Neural mechanisms underlying the reduction in behavioral variability during trial-and-error learning

A. Dubreuil[1,2] , Y. Burak[3] , T.M. Otchy[2,3] , B.P. Ölveczky[2,3]

1. ENS Cachan 2. Organismic and Evolutionary Biology departement, Harvard University 3. Center for Brain Science, Harvard University

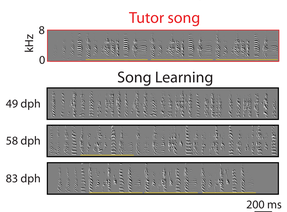
Question

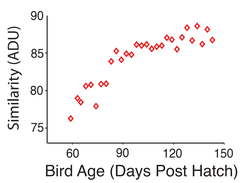
Motor exploration is essential for trial-and-error learning, yet as learning progresses motor variability is often reduced to yield a stereotyped performance. What neural mechanisms are responsible for this reduction in variability?

To address this question, we study the zebra finch, a songbird that learns its song by imitating a tutor.

Behavioral level

Motor exploration and reduction in vocal variability



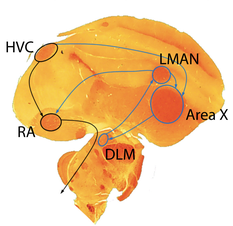


As sensori-motor learning commences, the song of juvenile zebra finches are first highly variable reflecting vocal exploration. As learning progresses the bird's vocal output becomes more stereotyped and more similar to the tutor.

Acoustic similarity of identified syllables increase with learning. All syllables of the same type are compared to each other using several accoustic features (pitch, amplitude, entropy...), and a similarity index is calculated.

Neural level

Song variability is driven by a source external to the descending motor circuit.



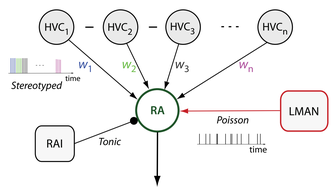
- The motor circuit in songbirds is composed of nucleus HVC that codes for the temporal sequence in which sounds are generated [1].
- RA receives inputs from both HVC and the learning pathway through LMAN, and projects to the respiratory and vocal muscles.
- LMAN, the output nucleus of a basal ganglia circuit, drives song variability [2].

Possible mechanisms for reduction in vocal variability

- If HVC is lesioned in adults, LMAN is capable of driving highly variable song, similar to what is observed in young birds [3] [4]. This suggests that LMAN contributes a variable input to RA throughout learning and beyond.
- The song learning process is thought to be driven by synaptic reorganization in the HVC-RA networks [5].

Here we explore whether strengthening and pruning of HVC-RA synapses can account for the reduction in LMAN induced song variability.

Model



Physiological parameters - taken from the literature.
Scaling factors of different inputs, trial-to-trial jitter in HVC firing, and weight distributions are adjusted to match recordings from RA neurons during singing.

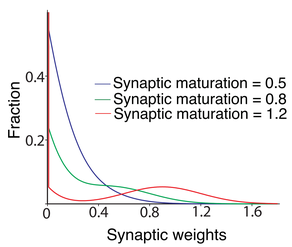
Age independent properties:

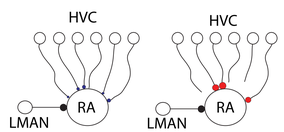
- Each RA projecting cell is modeled as a leaky integrate-and-fire neuron, receiving excitatory inputs from HVC and LMAN through voltage dependent conductances representing NMDA and AMPA channels.
- The RA interneuron network provides tonic inhibition.
- HVC is modeled as a synfire chain that provides a stereotyped input with same structure at all trials and ages.
- LMAN input is modeled as a Poisson spike train.

Age dependent properties:

- Learning is modeled by synaptic pruning and strengthening of HVC-RA synapses.
- Inhibition depends on $\langle W_i \rangle$, the mean of the HVC-RA weight distribution.

Synaptic strengthening and pruning:





Synaptic weight distribution: sum of two gaussians of mean μ_1 and μ_2:

- μ_1 shifts towards negative values with synaptic maturation : pruning.
- μ_2 shifts towards positive values with synaptic maturation : strengthening.

References

[1] Hahnloser, R. H., A. A. Kozhevnikov, and M. S. Fee, 2002, An ultra-sparse code underlies the generation of neural sequences in a songbird: Nature, v. 419, p. 65-70.

[2] Ölveczky BP, Andalman AS, Fee MS (2005) Vocal Experimentation in the Juvenile Songbird Requires a Basal Ganglia Circuit. PLoS Biol 3(5): e153.

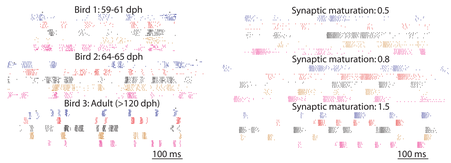
[3] Aronov D, Andalman AS, Fee MS . 2008. A specialized forebrain circuit for vocal babbling in the juvenile songbird Science 320 630-634.

