Master Thesis - Computational model of Zebra Finch song learning and the influence of sleep on it

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The 6th of June, 2017

Abstract

The Zebra Finches are songbirds which learn the song of their tutor. They learn it from 25 days post hatch (DPH) to 90 DPH (Liu, Gardner, & Nottebohm, 2004). Zebra finches are commonly used as a model of speech acquisition.

Derégnaucourt, Mitra, Fehér, Pytte, and Tchernichovski (2005) showed that sleep plays an important role in the learning of tutor songs. Indeed, they showed that sleeping has a negative impact on song restitution by zebra finches in the short term but a positive impact on the long run. Song restitution is less complex and less similar to the tutor song from one morning to the previous day evening, but the greater this loss in performance was overall for one bird, the better this bird was able to reproduce the tutor song at the end of its learning.

In addition to that, Dave and Margoliash (2000) have found neurons in the motor cortex which fires sequences during sleep that correspond to their activity pattern when the birds sing in adult zebra finches. This shows that motor neurons that are highly correlated with bird's own song (BOS) are activated during the night. These identified replays suggest that some learning may occur during sleep that use past experiences.

Our hypothesis is that during its sleep, the zebra finch restructures the knowledge it has acquired so far thanks to replay mechanisms. We hypothesize that this restructuring can account for the loss of performance in the short term and an improvement of performance in the long term.

The goal of this internship is to offer a model of the zebra finch song learning which can explain different behavioral data observed such as the correlation between the loss of performance every night and the overall performance at the end of learning.

Contents

1. Introduction

1.1 Zebra Finch song learning

1.1.1 Characteristic of the zebra finch song learning

insert zebra finch figure

The Zebra Finches are songbirds which learn the song of their tutor. Only males sing. Singing is part of the courtship of the bird. They learn their tutor song from 25 days post hatch (DPH) to 90 DPH (Liu et al., 2004). The songs have rather complex structure, with a chain of syllables. A syllable is defined by a sound surrounded by short silences. This chain of syllables forms a "motif" (Doupe & Kuhl, 1999; Margoliash, 2002). Zebra finches are close-ended learners (Margoliash & Schmidt, 2010). They learns only one song and will retain it their whole life, in comparison of open-ended learners such as canaries which learns a new song each year.

The Zebra Finch learning development has been described in two different phases. First of all, the Zebra Finch is in a sensory phase until 65DPH, when it only listens to the song of its tutor, which can be sung by a real Zebra Finch or by a song playback. This is a critical period in which the bird memorize fully the tutor song. Birds who have access to the tutor song for only ten days between 25DPH and 65 DPH sing the tutor song as good as the bird with access to the tutor song during their whole learning (Böhner, 1990; Roper & Zann, 2006). The second phase is the sensorimotor phase during which the bird sing and use its auditory feedback to improve its performance. It overlaps the sensory phase. Starting from 25DPH to 30DPH, the bird produces a *subsong*, a process similar to babbling. Then, the bird produce a *plastic song* starting from 50DPH. It tries to imitate the tutor song it has memorized. After 90DPH, the song has reached its *crystallization*. The song is fixed and will not change throughout the Zebra Finch adulthood. The song of the Zebra Finch gets highly stereotyped (Williams, 2004). Zebra Finches needs auditory feedback to learn to sing. Deafening in juvenile has severe impact on song acquisition, even if the tutor song has already been acquired. Deafening once the song is learned has a much smaller impact on performance (Scharff & Nottebohm, 1991; Doupe & Kuhl, 1999). Deafening a chicken, in opposition, has no impact on its calls. Zebra Finches raised in isolation will also develop abnormal songs. Therefore, Zebra Finches learns their vocalisation from a tutor and need to hear themselves to sing correctly.

1.1.2 Why is zebra finch song learning studied

Songbird and especially Zebra finches are commonly used as a comparison with human about vocal development. Indeed, the song they produce are not innate even though they have predispositions toward learning their songs. They produce song with complex structures composed of syllables.

The neuroanatomy of Zebra Finch has also been extensively studied and the different structures involved in singing has been identified (Nottebohm, 2005; Bertram, Daou, Hyson, Johnson, & Wu, 2014). Doupe and Kuhl (1999) even proposed parrallels between the areas involved in song production with songbird and the areas involved in speech with humans.

