

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

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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_juvenile_2004](#)). Zebra finches are commonly used as a model of speech acquisition.

[deregnaucourt_how_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_song_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.

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1. Introduction

1.1 Zebra Finch song learning

1.1.1 Characteristic of the zebra finch song learning

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_juvenile_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_birdsong_1999](#); [margoliash_evaluating_2002](#)). Zebra finches are close-ended learners ([margoliash_sleep_2002](#)). They learn only one song and will retain it their whole life, in comparison of open-ended learners such as canaries which learn a new song each year.

insert zebra
finch figure

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 ([bohner_early_1990](#); [roper_onset_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_birdsong_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_comparative_1991](#); [doupe_birdsong_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 learn 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_neural_2005](#); [bertram_two_2014](#)). [doupe_birdsong_1999](#) even proposed parallels 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. **deregnacourt_how_2005** for instance tracked from the syllables trajectories by clustering syllable productions over time.

* 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 G. B. Mindlin's song synthesizer to reproduce Zebra Finch song

G. B. Mindlin and his team built a model of the Zebra Finch vocal apparatus. They described with differential equations the behaviour of the components of this vocal apparatus (see Fig 1.1). The differential equations model the separation between the syringeal labia. Each labia are modeled as a spring and mass system that can produce sustainable oscillations. Depending of the parameters it receives, the synthesizer is able to produce a vast variety of sounds, either very pure or very rough, depending of the strength of the labia tension (**amador_beyond_2008**; **boari_automatic_2015**).

They simplified their model and obtained the dynamic system shown in equation 1.1.

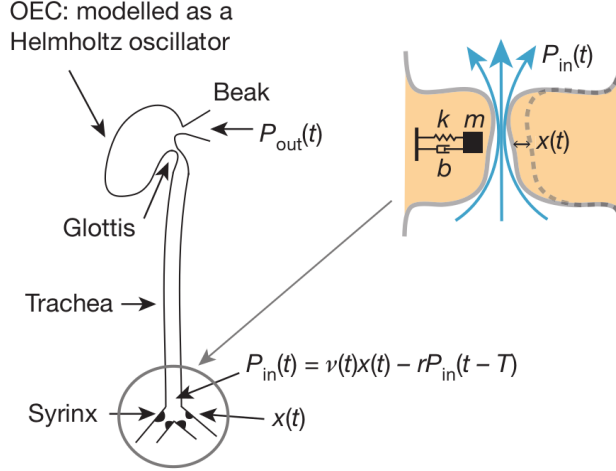


Figure 1.1: Model of the zebra finch vocal apparatus

The air ($P_{sub}(t)$) comes from the air sac below the syrinx, then goes up to the trachea, the glottis, resonate in the oro-esophageal cavity (OEC) and the beak ($P_{out}(t)$). Each component acts as a filter in G.B. Mindlin's team model of the zebra finch vocal apparatus. Figure 1b taken from **amador_elemental_2013**

$$\begin{cases} \frac{dx}{dt} = y \\ \frac{dy}{dt} = -\alpha\gamma^2 - \beta\gamma^2x - \gamma^2x^3 - \gamma x^2y + \gamma^2x^2 - \gamma xy \end{cases} \quad (1.1)$$

x describes the position of the syringeal labia. γ is a constant which takes into account values specific for the Zebra Finch vocal apparatus. α and β are unit-less time-dependant parameters. α is proportional to the air sac pressure, that is how much air is coming through the syrinx, and β is proportional to the syringeal labial tension. It can be hypothesized that these two parameters can be easily modified by motor actions. Therefore, the whole singing behaviour can be described as the dynamics of muscles acting on the air sac pressure and the syringeal labial tension. This synthesizer provides thus a way to bridge the gap between actual motor commands and song production. Even if the model is simplified, as it assumes a symmetry in the labial tensions, it is able to produce a rich variety of sounds. **amador_beyond_2008**; **perl_reconstruction_2011** studied the parameter space and even showed that different categories of sound productions can be found in different regions of the parameters space.

