Song development in zebra finch: modelling the growth and splitting of sequential chains of neural activity

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*Okubo, Mackevicius, Payne, Lynch, and Fee, Nature 2015*

1. Question

How are complex motor sequences formed from simple underlying components?

2. Approach

Network model of sequence formation and differentiation using STDP and heterosynaptic competition plasticity rules

Becoming an expert at producing complicated motor sequences requires breaking them into simple parts
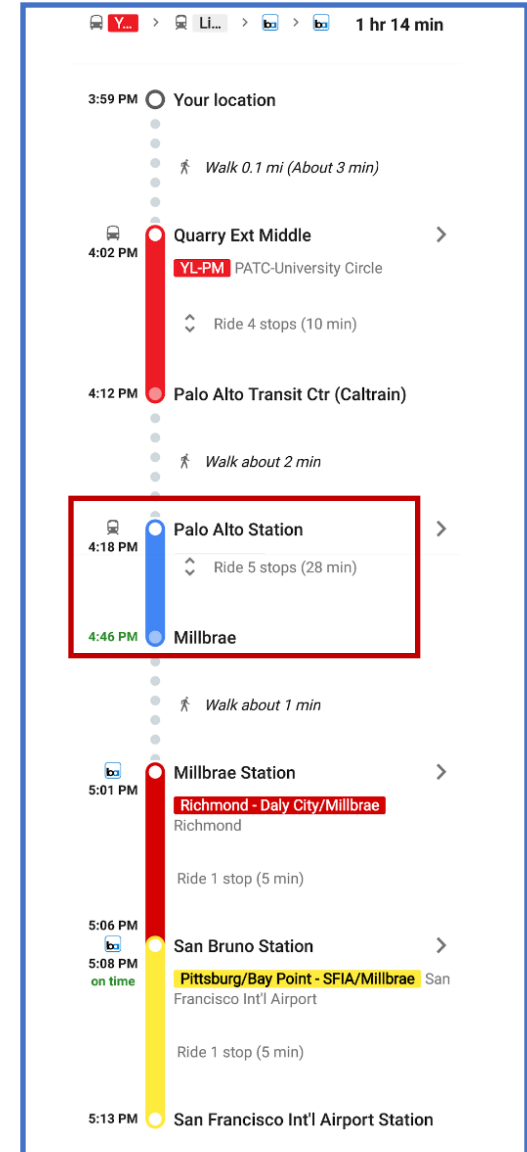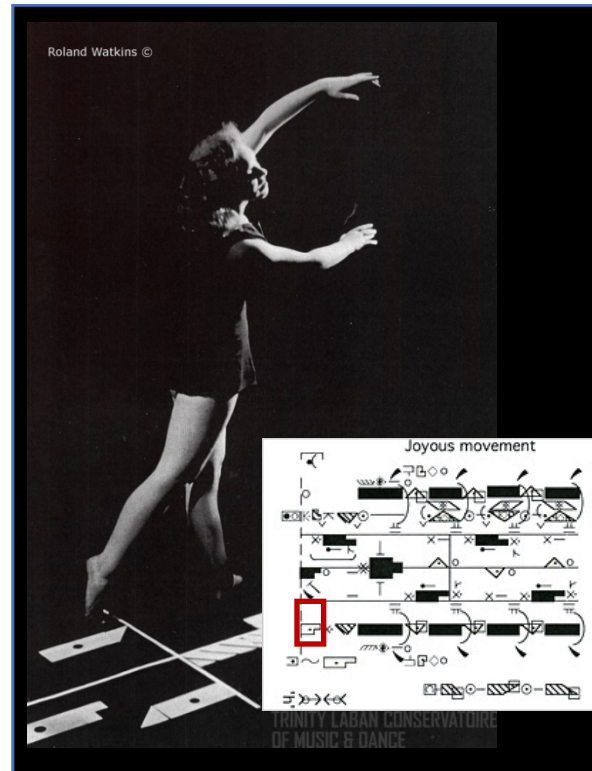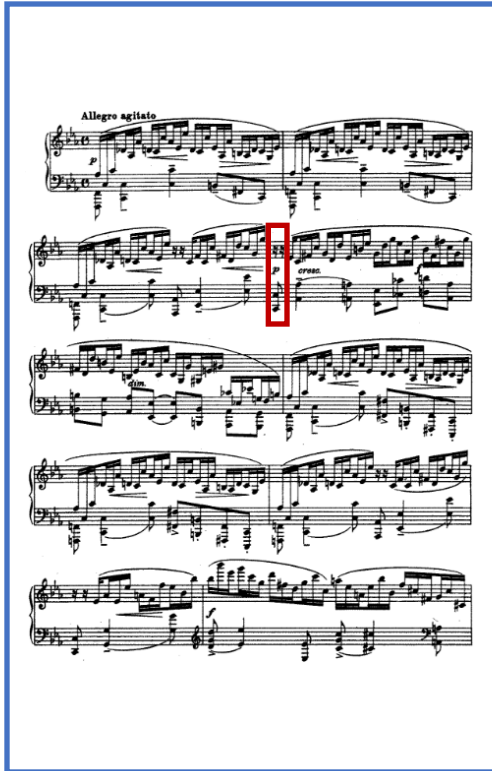
How can the brain learn complex motor programs from simple building blocks?

