Hidden Markov processes can explain complex sequencing rules of birdsong: A statistical analysis and neural network modeling

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Motivation
- What are neural substrates for sequential behavior?

Sequential behavior

- Speech
- Playing music
- Dancing

Generation

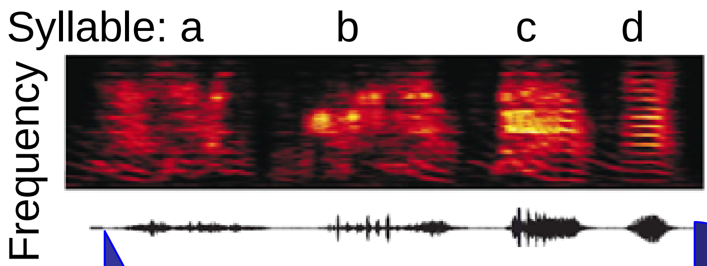
Perception

Learning

Motivation

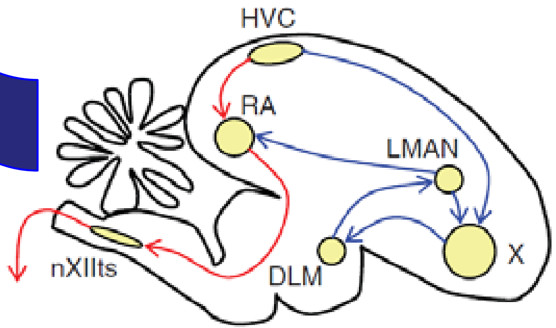
- What are neural substrates for sequential behavior?

Birdsong



Generation

Perception



Learning

Outline

1. Introduction
   – Neural substrates of birdsong
   – Neural network models
2. Statistics of birdsong
   – Higher-order history dependency
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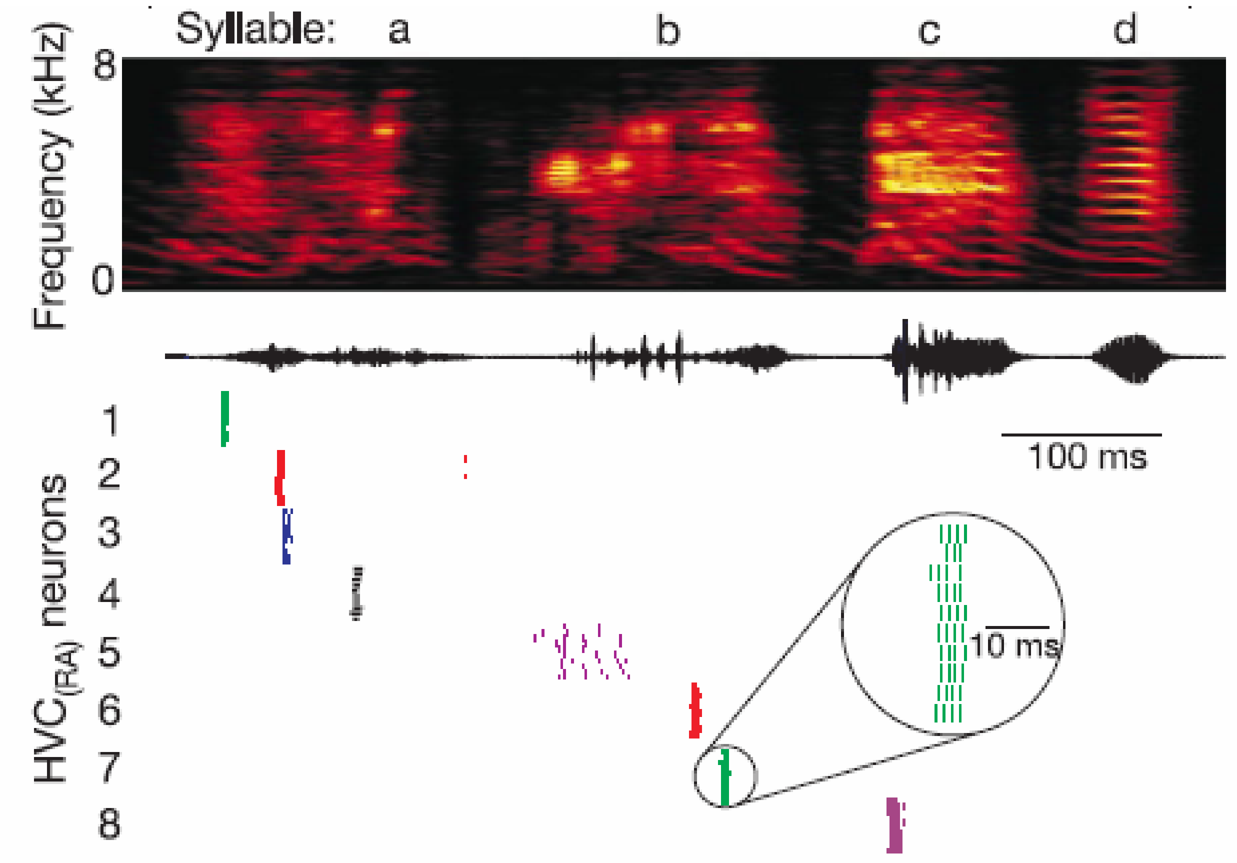
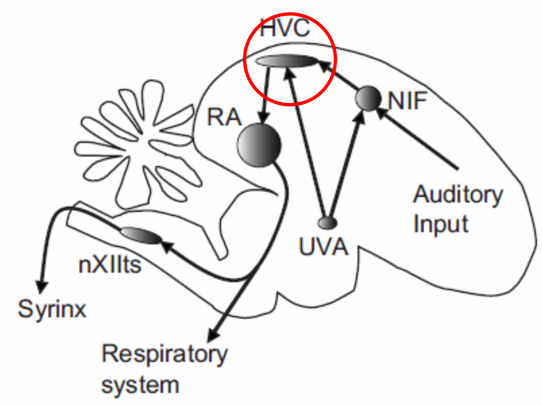
4. Discussion
   – Neural implementation
   – Future directions

Neural activity pattern during singing



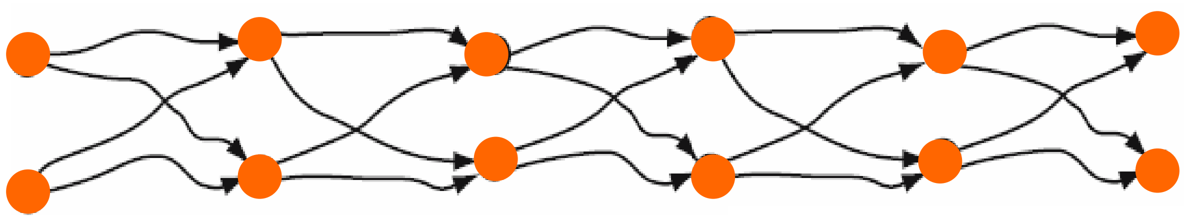
(Zebra finch)