[4] Thompson, J.A., Wu, W., Bertram, R. & Johnson, F. Auditory-dependent vocal recovery in adult male zebra finches is facilitated by lesion of a forebrain pathway that includes the basal ganglia. J. Neurosci. 27, 12308–12320 (2007).

[5] Kittelberger, J. M., and R. Mooney, 1999, Lesions of an avian forebrain nucleus that disrupt song development alter synaptic connectivity and transmission in the vocal premotor pathway: J Neurosci, v. 19, p. 9385-98.

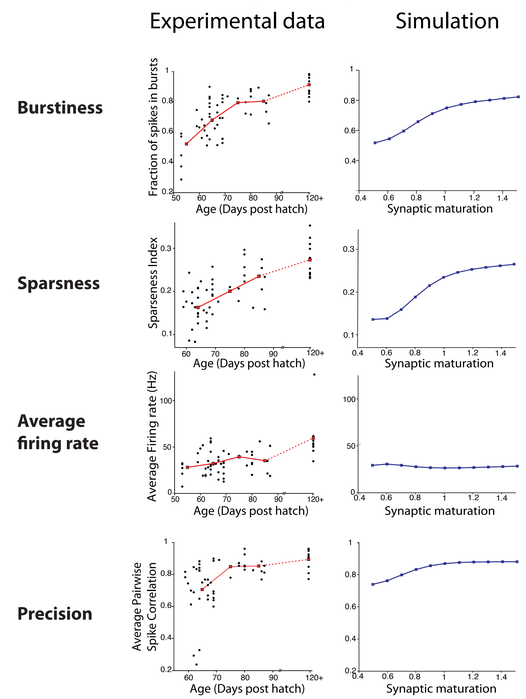
Model versus data

Our data comes from recordings from single RA neurons of 5 juvenile birds, whose age varied from 53 dph to 86 dph and from adult birds (age > 120 dph).

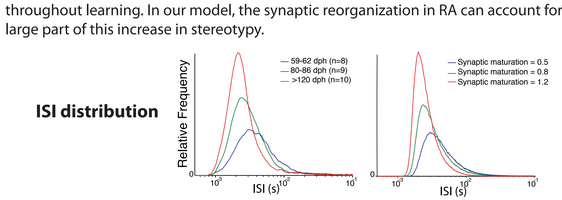


Song-aligned firing patterns in RA neurons change gradually during learning. As the song becomes less variable and more similar to the tutor, the firing patterns in RA become more precise, sparse and bursty.

Neural correlates of song learning



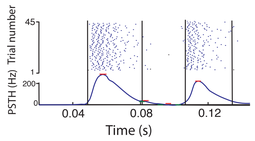
Precision: The average pairwise spike correlation of RA spike trains increases significantly throughout learning. In our model, the synaptic reorganization in RA can account for a large part of this increase in stereotypy.



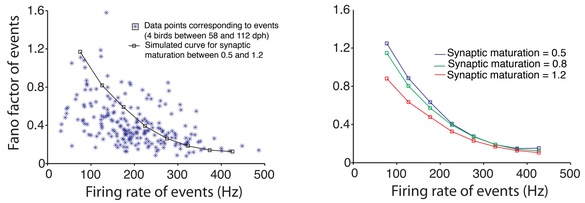
Dependence of variability on instantaneous firing rate

Selection of firing events

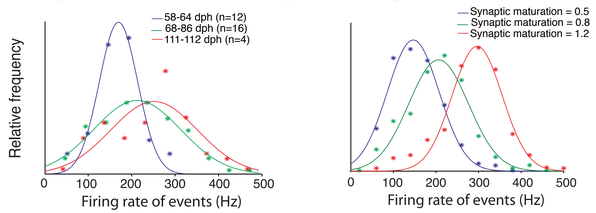
Spike trains are split into events using an automated method that recognizes maxima and minima of the smoothed PSTH. For each event we calculate a firing rate and we quantify variability by computing the Fano factor.



Variability depends on firing rate



Firing rates increase through learning



Conclusions

Maturation of HVC-RA synapses accounts, in a simple model of the HVC-RA-LMAN circuit, for two important trends observed in the neural recordings from RA neurons in singing juvenile zebra finches:

(1) Firing patterns gradually become more sparse and bursty.
(2) Trial-to-trial variability in RA is reduced with age.

Our results suggest a direct mechanistic link between the shaping and maturation of a learned motor program and the reduction in behavioral variability.

This work was supported by :

- A scholarship from the Physics Departement of the Ecole Normale Superieure de Cachan
- NINDS 1R01NS066408-01A1
- The McKnight Endowment Fund for Neuroscience
- The Esther and Joseph Klingenstein Fund
- The Swartz Foundation