Zebra Finches are also excellent laboratory animals. They are easily domesticated and easy to study compared to other songbirds or "speaking" animals. As they learn only one song, their learning is easily

not beautiful sentence

trackable. The developmental trajectory can be inferred. Derégnaucourt et al. (2005) for instance tracked from the

- Well studied Neuroanatomy
- Easy to study experimentally
  - Easily domesticated
  - Learn one song
  - Learn quickly (90DPH)
  - Easy to track song development

1.2 Neurobiology of the Zebra Finch

1.2.1 Neuroanatomy of the Zebra Finch song system

- Connection between RA, HVC, Area X, … Inhibition, excitation

1.2.2 Pattern of activation in RA and HVC

- HVC clock like, temporal structure (Ali et al.)
- RA activation while singing at very precise time and sparse coding
  - Motor control (Ali et al.) Ali et al. shows real two different learning: spectral and temporal

1.3 Models of song learning

Only very few models have been created. Even less are actual computational models.

1.3.1 Reinforcement learning

- Proposed but no real explanation of what could be the state space, the action space, the reward function (Dave&Margoliash).
- Used in paradigm to test different hypothesis (averse reward to force change in behaviour of the bird)

1.3.2 Song preferences in selection (Marler)

- Behavioural model to explain how the bird select its template
- TODO: Add more

1.3.3 Coen's model

- Clustering technique with babbling (multimodal)
  - Cluster the tutor song syllables thanks to their characteristics
  - Babbling, create a mapping between the motor space and the identified cluster
- Use of a real synthesizer but not actually built to model zf vocal apparatus
- No quantitative means to see how good is the song reproduction
- The learning is only babbling, nothing is driving the model in a specific direction.

1.4 Song synthesizer

1.4.1 Description of Perl song synthesizer to reproduce Zebra Finch song

- Presentation of anatomy simulation, mass and spring...
- Parameters
  - Air sac pressure
  - Syringeal Labial Tension
- Parameters are close to actual motor actions, so close to actual motor command

1.4.2 Zebra Finches are sensible to song produced by the synthesizer

- Show results of Amador where RA neurons were activated by Synth song but not by conspecific song.

1.4.3 Gestures and song structure

- Boari's Gesture concept and automatic extraction of the gestures
- Could have been correlated to HVC activation but in fact no.

1.5 Influence of Sleep in the Zebra Finch song development

1.5.1 Margoliash results with song replay

- RA neurons activated while singing
- Also activated when the bird is asleep and listen to his own song
- Spontaneous activity with part of the song: Replays
- Replays can be consolidation of memory
- Replays can have another role

1.5.2 Derégnaucourt results about positive impact of sleep for development

- Extraction of syllables characteristics and track over time
- Global trend for the trajectory of a syllable over time
- Each day, the syllables characteristics are closer

1.6 A computational model of birdsong learning to explain the sleep influence

1.6.1 Interest of a computational model of birdsong learning

- Computational model helps understanding what are the *implementation constraints* of the learning mechanisms
  - Use of synthesizer

  - Realistic computational budget

- Easily make hypotheses that can be tested experimentally afterwards
- Abstracted and controlled environment

1.6.2 Goal: Build a modular two-step learning model and look for learning algorithm that can account for Derégnaucourt's results.

2. Our Model

2.1 Global Architecture

2.1.1 Usage of Boari's implementation of the birdsong synthesizer

2.1.2 Measurement of song quality with standard measures

- Entropy, Pitch, Goodness, Amplitude, Frequency Modulation, Amplitude Modulation
- Imported from Matlab implementation, with qualitatively similar results

2.1.3 Two-step learning model

- Bird has several song models it trains to reach tutor
- tutor song is known
- day algorithm for parameters optimisation
- night algorithm for structure optimisation
- Hypothesis: structure optimisation yield unlearning short term, better learning long term

2.2 Song Model

2.2.1 Song Model

2.2.2 Gesture paradigm inherited from synthesizer

2.2.3 Song structure

- List of gestures and their duration
- Fixed duration of the song because of measurement

2.2.4 Gesture composed of two generators for the motor commands

- Abstracted in sum of sin & linear func

2.3 Day learning algorithm

2.3.1 goal

- Optimise gestures parameters

2.3.2 Hillclimbing

- really simple
- Choose song model, choose gesture
- Choose close parameters, if better keep, if worse trash
- Knows if better by comparison of weighted standard measurements
- Not whole song but only gesture trained to make faster computations
  - Actually creates unlearning

2.3.3 Prediction

- Should improve song production but get stuck in local maximum because bad structure

2.4 Night learning algorithms

2.4.1 Goal

- Find better structure to describe song motor command

2.4.2 Several variations of algorithm have been tested

- Evolutionary algorithm
  - Simple solution for structure variation
- with or without diversity

2.4.3 Algorithm

- Evolutionary algorithm Microbial GA
- Increase population size and add variation in structure
  - Remove, add, change, copy gesture
  - Song always the same length for comparison reasons.
- Compare by tournament
  - The winner put a variation of itself in place of the loser
  - Compare number of neighbour * score, lower the better