1. Start with a "prototype" building block
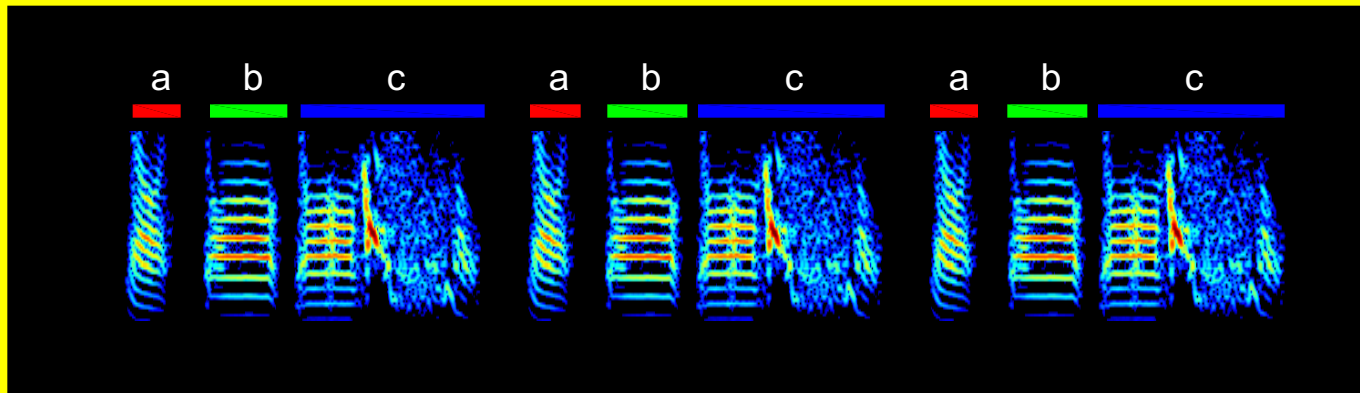   (short sequence of neural activity)
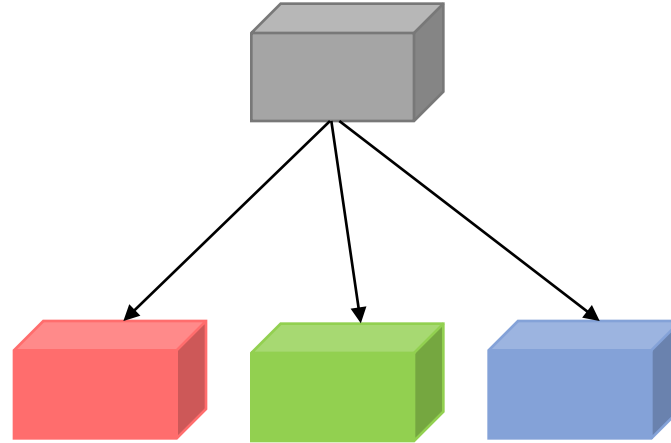
2. Replicate the prototype
   & differentiate the copies

