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# Variability in Singing and in Song in the Zebra Finch

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## **VARIABILITY IN SINGING AND IN SONG IN THE ZEBRA FINCH**

A Thesis Presented to the Faculty of  
The Rockefeller University  
in Partial Fulfillment of the Requirements for  
the degree of Doctor of Philosophy

by  
Cameron Wellock  
June 2012



# **VARIABILITY IN SINGING AND IN SONG IN THE ZEBRA FINCH**

**Cameron Wellock, Ph.D.**

**The Rockefeller University 2012**

Variability is a defining feature of the oscine song learning process, reflected in song and in the neural pathways involved in song learning. For the zebra finch, juveniles learning to sing typically exhibit a high degree of vocal variability, and this variability appears to be driven by a key brain nucleus. It has been suggested that this variability is a necessary part of a trial-and-error learning process in which the bird must search for possible improvements to its song. Our work examines the role this variability plays in learning in two ways: through behavioral experiments with juvenile zebra finches, and through a computational model of parts of the oscine brain.

Previous studies have shown that some finches exhibit less variability during the learning process than others by producing repetitive vocalizations. A constantly changing song model was played to juvenile zebra finches to determine whether auditory stimuli can affect this behavior. This stimulus was shown to cause an overall increase in repetitiveness; furthermore, there was a correlation between repetitiveness at an early stage in the learning process and the length of time a bird is repetitive overall, and birds that were repetitive tended to repeat the same thing over an extended period of time.

The role of a key brain nucleus involved in song learning was examined through computational modeling. Previous studies have shown that this nucleus produces variability in song, but can also bias the song of a bird in such a way as to reduce errors while singing. Activity within this nucleus during singing is predominantly uncorrelated



with the timing of the song, however a portion of this activity is correlated in such a manner. The modeling experiments consider the possibility that this persistent signal is part of a trial-and-error search and contrast this with the possibility that the persistent signal is the product of some mechanism to directly improve song. Simulation results show that a mixture of timing-dependent and timing-independent activity in this nucleus produces optimal learning results for the case where the persistent signal is a key component of a trial-and-error search, but not in the case where this signal will directly improve song. Although a mixture of timing-locked and timing-independent activity produces optimal results, the ratio found to be optimal within the model differs from what has been observed *in vivo*.

Finally, novel methods for the analysis of birdsong, motivated by the high variability of juvenile song, are presented. These methods are designed to work with sets of song samples rather than through pairwise comparison. The utility of these methods is demonstrated, as well as results illustrating how such methods can be used as the basis for aggregate measures of song such as repertoire complexity.

