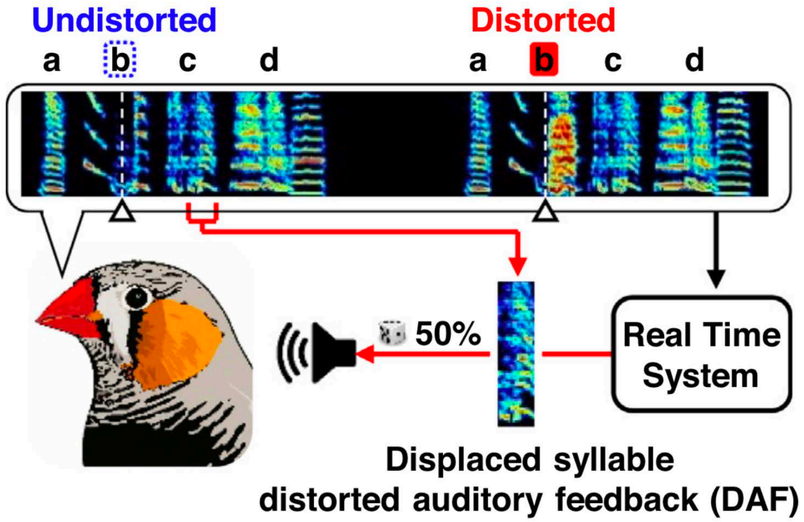
Q(s,a) = 'Quality' of taking action 'a' in state 's'

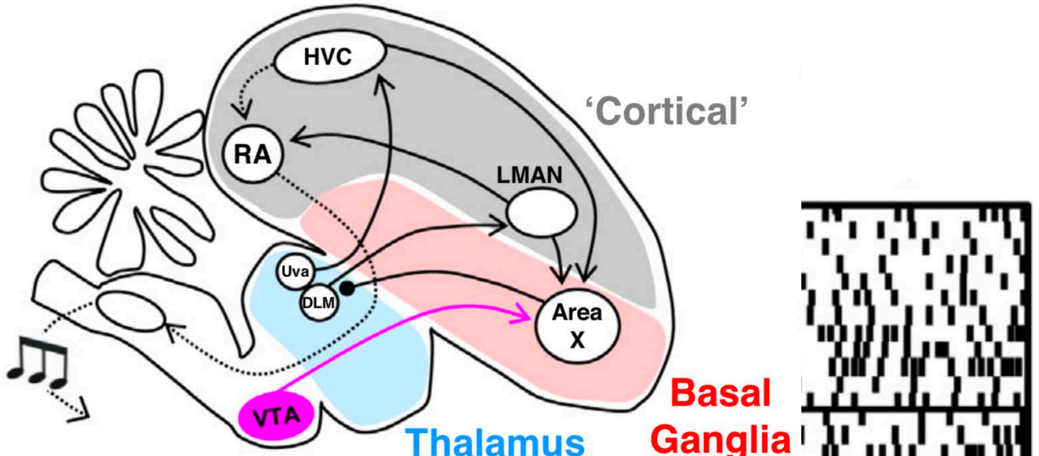
Schultz 1997
Chen 2020

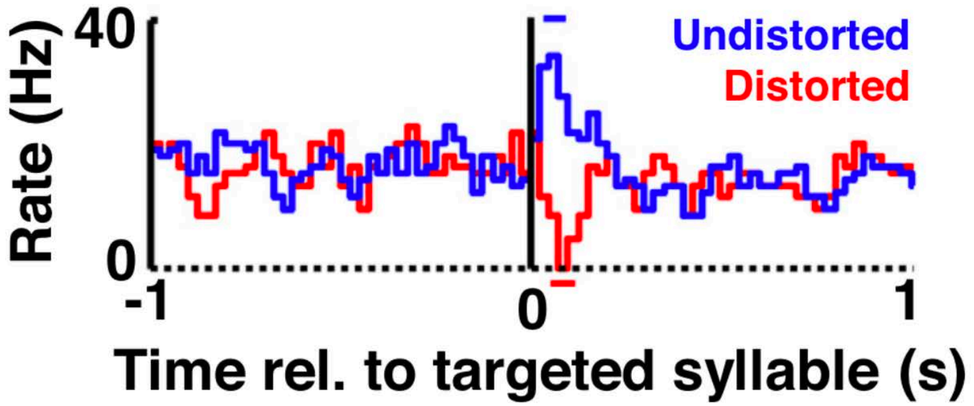
Principles of song evaluation

Dopamine Neurons in VTA signal RPE







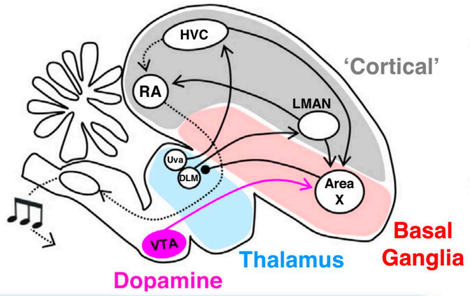


How does VTA compute song RPE?

Gadagkar 2016
Chen 2010
Chen 2020

Principles of song evaluation (Actor-Critic model)

Works for 10-50 ms time bins



'STATE' = Current time-step of the song

(Timing)

Uva (Thalamus) t_1 t_2 t_n

HVCx t_1 t_2 t_n

HVC: What 'piano key' is pressed

HVCra t_1 t_2 t_n

Performance Prediction error

(Required for learning)

$V(t)$

Critic (VP)

Predicted quality

$Q_{t,1}$ $Q_{t,2}$ $Q_{t,3}$ • • $Q_{t,n}$

Actor (Area X)

HVC+LMAN —> Eligibility trace

Biased Variability

π_1 π_2 π_3 • • π_n

Consolidator (RA)

RA=piano

Q

Thal.

Aud Cx

Actual song error

(Through AIV)

DA

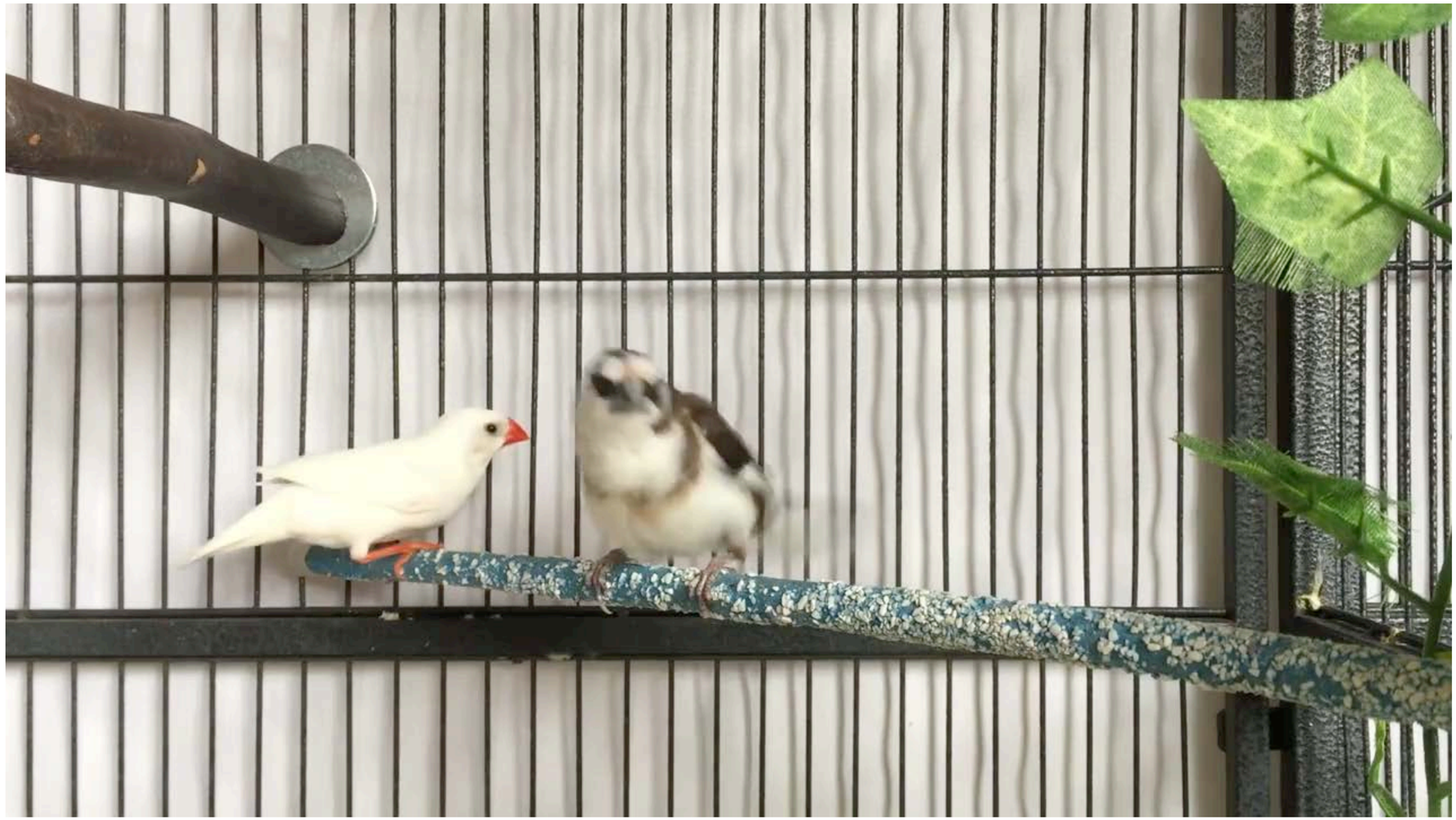
(VTA)

LMAN

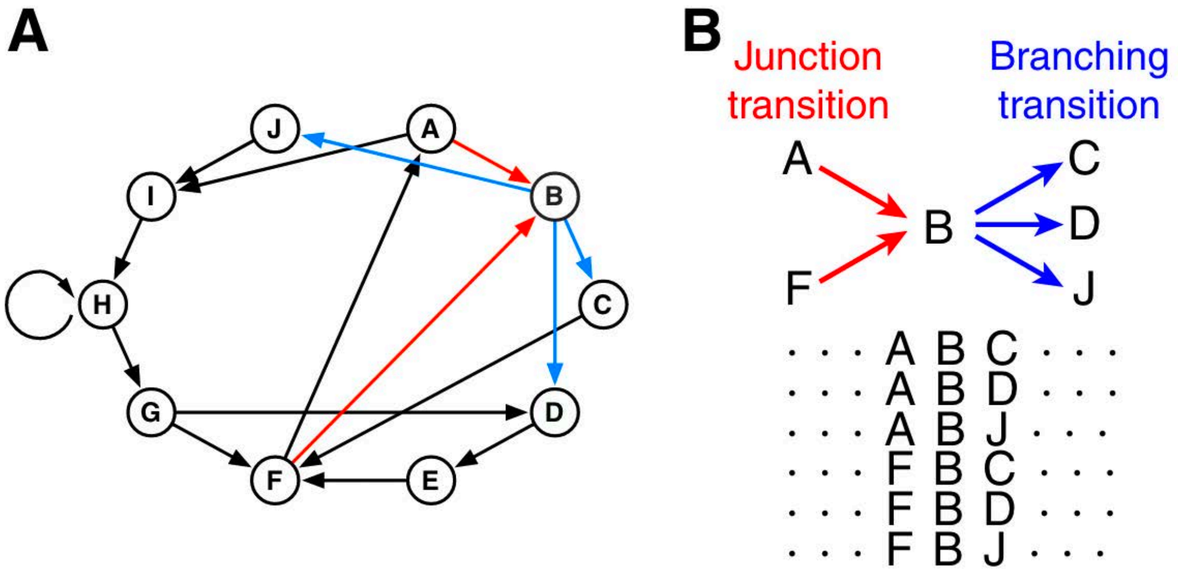
Vocal 'guess'

Vocal output (= LMAN + HVC)

Bengalese Finches: branching transitions

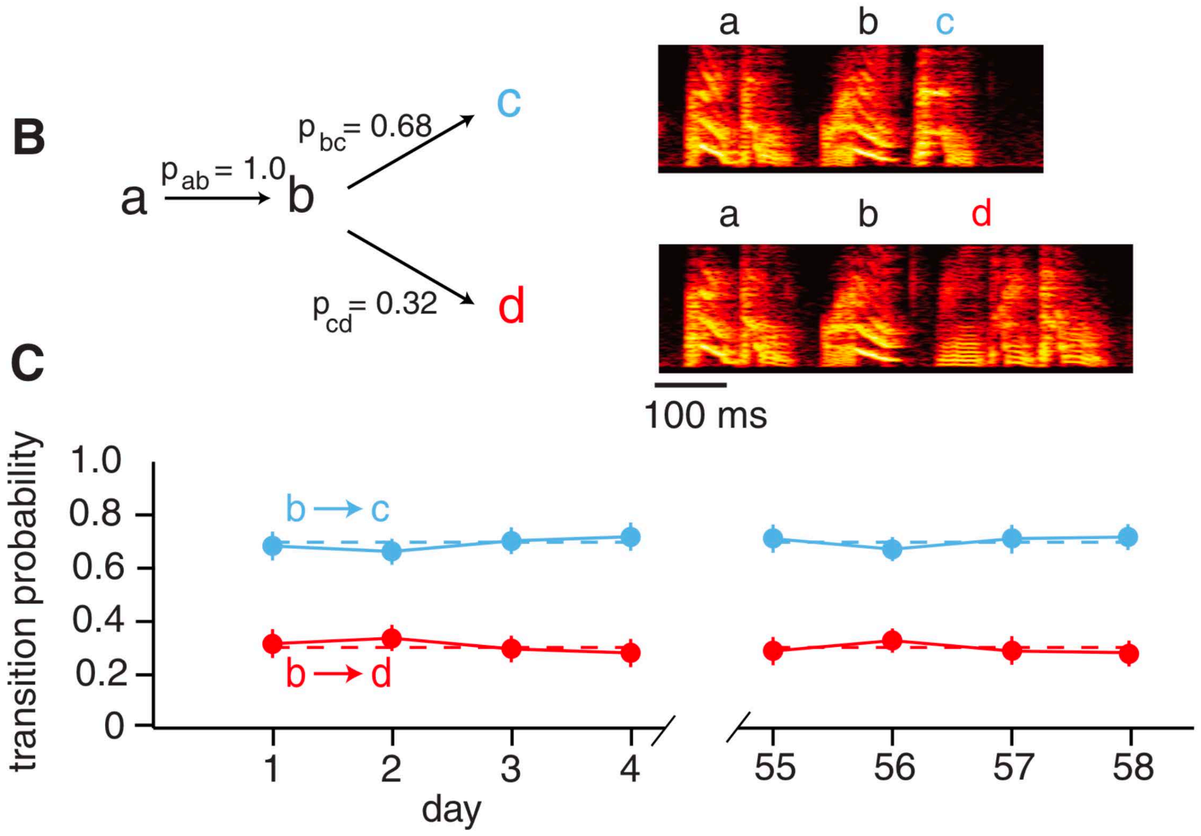


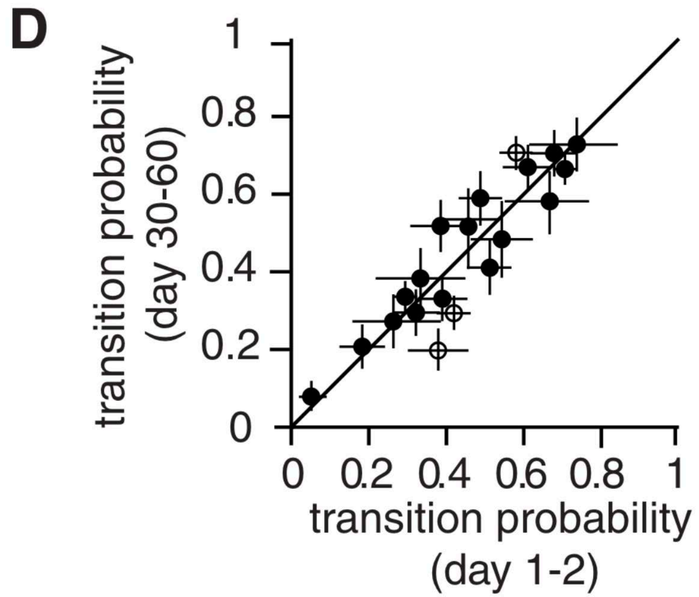
Bengalese Finches: branching transitions



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

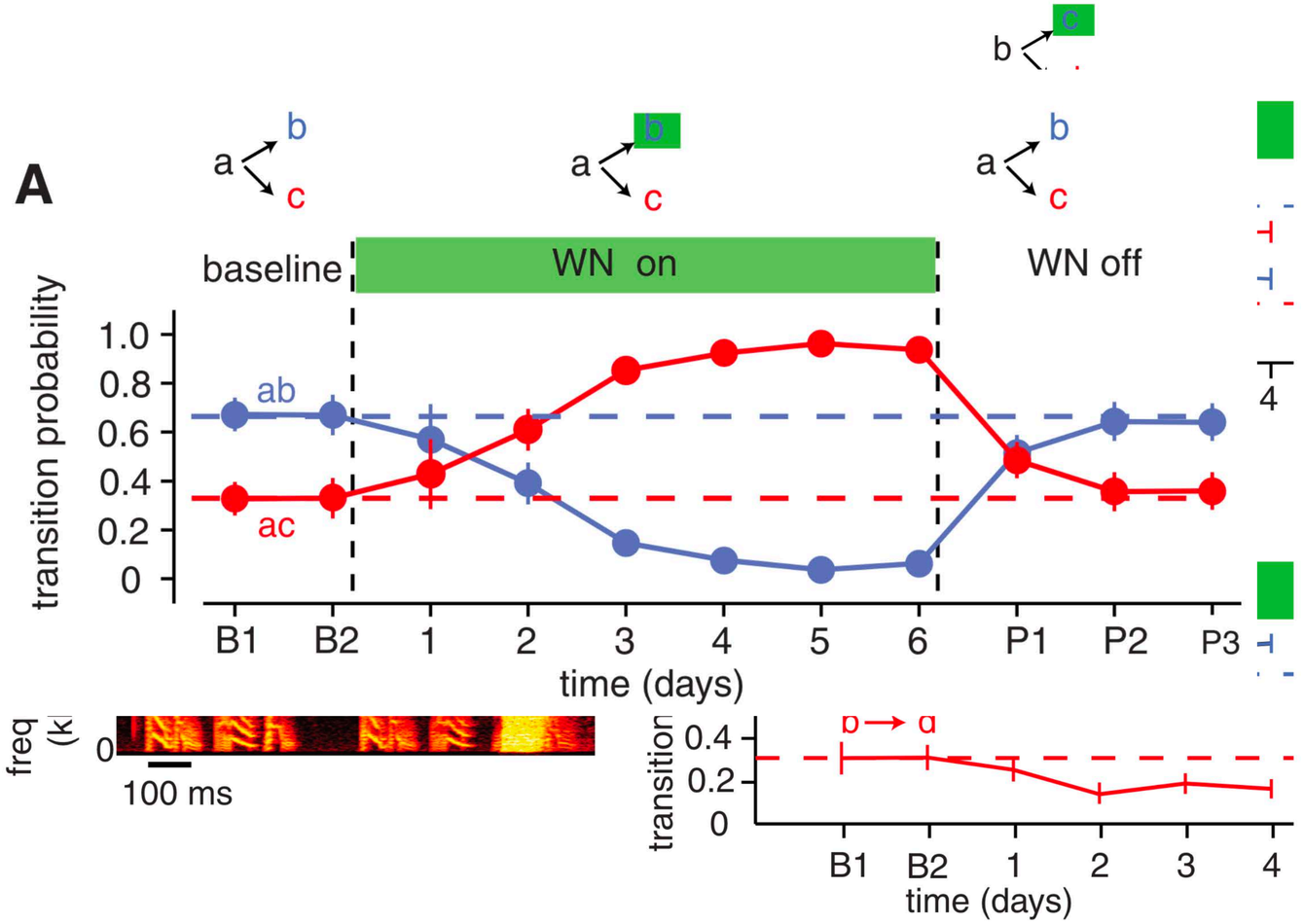
Bengalese finches crystallize transitions