This model of birdsong production shows that low dimensional but biologically realistic parameters can describe the singing behaviour. Simple variations in the motor space produces complex and diverse variations in the song production. This model simplifies greatly the study of song production behaviour, as it is possible to study the dynamics of song production in the motor space while keeping realistic constraints.

1.4.2 Zebra Finches are sensible to song produced by the synthesizer

The computational model of the zebra finch vocal apparatus is a real sound synthesizer. It produces sound waves which birds, as we, can listen to. As explained in 1.2, Zebra Finches have neurons which are highly selective to their BOS. When the bird is asleep and listen to their own song, these neurons fire in a very specific pattern. To assess the quality of their synthesizer, G.B. Mindlin team tested if their synthetical song, built from the BOS, will activate these neurons (**amador_low_2014**; **boari_automatic_2015**). They showed that even if the strenght of the activation was not as strong as the BOS, their synthesized song performed better than a conspecific song or the BOS played in reverse. This suggests that the synthesis is sufficiently good to trick a bird and therefore a good imitation of its song.

1.4.3 Gestures and song structure

The study of the parameters α and β over the time course of the song reveals interesting results. **amador_elemental_2013** propose to describe songs by the sequence of air sac pressure (α) and syringeal labial tension (β) trajectories, called gestures. A gesture starts and stops when there is a discontinuity in the trajectory of either the air sac pressure or the tension (see Fig 1.2). If notes and syllables are the primitives of a song in the sensory space, a gesture is the primitives of a song in the motor space. A syllable is most of the time generated by a succession of several gestures. Amador and her collaborators suggested that spiking pattern observed in HVC is correlated with the onset and offset of gestures. It would have suggested that HVC activity is not a clock-like pattern but the transmission of high level motor commands which defines the song structure. This has been contested by **lynch_rhythmic_2016** and **picardo_population-level_2016** with extensive statistical analyses. Even if HVC neurons do not actually fire on the onset and offset of gestures, the gesture framework is very interesting because it allows us to think about the song structure representation in the motor space, and especially motor discontinuities.

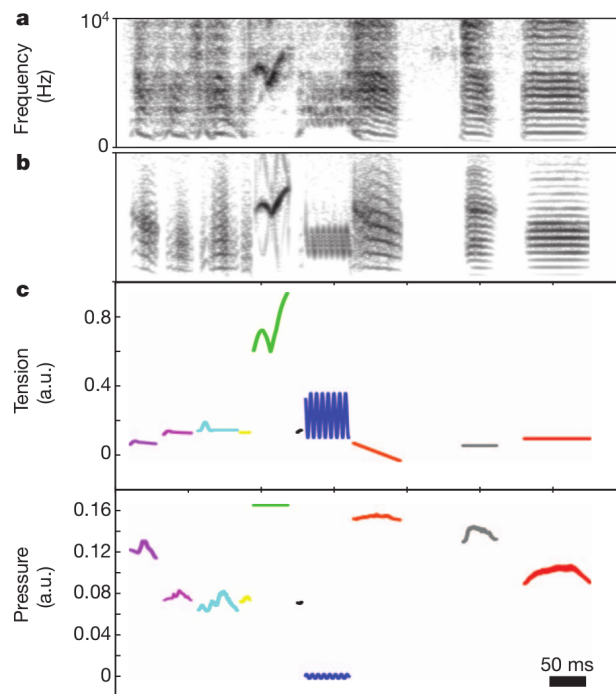


Figure 1.2: A birdsong and its associated parameters for reproduction segmented in gestures
a) spectrograph of a bird's song. b) spectrograph of the synthetic song. c) the parameters α and β for the song. There is several discontinuities in their trajectories. Each continuous segment forms a gesture. Figure from **amador_elemental_2013**

1.5 Influence of Sleep in the Zebra Finch song development

Several studies showed that sleep is involved in the song learning and maintenance. **dave_song_2000** shows thanks to electrophysiology recording the . **deregnacourt_how_2005** showed that sleep has

1.5.1 Song replays during sleep

As explained in the Section 1.2, the song system in the zebra finch brain is highly specialized. Neurons in HVC or RA have a very precise and stereotyped pattern of activation when the adult bird sings. **dave_song_2000** found surprising results. They recorded RA neurons while adult birds were asleep. Neurons in RA spontaneously burst in patterns similar to their activation patterns while the bird sing. Dave & Margoliash hypothesize that this replay activity could be the product of an off-line learning mechanism. Indeed, neural replays have already been found in the rat and it has been showed that these replays influence the construction of its cognitive maps (**de_lavilleon_explicit_2015**) or the suppression of the replays impairs the learning (**girardeau_selective_2009**).