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## LIST OF ABBREVIATIONS

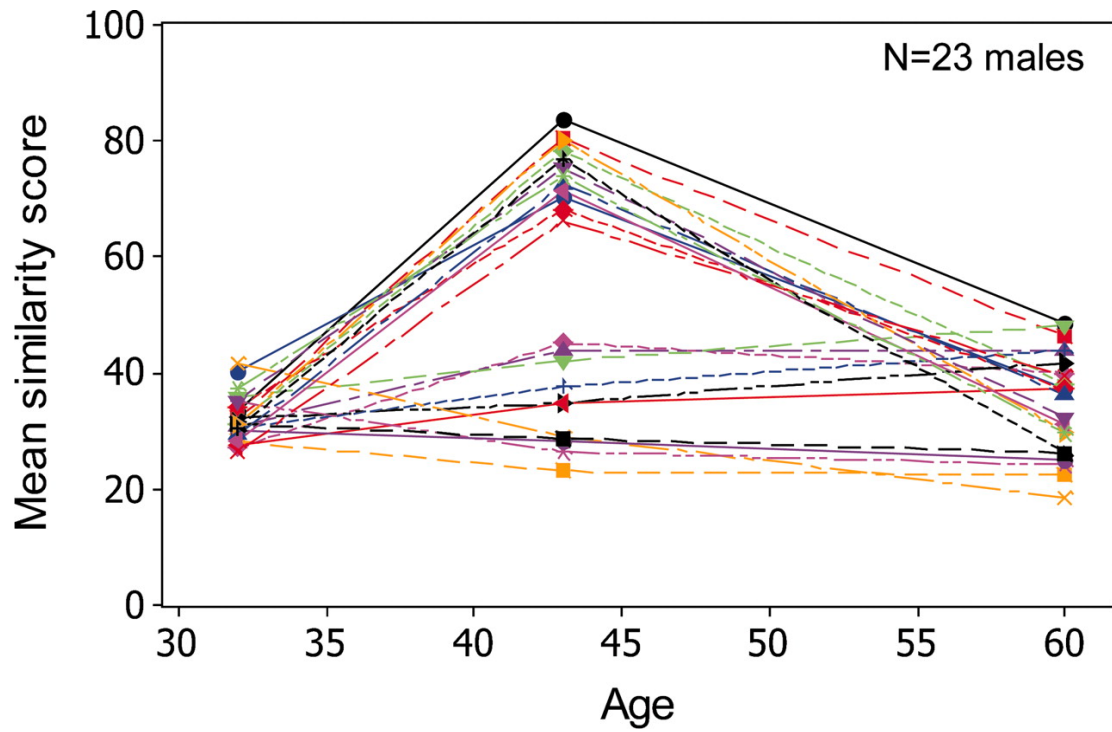
|        |   |
|--------|---|
| AFP    | Anterior forebrain pathway                                |
| AMPA   | Alpha-amino-3-hydroxy-5-methyl-4-isoxazole propionic acid |
| BOS    | Bird's own song   |
| CM     | Critic module (model component)                           |
| DAQ    | Digital acquisition                                       |
| DLM    | Medial nucleus of the dorsolateral thalamus               |
| DPSO   | Days post subsong onset                                   |
| DTFT   | Discrete time Fourier transform                           |
| DTW    | Dynamic time warping                                      |
| GABA   | Gamma-aminobutyric acid                                   |
| HVC    | Proper name (historically "high vocal center")            |
| LMAN   | Lateral magnocellular nucleus of the nidopallium          |
| LTD    | Long term depression                                      |
| LTP    | Long term potentiation                                    |
| MCC    | Matthews correlation coefficient                          |
| MCP    | Motor control pathway                                     |
| MMAN   | Medial magnocellular nucleus of the nidopallium           |
| NCM    | Caudomedial neostriatum                                   |
| Nif    | Nucleus interfascialis                                    |
| NMDA   | N-methyl-D-aspartate                                      |
| nXIIts | Hypoglossal nucleus 12, tracheosyringeal portion          |
| RA     | Robust nucleus of the arcopallium                         |
| REF    | Reference module (model component)                        |
| RL     | Reinforcement learning                                    |
| SAP    | Sound analysis pro (song analysis software)               |
| STDP   | Spike-timing dependent plasticity                         |
| STFT   | Short time Fourier transform                              |
| STRF   | Spectrotemporal receptive field                           |
| TM     | Timing module (model component)                           |
| Uva    | Thalamic uvaeform nucleus                                 |
| WSPR   | Windowed spectral pattern recognition                     |

## CHAPTER 1: INTRODUCTION

My interest in how songbirds learn to sing began with a single paper, “Juvenile zebra finches can use multiple strategies to learn the same song” [1]. In the paper, the authors demonstrated how the juvenile zebra finch, a songbird, could follow two seemingly distinct paths on its way to imitating an adult song model. In the first strategy described, young birds tended to produce an approximation of the entire song, which gradually gained in similarity to the birds’ adult songs. In the second strategy, young birds tended to repeat a short vocalization, again and again. This vocalization was an approximation to one of the model’s song syllables. These serial repetitions were subsequently altered, gradually to match each of the model’s syllables. Most surprising was the way in which birds seemed to split almost evenly between these two very different ways of achieving a good model imitation, with half of birds pursuing the former strategy and half pursuing the latter (Figure 1).

At about the same time, I read another paper describing neural activity in one of the key brain nuclei involved in producing the vocal variability of songbirds [2], the lateral magnocellular nucleus of the nidopallium (LMAN), a nucleus implicated in generating vocal variability—the same kind of variability seen in the first paper [3a]. Perhaps not surprisingly, the activity patterns seen in LMAN during adult singing tended to be highly variable, with little stereotypy in firing patterns from one performance of the bird’s song to the next [4]. This paper, however, presented a surprising new detail: although much of the activity in LMAN was highly variable, some of it was tightly locked to the timing of the song. I was struck by the apparent





**Figure 1** Zebra finches display two strategies during song learning. Mean similarity of three consecutive syllables as sung by each bird, as measured on three different days. This figure clearly shows the divergence between birds that were highly repetitive and birds that were not. From Liu, Gardner, and Nottebohm [1].

relationship between variability and stereotypy found in both the behavior of the birds and in the activity within their brains; this relationship became the basis of my research.

My research has pursued this relationship between variability and stereotypy on three fronts. Experiments with live birds were conducted to try to discover what factors cause a bird to choose one strategy over another, and to discover what effect strategy choice has on the song learning process. Prior to this effort, all studies of singing strategy had been observational in nature; this represented the first effort to examine this phenomenon experimentally. By studying birds that learn with reduced vocal variability, we may be able to shed light on the details of the song learning process; such work may in turn help to shed light on motor learning in general.

Through computational modeling I examined possible roles for the timing-locked signal in LMAN, along the way developing a novel hypothesis about the origin of this signal. My model suggests that while the hypothesis is broadly compatible with observed behavior—indeed, it was the most compatible amongst the alternatives tested—there may be more to the story as the model performed best with more timing-locked activity than has been observed *in vivo*. This model both suggests possible mechanisms of song learning, and highlights aspects of the process that need additional study.