3. Build complex sequences
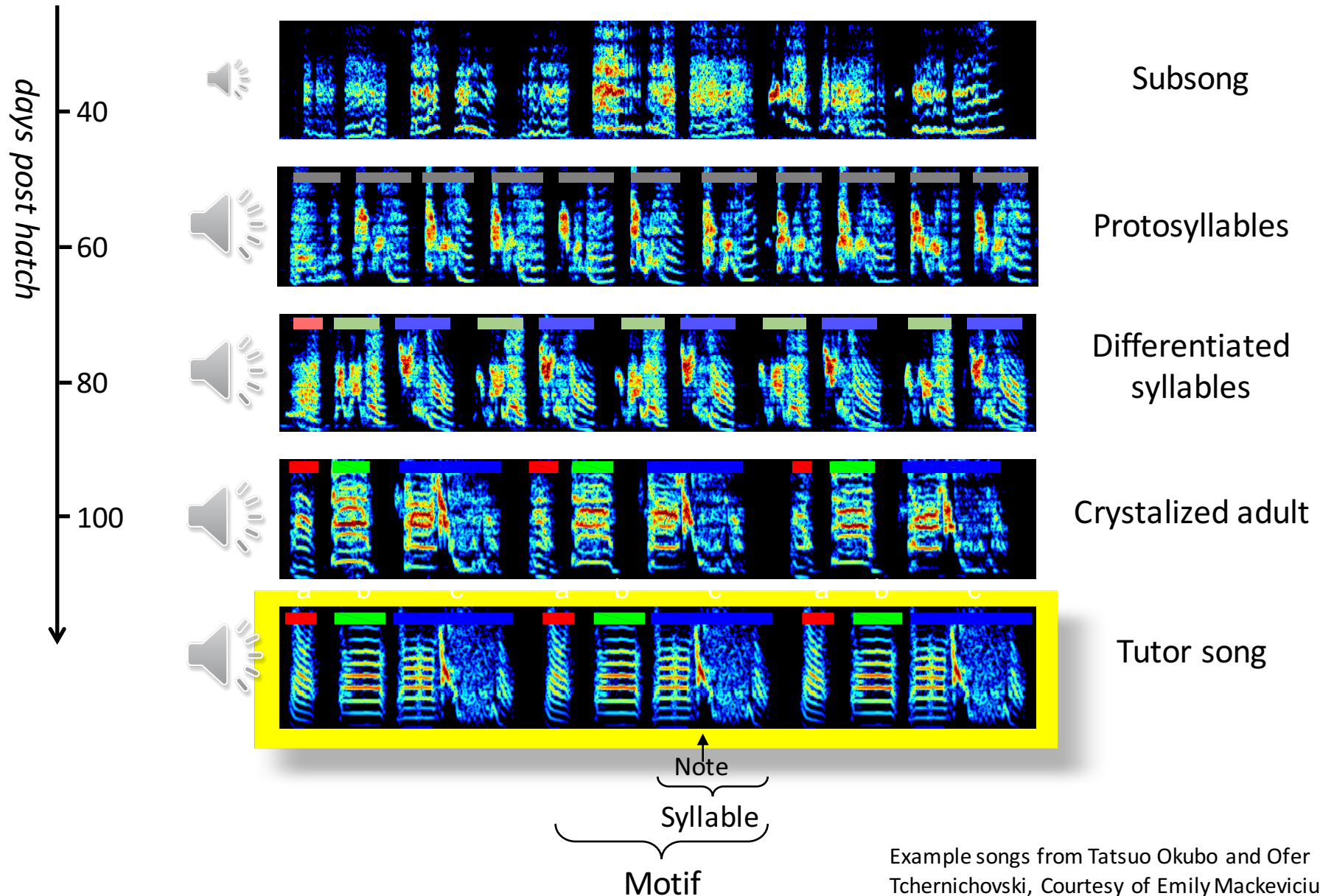   (long, flexible sequence of neural activity)
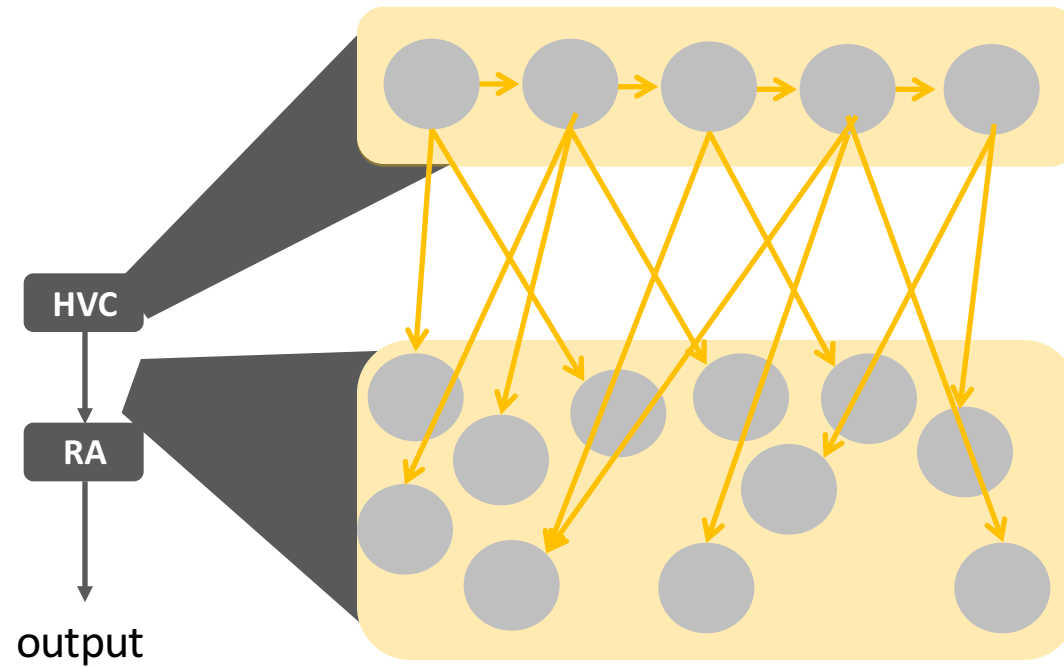
Birdsong is organized into syllables
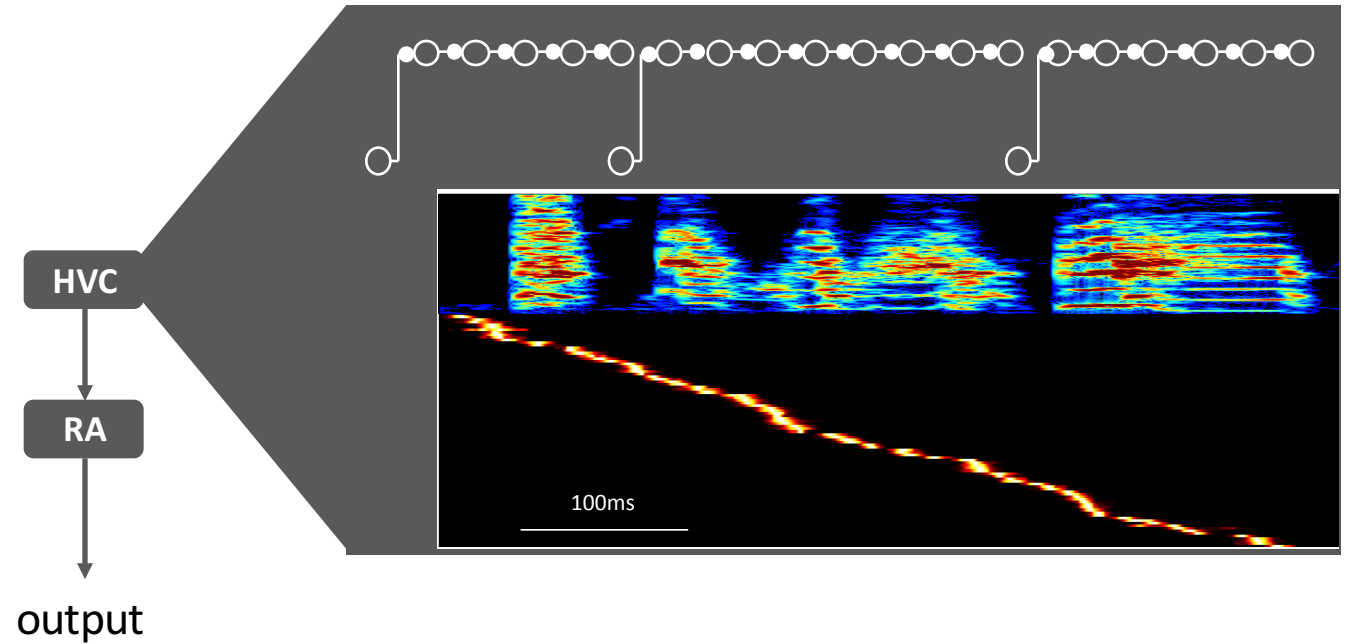

Tutor song

Songbirds learn to sing through a series of stages

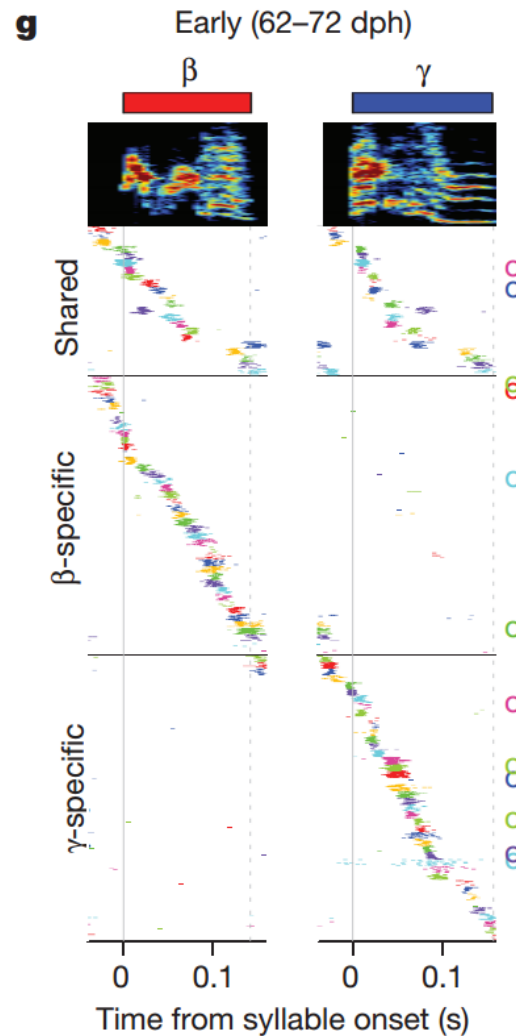Example songs from Tatsuo Okubo and Ofer Tchernichovski, Courtesy of Emily Mackevicius