Hahnloser, Kozhevnikov and Fee, Nature, 2002

Feedforward chain hypothesis

- Spikes propagate on feedforward chain network

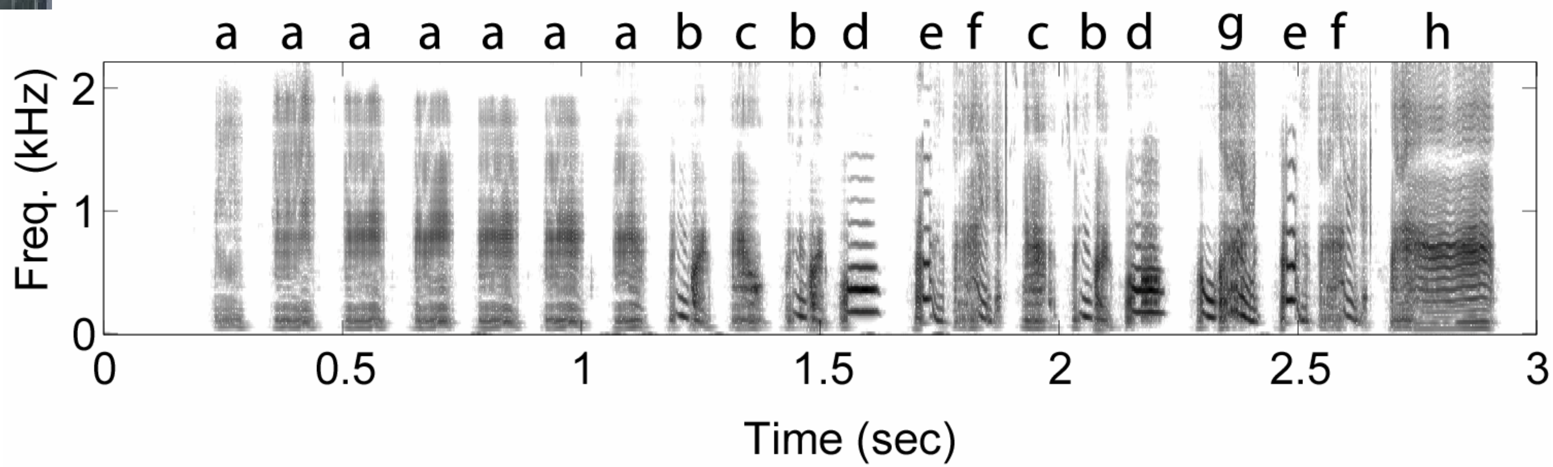


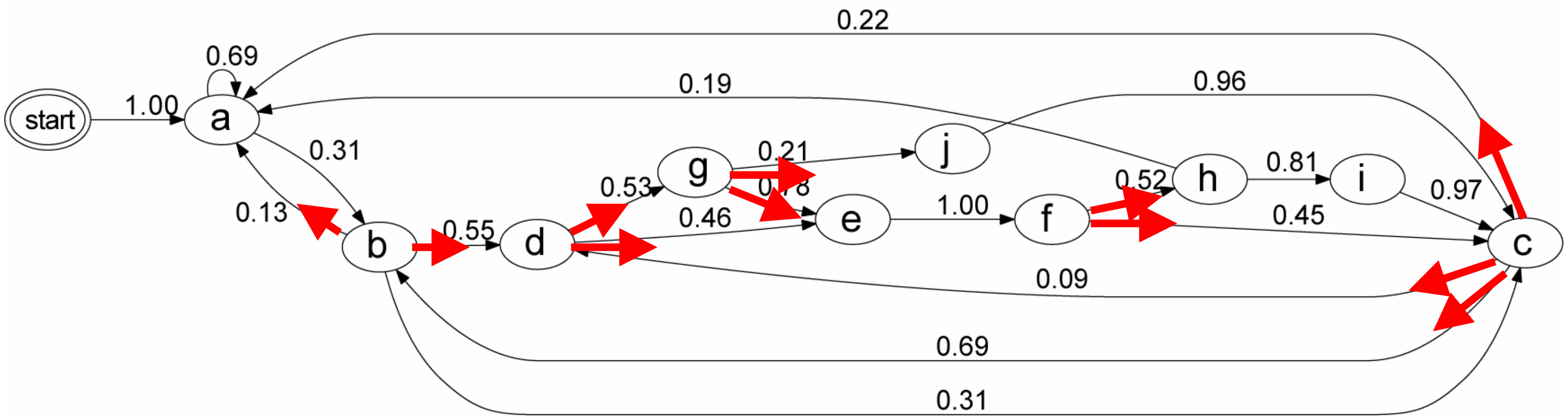
Li & Greenside, Phys. Rev. E, 2006.
Jin, Ramazanoglu, & Seung, J. Comput. Neurosci. 2007.

Experimental evidences:
Long & Fee, Nature, 2008; Long, Jin & Fee, Nature, 2010

It is suitable for *fixed* sequences.
But how about *variable* sequences?

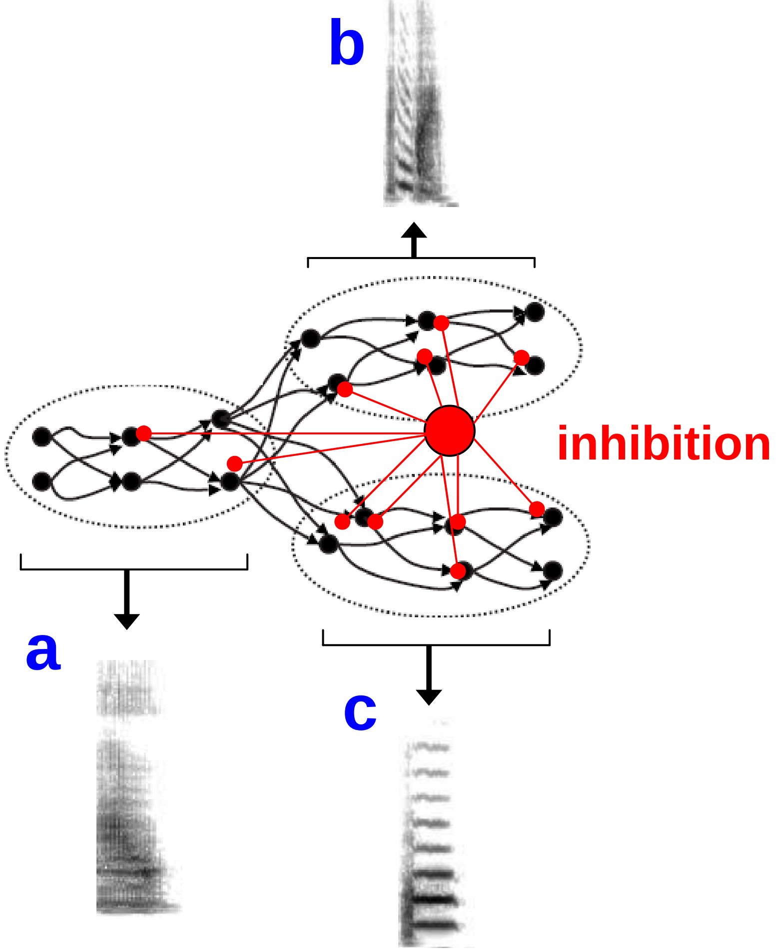
Song of Bengalese finch
- Variable sequences including branching points