Finally, practical issues in analyzing the recordings of juvenile birds gave rise to a new approach for looking at their song. Existing tools for comparing and sorting birdsong were intended primarily for use with adult birds, the songs of which are highly stereotyped, despite the fact that many studies focus on song learning in juveniles, the

songs of which lack such stereotypy. This lack of stereotypy means that direct comparison of any two samples of juvenile song may be impractical—the song of a juvenile zebra finch may change substantially from moment to moment. To overcome this difficulty, I took a different approach, mining large sets of song samples for recurrent patterns that can be found even in the absence of stereotypy. This work, so far as I know, represents the first attempt to develop methods of song analysis targeted specifically at the songs of juveniles, and the first attempt to develop methods designed to look at birdsong in aggregate. In addition to providing useful tools for the research community, this method opens up new means of quantitatively describing birds' songs and provides a foundation for the analysis of features of birdsong that can only be described in aggregate, such as the complexity of a bird's repertoire.

In the rest of this chapter I provide an overview of relevant historical and current research in these fields. In subsequent chapters I describe experiments with zebra finches studying repetitiveness in juveniles, our computational modeling experiments examining the role of LMAN's timing-locked signal in learning, and our novel methods for examining highly variable birdsong; I conclude with a brief discussion of future directions for this work.

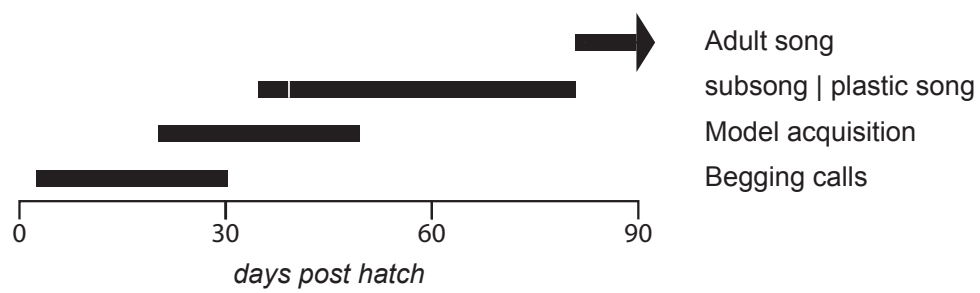
### **Songbirds and the song learning process**

We begin first, straightforwardly enough, with birdsong. A bird's song can be a powerful marker of identity, used by other birds—and humans—to identify the singer's species or even to identify a single individual. In many species this song is innate. Of the twenty-seven orders of birds, only three—the passerines, parrots, and hummingbirds—

have the capacity for learned vocalization; these orders may share similar brain structures for song learning, although these structures do not appear to be derived from a common ancestor [5]. Songbirds (oscines) are members of the passerine order and comprise the great majority of the bird species with learned vocalizations; for these species, every individual must acquire its own song [6, 7].

The details of the song learning process vary greatly from one species to another. Canaries (*Serinus canaria domestica*), for example, are seasonal learners, typically changing their song each year before the beginning of breeding season [8]. Zebra finches (*Taeniopygia guttata*) on the other hand learn a single song that is maintained for their adult lives [9]. Species can vary in terms of how many motifs or syllables they possess in their repertoires [10], the degree to which improvisation is exhibited [11], and the overall complexity of their songs [12]. In some species there is a strong link between repertoire size and sexual preference [10, 13-18], highlighting the role of song in mating [13].

For the zebra finch, song learning takes place when the animal is young. Only the males sing, and this song is learned from nearby adult males such as the bird's father [6]. There are two stages to the learning process: memory acquisition, when the bird internalizes the song it will eventually produce; and sensorimotor learning, in which the bird learns to perform its internalized song [19] (Figure 2). In the zebra finch, these two stages overlap [20]; the acquisition stage lasts approximately from day 20 to day 50 post-hatch [1], and the sensorimotor stage lasts roughly from day 35 to 80 post-hatch [9], although environmental factors can affect these schedules [21].