Dave & Margoliash's results were obtained on adult birds which have already learned their song. Though, we can hypothesize that RA replays also occur in the juvenile bird and impacts its learning. The actual function of the mechanism that produces these replays must still be determined.

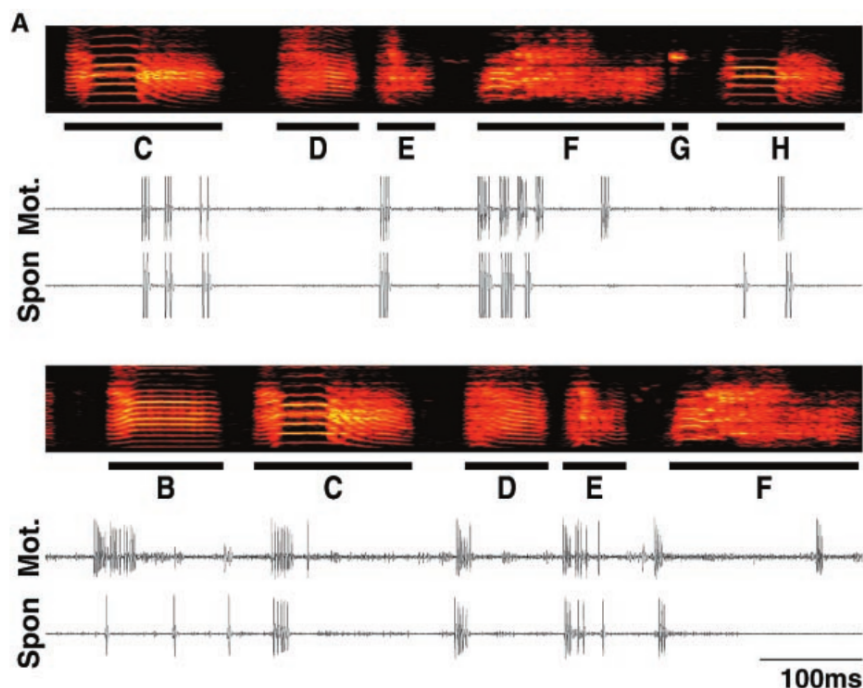


Figure 1.3: Neuronal replay during sleep

Recording of trace of activity of two different neuron for one bird. For each neuron, a premotor activity is shown with the spectrograph of the song the bird sang and the raw trace of a spontaneous activity during sleep that matches the premotor pattern. Taken from **dave_song_2000**

1.5.2 The impact of sleep on the birdsong learning

deregnaucourt_how_2005 recorded entire song developments of Zebra Finches and studied the vocal trajectories during the whole learning process as during the cycles of sleep and wakefulness. They tracked the development of syllables and clustered them. Thanks to this database, they computed the shift in the mean of the clusters for each syllable either in the same day (2 random samples of 100 songs), from evening to the morning (last 100 songs compared to the first 100 songs of the next day) or from the middle of one day to the middle of the next day (random sample of 100 songs compared to a random sample of 100 songs of the next day). They computed the total vocal change for each of these cluster, that is the relative

variation of syllable features **tchernichovski_procedure_2000**¹. They found that vocal change was the most important with the comparison of the cluster of the evening songs compared to the next day morning song, compared to the changes that occur for one day to the next or in the same day (see Fig 1.4). This result shows that sleep has a big impact in the development of the birdsong, because it cannot be explained by the day to day vocal change.