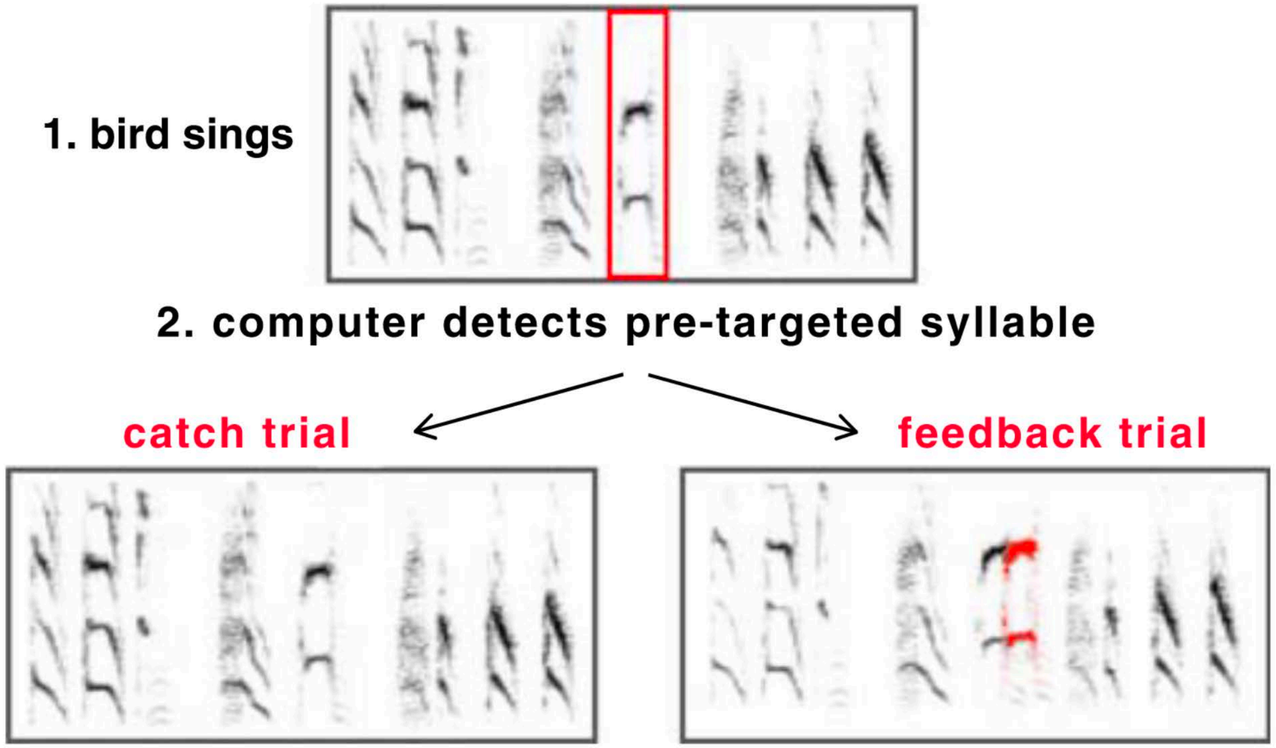
Warren 2012

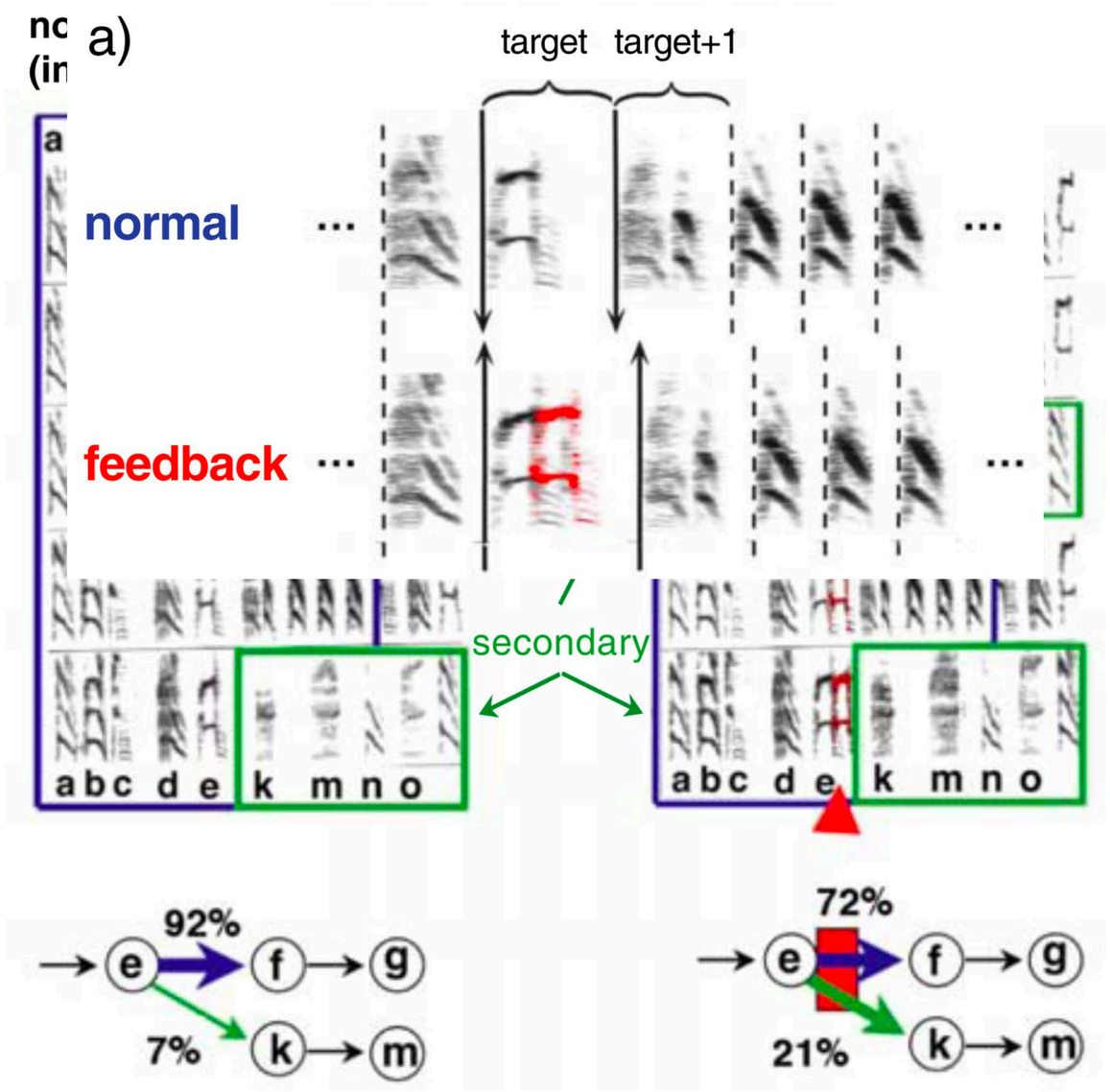
Bengalese finches crystallize transitions



Warren 2012

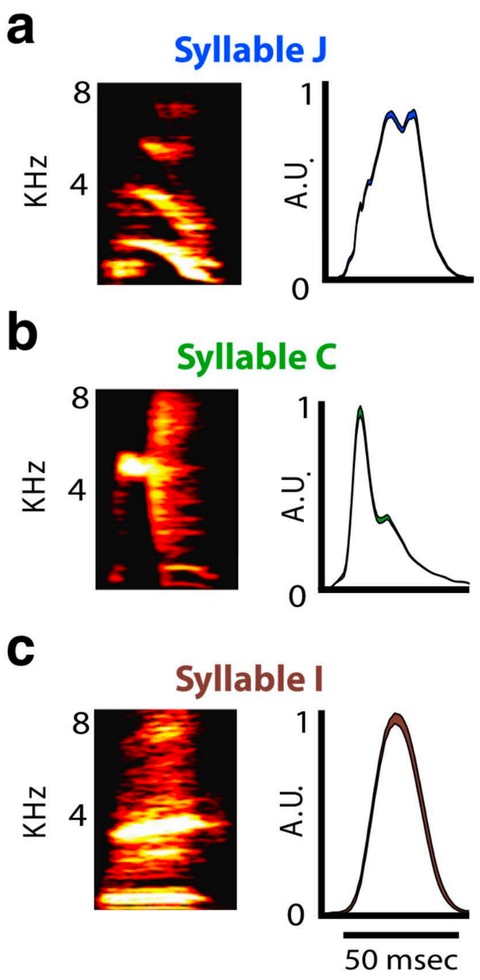
Branching transitions involve auditory feedback

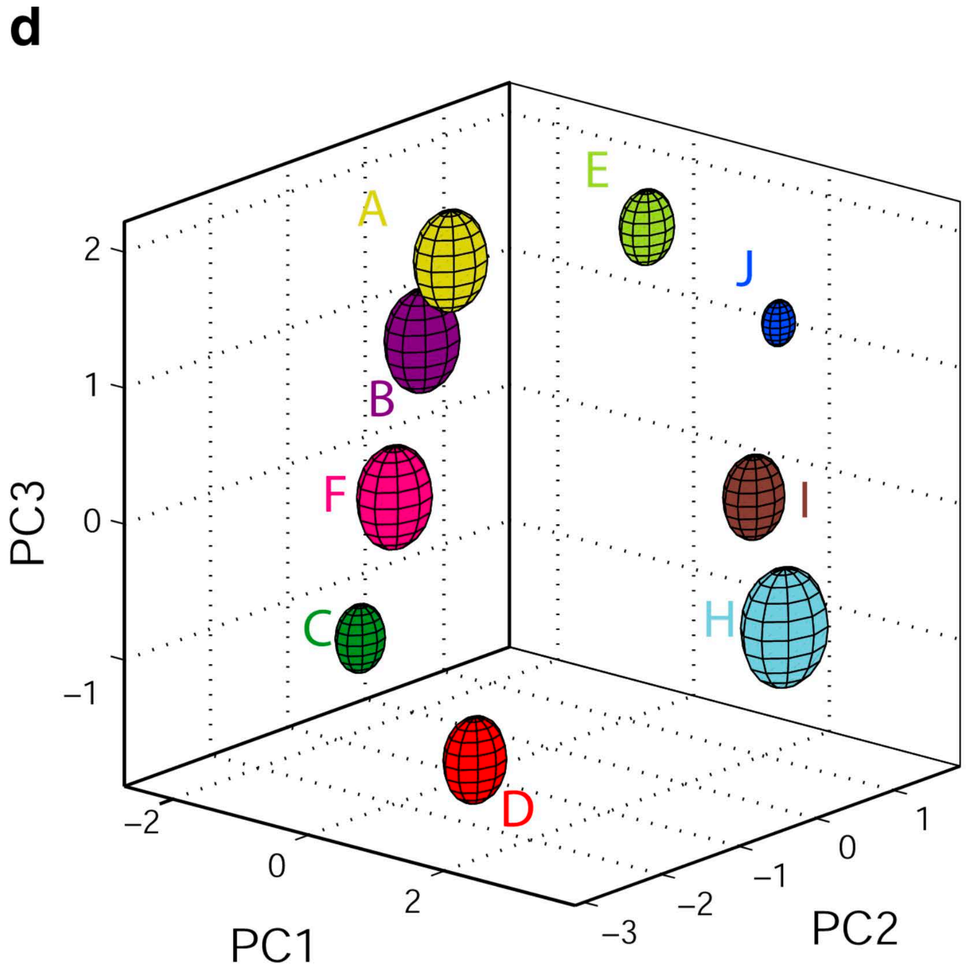




Sakata 2006

Are sequence and phonology related?





Syllable phonological metrics:

duration,

fundamental frequency,

time to half-peak amplitude,

frequency slope,

amplitude slope,

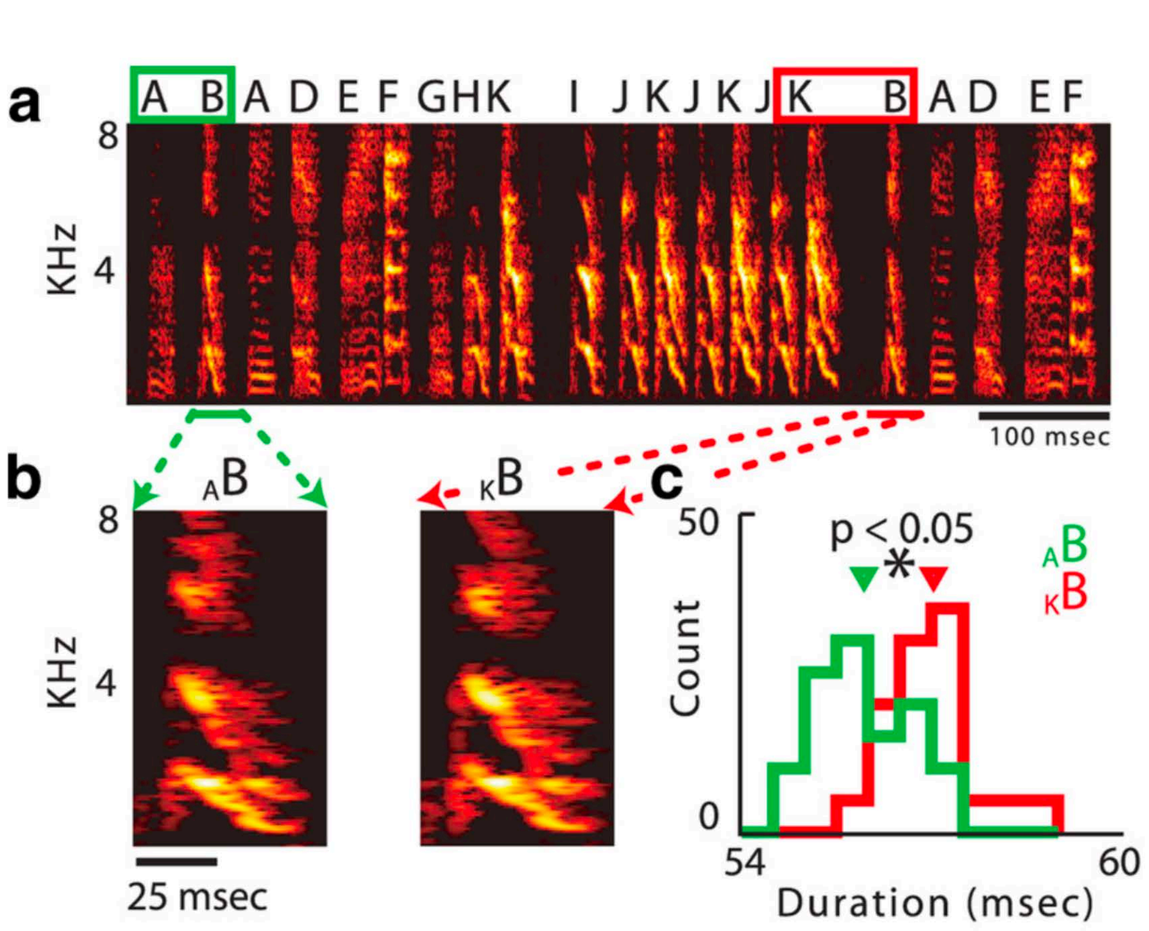
spectral entropy,

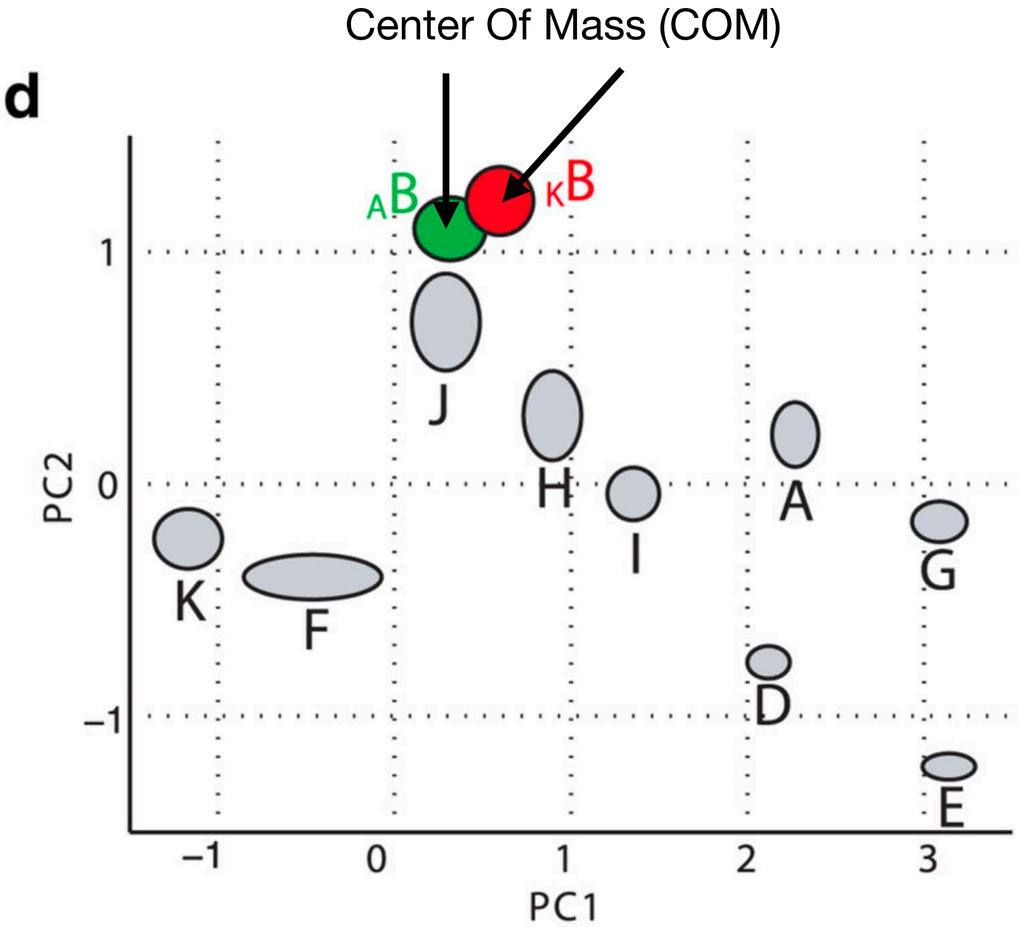
temporal entropy,

spectrotemporal entropy

Bouchard 2013
Wohlgemuth 2010
Tchernichovski 2001

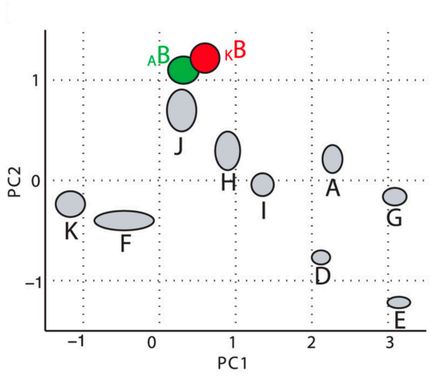
Are sequence and phonology related?

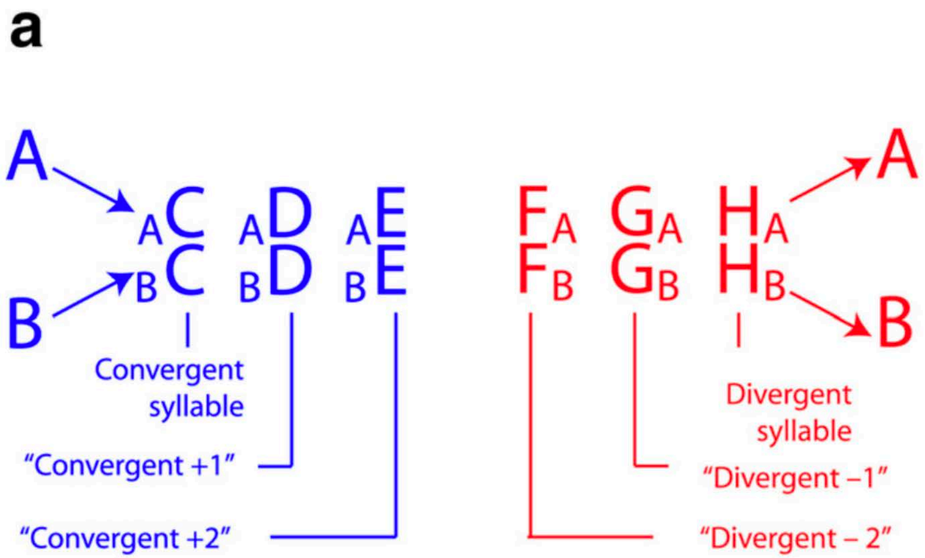


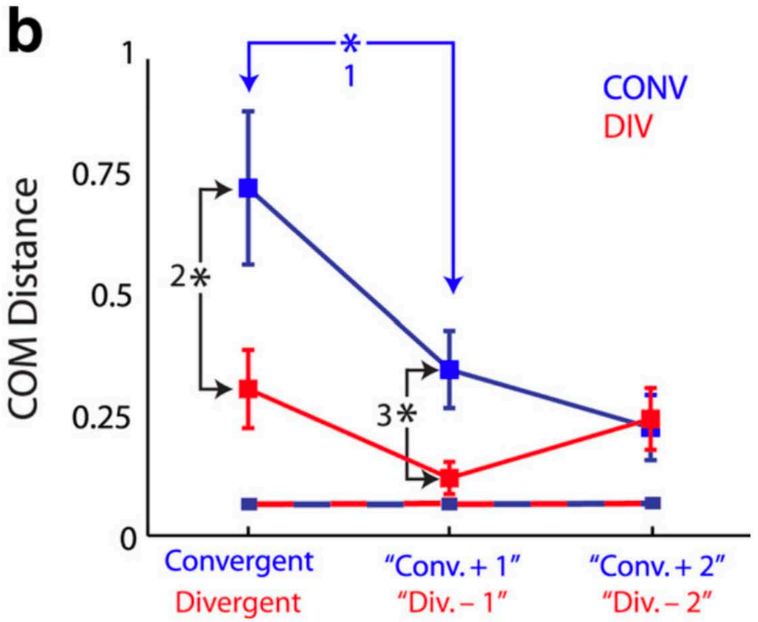


Bouchard 2013
Wohlgemuth 2010
Tchernichovski 2001

Are sequence and phonology related?