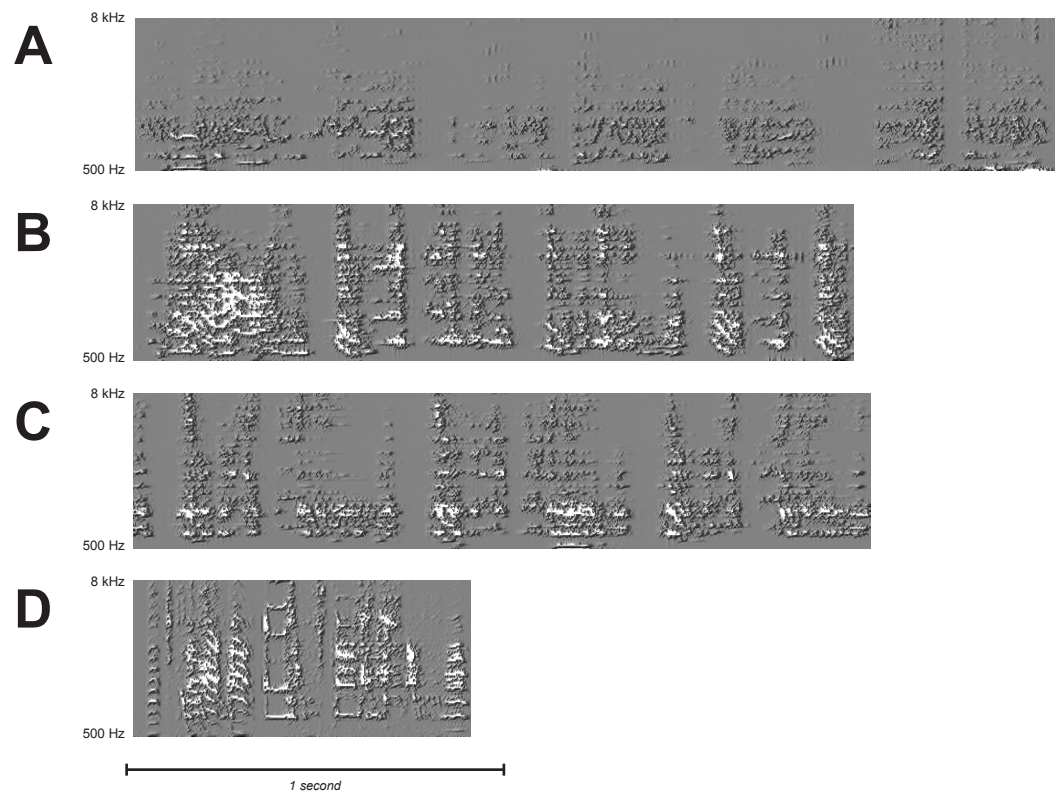


**Figure 2** Song learning schedule of the zebra finch.

Prior to the beginning of sensorimotor learning, zebra finches do not sing but do make use of begging calls; Liu, Wada and Nottebohm have argued that these calls are a precursor to song [22].

During the memory acquisition process, the young zebra finch hears the songs of nearby adult males and somehow internalizes a representation of the song it will learn to produce, its song template. This “template model” has become a central tenet of the larger birdsong learning model [23-28], although the location(s) of the template within the oscine brain has not been conclusively identified (see Bolhuis *et al.* [29] and Bolhuis and Eda-Fujiwara [30] for a hypothesis) and the mechanism by which this template is transferred to the song motor system remains essentially unknown.

In the earliest stage of a juvenile’s song production vocalizations tend to sound very little like the song of an adult. At this stage the sound produced by the juveniles is like a kind of babbling [31]; this earliest stage of vocalization is called “subsung” [6, 32] and it typically lasts for three to five days. From subsung the juvenile progresses to a style of vocalization, “plastic song” [6], a style of vocalization that is low in stereotypy but in which the precursors of adult-like sounds can be identified. During this phase the bird begins to develop a consistent song motif and variability declines [33, 34]. By approximately 80 days post-hatch the juvenile learns to produce its song with a high degree of stereotypy and the song crystallizes [35], becoming largely static, at which point its song-learning process is complete, although an adult’s song can still be changed [36-38]: since deafening is followed by song deterioration, some kind of song learning or learning consolidation appears to continue after song crystallization.



**Figure 3 Song ontogeny in the zebra finch. Spectrograms indicating the ontogenetic development of a bird's song: (A) subsong, (B) early plastic song, (C) late plastic song, (D) adult song.**

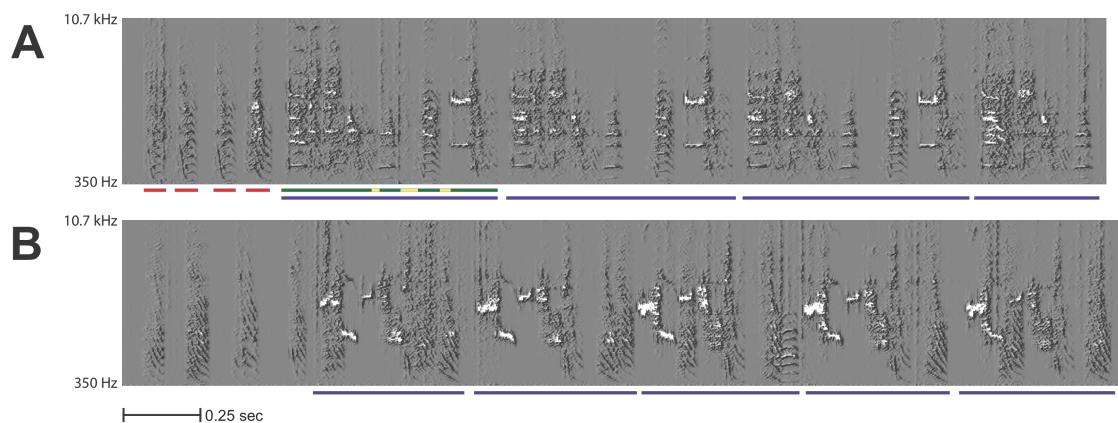
Examples of song at each of these stages are found in Figure 3. Auditory feedback is a crucial part of the sensorimotor learning process; birds must be able to hear themselves sing or they will not develop normal song [39], although the importance of auditory feedback for maintenance of the learned pattern diminishes as time goes by.