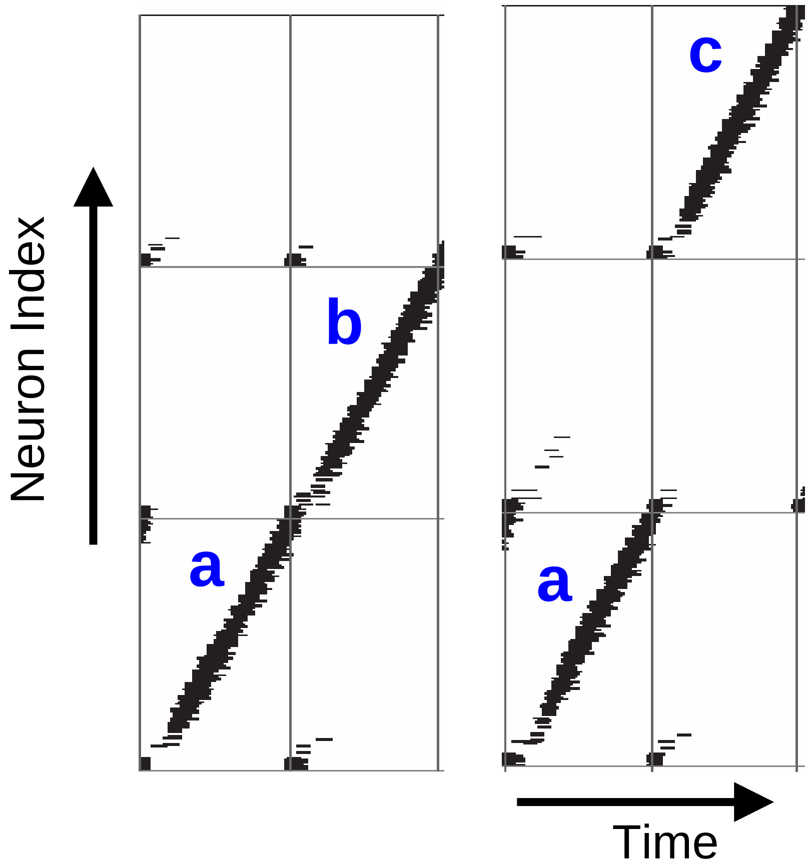




Branching-chain hypothesis

- Mutual inhibition between branching chains

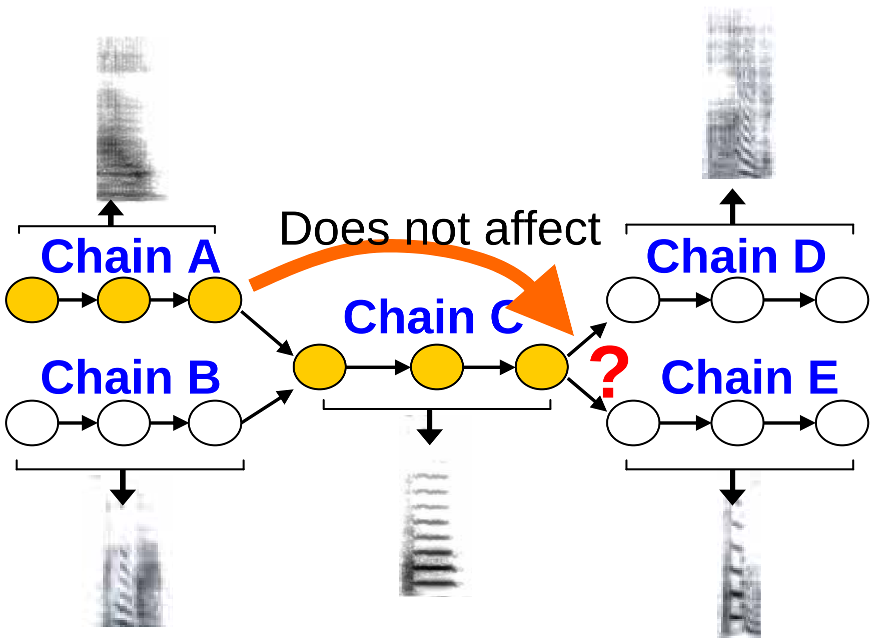




(Jin, Phys Rev E, 2009)

Limitation of branching-chain model

- The transition is a simple Markov process
  - The present active chain depends only on the last active chain



Question: Syllable sequences of Bengalese finch songs are Markov processes?

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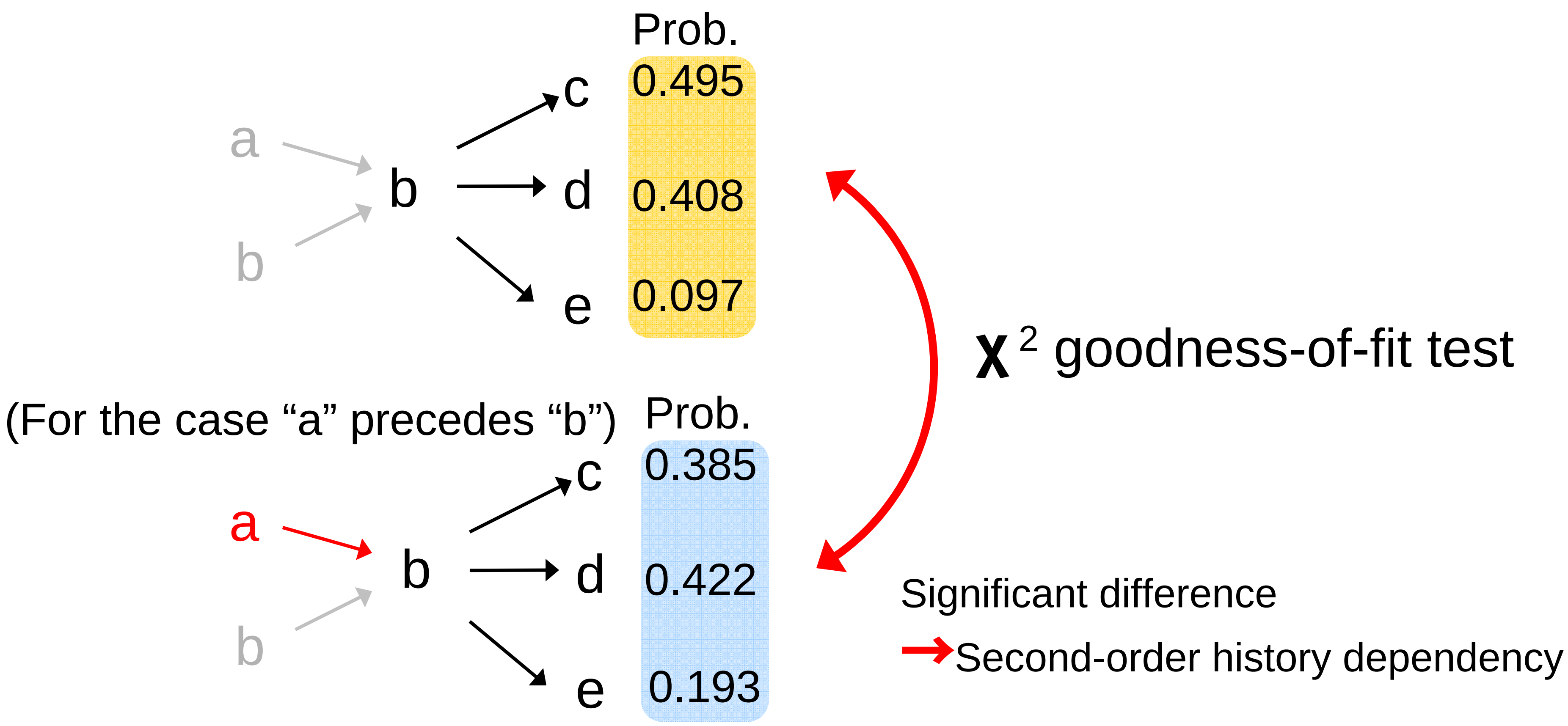
Test of (first order) Markov assumption

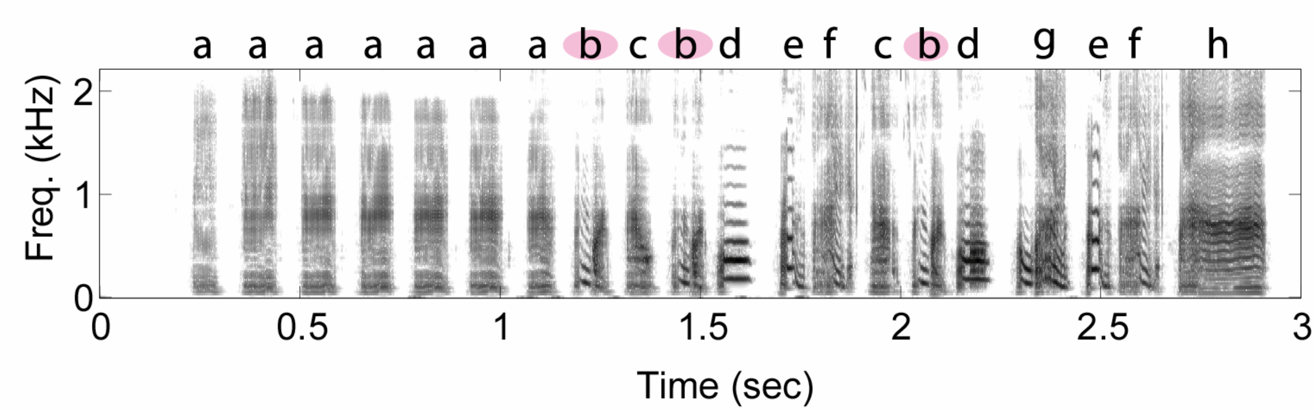
Null hypothesis：

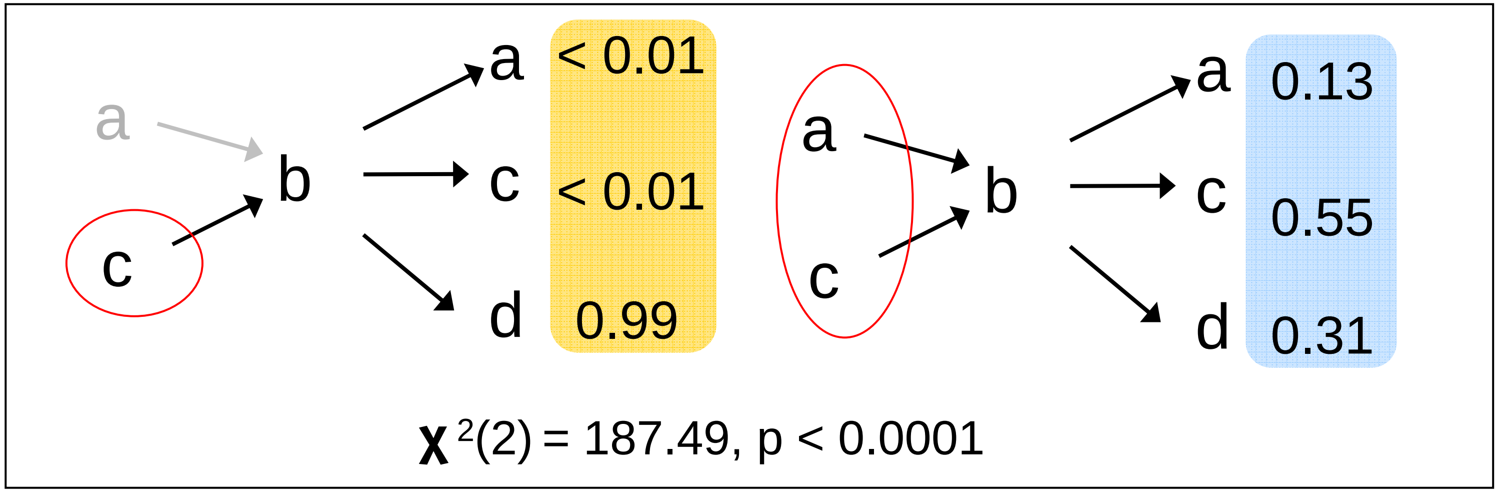
The transition probability to next syllable does not depend on preceding syllable (Markov assumption)