How the songbird brain produces song

HVC

RA

output

Courtesy of Emily Mackevicius

How the songbird brain produces song

(Hahnloser, Kozhevnikov and Fee, 2002
Lynch, Okubo et al., under review)

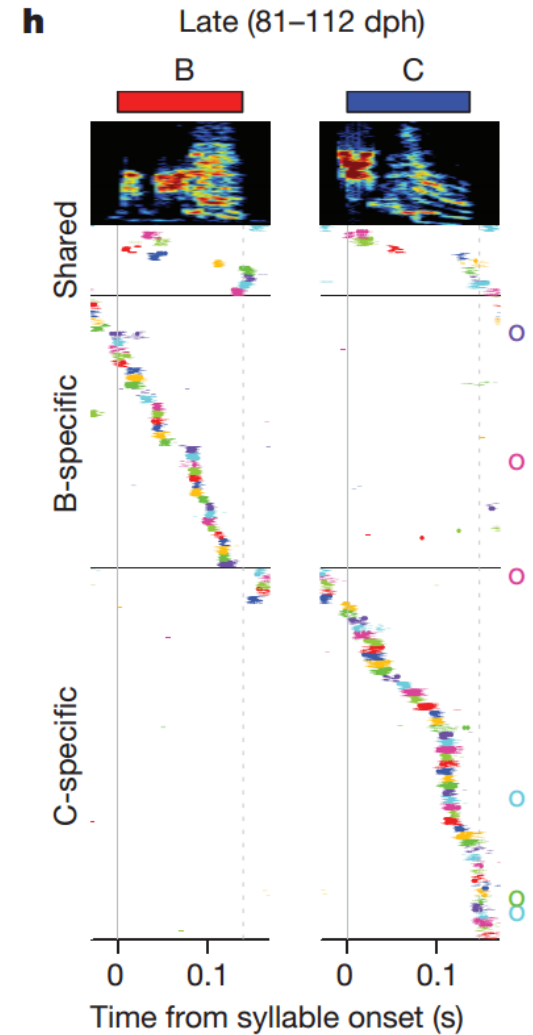# The protosequence starts to split as birds develop new syllable types