The song of the adult zebra finch has multiple levels of organization [40], illustrated in Figure 4. The fundamental component of zebra finch song, as identified by human listeners, is the note, a short (<50 millisecond) utterance of consistent tone or sound quality: the note may rise in pitch slowly, for example, but an abrupt change would indicate a transition to a new note. Notes are combined into larger assemblies called syllables, which are separated by the brief pauses that a bird takes between them. A syllable may consist of one note or several, but typically no more than four (personal observation).

Syllables in turn are sequentially combined into a motif, a sequence of syllables and the highest level of organization in a zebra finch's song. Each zebra finch normally has a single motif. The adult motif is highly stereotyped, with little variability between motif repetitions in terms of pitch or timing and with all elements consistently appearing in the same order. When a bird sings its motif, it typically does so in a bout. Bouts comprise a variable number of repetitions of the bird's motif that are sometimes prefaced by a number of introductory notes.

In addition to song, zebra finches produce other vocalizations, including a variety of short calls, which can serve multiple purposes [7] and are produced by both sexes. Calls are typically short (50-500 ms) continuous sounds; Zann [41] provides a comprehensive listing of these calls and their uses.





**Figure 4 Parts of zebra finch song. (A) Spectrogram of a bout of singing from an adult zebra finch. Noted in the figure are the following song parts: introductory notes, underlined in red; syllables, underlined in green; the silent interval between syllables, underlined in yellow. The blue lines mark the repetitions of the bird's motif. Note that each performance of the motif appears much like the others, except for the truncated final motif. (B) Spectrogram of a bout of singing from a different zebra finch. Although its song is also highly stereotyped, it is visibly different from the song of the bird featured in panel A. For convenience, blue lines once again mark repetitions of the bird's motif.**

## **Singing style in juvenile male zebra finches**

As mentioned earlier, Liu, Gardner, and Nottebohm argued that zebra finches can employ multiple strategies for song learning: in a cohort of young males, some would produce plastic song with considerable variability from syllable to syllable, while others would produce song with very low inter-syllabic variability [1].

In one set of experiments on 37 family-reared males, 18 chose the repetitive strategy, and 19 chose the non-repetitive strategy. A second set of experiments on 23 additional family-reared young males revealed similar divisions, with approximately half the birds following each strategy. In a third set of experiments with twelve males raised with a tutor but in isolation from siblings, four were classified as non-repetitive, one was classified as repetitive, and the remaining seven engaged in both behaviors. Both repetitive and non-repetitive strategies produced final adult songs of similar quality; neither appeared superior. It was stated by Liu *et al.* [1] that in some cases birds could switch from one strategy to another, although data were not given on how many birds switched strategies or when. They also noted males raised without a cohort tended to pursue both strategies simultaneously.

Only one other study has addressed the phenomenon of juvenile repetitiveness. Tchernichovski, Mitra, Lints, and Nottebohm describe a somewhat different outcome: in their study essentially all birds initially adopted a repetitive strategy [20]. In this study, however, birds were not presented with a tutor's song until day 43: a late start that may have had substantial effects on behavior.

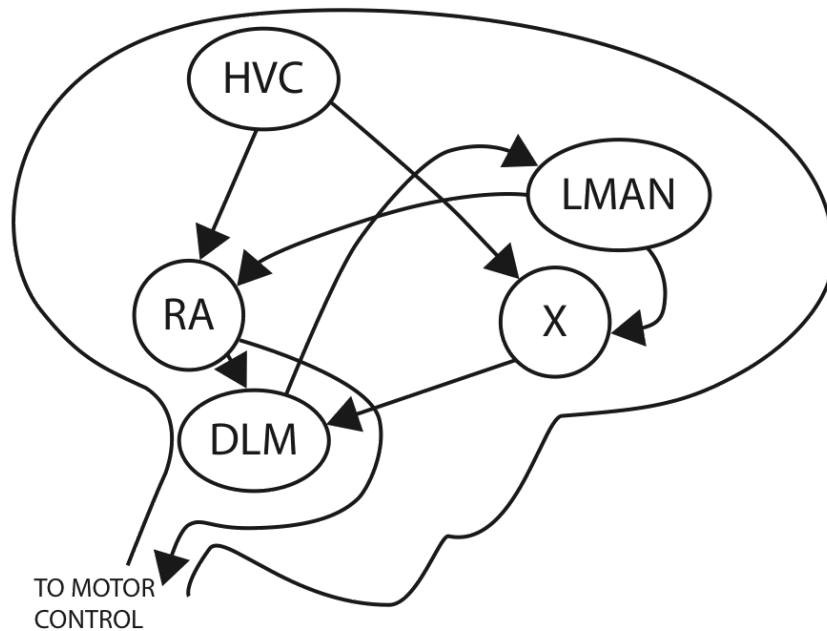
## **Known issues in designing behavioral experiments with the zebra finch**