Result

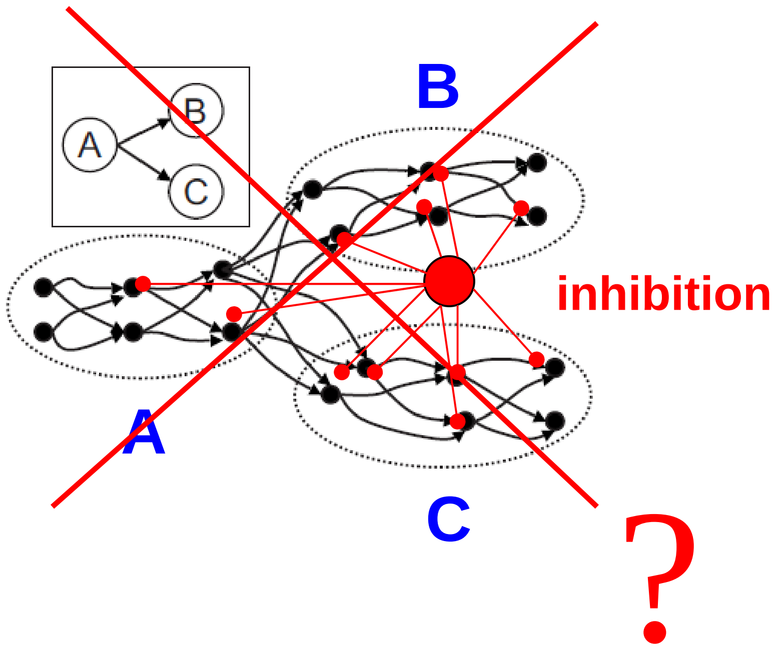
We found more than one significant second-order history dependency in all 16 birds.
(p < 0.01 with Bonferroni correction)



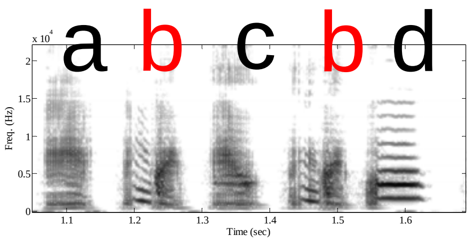


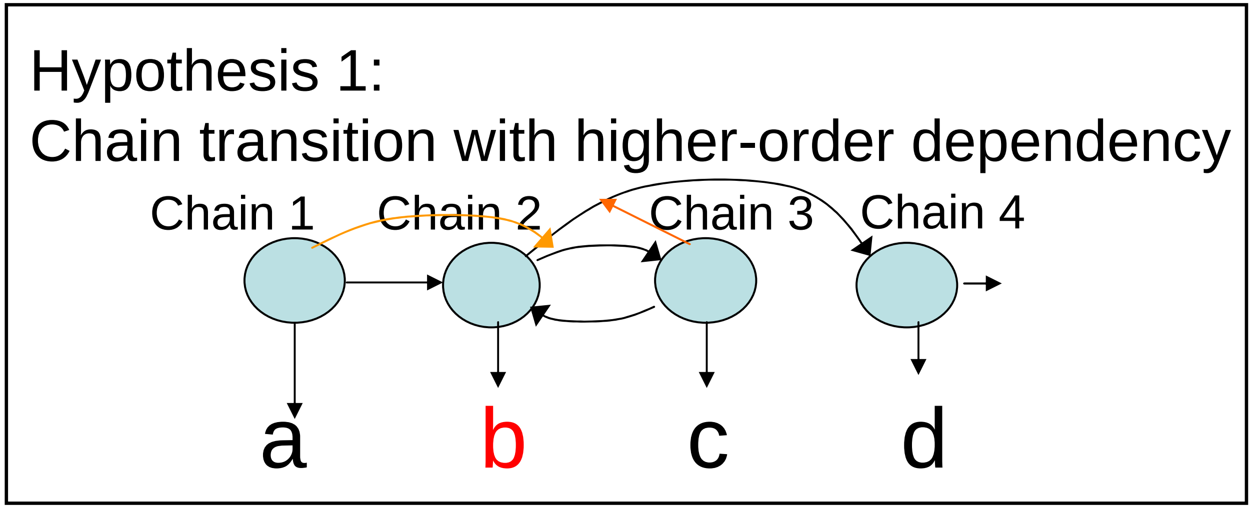
Then,…

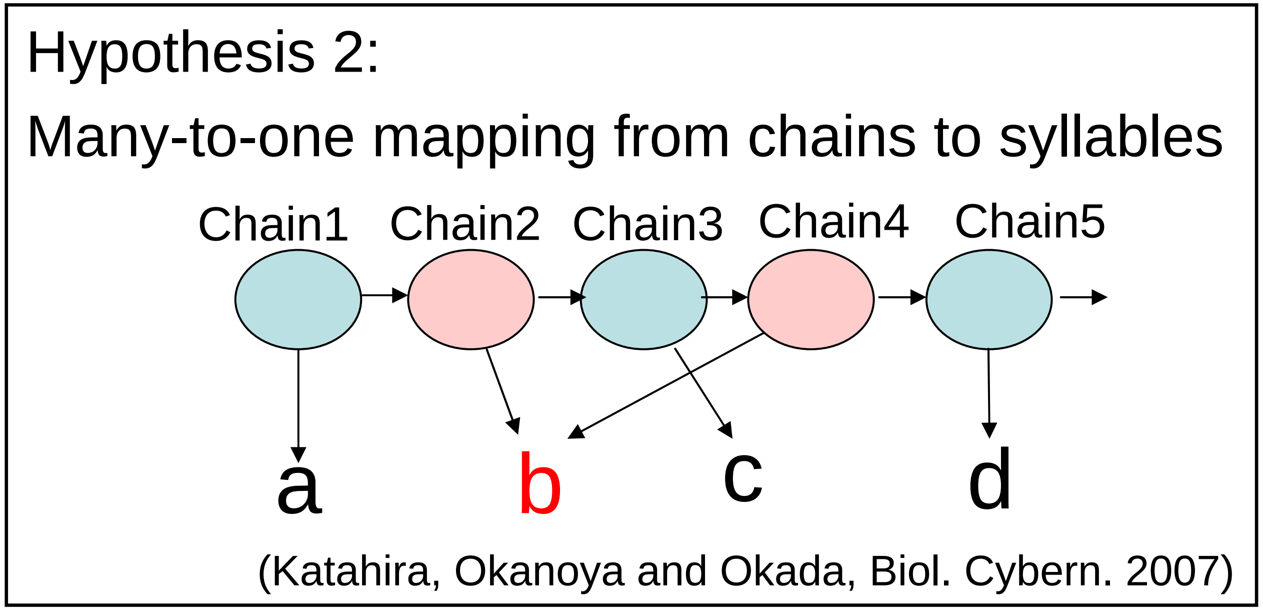
- The branching-chain model is incorrect?