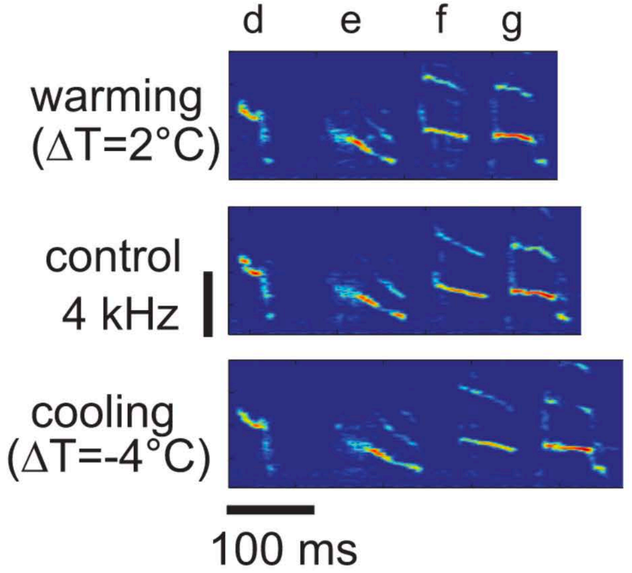


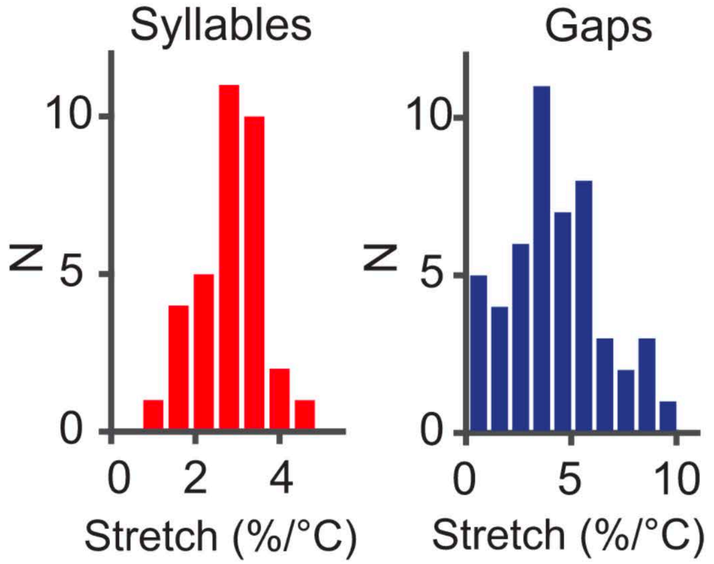


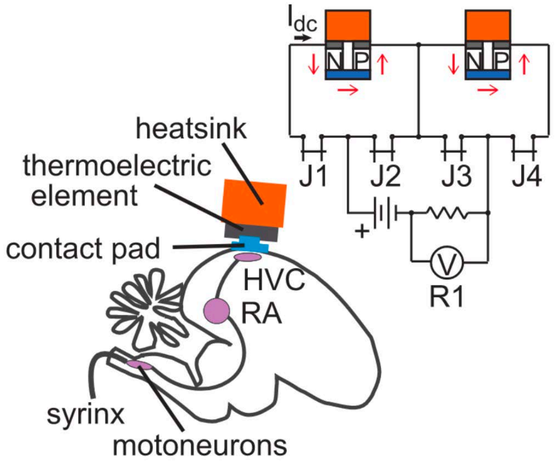


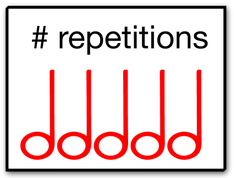
Bouchard 2013
Wohlgemuth 2010
Tchernichovski 2001

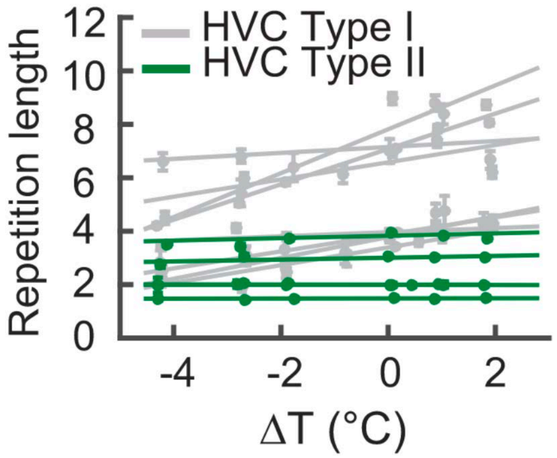
HVC cooling changes Bengalese finch syntax

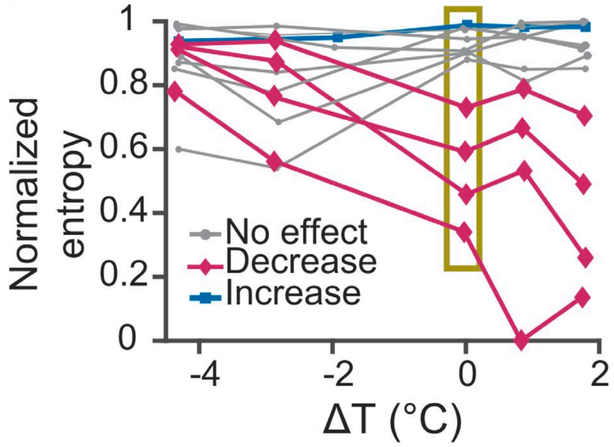


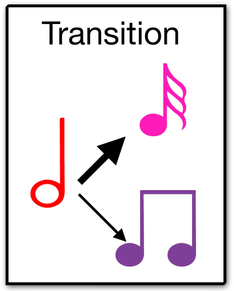










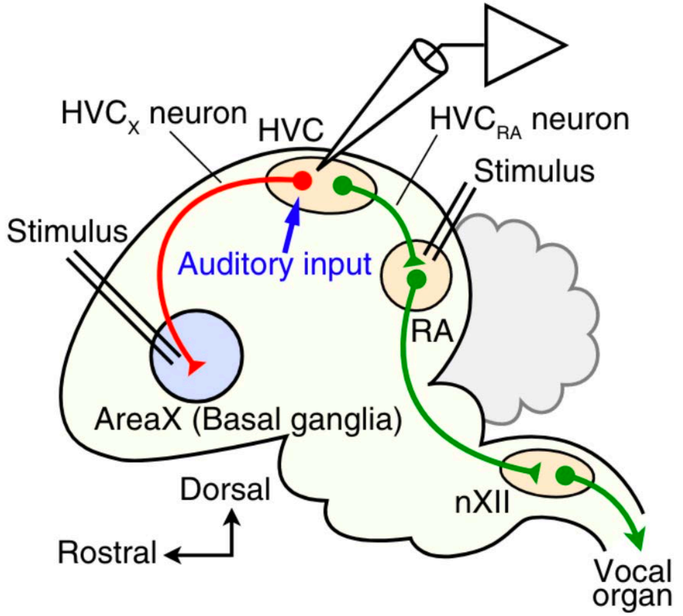


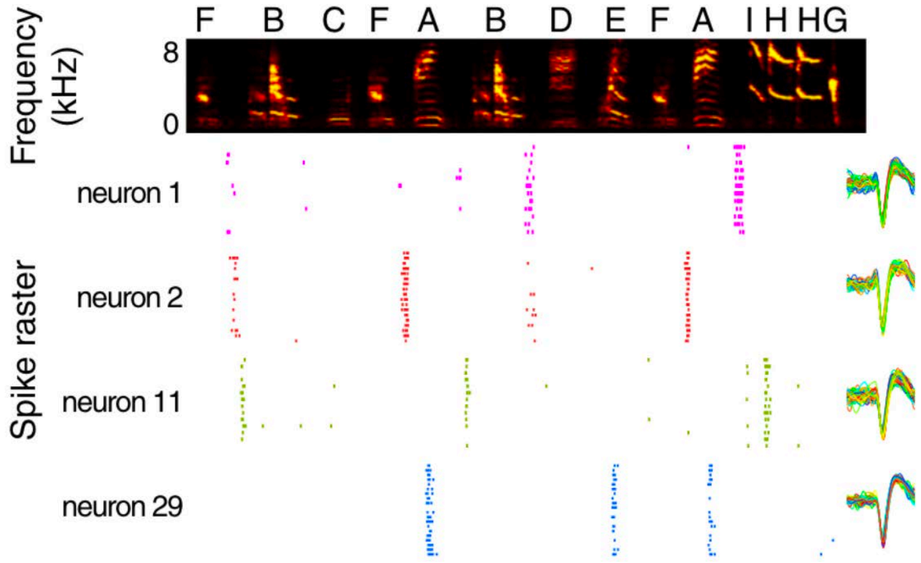
What syntax properties are reflected in HVC activity?

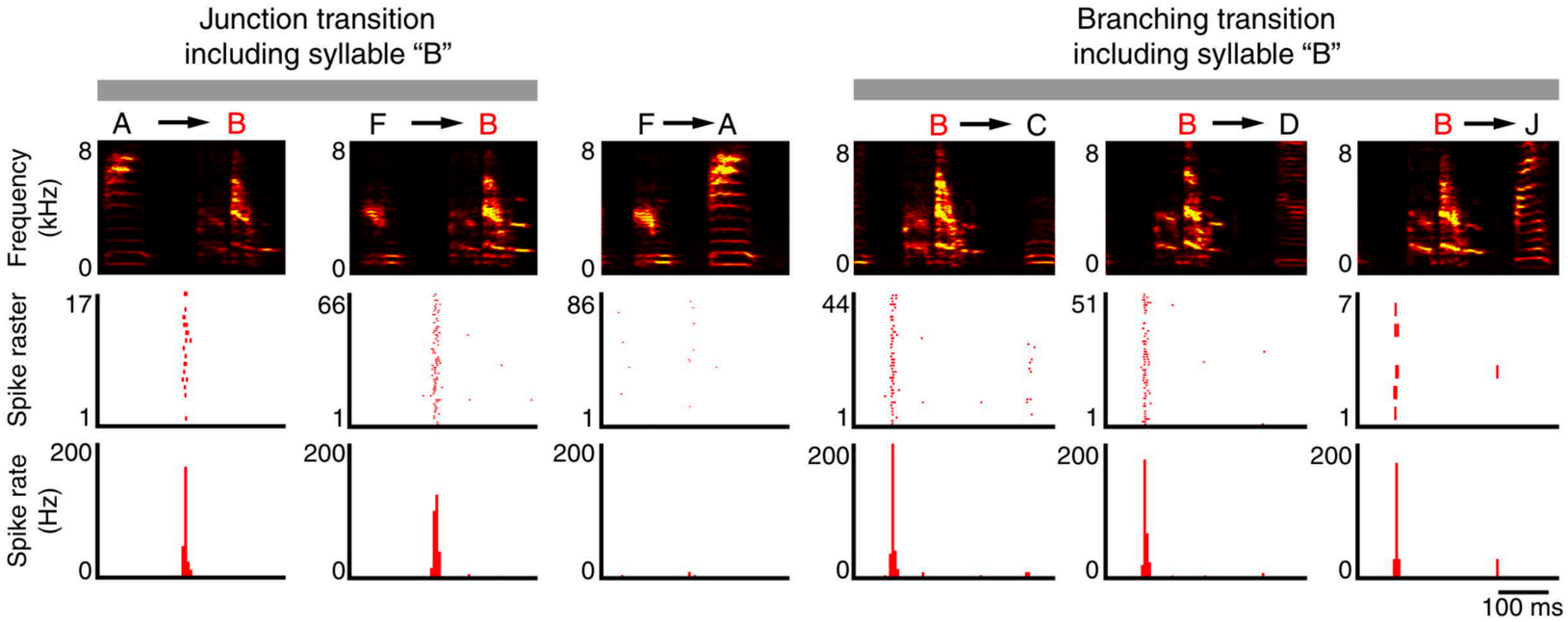
Zhang 2017

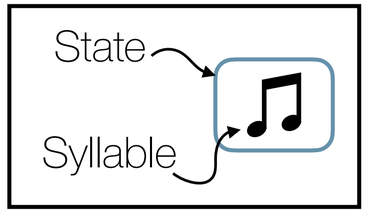
Neural encoding of Bengalese finch syntax

Fujimoto 2011





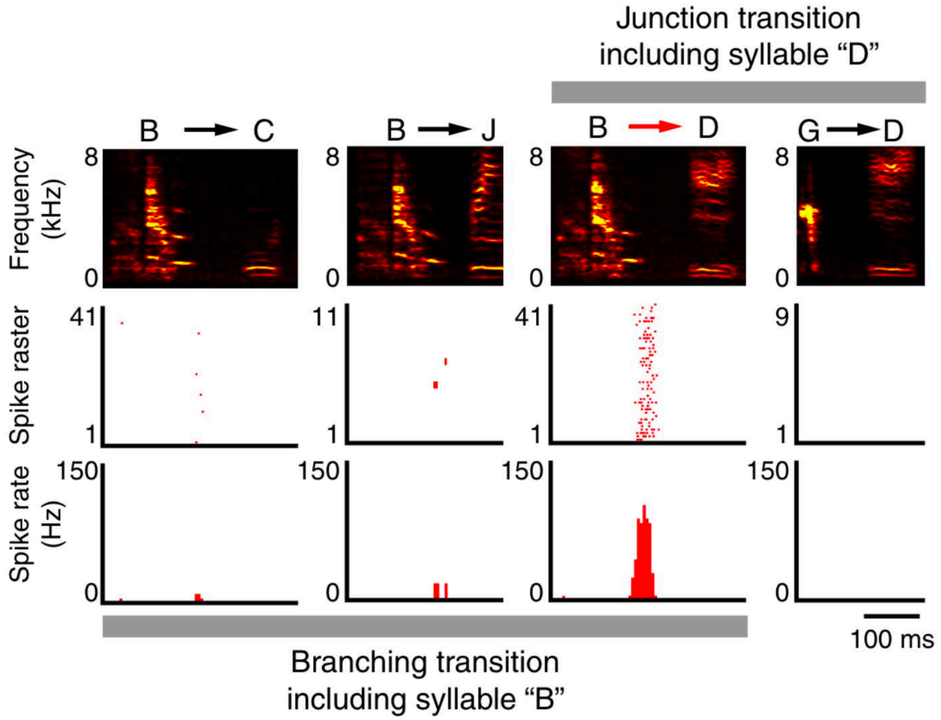


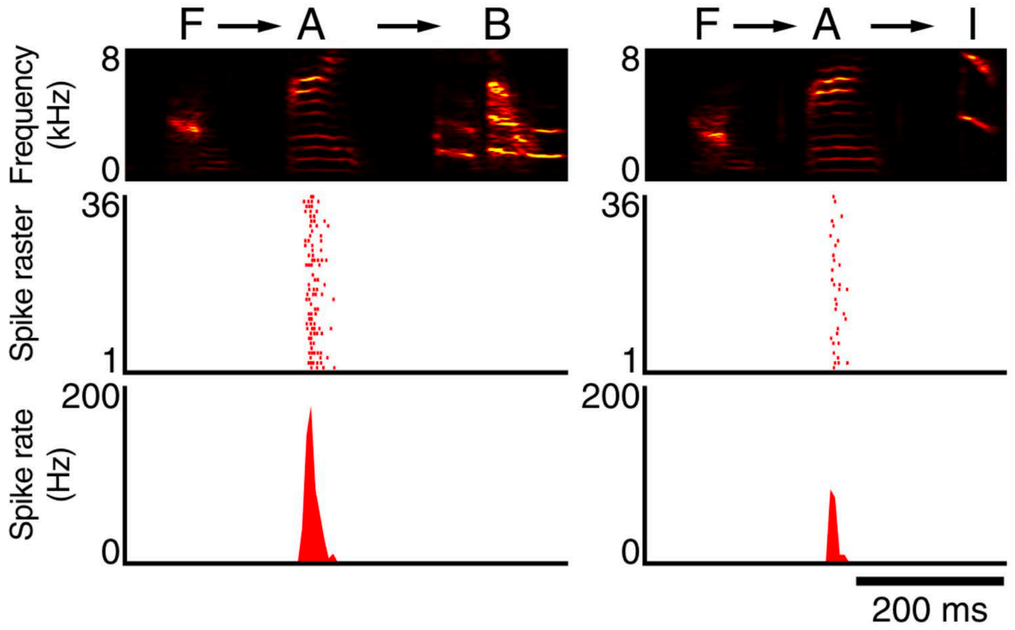


Neural encoding of Bengalese finch syntax

Fujimoto 2011

Transition specific activity

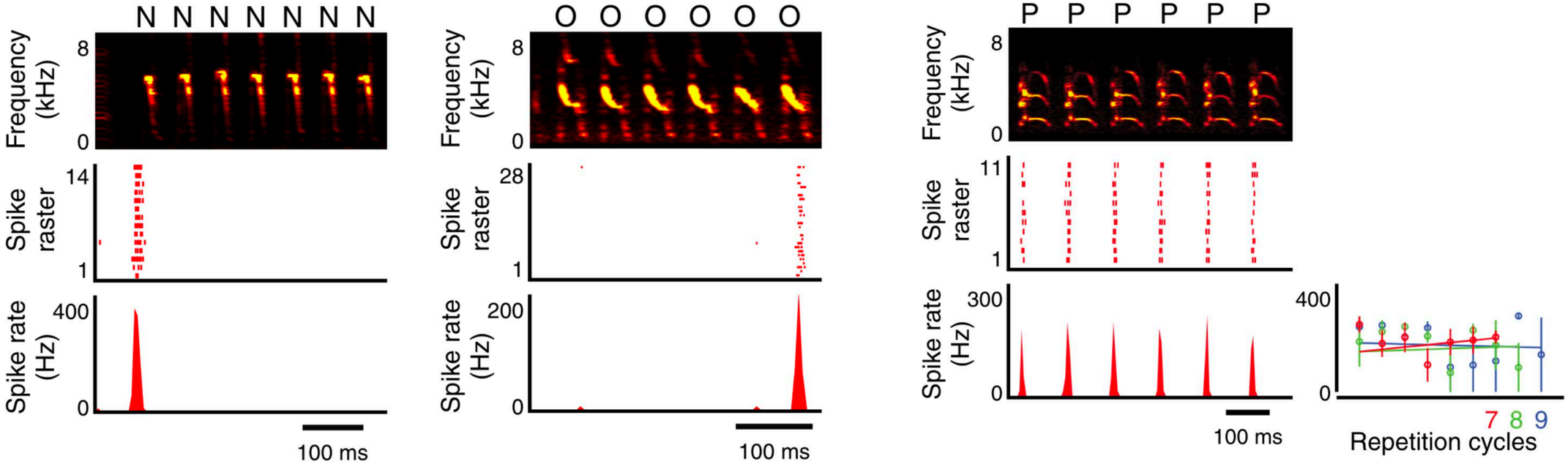




Neural encoding of Bengalese finch syntax

Fujimoto 2011

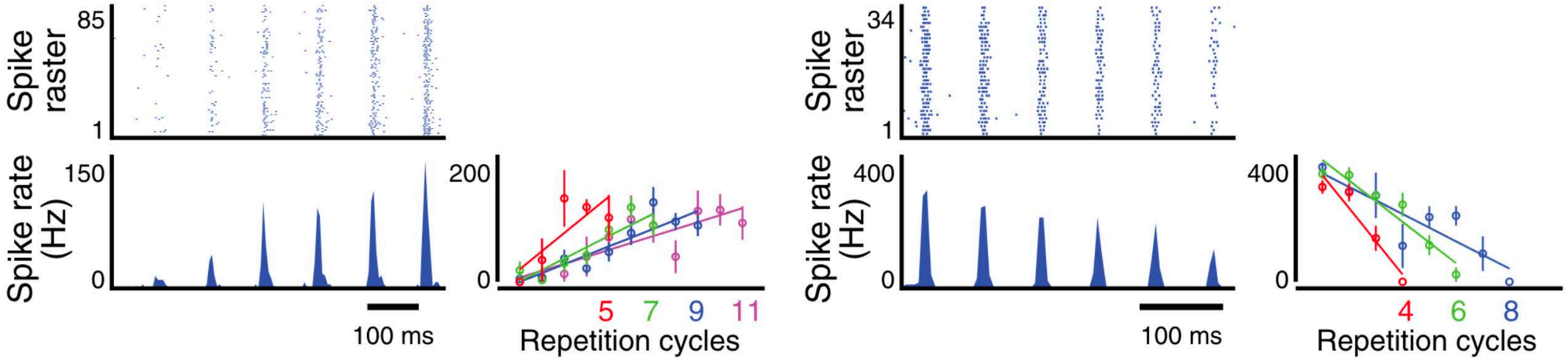
Repetition specific activity

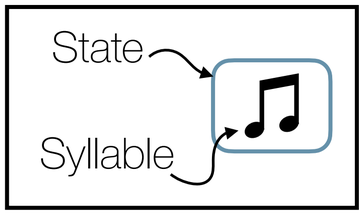


Neural encoding of Bengalese finch syntax

Fujimoto 2011

Repetition specific activity





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

Interim summary - extending a stereotyped behavior

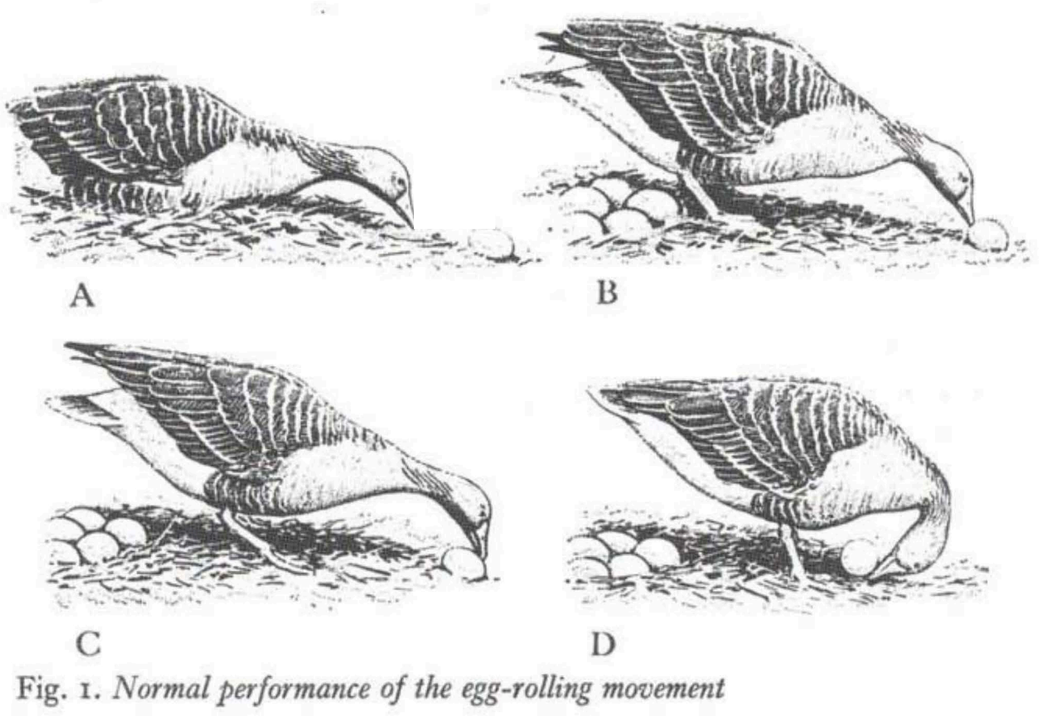
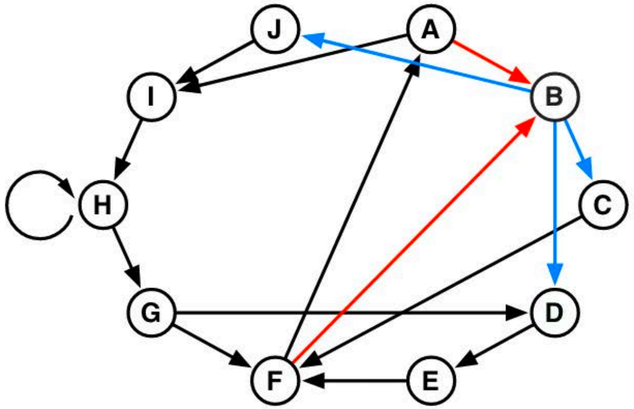