Okubo, Mackevicius, Payne, Lynch and Fee, Nature 2015
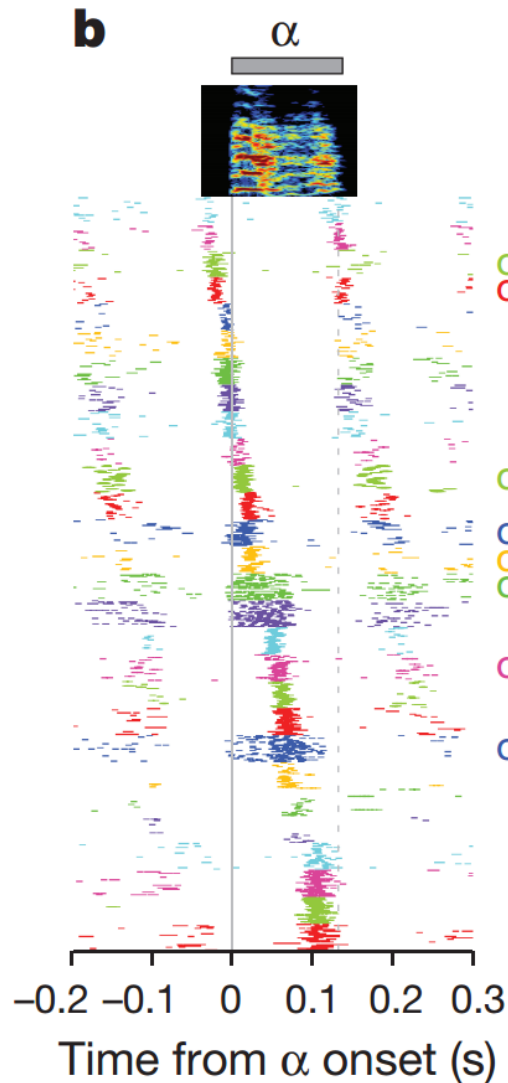
The protosequence keeps splitting as syllables differentiate
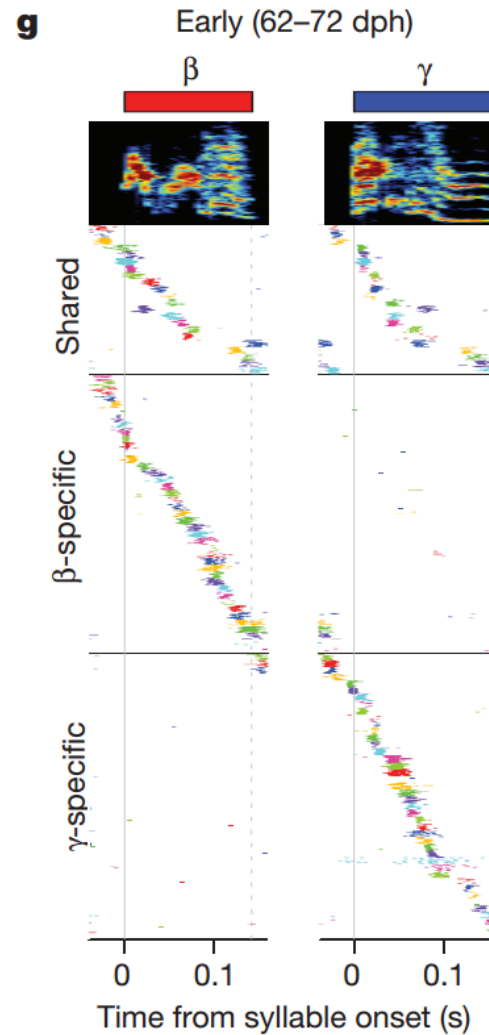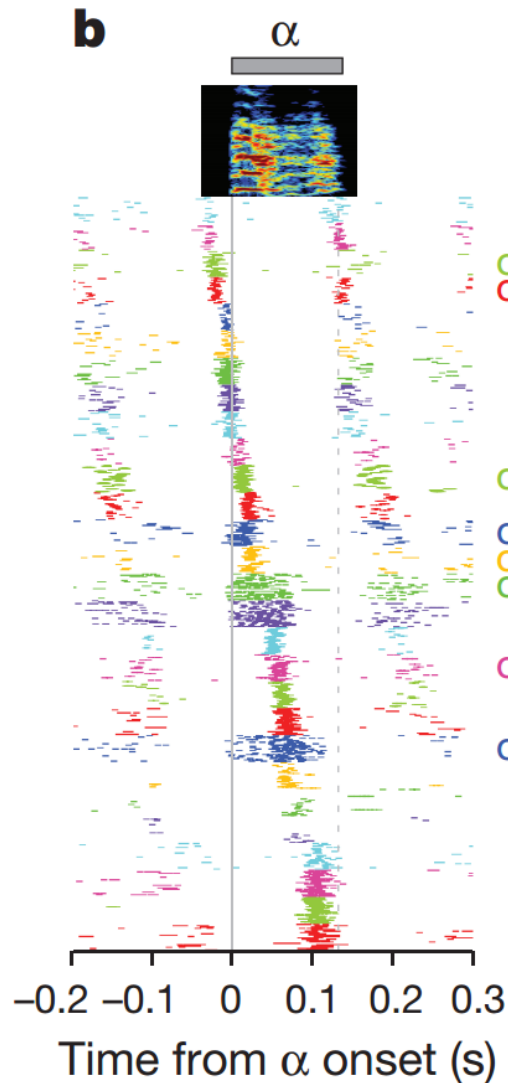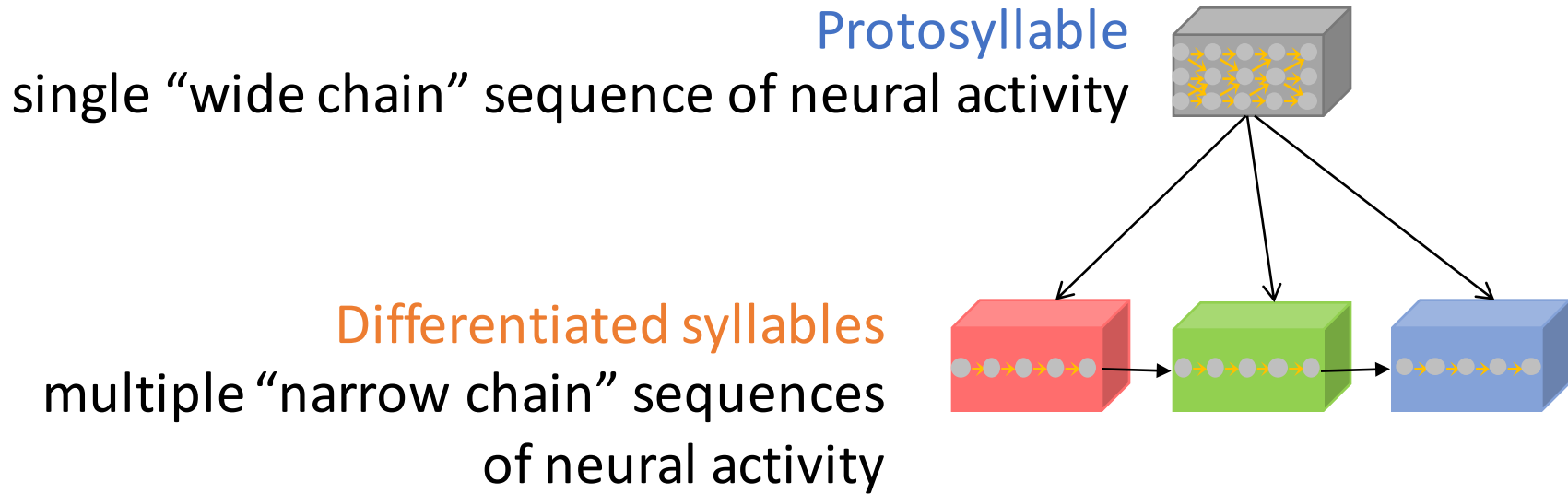
Okubo, Mackevicius, Payne, Lynch and Fee, Nature 2015

Protosyllable
single "wide chain" sequence of neural activity

Differentiated syllables
multiple "narrow chain" sequences
of neural activity

Question

How are complex motor sequences formed from simple underlying components?

Hypothesis

Differentiation of protosyllables through splitting of the underlying neural sequence

Approach

Network model of sequence formation and differentiation

Movie of model HVC development: sequence growing and splitting
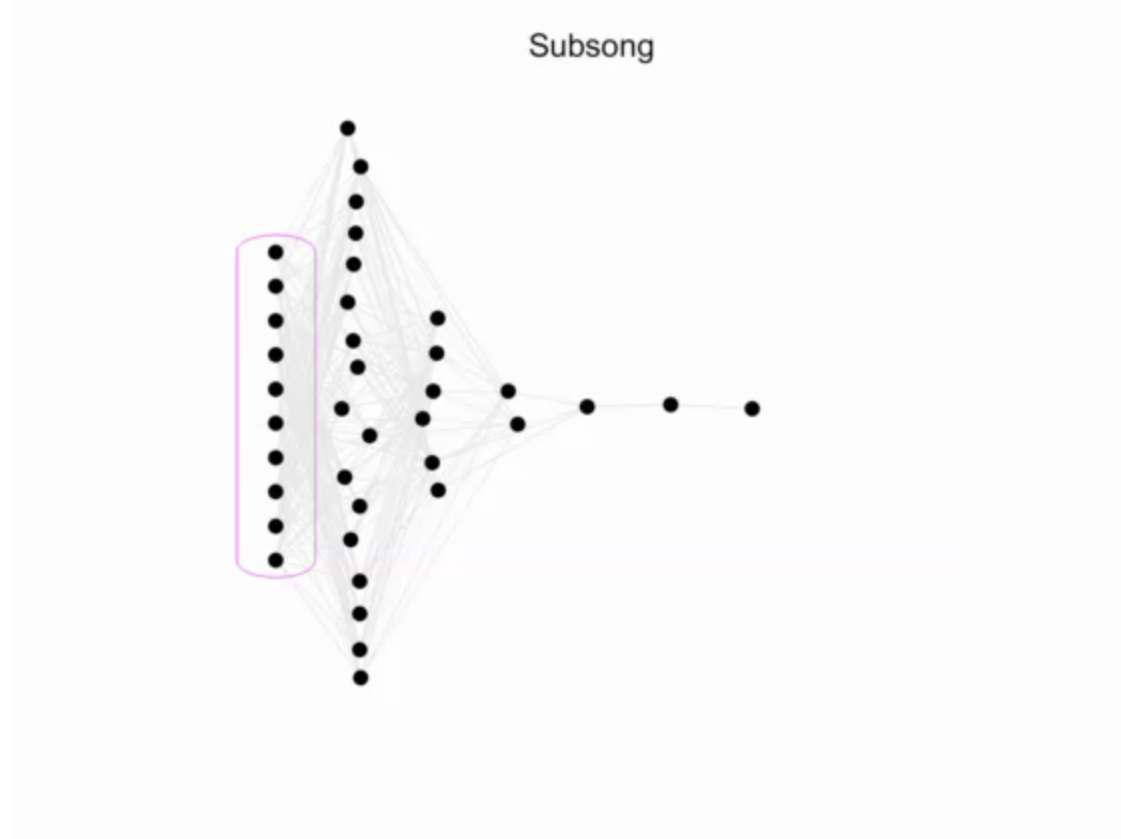
Subsong