Two possible mechanism for history dependency



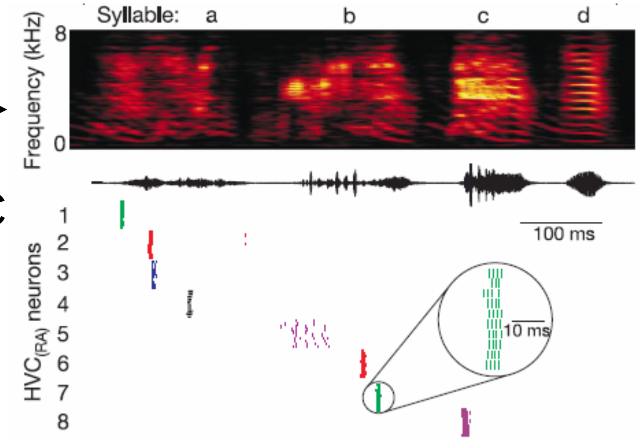




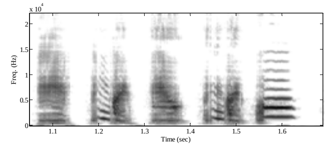
However…

- The neural activity data from HVC of *singing Bengalese finches* are *not* available.

HVC



Zebra finch



HVC

Bengalese finch

?

- We examined two hypotheses based on song data by using statistical models.

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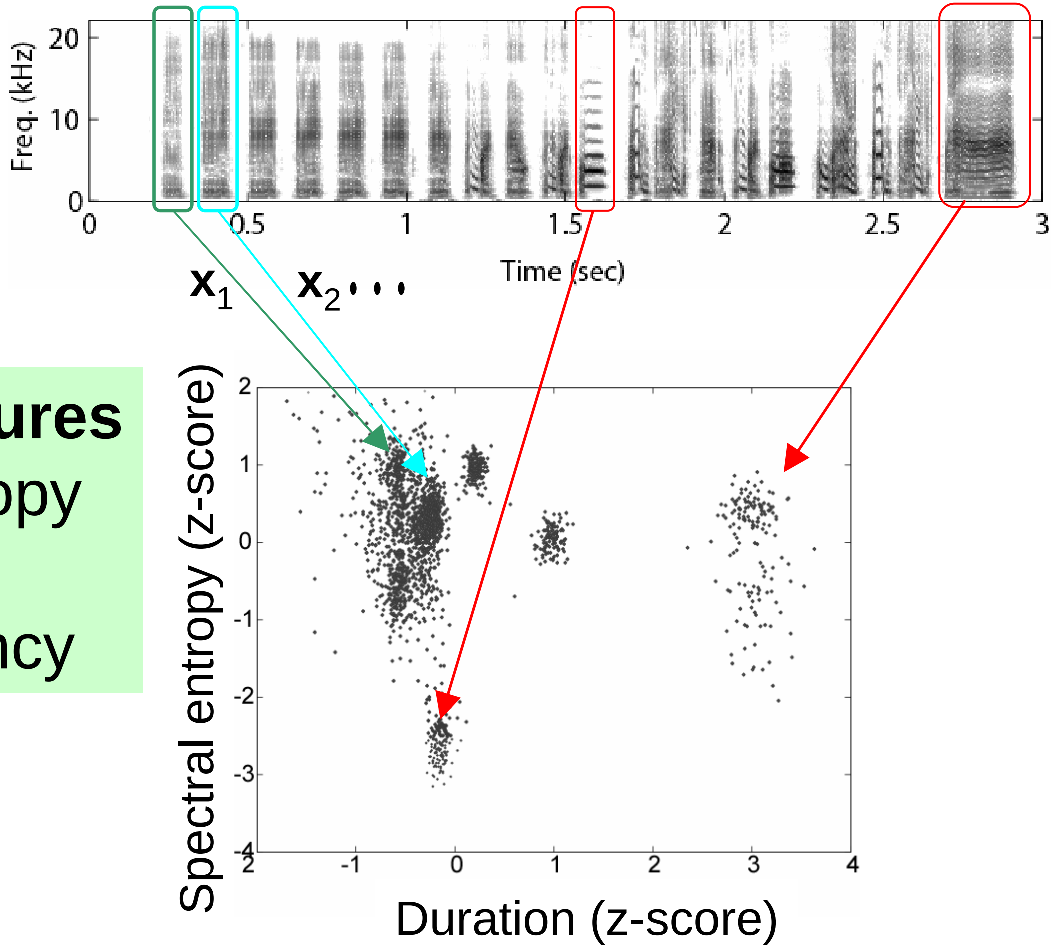
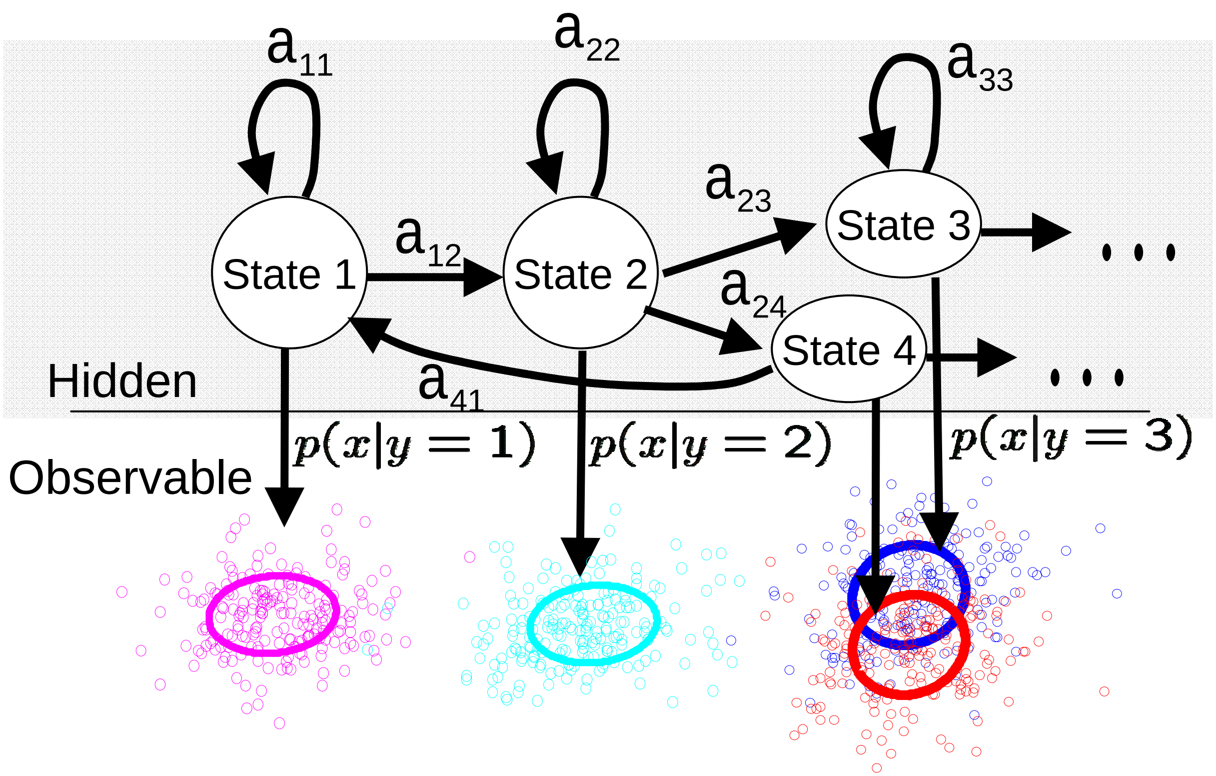
Feature extraction - Auditory features



Auditory features
- Spectral entropy
- Duration
- Mean frequency

(c.f. Tchernichovski et al. 2000)

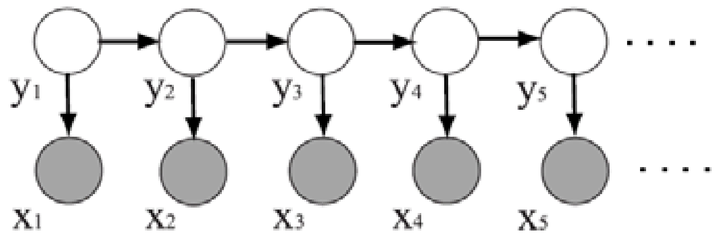
Hidden Markov Model (HMM)



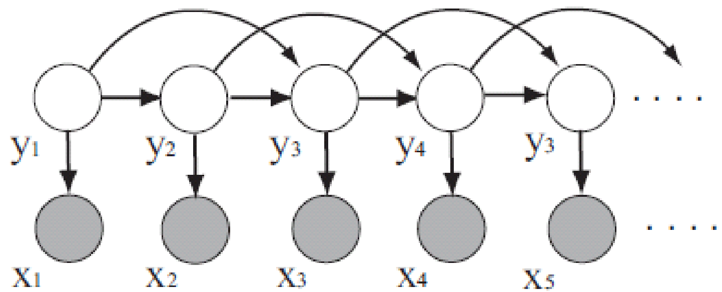
$$p(x|y=i) = \frac{1}{(2\pi)^{D/2}} \frac{1}{|\Sigma_i|^{1/2}} \exp\left\{-\frac{1}{2}(\boldsymbol{x}-\boldsymbol{\mu}_i)^T \Sigma_i^{-1}(\boldsymbol{x}-\boldsymbol{\mu}_i)\right\}$$