2.4.4 Predictions

- Structure variation yields unlearning short term but positive impact long term
- Diversity will increase this

2.5 Parameters

- Tried to be realistic
- most are fit through gridsearch
- Realistics: Number of days, number of syllables sung during all dev
- Gridsearch optimisation
- Default value for gesture parameters
- Learning rate
  - Prevent part of unlearing
  - Could be fitted to match real song learning rate
  - Coefficient for score optimisation
- Algorithm way better in score than Boari but qualitatively very different to the ear
- Look at which parameters boari's method was better than algo and put priority on them
- Amplitude and entropy
- Diversity threshold to maximise variance in diversity score
  - Value: 5000
  - Other parameters
- Number of song models during day and night: Depend of runs
- Boundaries for parameters values: Fixed
- Number of tournaments during night: depend of runs
  - Correlated with replay? By how much?

3. Analyses and results

3.1 Learning method is as good Boari's method or better

- Using standard measure criteria in the birdsong community
- Simple description of motor params sufficient to produce good songs
- Qualitatively same amount of gestures
  - Can be due to luck

3.2 Too little training per model cause divergence

- maybe due to global vs local error

3.3 Derégnaucourt results not reproduced

- Syllables extracted by time of begin and end
- Without or with diversity
- No night deterioration
- Night deterioration has no impact in overall learning

4. Discussion

4.1 The synthesizer which cannot produce every sounds

- Our score really close to boari's method (not way better or way worst), maybe we reached synthesizer limits

4.2 The parameters description we choose

- more simple/complexe possible than sum of sin and affine?

4.3 The unlearning during day due to the gesture learning

4.4 Fixed duration of songs in learning

- Dynamic Time Warping can correct that

4.5 Big artificial separation between structuration and gestures optimisation

4.6 Diversity not strong enough? What if only diversity during night?

- Maybe not convergence
- Maybe what we are looking for

5. Conclusion

5.1 Learning algorithm with two step learning

- Very few of them
- Working with realistic synthesizer
- modular architecture, easy to test new models

5.2 Restructuration didn't yield the expected effect

- More parameters search might be able to fix it

Bibliography

Bertram, R., Daou, A., Hyson, R., Johnson, F., & Wu, W. (2014, September). Two neural streams, one voice: Pathways for theme and variation in the songbird brain. *Neuroscience*, *277*, 806–817. doi:10.1016/j.neuroscience.2014.07.061

Böhner, J. (1990, February). Early acquisition of song in the zebra finch, taeniopygia guttata. *Animal Behaviour*, *39*(2), 369–374. doi:10.1016/S0003-3472(05)80883-8

Dave, A. S. & Margoliash, D. (2000, October 27). Song replay during sleep and computational rules for sensorimotor vocal learning. *Science*, *290*(5492), 812–816. doi:10.1126/science.290.5492.812

Derégnaucourt, S., Mitra, P. P., Fehér, O., Pytte, C., & Tchernichovski, O. (2005, February 17). How sleep affects the developmental learning of bird song. *Nature*, *433*(7027), 710–716. doi:10.1038/nature03275

Doupe, A. J. & Kuhl, P. K. (1999). Birdsong and human speech: Common themes and mechanisms. *Annual review of neuroscience*, *22*(1), 567–631.

Liu, W.-c., Gardner, T. J., & Nottebohm, F. (2004). Juvenile zebra finches can use multiple strategies to learn the same song. *Proceedings of the National Academy of Sciences*, *101*(52), 18177–18182.

Margoliash, D. (2002, December 1). Evaluating theories of bird song learning: Implications for future directions. *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology*, *188*(11), 851–866. doi:10.1007/s00359-002-0351-5

Margoliash, D. & Schmidt, M. F. (2010, October). Sleep, off-line processing, and vocal learning. *Brain and Language*, *115*(1), 45–58. doi:10.1016/j.bandl.2009.09.005

Nottebohm, F. (2005, May). The neural basis of birdsong. *PLoS Biol*, *3*(5). doi:10.1371/journal.pbio.0030164

Roper, A. & Zann, R. (2006, May). The onset of song learning and song tutor selection in fledgling zebra finches. *Ethology*, *112*(5), 458–470. doi:10.1111/j.1439-0310.2005.01169.x

Scharff, C. & Nottebohm, F. (1991). A comparative study of the behavioral deficits following lesions of various parts of the zebra finch song system: Implications for vocal learning. *Journal of Neuroscience*, *11*(9), 2896–2913.

Williams, H. (2004, June). Birdsong and singing behavior. *Annals of the New York Academy of Sciences*, *1016*(1), 1–30. doi:10.1196/annals.1298.029