Okubo, Mackevicius, Payne, Lynch and Fee, Nature 2015

Model of the growth and splitting of sequential chains of activity in HVC

1. **Start with a randomly connected recurrent network**
2. **Include simple learning rules:**
   STDP and synaptic competition
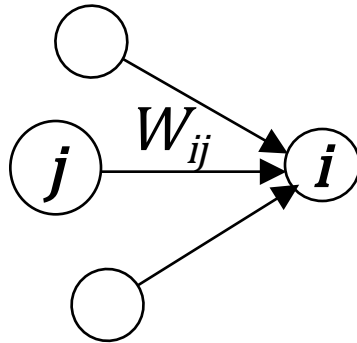   (Jun & Jin 2007, Fiete et al. 2010)
3. **Drive it with seed inputs**

Achieve:

- Growth of a protosyllable chain
- Splitting into multiple daughter syllables

External input

HVC

Seed neurons

Okubo, Mackevicius, Payne, Lynch and Fee, Nature 2015
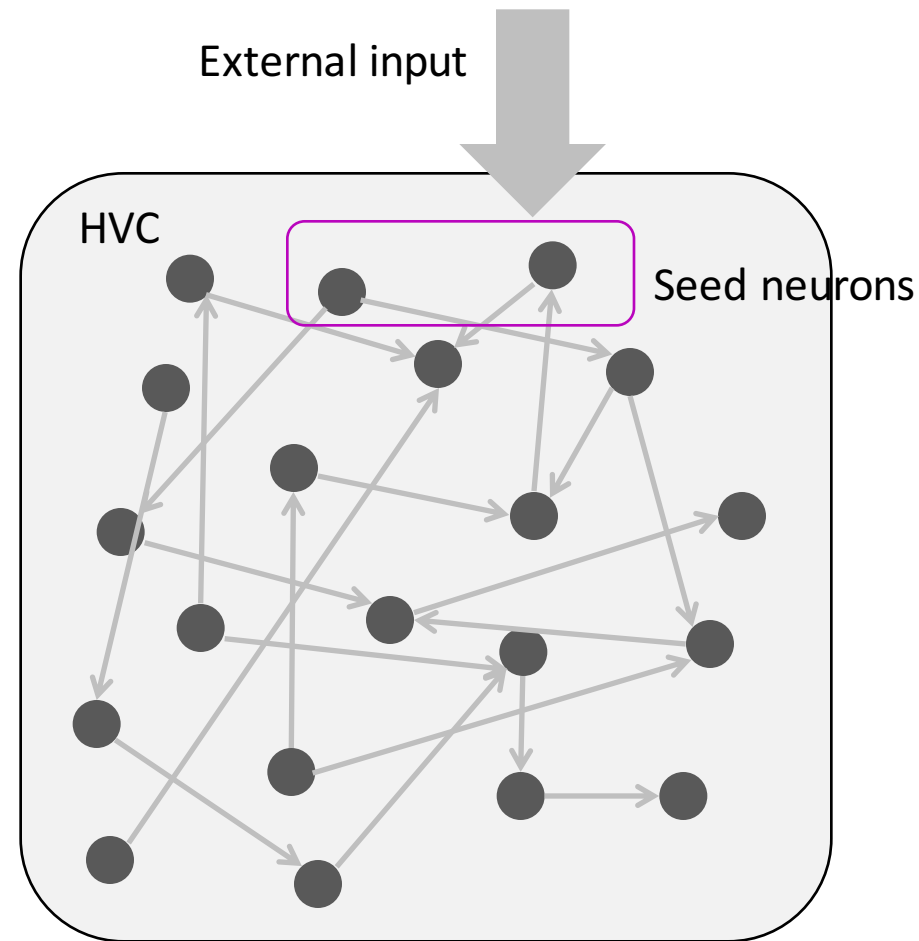
Binary neuron model

Based on Fiete et al. 2010

Feed forward-inhibition

$$\vec{x}(t) = \left(\boldsymbol{W}\vec{x}(t-1) - \overbrace{\beta I_{feedforward}} - \underbrace{\alpha \vec{I}_{adapt}}\right) > 0$$