State transition dynamics in HMM

1st order HMM: $a_{ij} = p(y_t = j | y_{t-1} = i)$



2nd order HMM: $a_{ijk} = p(y_t = k | y_{t-1} = j, y_{t-2} = i)$

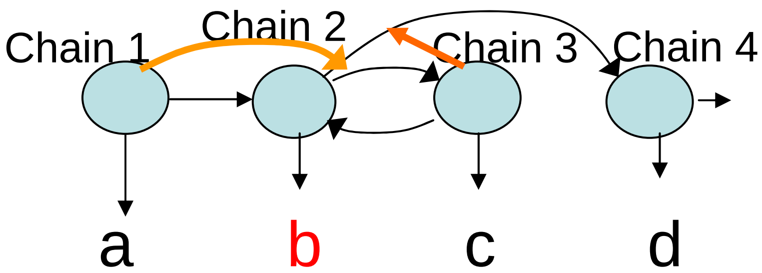


0th order HMM (Gaussian mixture):

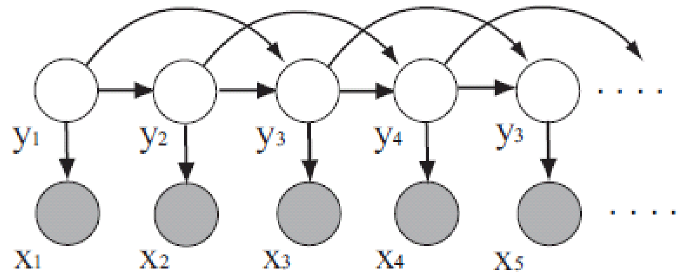
$$a_i = p(y_t = i)$$

Relationship between two hypotheses and statistical models

Hypothesis 1:
Chain transition with higher-order dependency

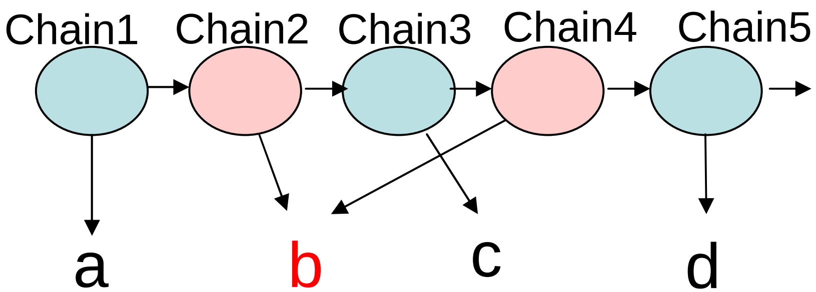


→ 2^{nd} order-HMM

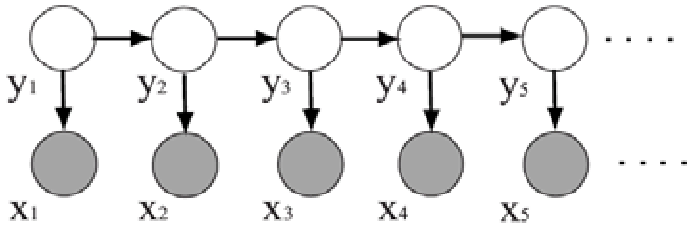


Hypothesis 2:

Many-to-one mapping from chains to syllables



→ 1^{st} order-HMM



Bayesian model selection

Given data (auditory features): $X = \{\boldsymbol{x}_1, \boldsymbol{x}_2, \ldots\}$

Model structure $\mathcal{M} = \{L, K\}$
- L : Markov order (0,1,2)
- K : the number of hidden states

Model posterior: $p(\mathcal{M}|X) \propto p(X|\mathcal{M})p(\mathcal{M})$

Marginal likelihood: $p(X|\mathcal{M}) = \int d\theta \, p(X|\theta, \mathcal{M})p(\theta|\mathcal{M})$

($\boldsymbol{\theta}$: model parameter set) (→difficult to compute!)

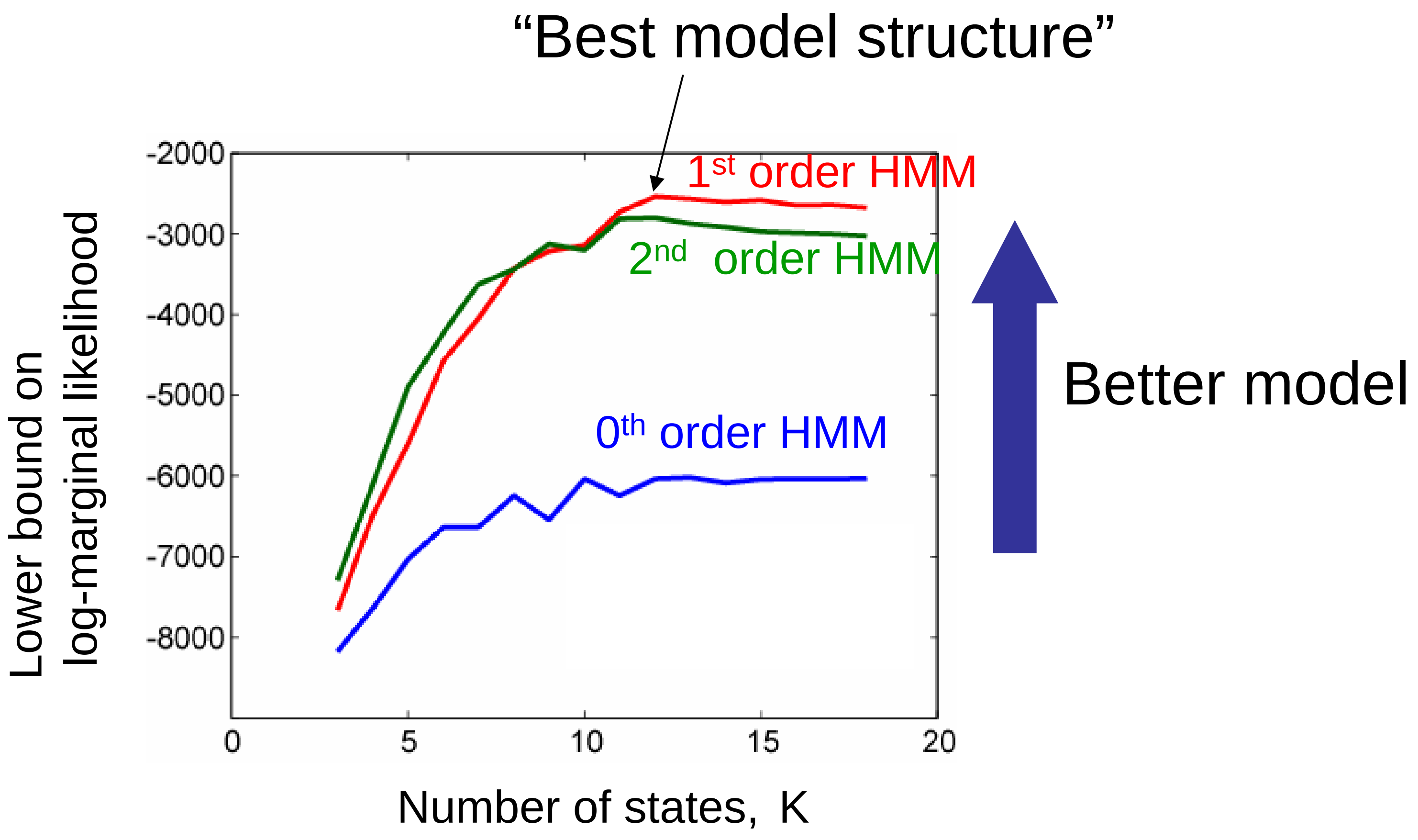
Approximation

$$\log p(X|\mathcal{M}) \geq \underline{\mathcal{F}_{\mathcal{M}}}$$

Lower bound
(variational free energy)

(can be computed by variational Bayes method)