A question of practical importance to our research is the extent to which zebra finches will learn from song sources besides other zebra finches, namely electronic playback. There is no clear consensus here: Adret [42] and Bolhuis, Van Mil, and Houx [43] reported that zebra finches would learn readily from a recording of an adult, although not necessarily producing a good imitation of the provided song model; on the other hand, Immelmann [9], Eales [44], and Houx and ten Cate [45] reported that zebra finches generally would not learn from recordings. Tchernichovski, Lints, Mitra, and Nottebohm, in a new twist, reported that they would if the animals were allowed to elicit song playback by pecking at a key, but that learning accuracy would decrease as the amount of song played increased [46]. It is difficult to know what to make of these conflicting reports except to say that one must exercise caution when planning to play songs to zebra finches electronically.

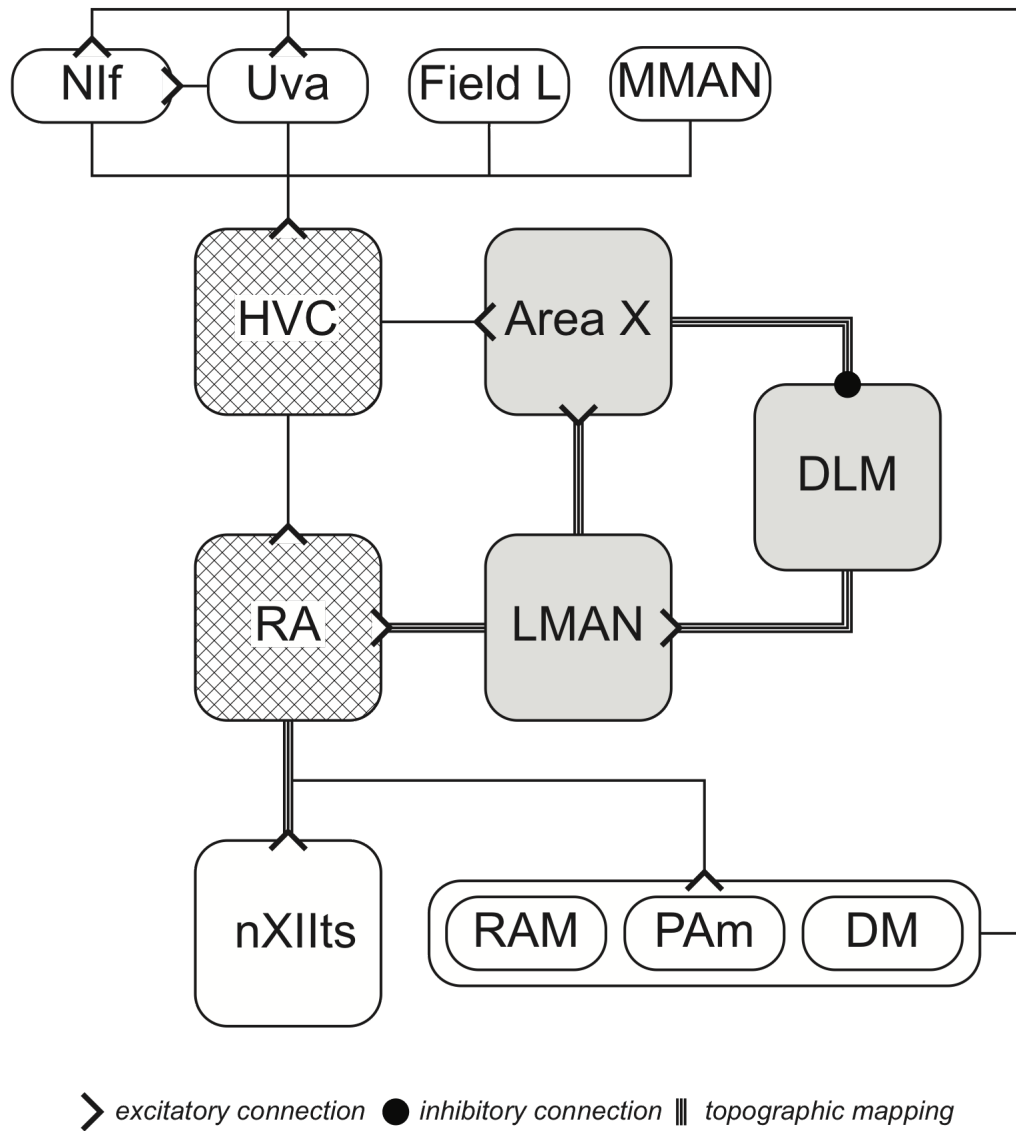
Another relevant question is whether or not zebra finches will consider the songs of more than one tutor; this has possible implications for our behavioral study. Research has shown that zebra finches will learn from more than one tutor if given the chance. Both Böhner [47] and Williams [48] reported that birds raised with access to two tutors can “mix and match” pieces of each tutor’s song to create a unique synthesis. This effect has been observed in other species in the field [49], suggesting that for many species this synthesis may be a routine part of song learning. Certainly there is no evidence that zebra finches would be inclined to reject a new tutor’s song out of hand.