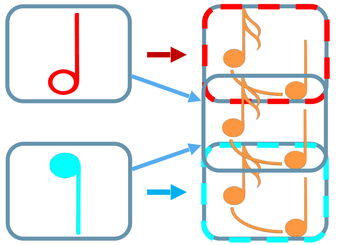
Fig. 1. *Normal performance of the egg-rolling movement*

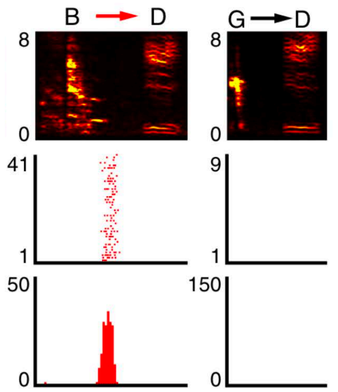
Lorenz and Tinbergen 1938

Konrad Lorenz and Nikolaas Tinbergen

Flexible syntax





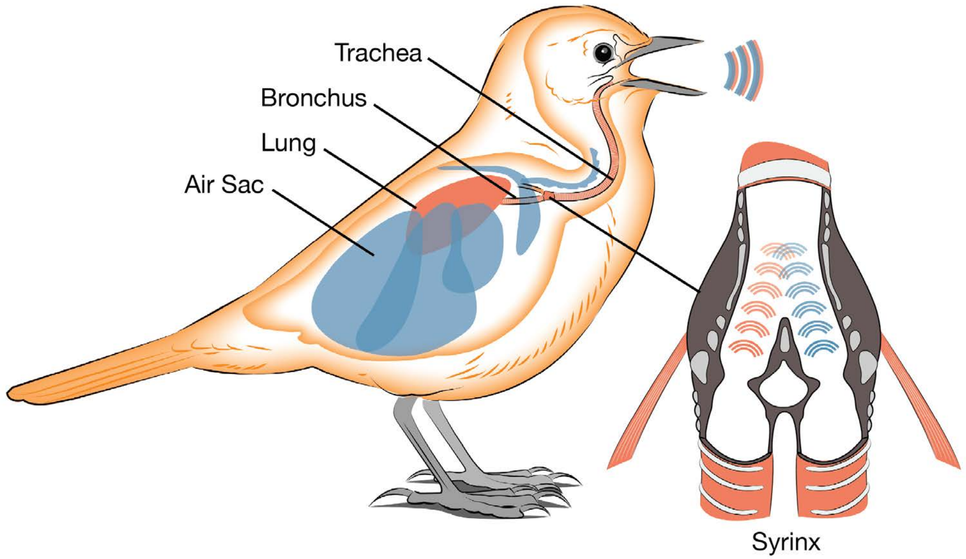


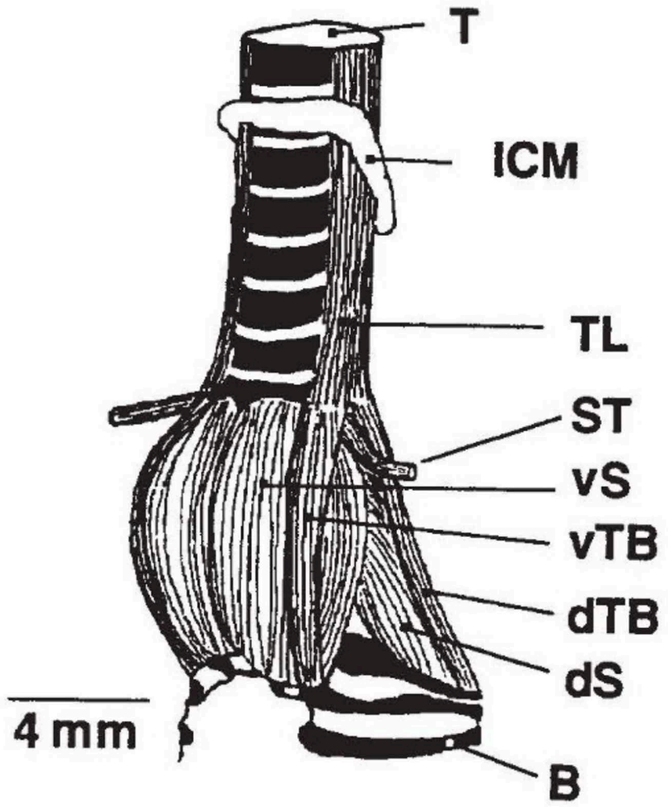
Open-ended learner

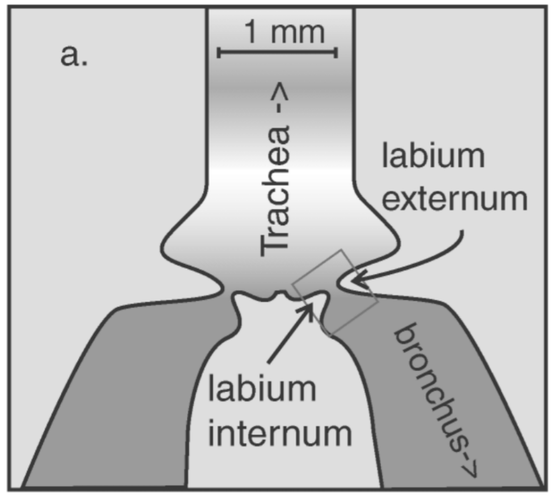
Canaries: Long-range, hierarchical, syntax rules

(Motor syntax and working memory)

Interlude: Physics of song

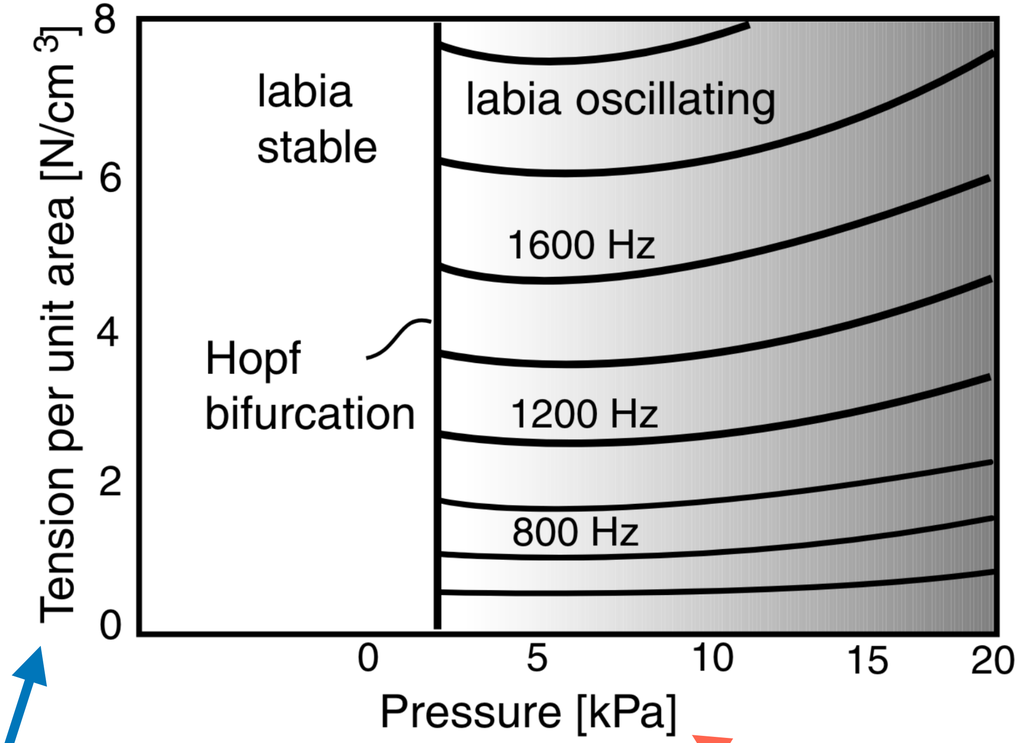






Gardner 2001

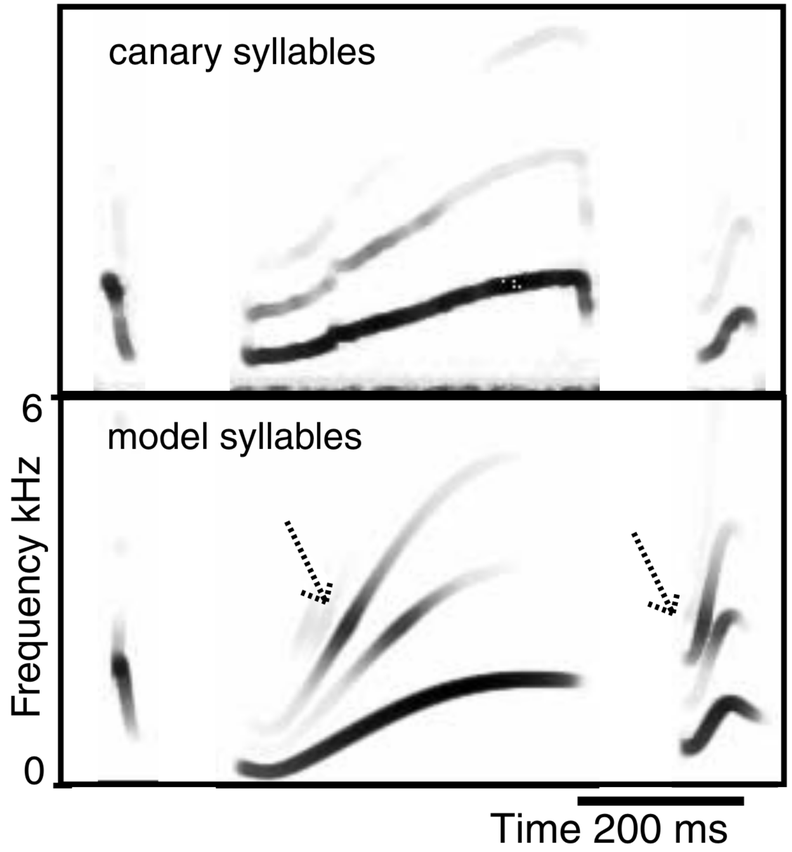
Oscillatory solutions of the labia equations of motion

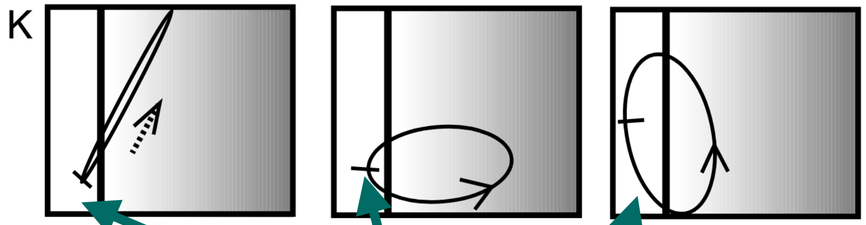


Muscles

Bronchi air pressure

Also:
Beak and trachea filter
Beak clicks

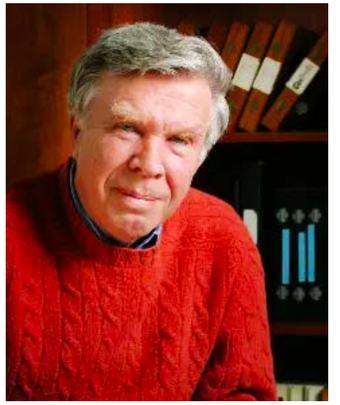




Mini breaths

Gardner 2001

Canary song syntax: Syllable repertoire



Fernando Nottebohm

Hatch ~04/1981

Initial learning

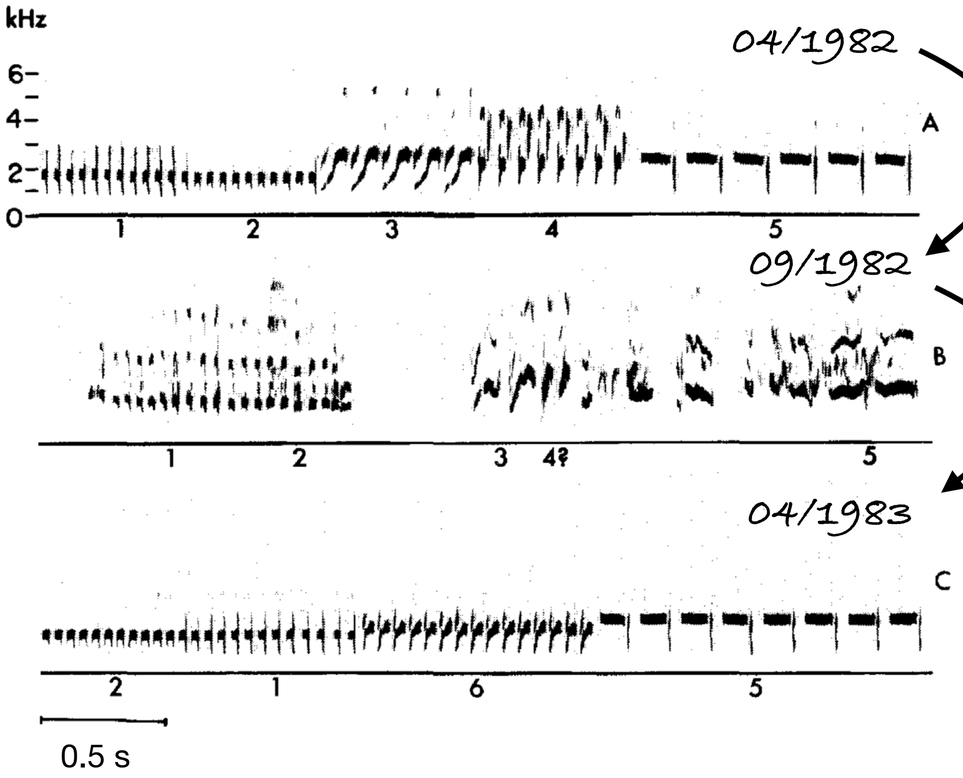
04/1982

Stop, then relearn

09/1982

Crystallize?

04/1983



~38

~25 sylables

Hatch (spring or summer)

1 year (1st mating)

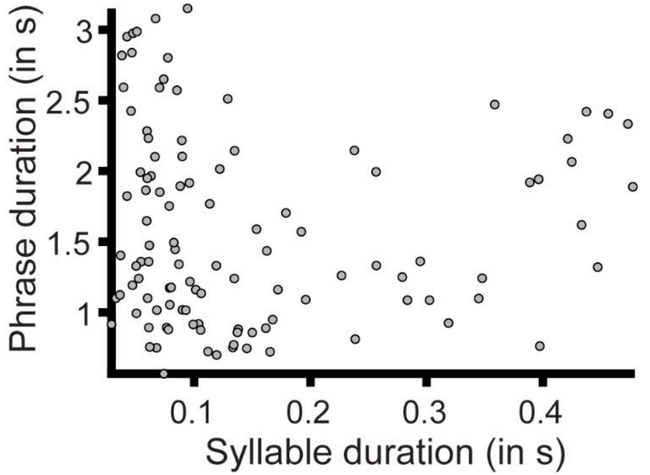
2 years

3 years

Canary song syntax: Hierarchical sequences

Syllables compose phrases:

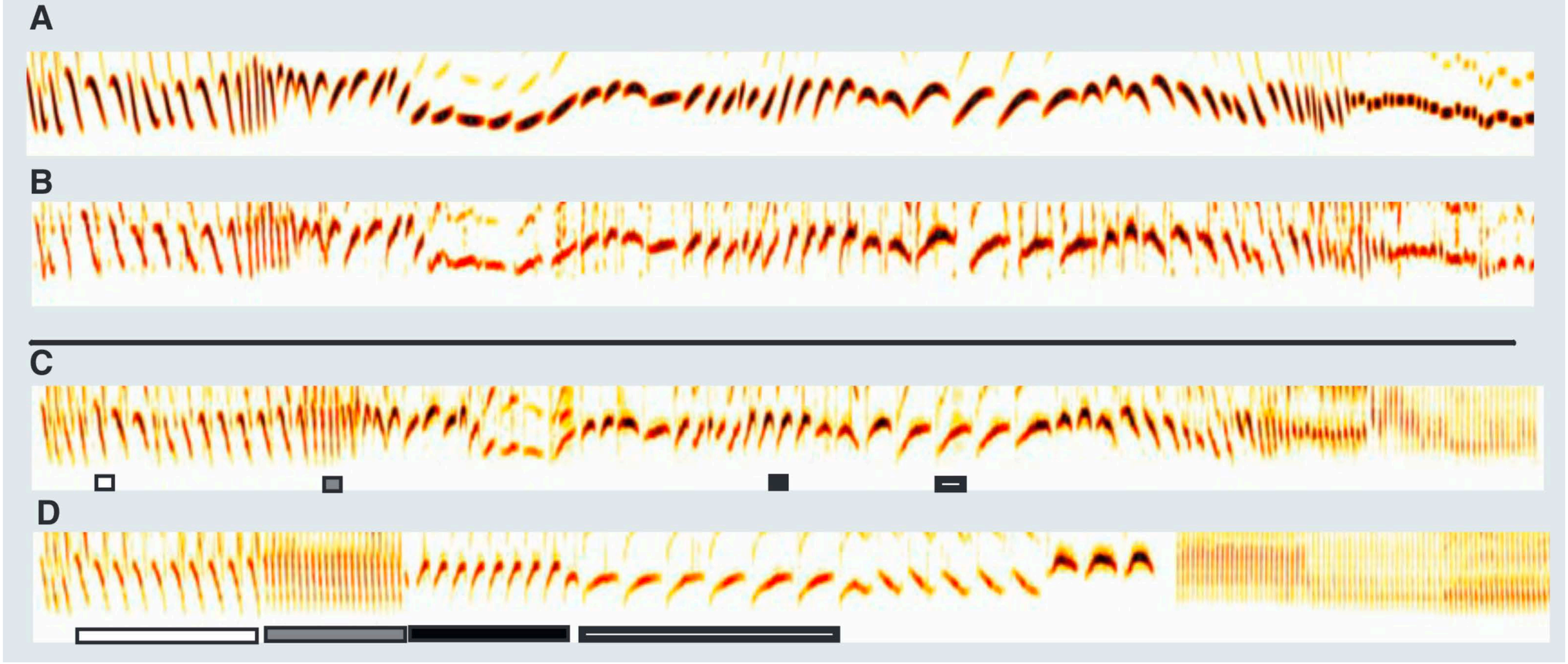
Phrase 1 Phrase 2 Phrase 3



Waterslager canaries
(Markowitz 2013)