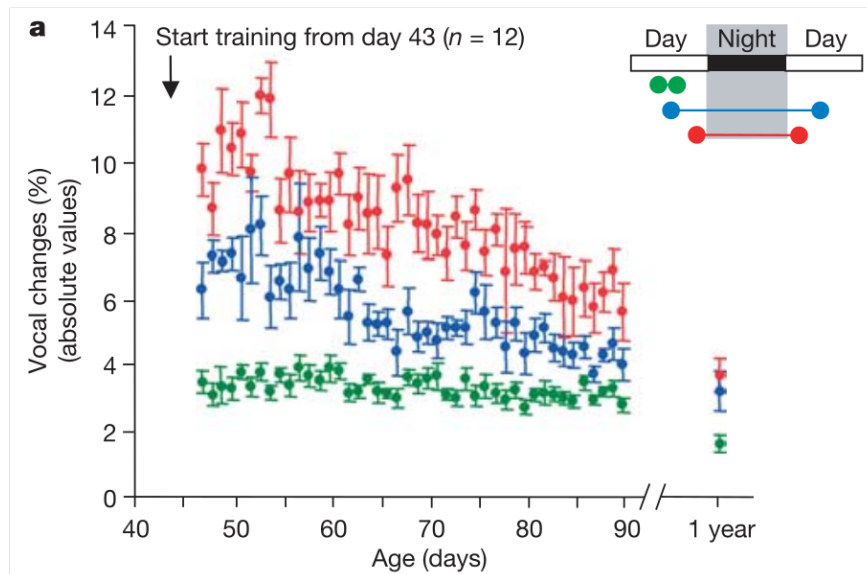


Figure 1.4: Absolute vocal change during song development

Vocal changes in absolute values (median + s.e.m). Green is the change across random sample during the same day (baseline). Blue is the change between random sample from one day to the next. Red is the vocal change from one evening to the next morning. Taken from **deregnaucourt_how_2005**

The vocal change measure Derégnaucourt and his team used is an absolute measure. That means that this measure cannot tell if the change goes in the same trend as the whole learning or in the opposite direction. Thus they introduce a signed measure of vocal change. If the change goes in toward the value of the feature at the end of the learning, the signed vocal change is positive, otherwise, it is negative. The signed vocal change showed that sleep actually has a *negative impact* on learning. Indeed, the effect of night-sleep is almost always negative (see Fig. 1.5a). The effect cannot be explained by the fact the bird has not sung for a long time. Indeed, preventing the bird of singing for 8 hours does not yield the same effect. Thus, this unlearning is due to a mechanism which occur during sleep.

The authors computed the performance of the bird to reproduce its tutor song at the end of its development thanks to a similarity measurement (**tchernichovski_procedure_2000**). Surprisingly, they found that the more the post-sleep deterioration was important overall, the better the bird was able to imitate the song of its tutor, as seen on Fig. 1.6. The negative impact sleep has on learning on the short term (day to day) has a positive impact in the long run. It shows that a learning mechanism is at play during sleep. This learning mechanism has a different function than the learning mechanism during the day. The author suggest that the oscillations in vocal learning may help the bird get out of local maxima in development. Several learning algorithm can be investigated to explain these results.