Adaptation term
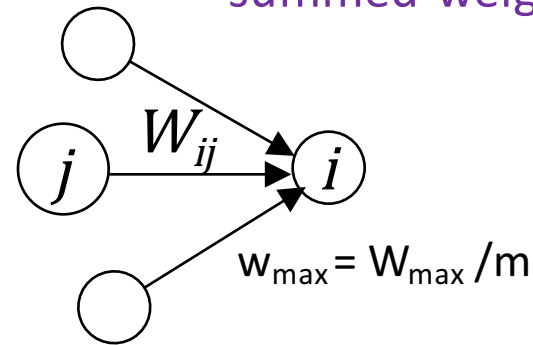
Plasticity rules

$$\Delta W_{ij} = \eta \Delta_{ij}^{STDP} - \eta \epsilon \Delta_{ij}^{hLTD}$$

STDP (simplified)
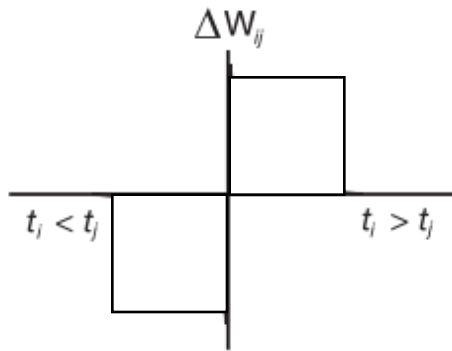
$$\frac{dw_{ij}}{dt}(t) = x_i(t)x_j(t-1) - w_i(t-1)x_j(t)$$

Heterosynaptic LTD:
summed-weight limit rule

$w_{max} = W_{max}/m$
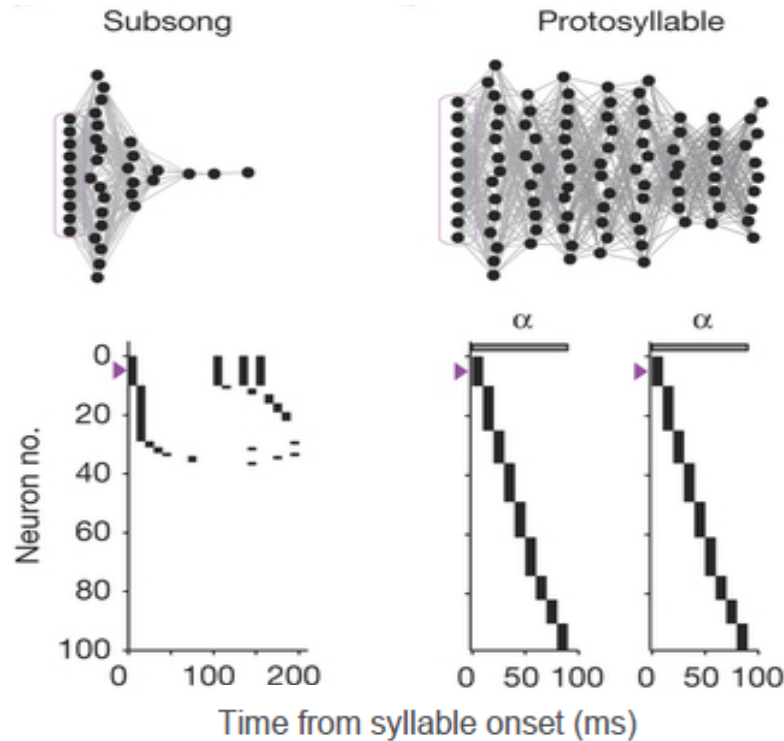
For incoming synapses to neuron i:
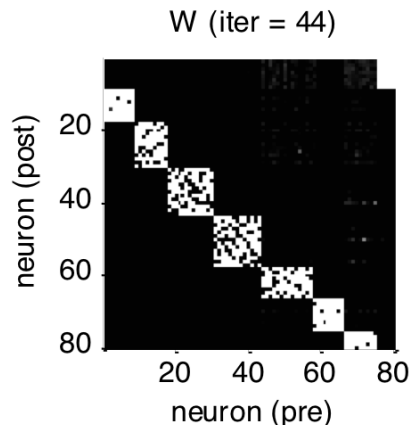
$$\Delta_{i*}^{hTLD} = \left(\sum_k W_{ik} + \eta \Delta_{ik}^{STDP} \right) - W_{max}$$

$$if > 0, \ else \ \Delta_{i*}^{hTLD} = 0$$

Fiete et al. 2010

Formation of a synaptically-connected protosyllable chain

- Before learning, transient inputs trigger a brief ripple of activity

- After learning, activity propagates along a robust protosyllable chain

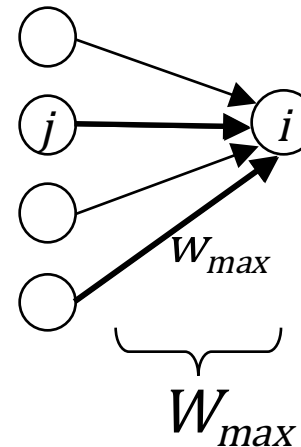- Weight matrix is a block-permutation matrix