## **Song production, control, and learning in the oscine brain**

Oscines possess an organ for producing sound, the syrinx. Unlike mammals, which have a single larynx, the syrinx is divided into anatomically symmetric left and right halves, with each connecting the bronchi on its side to the trachea. Each syringeal half has its own complement of muscles [50] that manipulate membranes known as the labia; as air is expelled through the syrinx, these labia vibrate, producing sound [51, 52]. Directing the syringeal muscles is an interconnected set of brain regions that control song performance and song learning [53, 54]. These are divided into two primary pathways: the motor control pathway, which is necessary for the production of song, and the anterior forebrain pathway (AFP), which is necessary for song learning but at least in adults is not necessary for song production [3] (Figure 5, Figure 6). The AFP is a basal ganglia-thalamocortical loop, analogous to pathways in mammals that are implicated in sensorimotor learning [55]; the nuclei found in this pathway are the lateral magnocellular nucleus of the nidopallium (LMAN), Area X (proper name), and the medial nucleus of the dorsolateral thalamus (DLM). The motor control pathway is located in the posterior of the pallium, with connections descending to motor control nuclei in the midbrain; the key nuclei, for our purposes, are the robust nucleus of the arcopallium (RA) and the high vocal center of the nidopallium (HVC). HVC is perhaps the most studied nucleus in the song system: it was in HVC that adult neurogenesis was first demonstrated, a subject that has brought HVC considerable attention [57-70]. Within HVC there are three major classes of neuron: RA-projecting neurons, Area X-projecting neurons, and interneurons [71-73]; the interneurons themselves are a heterogeneous population. HVC→RA synapses are glutamatergic and display both



**Figure 5 Key brain nuclei in the oscine song system. Simplified diagram of some of the key brain nuclei involved in the singing and song learning processes. RA and HVC are part of the motor control pathway (MCP), and are essential for singing in both juveniles and adults; LMAN is part of the anterior forebrain pathway (AFP), and is essential for song learning but is not necessary for singing in adults [3]. RA sits at a junction of these two pathways, both of which have a common origin in HVC. RA controls singing through projections to motor control nuclei in the brainstem [56]. Area X and DLM are known to connect to both the MCP and AFP.**



**Figure 6 Schematic of the song system. Includes all nuclei and connections discussed in this section. Area X, DLM, and LMAN, marked in grey, comprise the AFP; HVC and RA, marked in crosshatch, comprise the motor pathway.**

NMDA-type receptors and  $\alpha$ -amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid (AMPA) receptors [734]. HVC's connections to both RA and Area X have no known organization, with each HVC neuron connecting widely throughout these regions [75]. HVC receives input from other brain regions including the uvulaeform nucleus (Uva), the medial magnocellular nucleus (MMAN), and Nif [75, 76].

The striking feature of HVC's activity during singing is its highly stereotyped output to RA. Hahnloser, Kozhenikov, and Fee have shown that a "sparse coding" exists within RA-projecting HVC neurons such that during singing individual neurons fire with extreme temporal accuracy in a rigidly defined sequence, typically each at one specific time point in the song [77]. In a clever experiment, Long and Fee were able to change the tempo of the bird's song by physically cooling HVC [78]; this suggests that HVC's sparse firing pattern provides timing information about the song to RA.

RA sits at a junction of the motor control pathway and the AFP. RA contains at least two types of neurons: projection neurons, whose efferent targets are located in the tracheosyringeal portion of the hypoglossal nucleus twelve (nXIIts) [79], and GABAergic interneurons [80]. In addition to receiving input from HVC, RA projection neurons are the synaptic targets of neurons in LMAN [80-82]. These connections from LMAN to RA are myotopically organized [83, 84]. The LMAN→RA synapses form earlier than the HVC→RA synapses [74, 85-87] and LMAN→RA, but not HVC→RA, synapses primarily use N-methyl-D-aspartic acid (NMDA) as their neurotransmitter [80, 81]. RA in turn projects, as already mentioned, to the tracheosyringeal portion of hypoglossal nucleus XII in the brainstem (nXIIts); these projections show a strong topographic organization [83, 84]. RA also projects to brainstem nuclei involved in the control of respiration: DM,

RAm, and PAm, which in turn project to the nucleus interfascialis (Nif) and the thalamic uvaeform nucleus (Uva) [88].