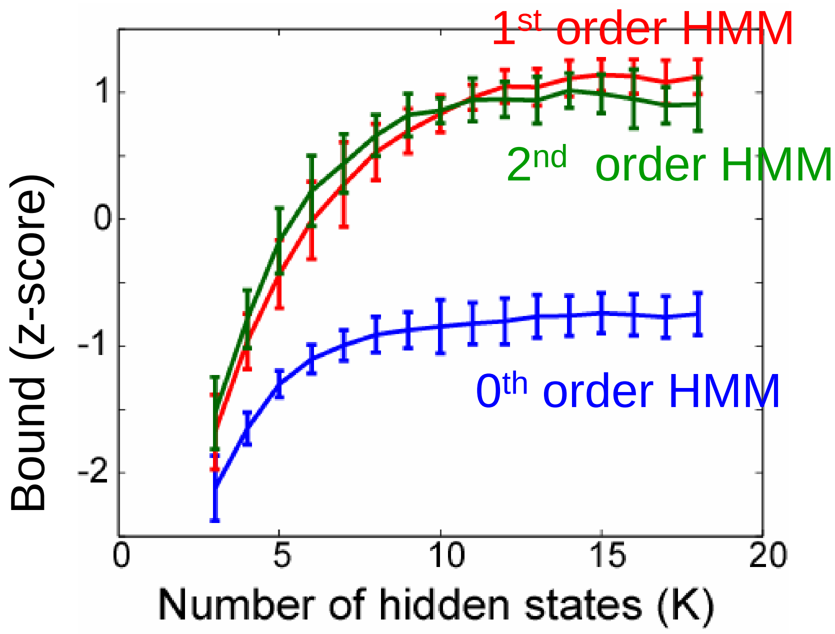
Result – model selection (one bird)



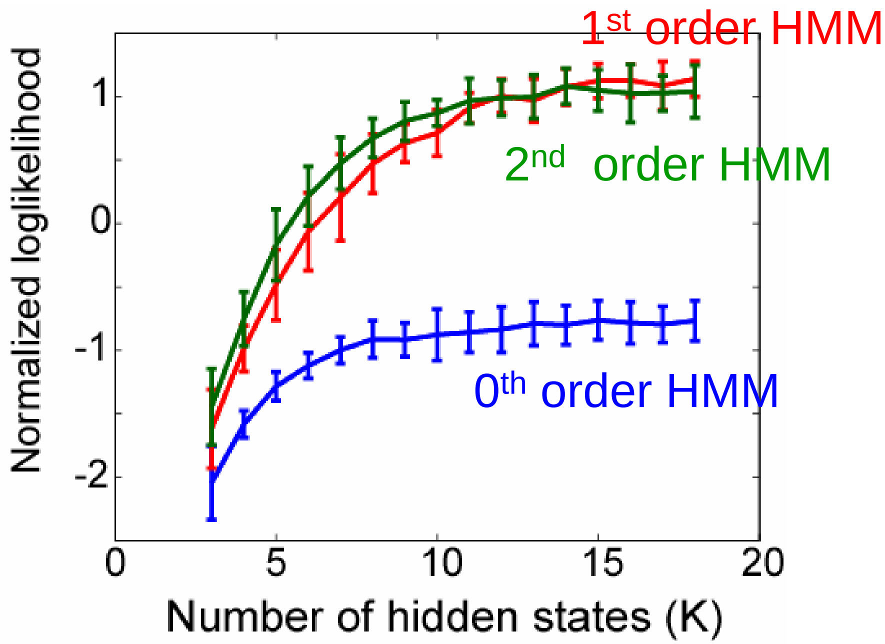
- With **small** number of states → 2nd order HMM
- With **large** number of states → 1st order HMM

Results – model selection, cross validation (averages over 16 birds)

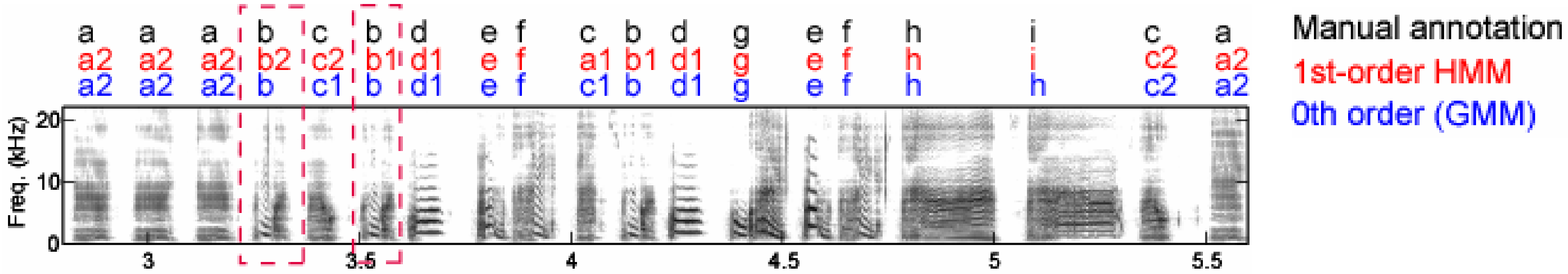
Lower bound on log-marginal likelihood

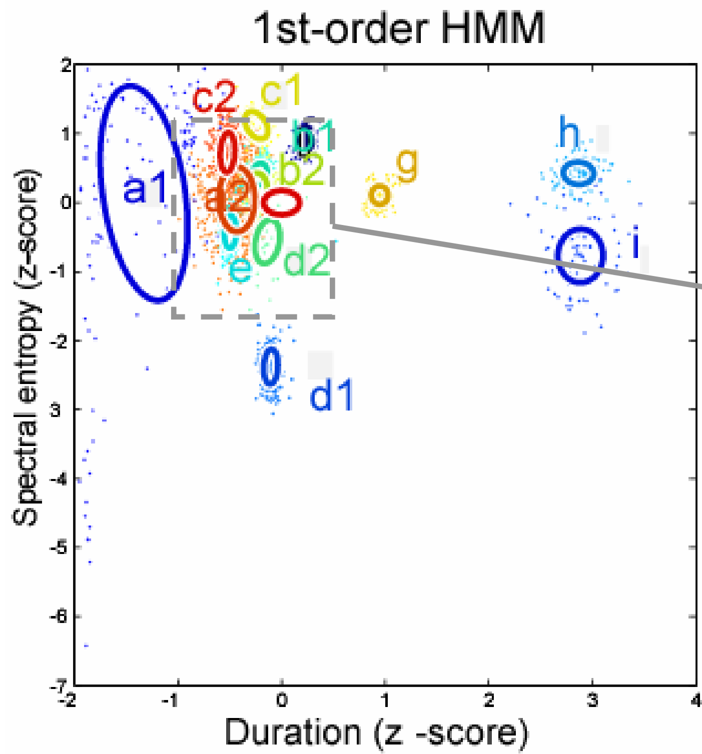


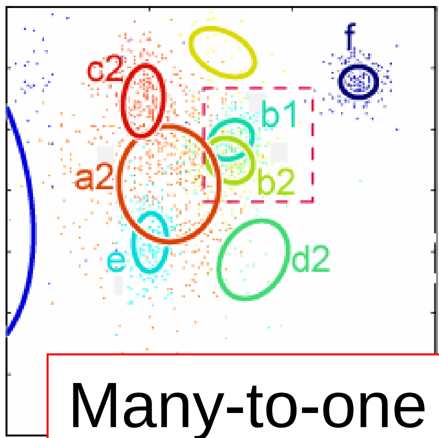
Predictive likelihood (cross validation)



HMM learns many-to-one mapping







Many-to-one mapping from the states to a syllable “b”

(Similar results were obtained for 30 syllables of the 54 syllables where significant second-order dependency was found)