Canary phrases are an innate syntactic structure

Noam Chomsky



'Tutor'

200dph

250dph

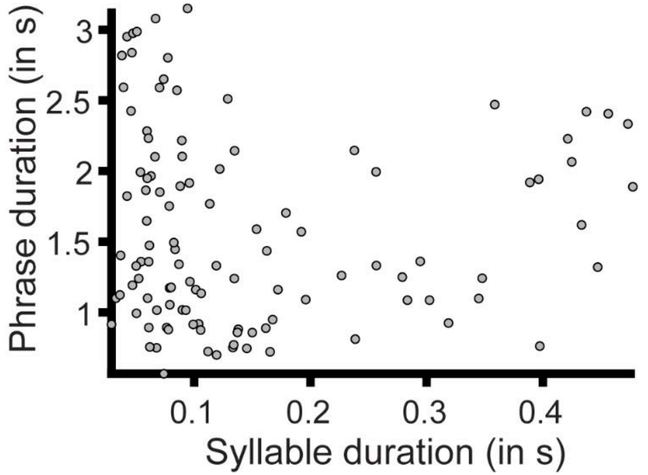
300dph

Gardner 2005

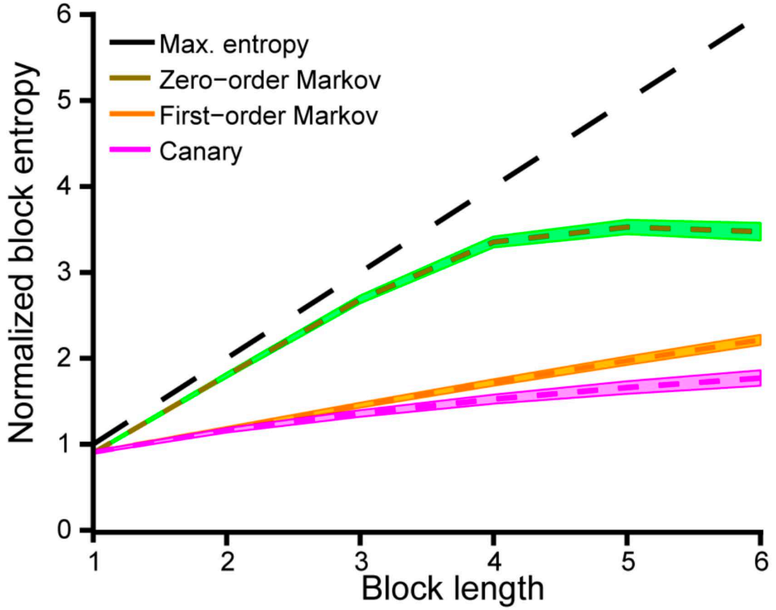
Canary song syntax: Hierarchical sequences

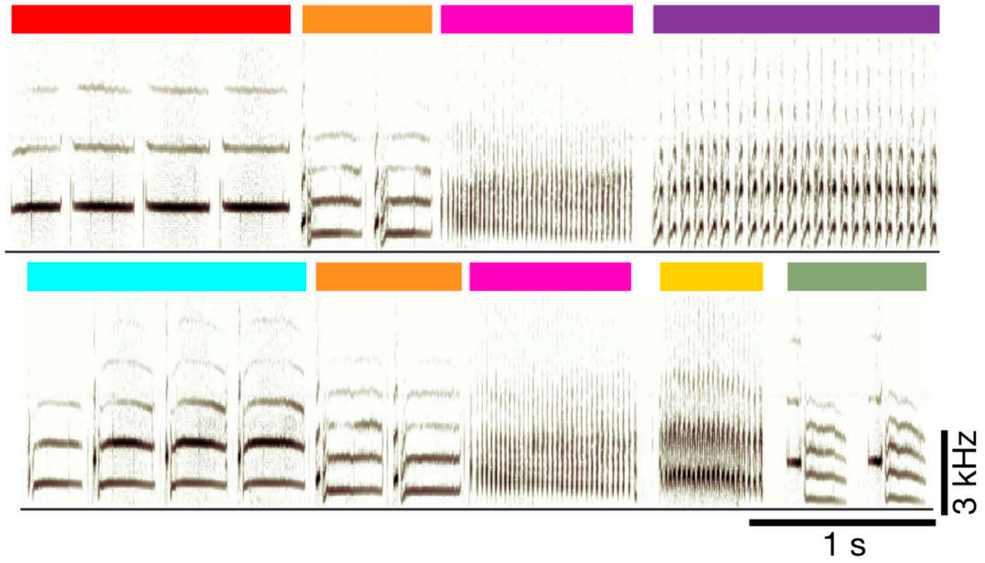
Syllables compose phrases:

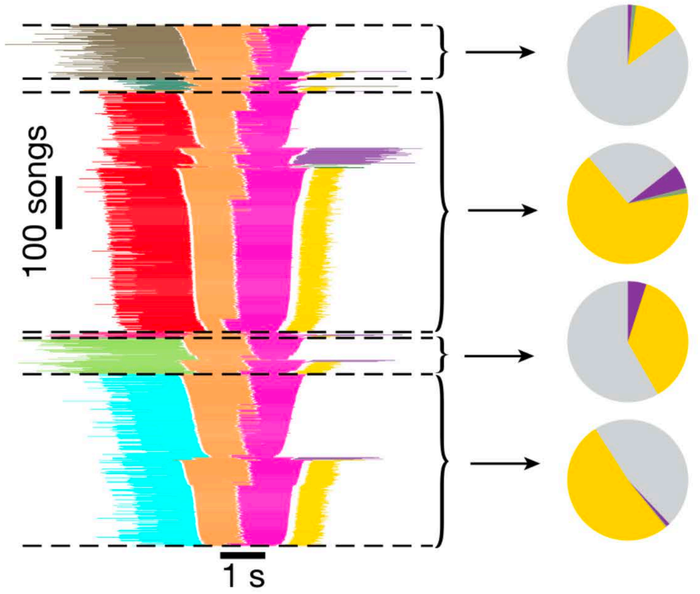
Phrase 1 Phrase 2 Phrase 3



Phrase sequences obey long-range syntax rules

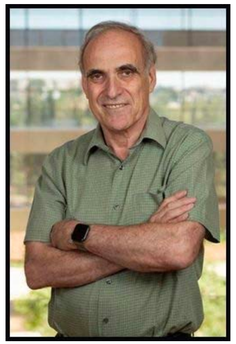




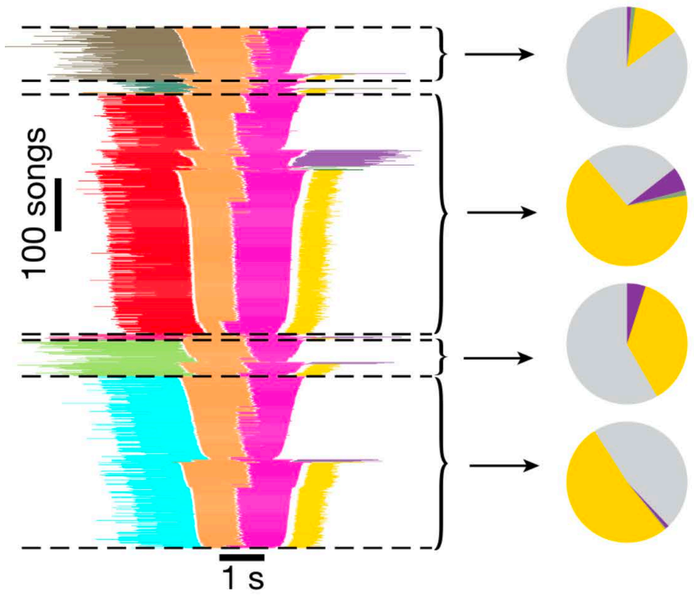


Cohen 2020

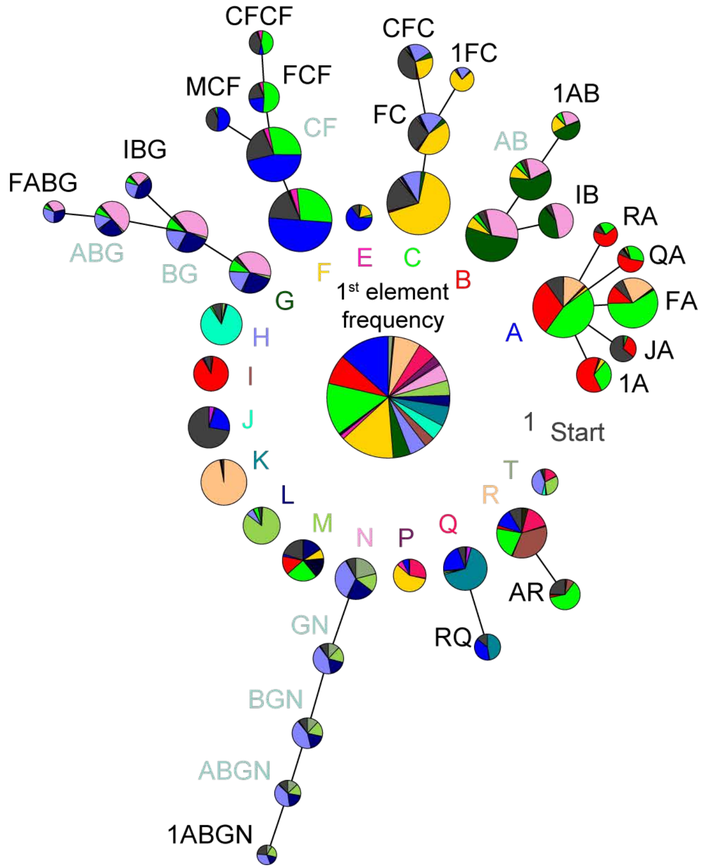
Canary song syntax: Long-range order



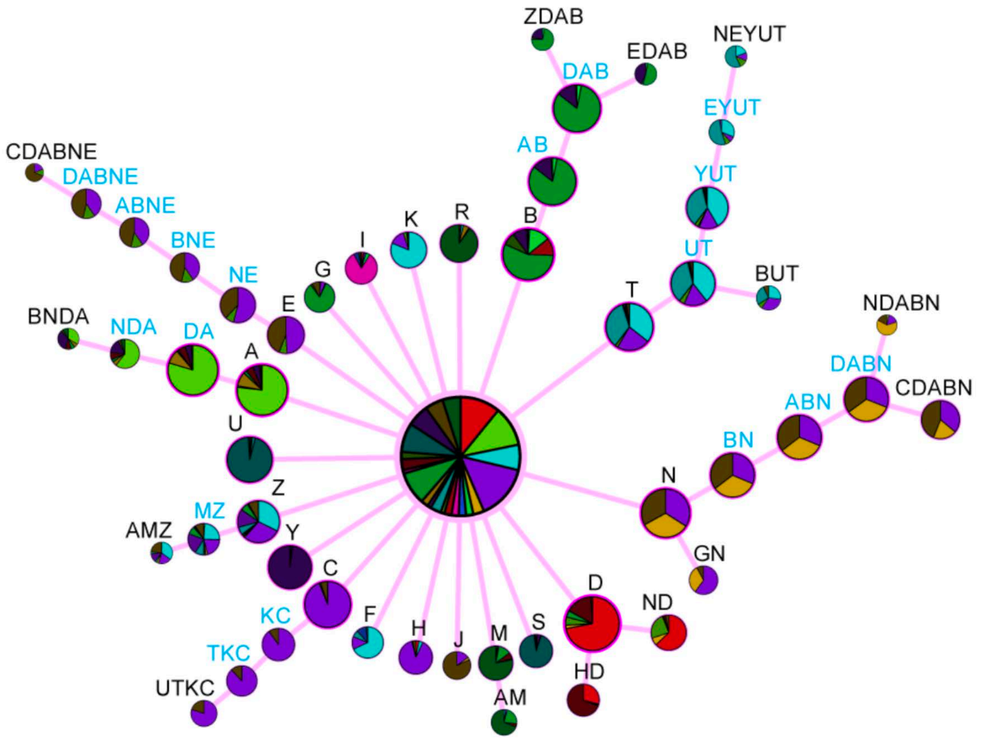
Naftali Tishby



Domestic Canary



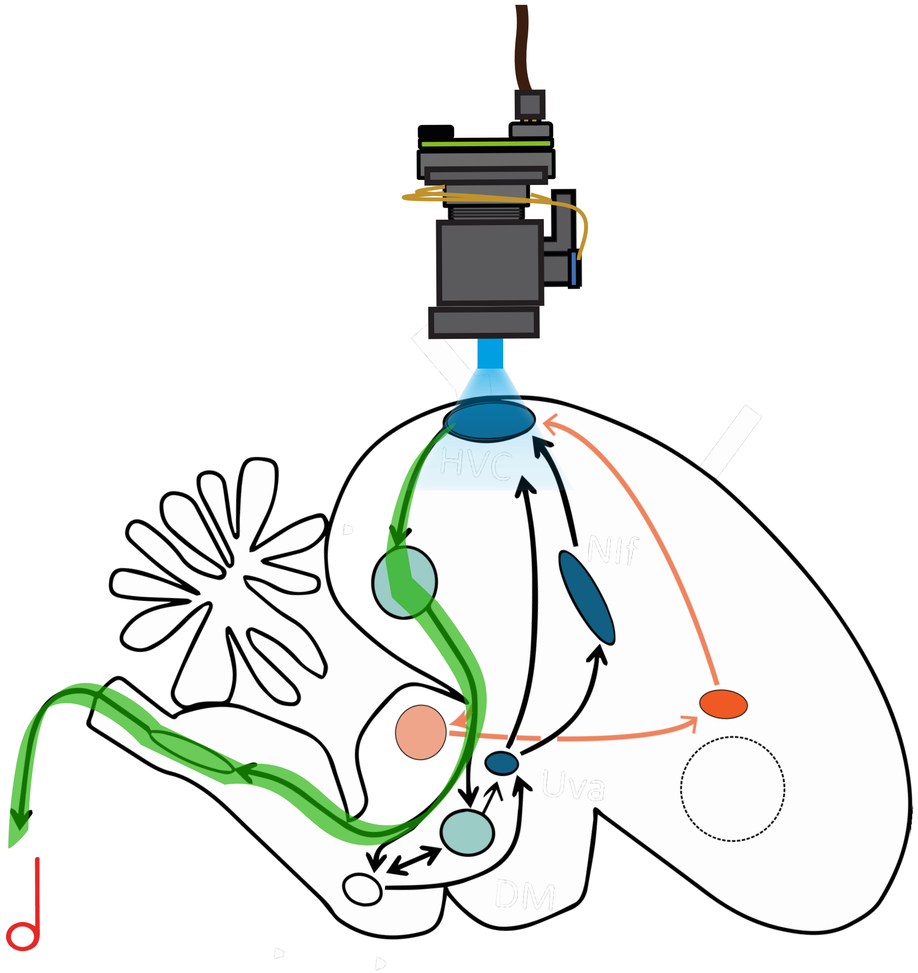
Belgian Waterslager Canary



How does the canary brain carry long-range (working) memory?

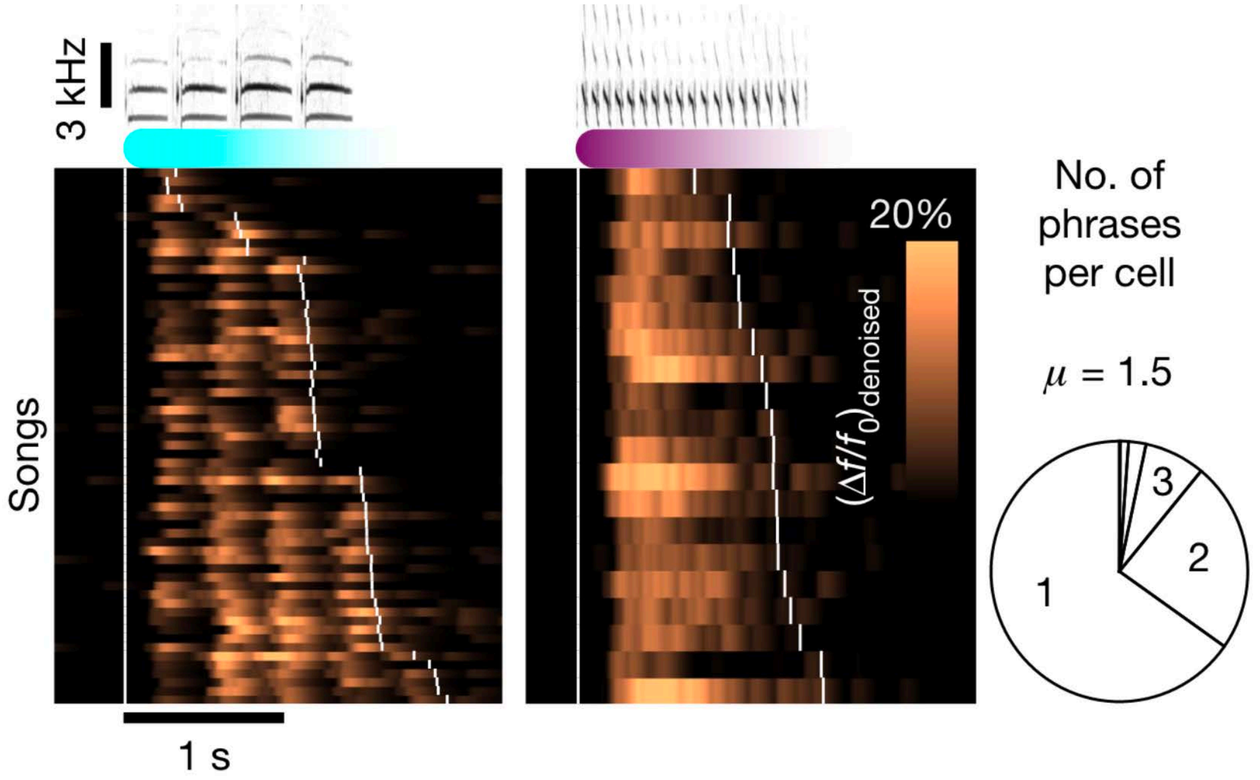
Ron 1996
Markowitz 2013
Cohen 2022

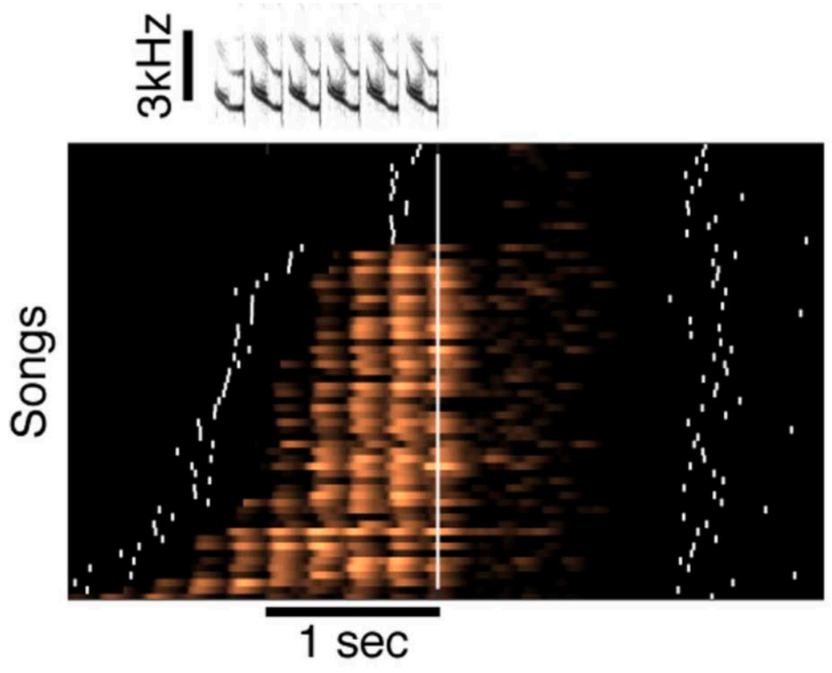
Song-locked canary premotor activity is syllable specific