¹These measures are detailed in Section 2.1.2

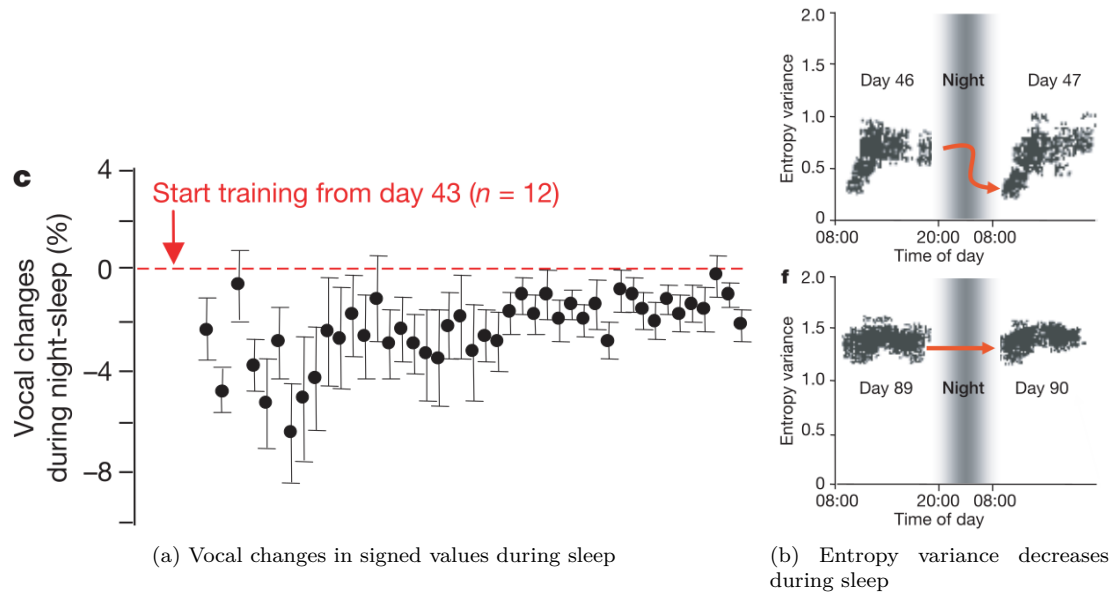


Figure 1.5: Sleep has a negative impact on vocal development

a) Vocal changes in signed values (median + s.e.m) during night-sleep compared to overall development trend.
b) Entropy variance increase overall song development but decrease during night when the bird is still learning. At 90DPH, the bird has reach crystallisation of the song and sleep has little to no impact. Taken from [deregnaucourt_how_2005](#)

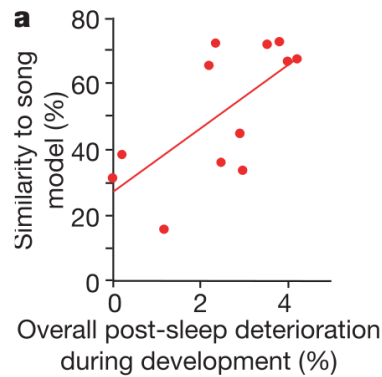


Figure 1.6: Correlation between post-sleep deterioration and similarity of the tutor song at the end of learning.

The more the sleep deteriorate the bird's learning from one day to the next, the better the bird reproduces its tutor song at the end of its learning. Taken from [deregnaucourt_how_2005](#)

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

The goal of this internship is to build a computational and behavioral model of birdsong learning with realistic constraints and try to model the impact of sleep on song development as presented in the Section 1.5.2. The model is developed from scratch in Python 3. It uses the birdsong synthesizer built by G.B. Mindlin and his team and the standard measures used to analyse birdsong.

The Model is a two-step learning model. The model alternates between two different learning algorithm. The strong hypothesis we make is that one of these learning algorithm correspond to the learning algorithm the bird uses during the day, and the second algorithm is the algorithm used by the bird during its sleep. We hypothesize that the algorithm used during sleep should focus on restructuration of the song models the bird has and to the diversity . We think that an algorithm targetting these yields the negative impact of sleep in the short term with a positive impact at the end of learning as `deregnacourt_how_2005` observed.

The source code of the model is available at <https://github.com/PaulEcoffet/birdsonglearningmodel>.

2.1 Global Architecture

The model is built in several modules. First of all, the model uses G.B. Mindlin's team synthesizer to produce realistic song with biologically plausible parameters (see Section 1.4). Then, song features measurement and songs comparison methods have been implemented and used as the hearing system. The song feature measures were taken from the litterature (`tchernichovski_procedure_2000`). They are the standard measures used to describe songs and syllables in the birdsong research community.

As we are building a computational model, we had to explicit every aspect of the song learning.

The birdsong learning model I built is a two step learning algorithm. One algorithm models the learning process of the bird during the day, the other models the learning during the night. These day and night models can be easily changed in the program I wrote.

2.1.1 Boari's implementation of the birdsong synthesizer

We want to use G.B. Mindlin's synthesizer because it allows us to build a computational model with realistic constraints. It bridges the gap between the motor command and the song production thanks to a biophysical model of the Zebra Finch vocal apparatus. Our model can produce simple streams of α and β parameters and send it to the synthesizer. The synthesizer produces real sound waves that can be analyzed by the hearing system.