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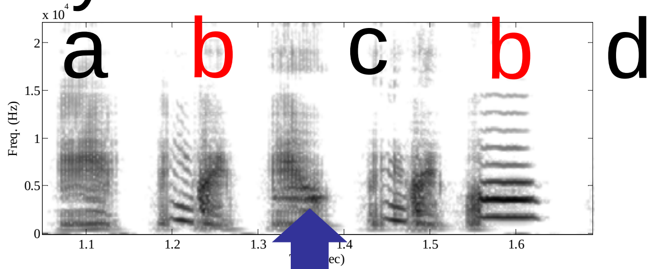
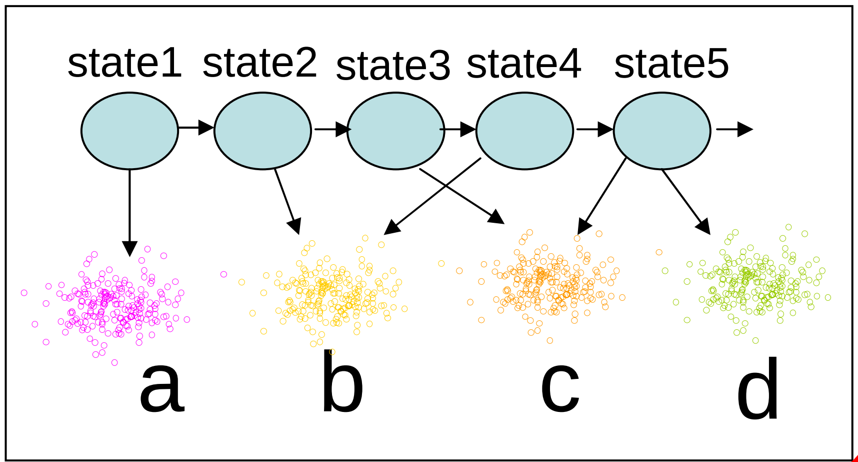
Summary of results

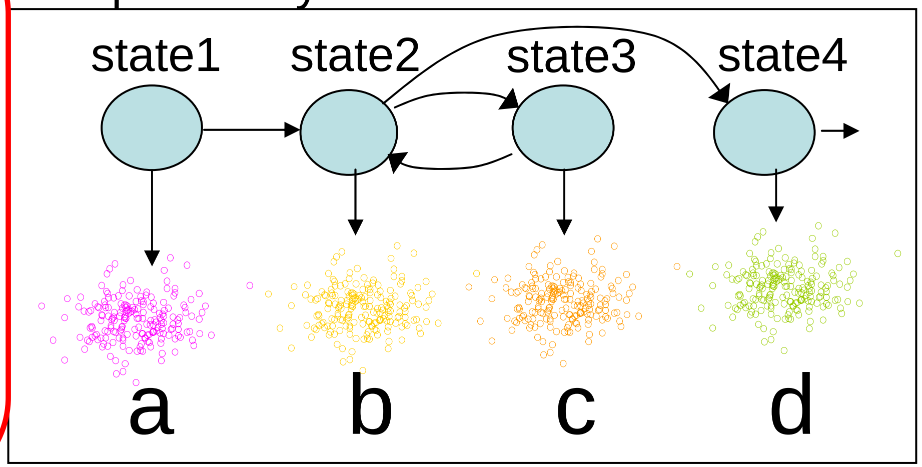
- Bengalese finch songs have at least second-order history dependency.



Many-to-one mapping – 1st HMM



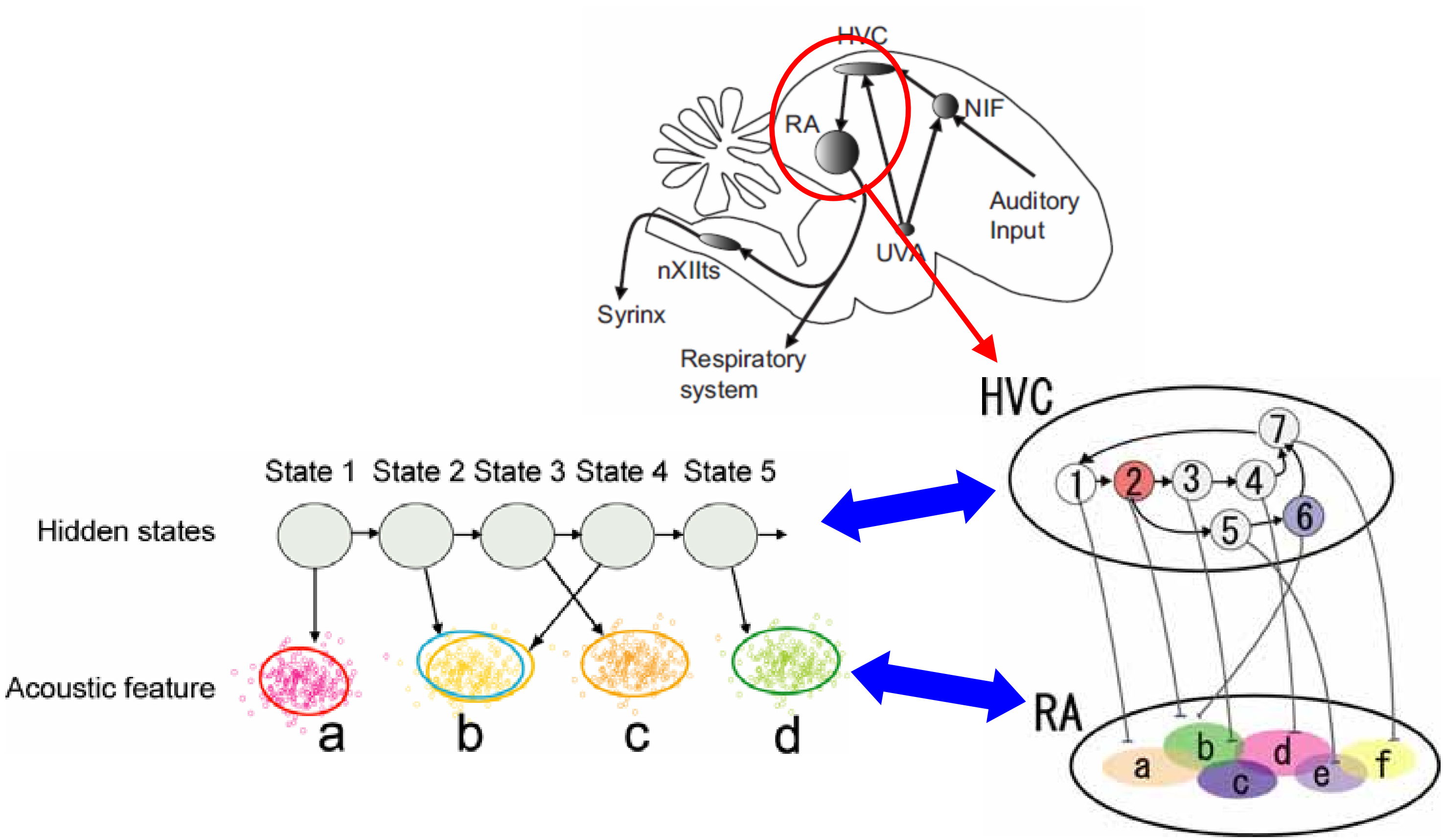
State transition with higher-order dependency - 2nd-order HMM



This mechanism is sufficient for Bengalese finch song

Mapping onto neuroanatomy

- HVC - hidden state (branch ⇔ state)
- RA - auditory features of each syllable



(Katahira, Okanoya and Okada, 2007)

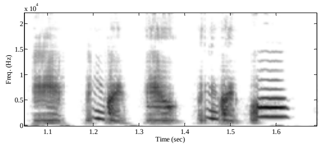
Future directions (ongoing research)

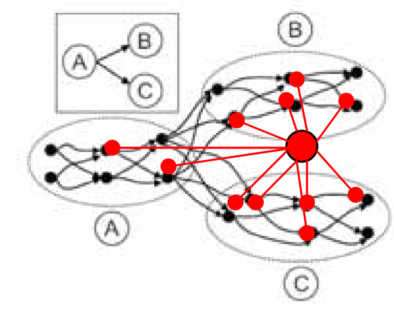
- How the brain can *learn* this representation?
  - Analysis of development of song from a juvenile period.
  - Developing a network model with synaptic plasticity for learning the many-to-one mapping.
    (e.g., Doya & Sejnowski, NIPS, 1995;
    Troyer & Doupe, J Neuropysiol, 2000;
    Fiete, Fee & Seung, J Neuropysiol,2007)

- Applying HMMs to spike data recorded from songbird
  (Katahira, Nishikawa, Okanoya & Okada, Neural Comput, 2010)

Overbiew of our approach

Behavior





Parameter fitting,
Model selection

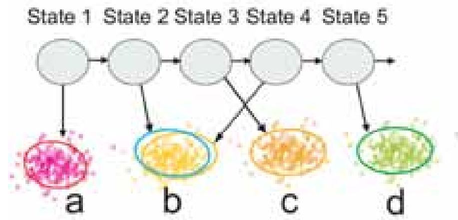
Constraints

Neural network model

Statistical model

Support,
Refinement

Mapping



Constraints

Anatomy,
Physiology