Okubo, Mackevicius, Payne, Lynch and Fee, Nature 2015

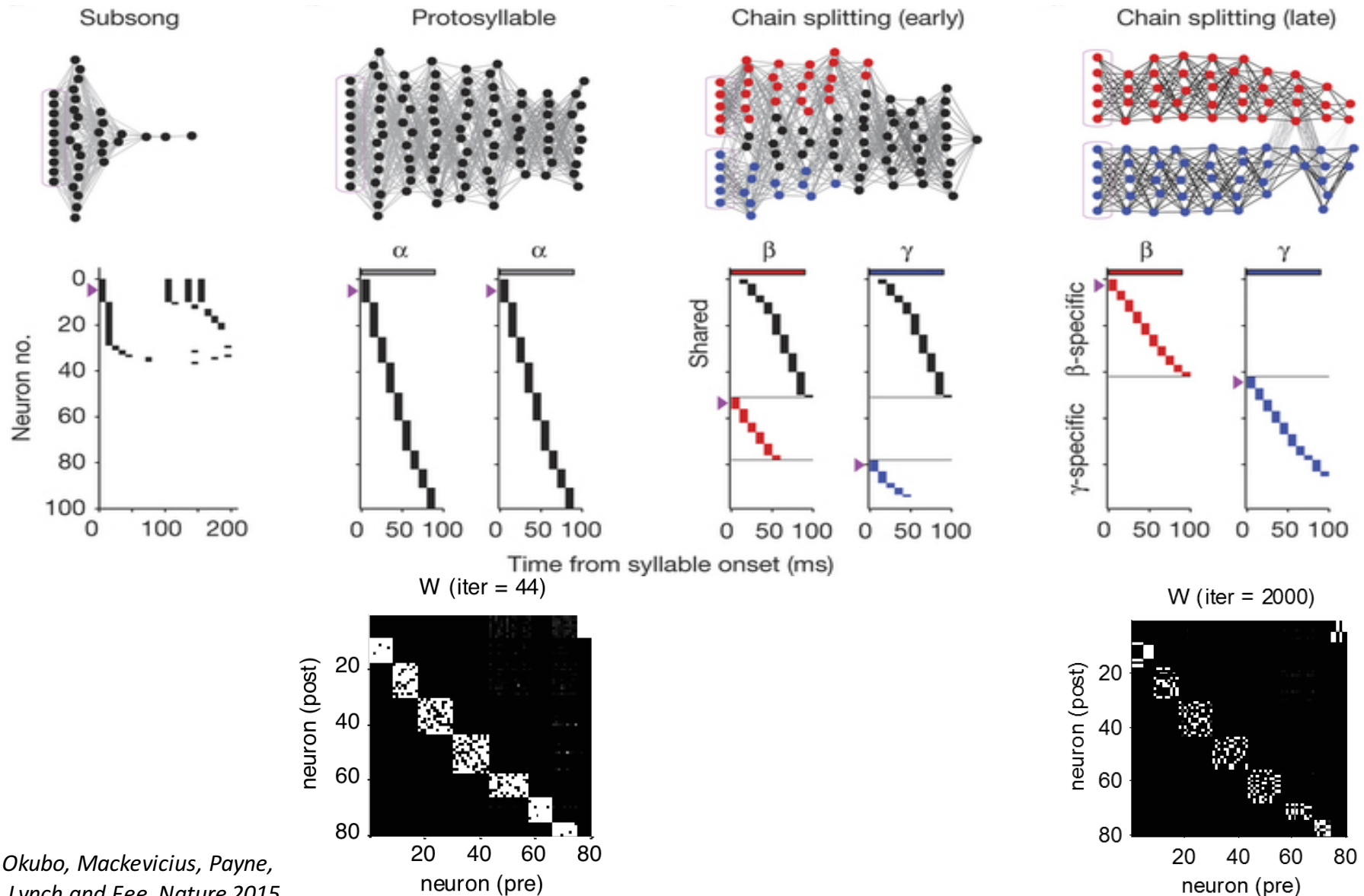# Splitting of the protosyllable chain into two daughter sequences
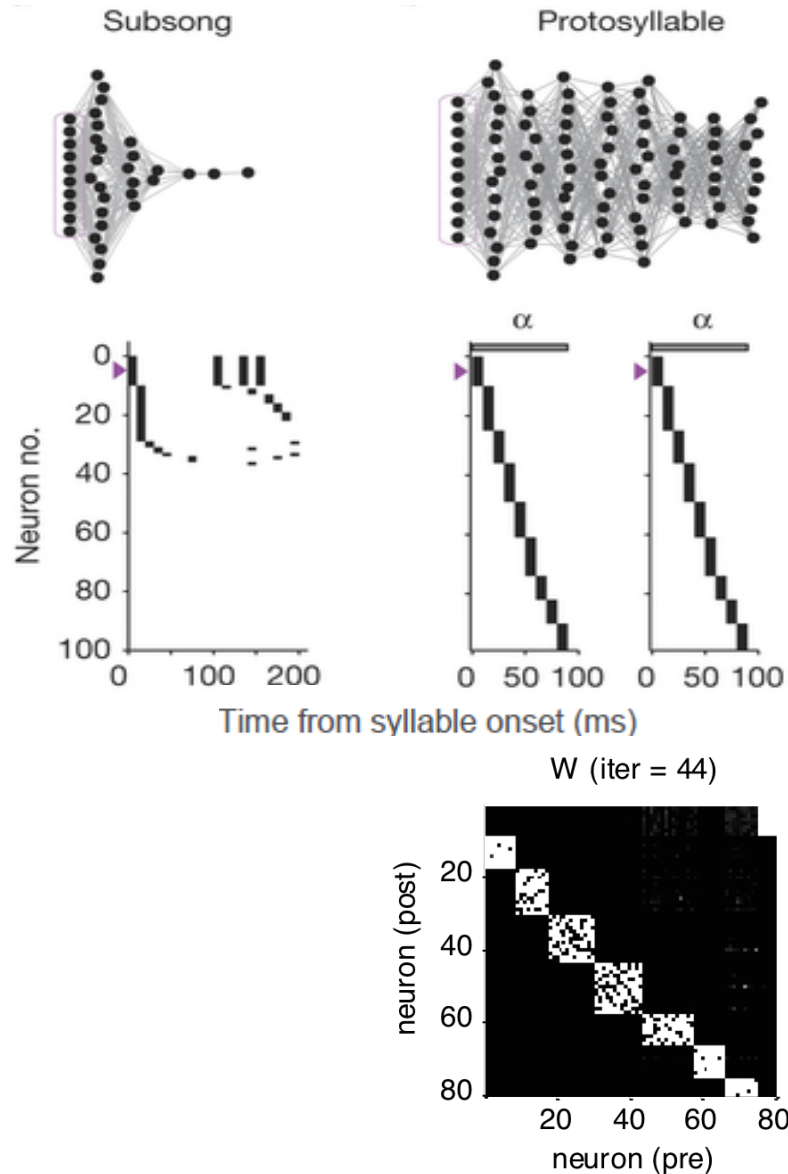
Idea: Increase synaptic competition by allowing fewer, stronger synapses per neuron

W_{max} *stays the same (total synaptic input)*
w_{max} *doubles (hard limit on each synapse)*

Also increase lateral inhibition to encourage splitting, and divide seed inputs into two groups

Okubo, Mackevicius, Payne, Lynch and Fee, Nature 2015

Splitting of the protosyllable chain into two daughter sequences

Okubo, Mackevicius, Payne, Lynch and Fee, Nature 2015

Question

How are complex motor sequences formed from simple underlying components?

Hypothesis

Differentiation of a prototype syllable through splitting of a neural sequence

Approach

Network model of sequence formation and differentiation using STDP and heterosynaptic competition plasticity rules

Further questions

- Dependence on specific formulation of plasticity rules, systematic exploration of parameter sensitivity

- We used increasing lateral inhibition + increased heterosynaptic competition to break up initial wide chain, other mechanisms?

- Extension to non-binary neurons