We used the implementation of the synthesizer available for download on the Dynamical System laboratory of the University of Buenos Aires (<http://www.lsd.df.uba.ar>) (`boari_automatic_2015`). The downloaded program was actually a combination of a α and β parameter extractor from an audio file and the synthesizer from the extracted parameters. I extracted the synthesizer from the source code and adapted it so that it can receive arbitrary parameters. The synthesizer had several bugs. It is suppose to generate a sound stream of the same length of the parameter stream, that is, if there is 10 000 values of α and β sampled at 44 100 Hz, the synthesizer should return a sound wave composed of 10 000 values sampled at 44 100 Hz. But it actually dismiss 2 values, returning only 9 998 values. As the implementation of the

synthesizer was badly documented and the source code was not self explanatory at all, I decided to pad the α β streams with 2 dummy values to prevent this bug.

I have also developped a small Cython package to call Boari's C synthesizer from Python. The source code of this package is available at <https://github.com/PaulEcoffet/birdsynth>.

2.1.2 Characterizing and comparing songs

As we wanted to work on real audio signal, our algorithm must use relevant features of the songs to describe them. Indeed, it needs to compare its production to the tutor song so as to correct its errors and improve itself.

Measurement of the song features

tchernichovski_procedure_2000 suggested several measures to characterize compare songs. To apply these measures, the song is first cut into several time windows, and the measures are computed for each time windows. These measures give us a fine-grained description of the song throughout time. Tchernikovski and his colleague proposed also a measure of similarity between two songs.

They are extensively used in the birdsong research community (**coen_learning_2007**; **deregnacourt_how_2005**; **lipkind_stepwise_2013**; **liu_juvenile_2004**).

The measure we used are the Amplitude, the Frequency Modulation, the Amplitude Modulation, the Pitch, the Goodness and the Wiener Entropy of the signal. Tchernikovski and his team developped a software called Sound Analysis Pro 2011 to compute these features. Though, this software runs only on Windows and its function cannot be called by another program. I have thus ported the implementation of the song features measurement from a Matlab implementation (called Sound Analysis Toolbox) to a Python implementation. The values of the features for the same song computed by my implementation matched qualitatively the values of the Matlab implementation (see Figure ??).

I have also reimplemented the spectral derivative plot which is extensively used in the songbird research community to represent songs.

Comparison of two songs

tchernichovski_procedure_2000 introduced also a similarity measurement. This similarity measurement compares how a song is related to its tutor song. To do so, the algorithm of similarity measurement look for matches in the features for each sound window of the tutor song and the pupil song. The similarity score is the percentage of the tutor song that has been matched to the pupil song. The similarity score does not punish wrong order of syllables. For instance, if the pupil sings the syllables A-C-B instead of A-B-C, the similarity will be very high even if the syllables are sung in the wrong order.

Similarity is really long to compute and is only meaningful when comparing two complete songs. It is also almost unaffected by temporal mismatches. Other methods are used to compare syllables or notes. For simplicity, syllables are compared by the study of means and variance of every features (Pitch, Entropy, ...) during the syllables. Two syllables are considered similar if they have the same mean and variance for every features.

The Python module I wrote to compute song features and similarity scores is called *birdsonganalysis* and is available for download at <https://github.com/PaulEcoffet/birdsonganalysis/>.

2.1.3 Song Model

The computational model works on the motor representations of songs. The goal of this model is to adjust these representations so that they generate an accurate imitation of the tutor song with G.B Mindlin's synthesizer. I call these motor representations *Song Models*. The representation we choose for the Song Model is highly inspired from **amador_elemental_2013** works on gestures.

insert graph
to show the
match

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

Gesture composed of two generators for the motor commands

- * Abstracted in sum of sin & linear func

2.1.4 Two-step learning model

Our model is divided in two different phases.

- * 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 Day learning algorithm

2.2.1 Goal

- * Optimise gestures parameters

2.2.2 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

2.2.3 Prediction

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

2.3 Night learning algorithms

2.3.1 Goal

- * Find better structure to describe song motor command

2.3.2 Several variations of algorithm have been tested

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

2.3.3 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

2.3.4 Predictions

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

2.4 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 unlearning * 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/complex 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