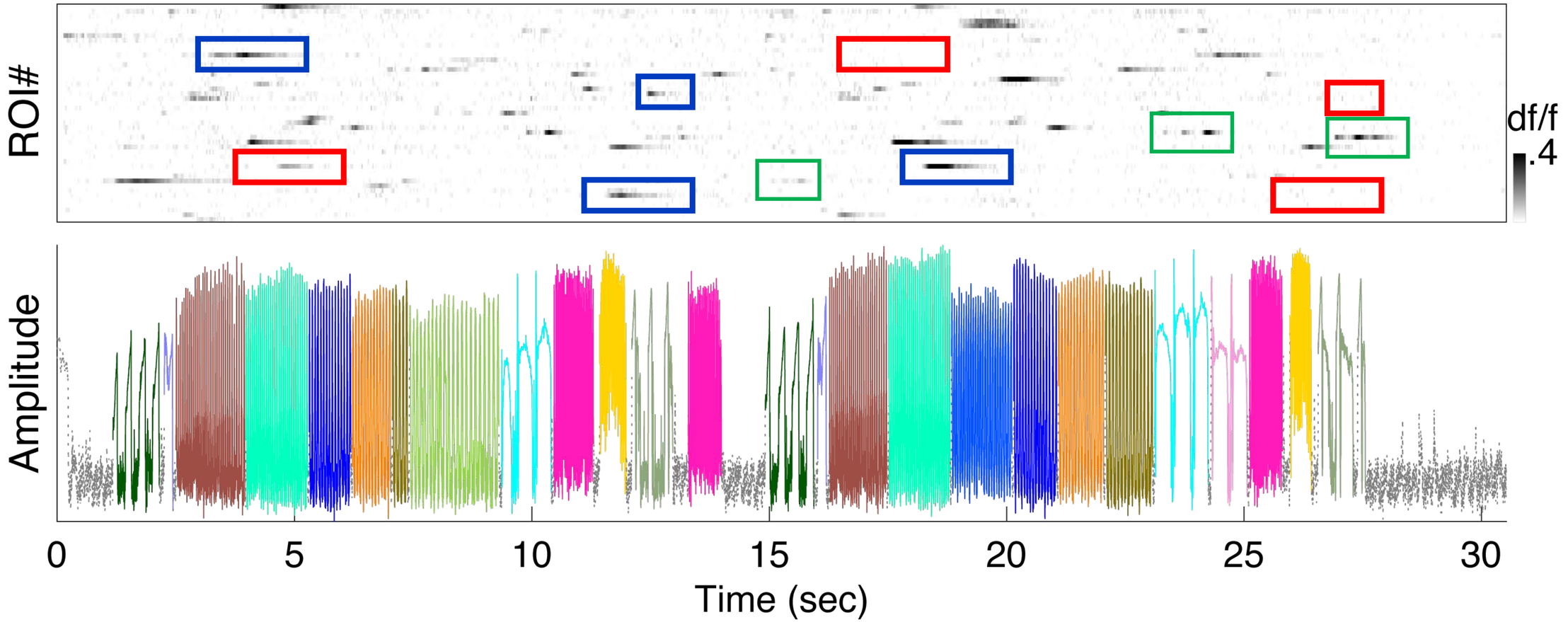
The premotor song circuit

HVC activity is locked to behavior



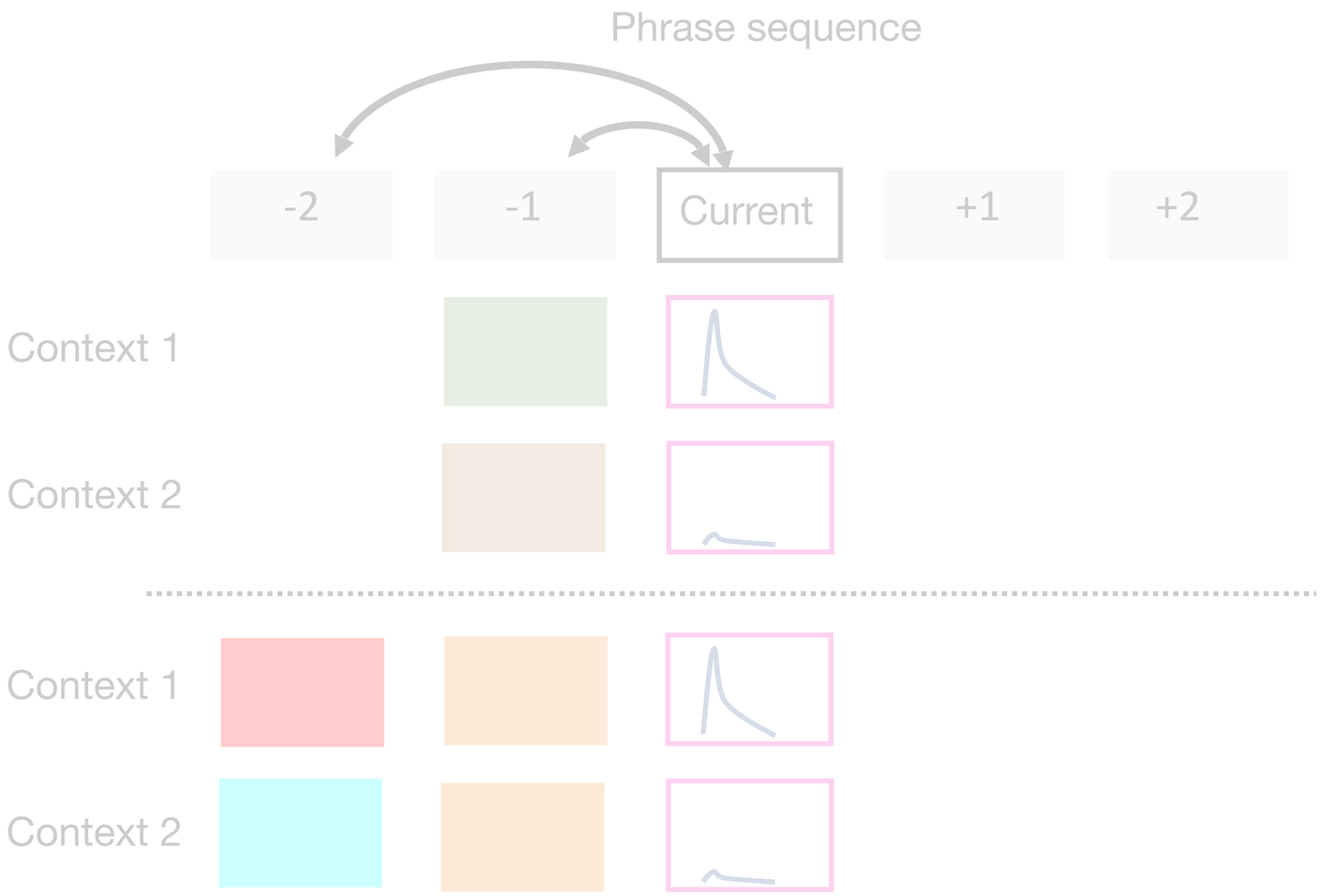


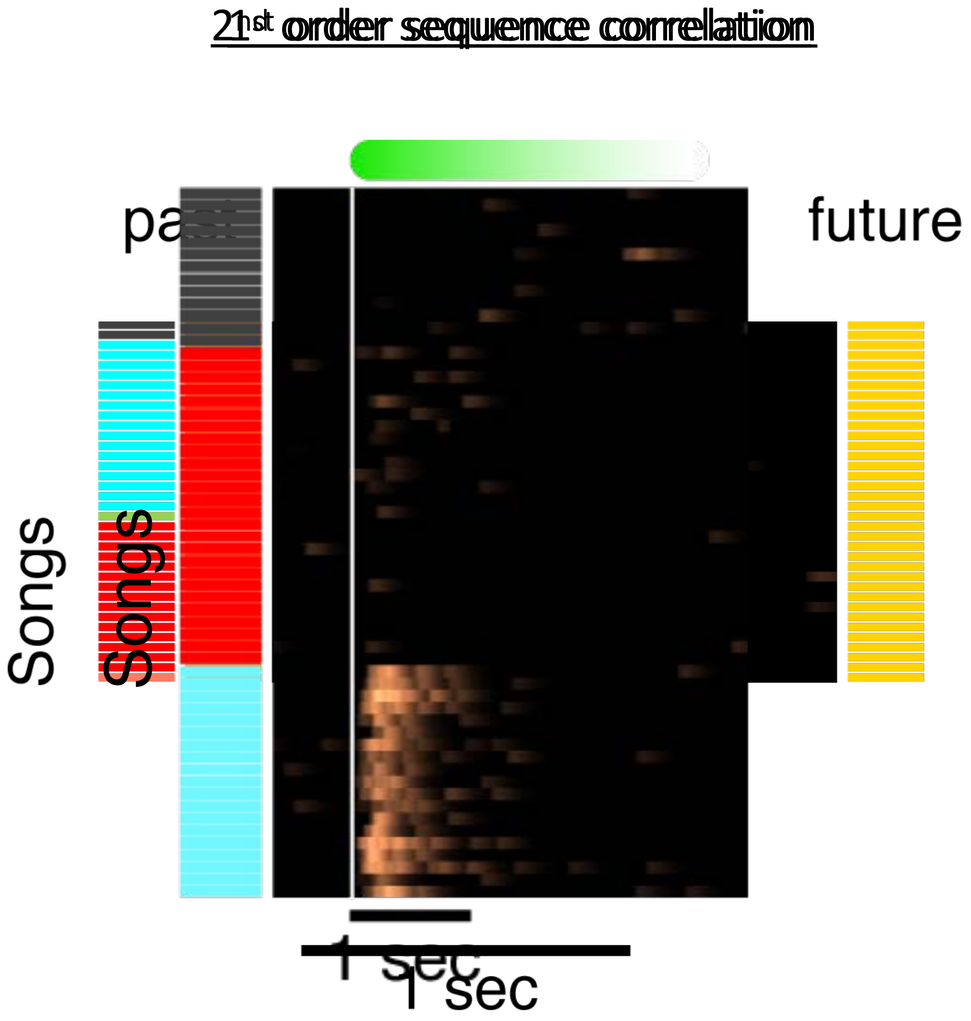
HVC activity is context dependent



Cohen et al. 2020

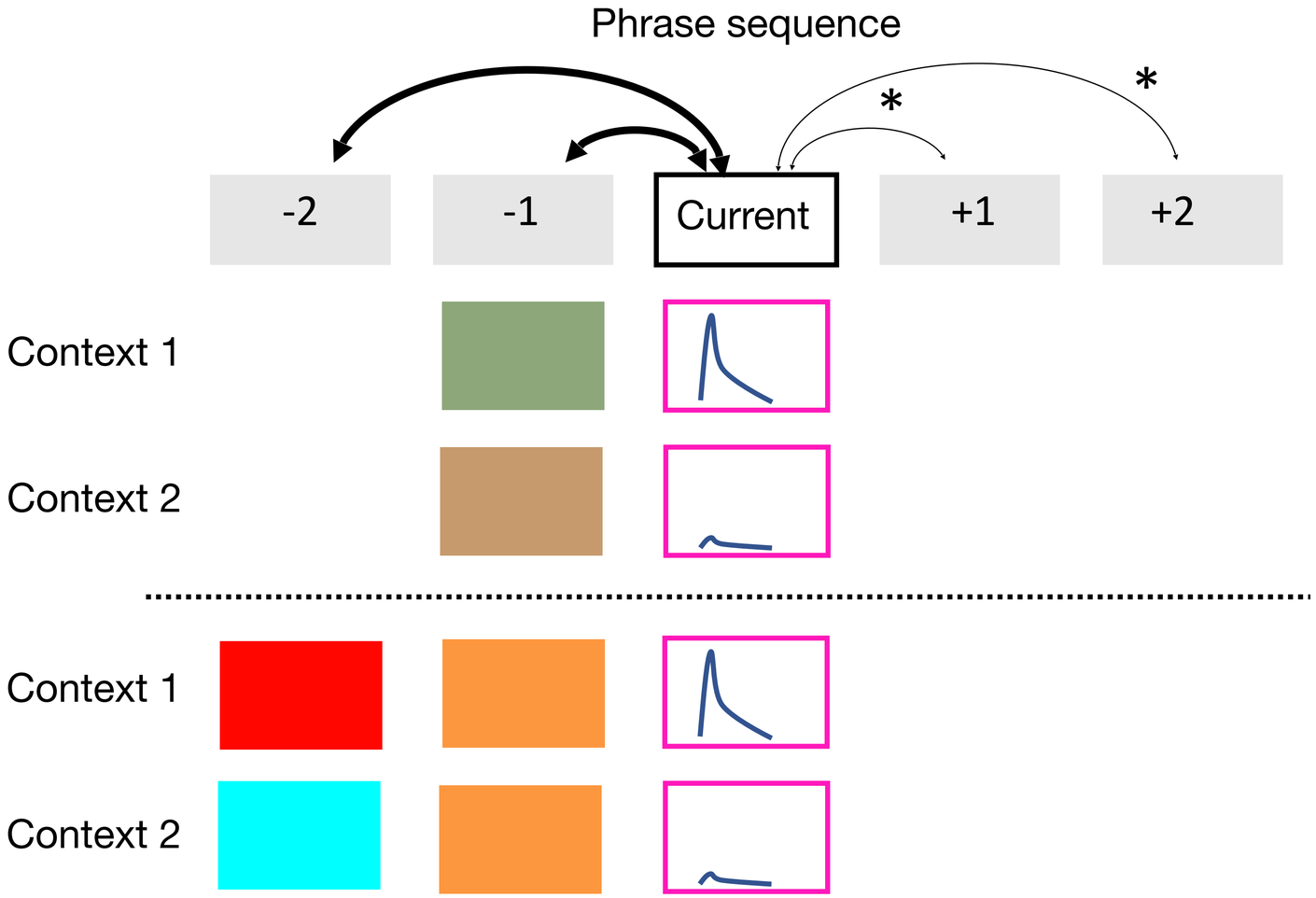
HVC neurons reflect long-range sequence information





Cohen et al. 2020

HVC neurons reflect long-range sequence information

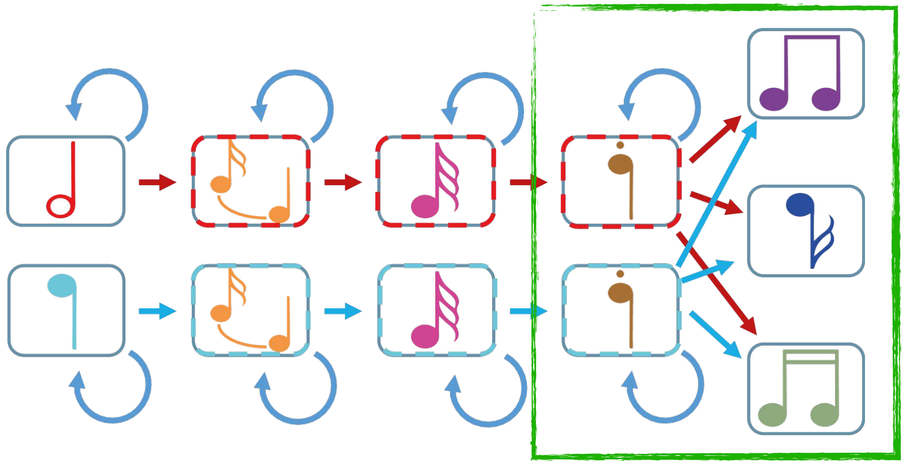


* : $p<10^{-6}$

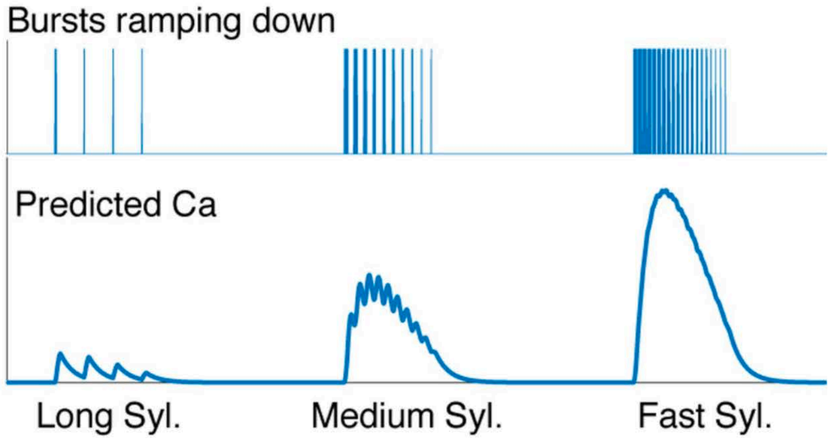
Cohen et al. 2020

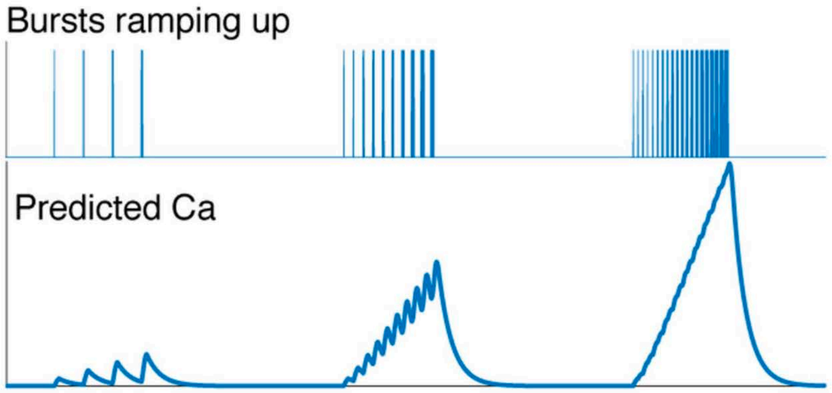
The hidden neural states underlying canary syntax

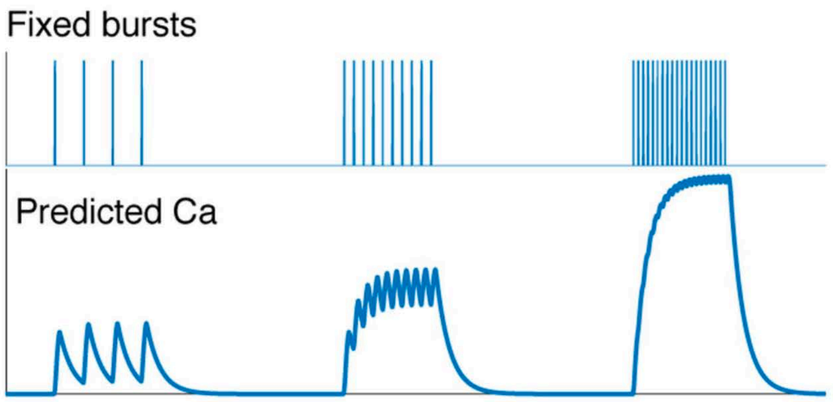
—> Phrase sequence —>

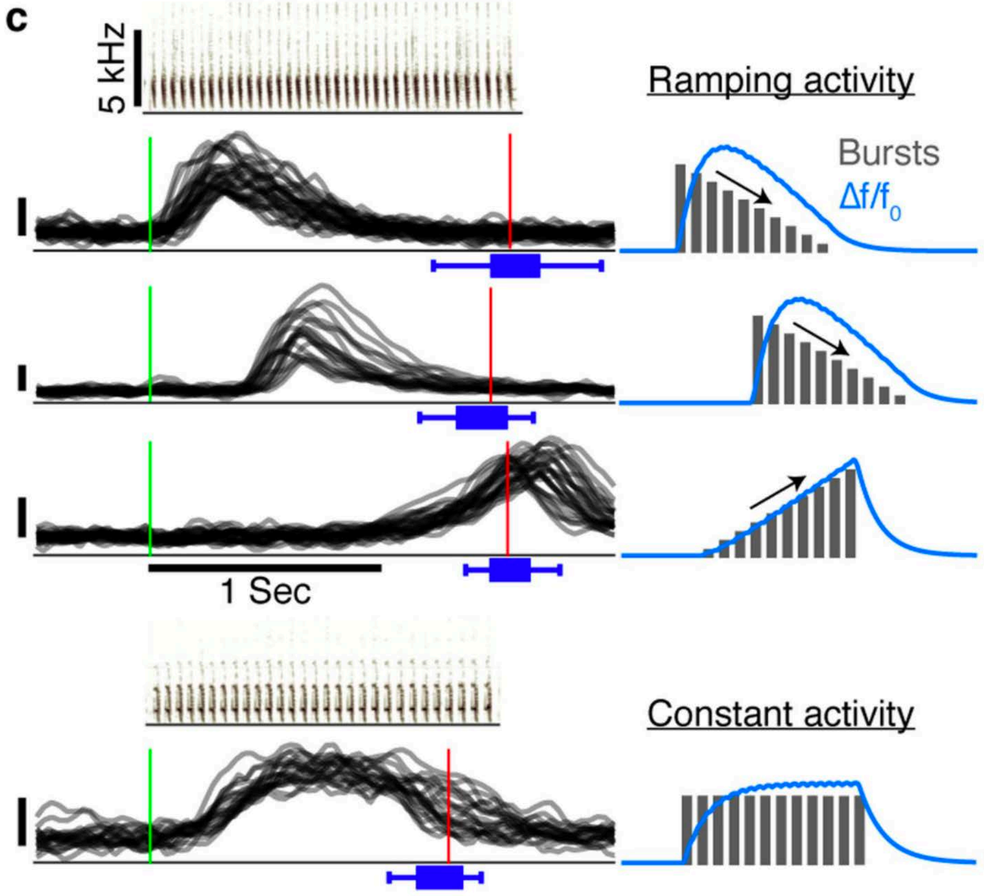


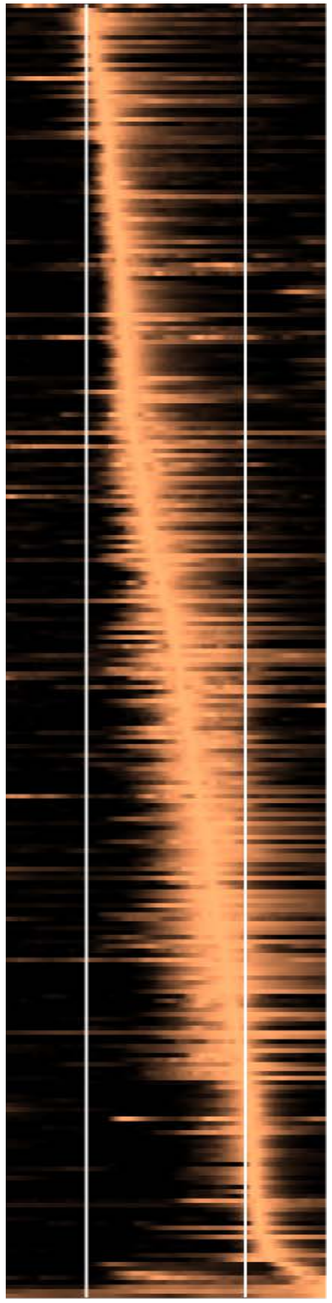
HVC neurons also reflect timing information



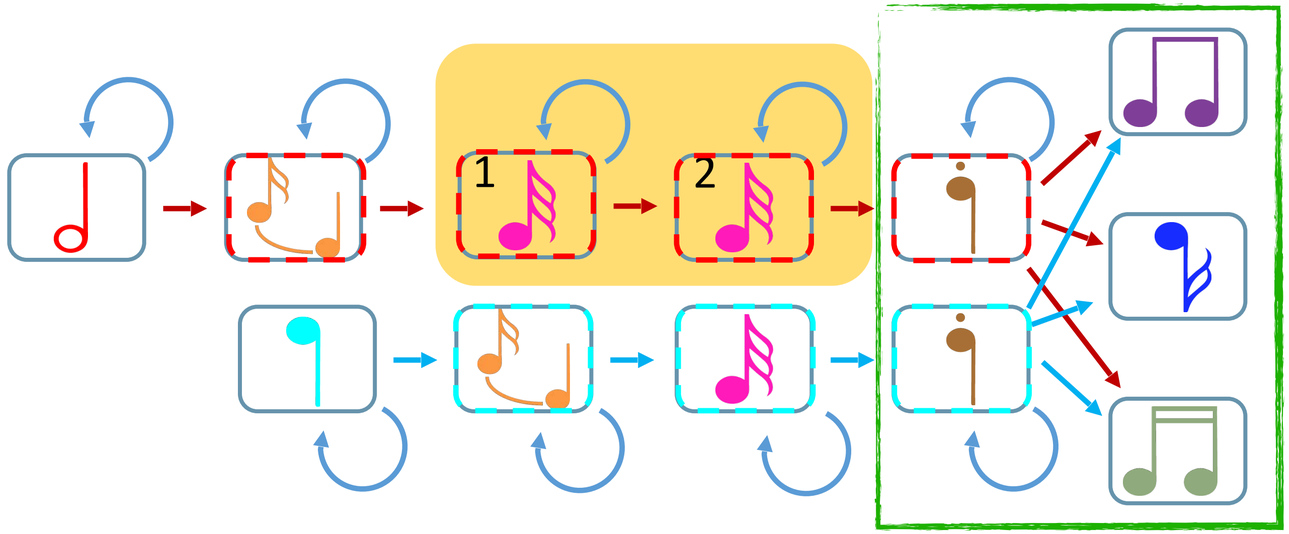




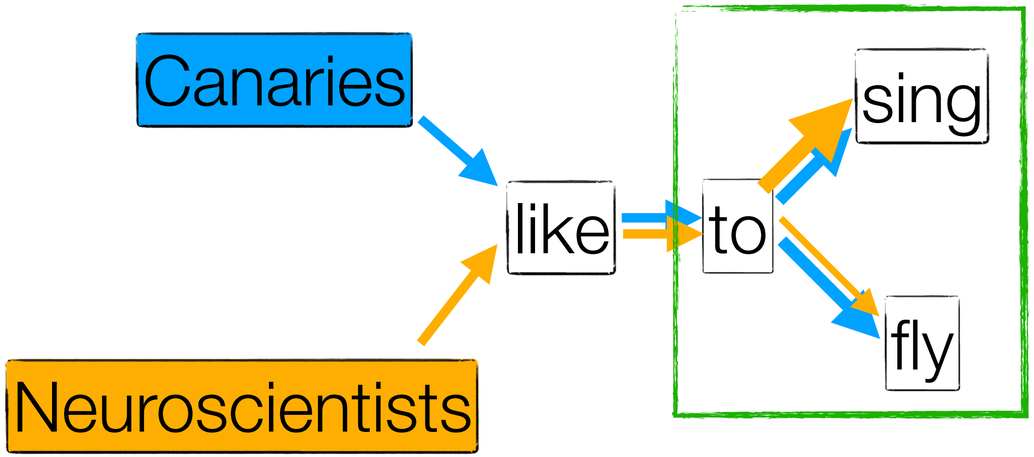




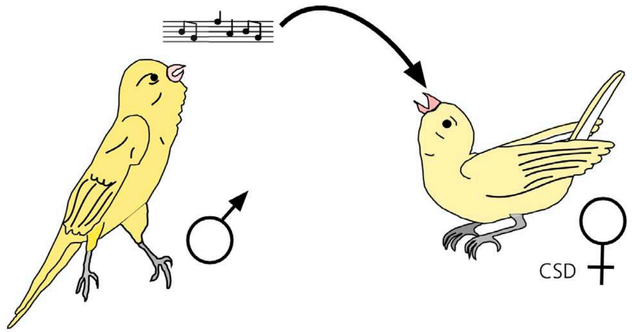
Interim summary -
Motor working memory model - time scale of 1-7 sec

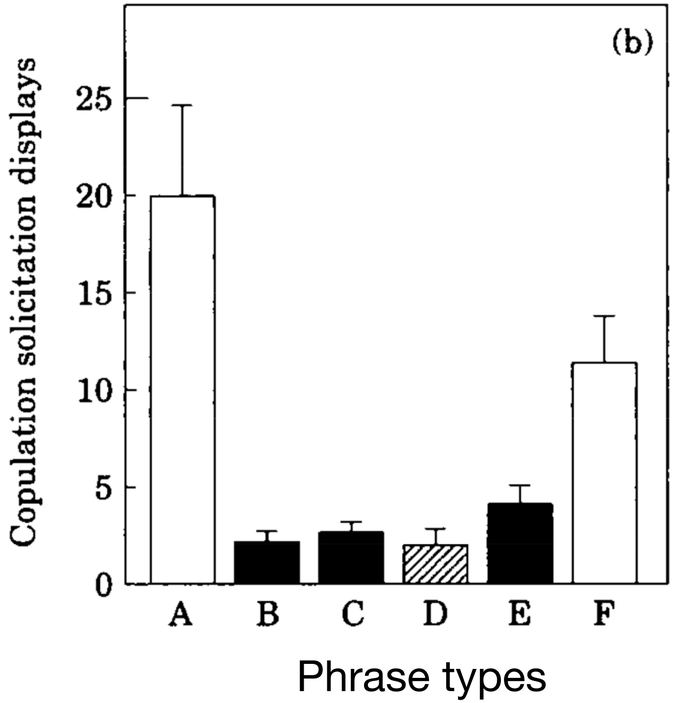


High order syntax rules

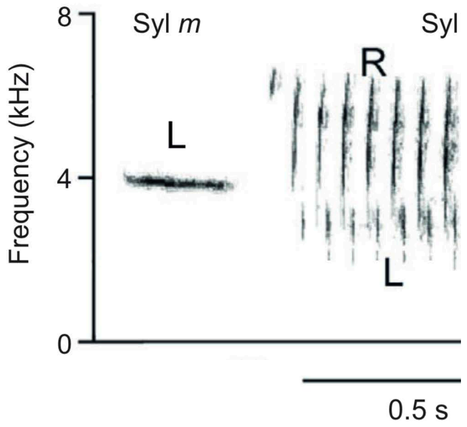


Canary song preferences

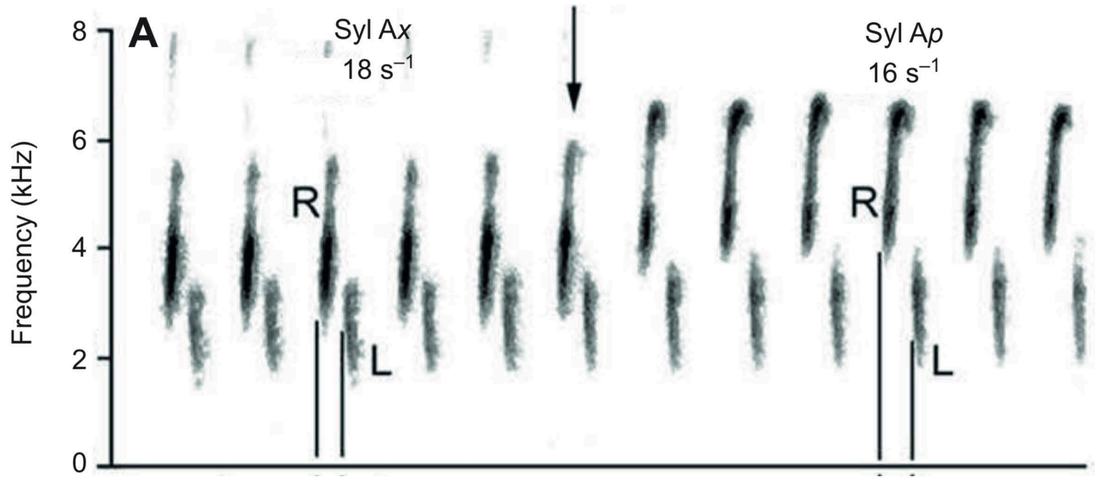




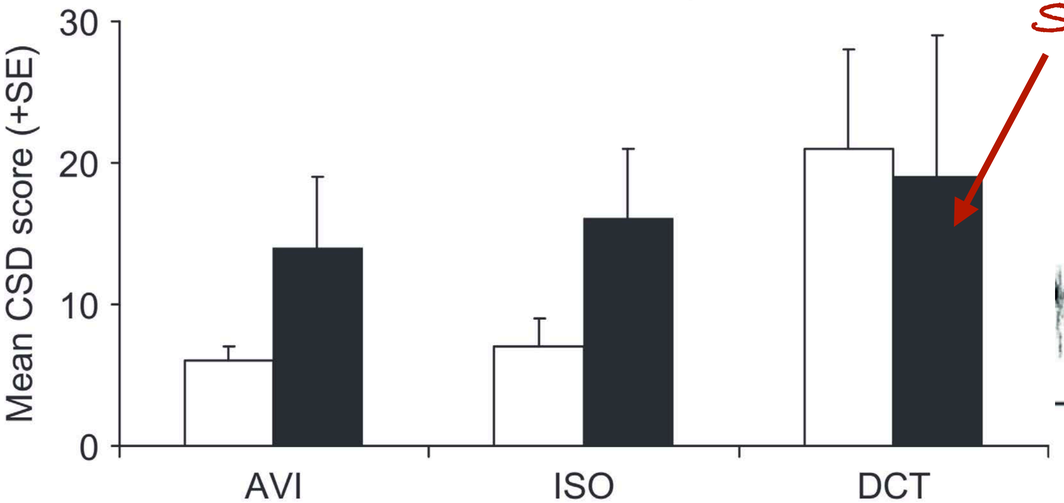
high repetition rate
wide-band
multi-note syllables



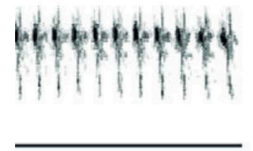
Rapid inter hemispheric coordination



Females learn their preference



Song with 'A'



T=Tutored

Vallet 1995
Del Negro 2000
Leboucher 2012
Suthers 2012

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

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

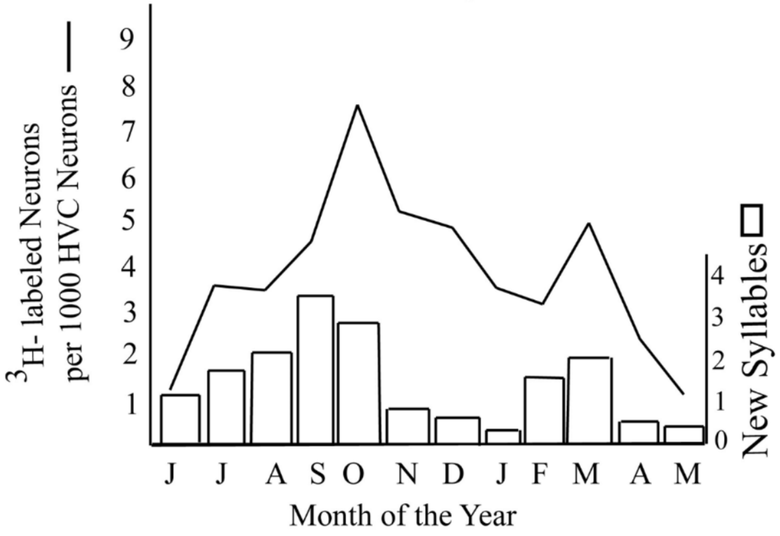
Seasonal anatomical changes
Neurogenesis and neuronal recruitment
Hormones, circuit, and song interaction

What are the potential benefits?

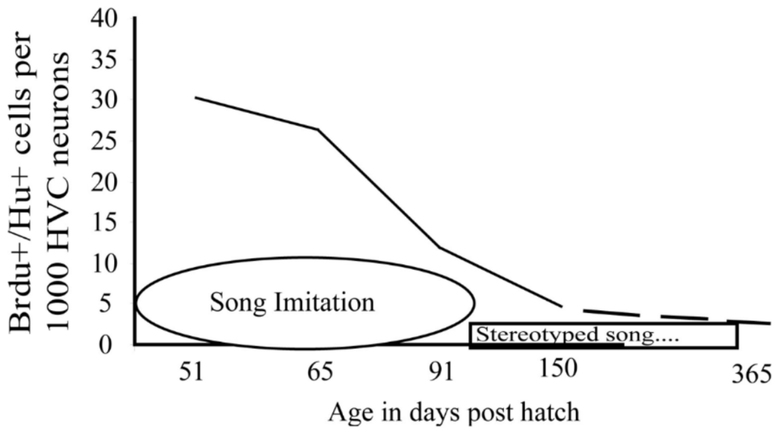
Nottebohm 1981

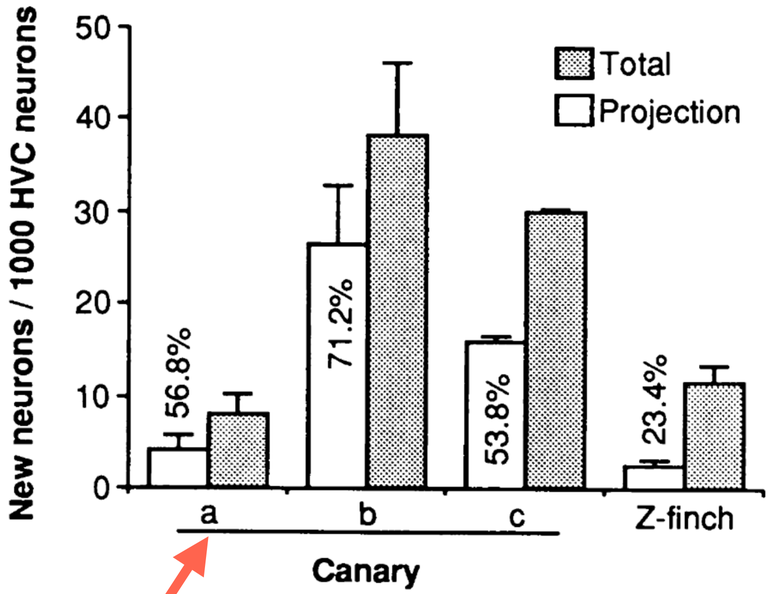
Canaries: Neurogenesis and adult plasticity

Canary



Zebra Finch





1yr, spring

1yr, fall

4yr, 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

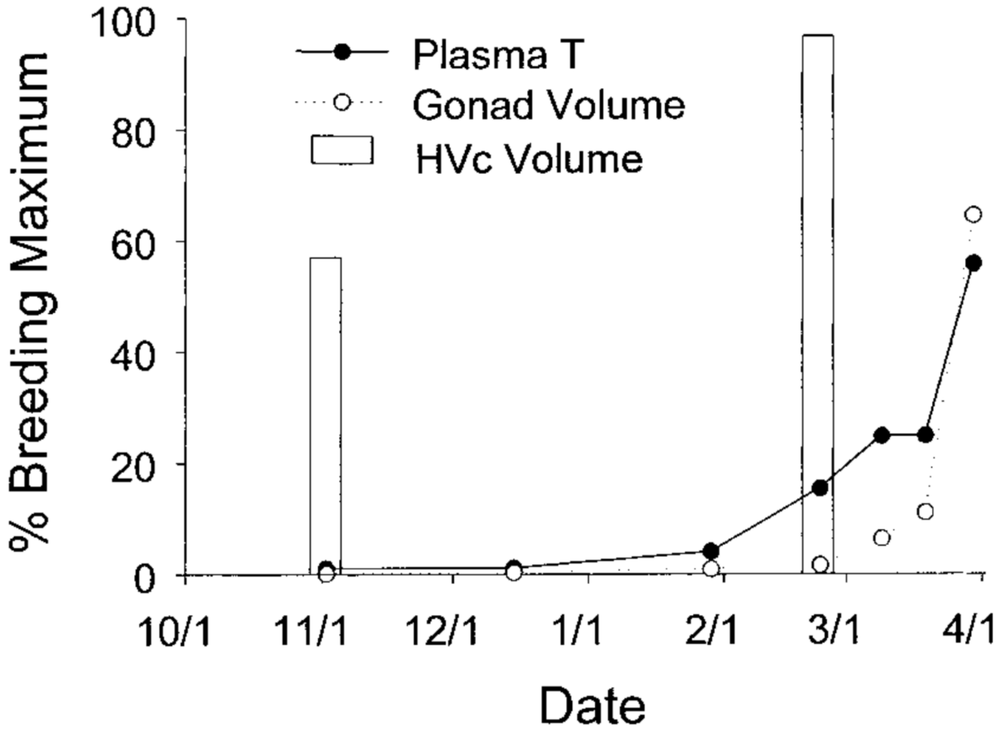
In HVC, mostly HVCRA, some interneurons
About 50% replaced every year

Goldman 1983
Nottebohm 1986
Kirn 1994
Gahr 1997

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

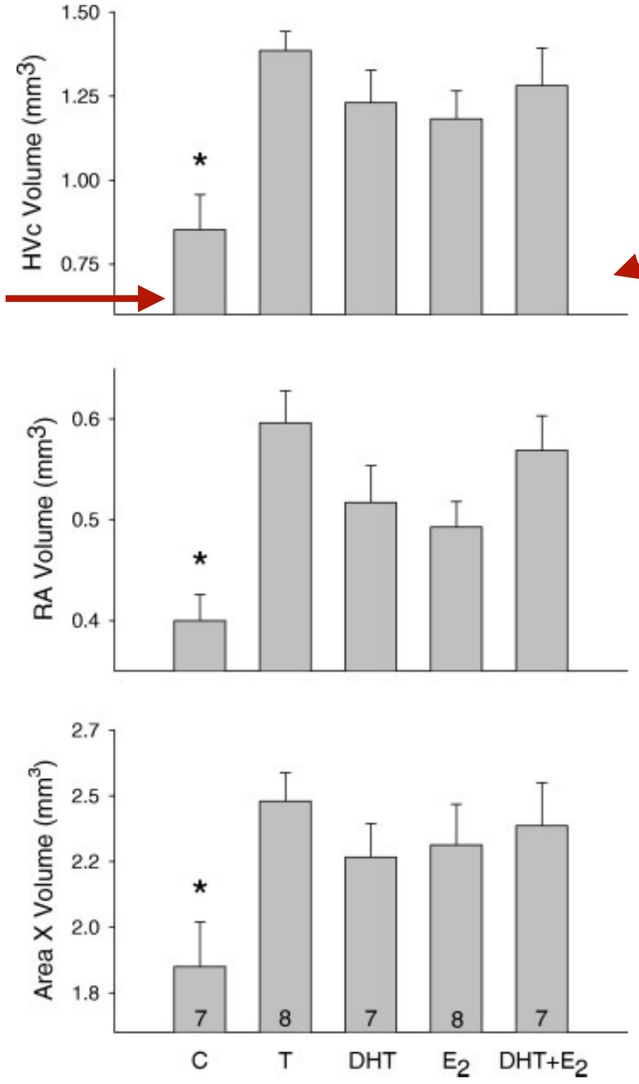
HVC grows (and decays) faster than RA and X
Further studies show that growth in RA,X needs Testosterone affecting HVC first

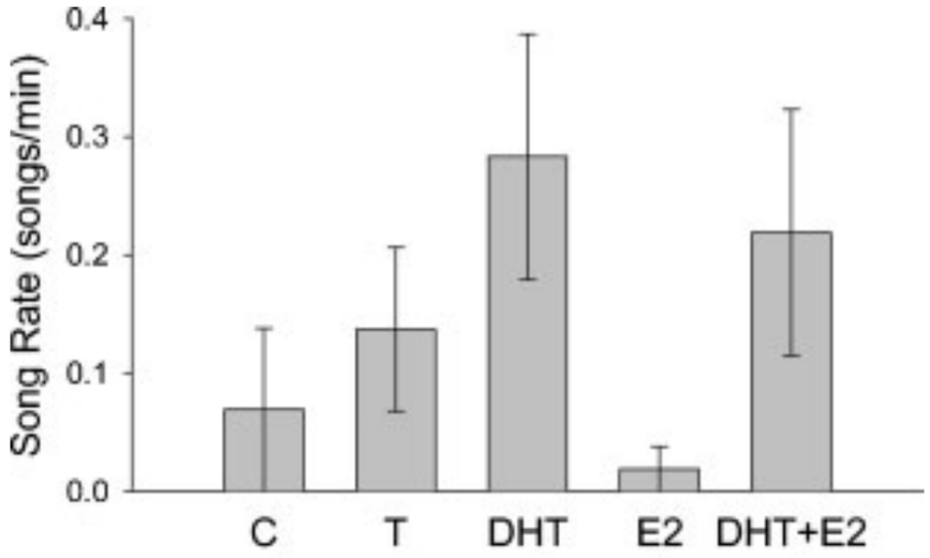
Mass of syrinx (also has androgen receptors) shrinks in non-breeding season.

Testosterone and adult plasticity

Control

Testosterone
Estradiol (and variations)





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

Tramontin 2003

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

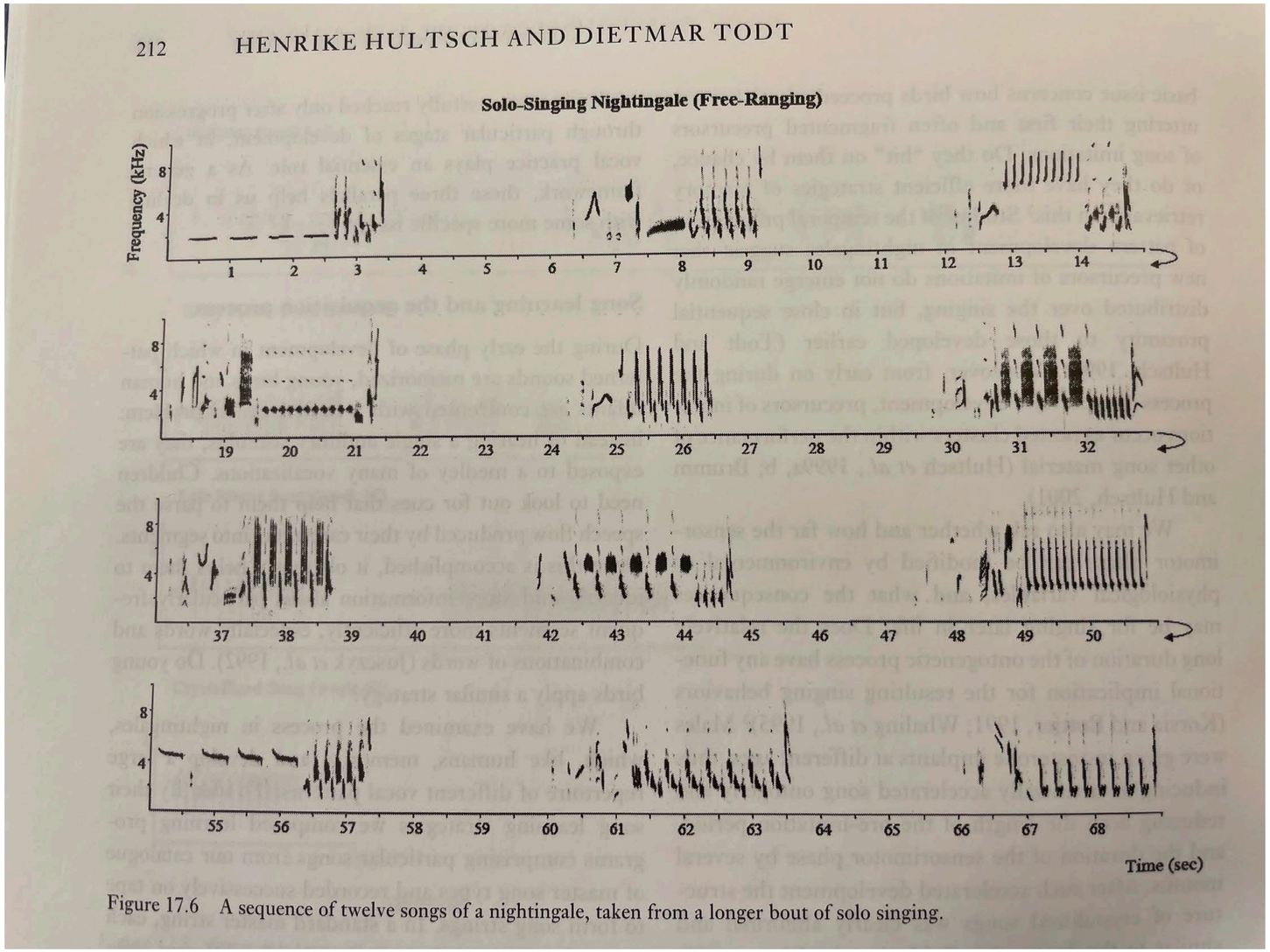


Figure 17.6 A sequence of twelve songs of a nightingale, taken from a longer bout of solo singing.

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

What processes occur between initial acquisition and adult production?

Learn: 15-40 dph

Omission, Addition
Invention, Recombination

Test: 9-11 months

Age (months)

Experiment: play so

Result: 30% songs learned

Experiment: play so

Result: 75% songs learned
Similar with 20 or 60 songs

Experiment: play so

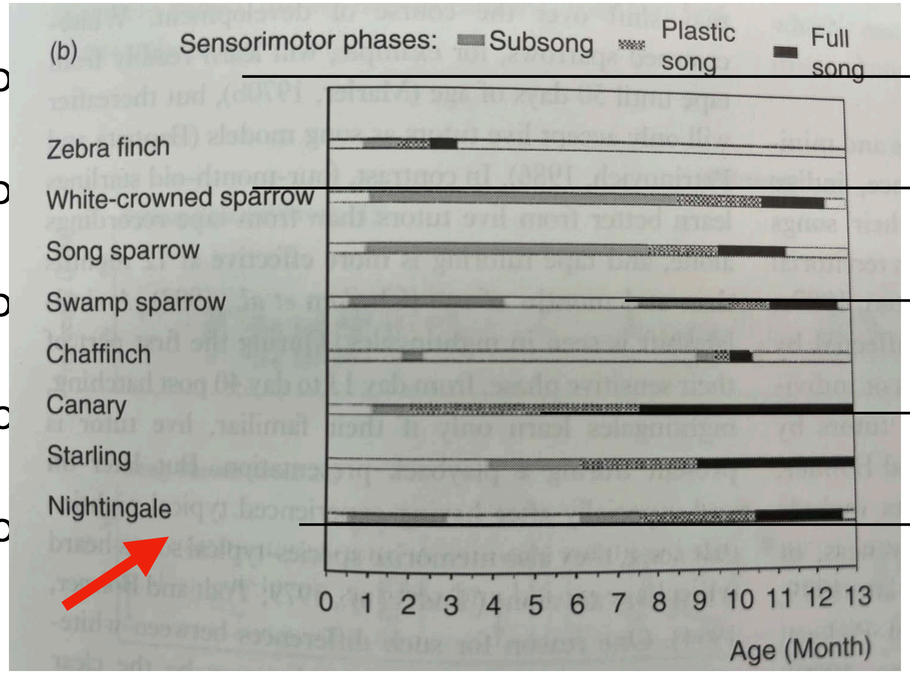
Result: A live tutor is needed at 13-40 dph
Playback learning works in later stages

Experiment: Play sc

Result: Improve learning

Experiment: play co

Result: segmented song



Nightingales: Evidence for hierarchical memorization and (or) retrieval

Learn: 15-40 dp

9-11 months

Age (months)

Experiment: play large co

kages of 3-4 songs
short term memory

Experiment: play dense o

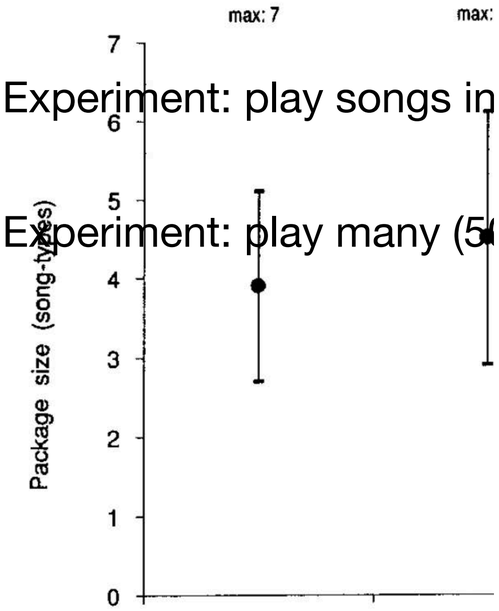
kages have typical size
uisition time window

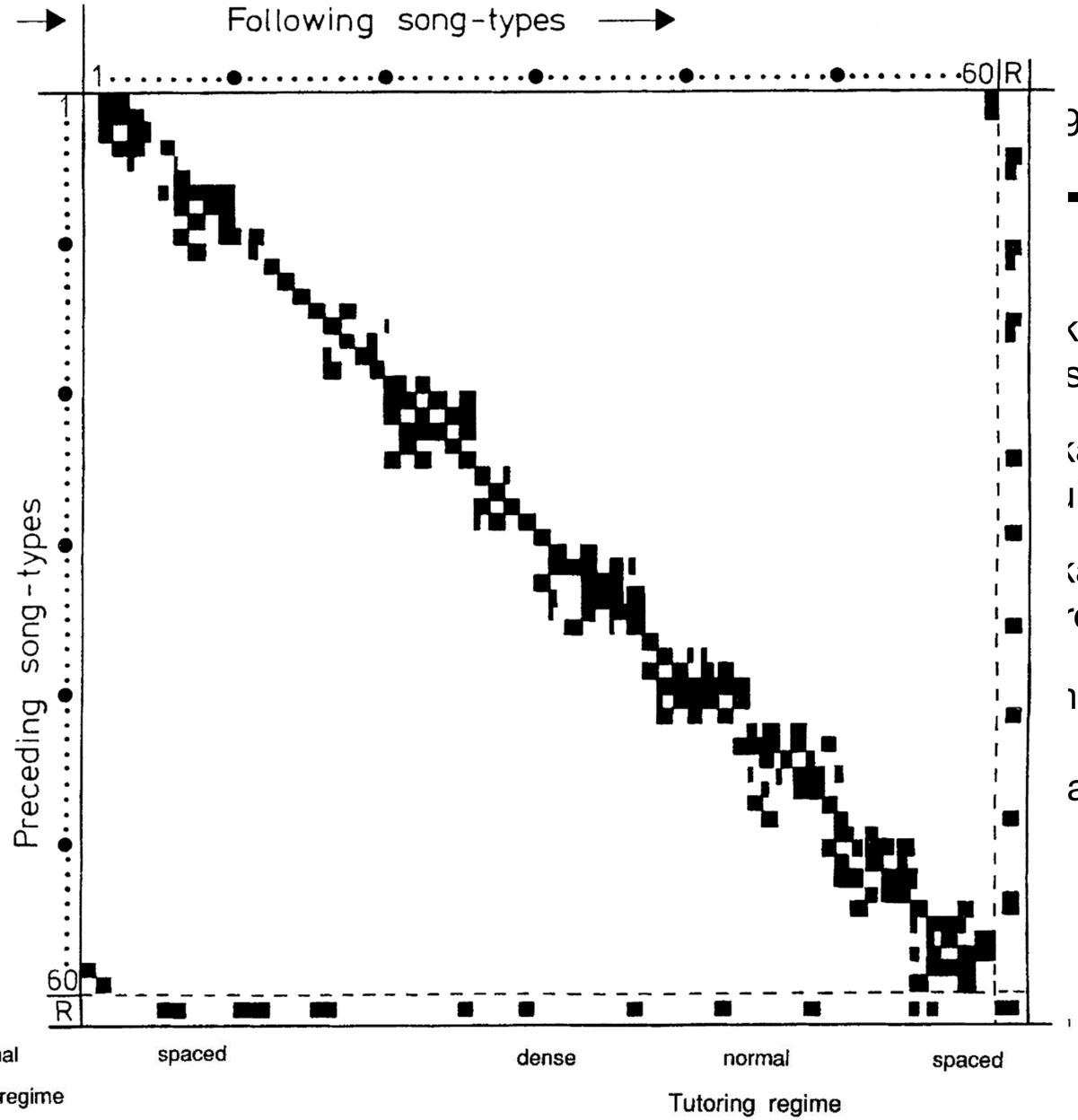
Experiment: play songs in

kages are normal and
rder of the first playback

Experiment: play many (5

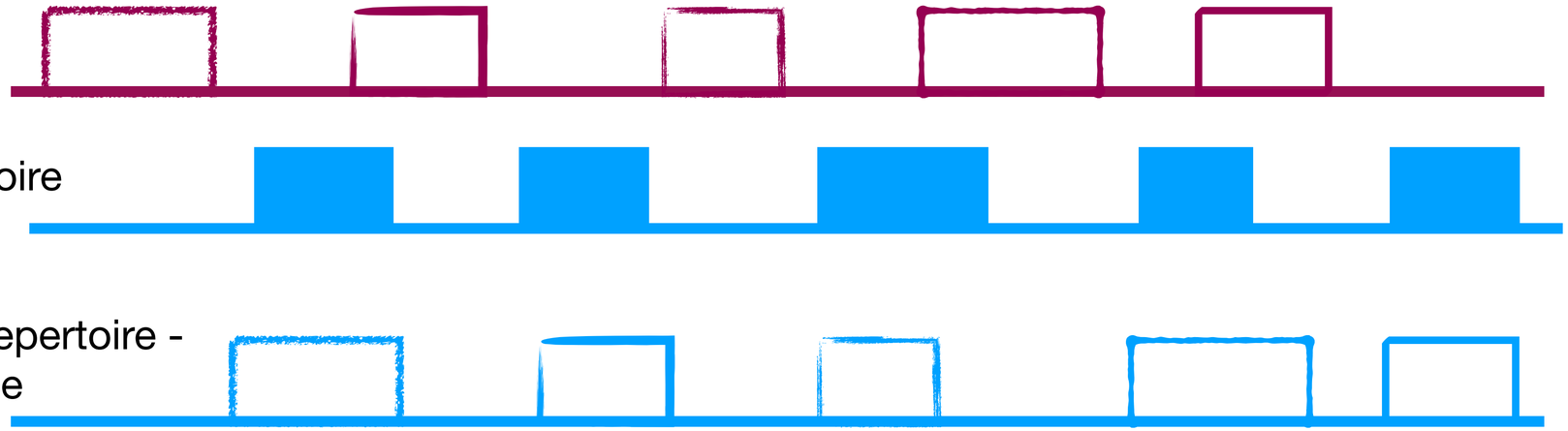
norization of entire sequence,
first.
a hierarchical process





Interaction effects on song retrieval

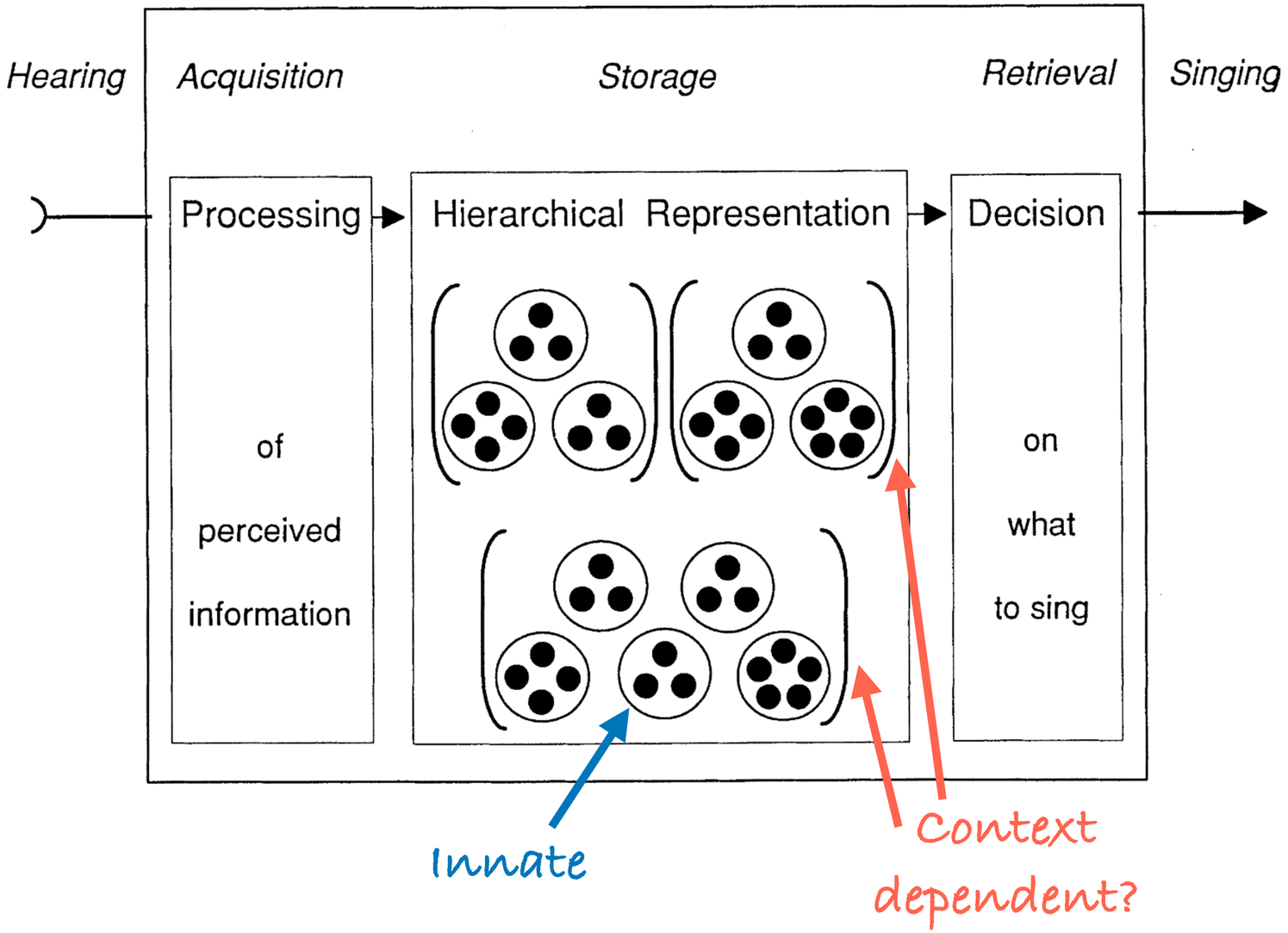
What to expect from vocal interaction?
Nightingale songs = sentences?



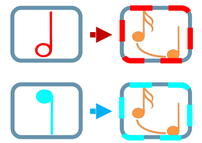
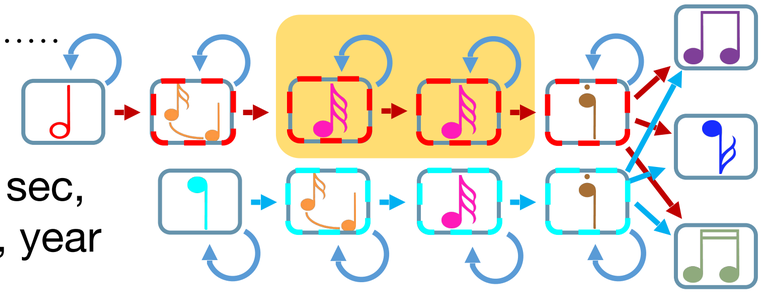
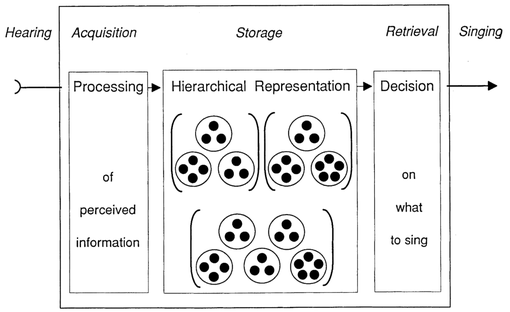
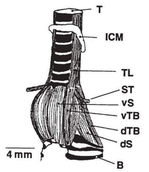
Stimulus is a reply to a previous song -
Aggressive or friendly? Determined by overlap.

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	Life time. Moment-to-moment (~10ms)	
		Branching transitions	Production: 100-200 ms (Auditory: ~1 sec)	
Open-ended learners		Hierarchical song Long-range syntax	Syllables: 8-500ms, Phrase sequence rules: 1-7 sec, Seasonal plasticity: months, year	
		Extensive repertoire, Hierarchical memorization and retrieval, Acoustic matching	Acquisition: months, year Retrieval: 1 second	 

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