RA neurons have high spontaneous firing rates. During singing, neurons in RA have a highly stereotyped firing pattern, albeit different from that seen in HVC. An RA neuron fires in short bursts, at different time points during song, and is generally inactive during other parts of the song [77, 89, 90]. Yu and Margoliash observed that the firing times for specific RA neurons corresponded with the type of note being produced at that time, rather than with the syllable or the time point within the song [89]; because of this, RA is generally associated with the production of notes rather than the sequencing of larger parts of the bird's song [91].

The AFP influences the motor pathway through LMAN, which is essential for song learning. Lesioning studies have demonstrated LMAN's necessity during the sensorimotor learning phase [3, 92] and in adult song plasticity [93] but not in adult song production [94]. Additionally, the window of synaptic plasticity for LMAN neurons coincides with the window of sensory learning: as a bird approaches the end of the memory acquisition phase of song learning, synaptic plasticity of neurons within LMAN declines [95]. LMAN receives input from the medial nucleus of the dorsolateral thalamus (DLM) and also contains a large number of intrinsic, NMDA-type glutamatergic connections [73]. LMAN neurons project to RA [80, 81] and also to Area X [96]. LMAN, DLM, and Area X form a closed loop with topographically organized connections throughout [97].

Although part of the AFP, LMAN both influences and is influenced by motor activity, at least for adults: LMAN can effect changes in song through its projections to



RA [98], and LMAN may be driven by motor control signals [2]. During singing, early electrophysiological work suggested that LMAN's activity pattern was only broadly related to song timing [4]; however later research suggested that LMAN displays a mixture of firing events that are time locked with the song and firing events that are not time locked with song [2], a point we will return to.

There are a number of other nuclei that are either part the song system or peripheral to the song system, however the understanding of the roles these nuclei play is less well understood than the roles of HVC, RA, or LMAN. Area X, which receives inputs from both HVC and LMAN, is clearly important in song learning: lesioning Area X prevents song imitation and crystallization [3]. DLM, a thalamic nucleus in the AFP, is essential for babbling during subsong [99]. Uva, which innervates HVC and Nif, is involved in regulating the temporal structure of song [100, 101], and appears to have a role in coordination between brain hemispheres [102, 103]. Nif innervates HVC and appears to have a role in transmitting auditory signal into HVC, although lesioning studies indicate that it is not necessary for song production [104]. Likewise Field L, an auditory region of the caudal forebrain, also connects to HVC and displays a general sensitivity to conspecific song [105-107] but appears primarily involved in conveying auditory information rather than in song production [108]. Finally MMAN, the medial magnocellular nucleus of the nidopallium, also innervates HVC but is posited to have a role in regulating singing behavior rather than song production [109].

Most of the nuclei involved in the song system that have been examined display a response to the auditory stimulus of the bird's own song (BOS), including HVC [72, 110, 111]; HVC's neurons fire in a time-locked manner along with the song [112, 113].

LMAN neurons are also responsive to BOS, albeit not with the same time-locked behavior seen in HVC [114, 115], and with a varying degree of selectivity depending on the age of the animal [116]. RA [117], nXIIIts [118], and Area X neurons are also responsive to BOS [114]. There has been considerable debate about the significance of these responses: see Konishi [119] and Theunissen *et al.* [120] for reviews. The curious part of this feedback response is that many of these nuclei are not responsive to playback when the bird is awake or singing; HVC does not respond to presentation of BOS when the animal is awake [121], perhaps due to modulatory input from Nlf [122] and Uva [123], and LMAN does not respond to presentation of BOS during singing [2, 4].

On the other hand, there is considerable evidence that the song system is actively reshaping its motor programs during sleep. Rauske, Chi, Dave, and Margoliash observed changes in RA activity during singing after sleep [124], and Crandall, Adam, Kinnischtzke, and Nick found that nighttime activity in RA in juveniles corresponded with subsequent changes in song [125]. Additional inquiries have shed more light on the nature of this process: Dave and Margoliash observed that bursting activity in RA at night could mirror daytime activity during singing [126]; Shank and Margoliash observed that nighttime activity in RA and subsequent changes in song could be caused by playback of tutor song at night [127]. Dave and Margoliash have argued that this process might represent a kind of song playback during sleep that may be used to support a form of “off-line” learning, solving the problem of feedback delay found in “on-line” learning [128].

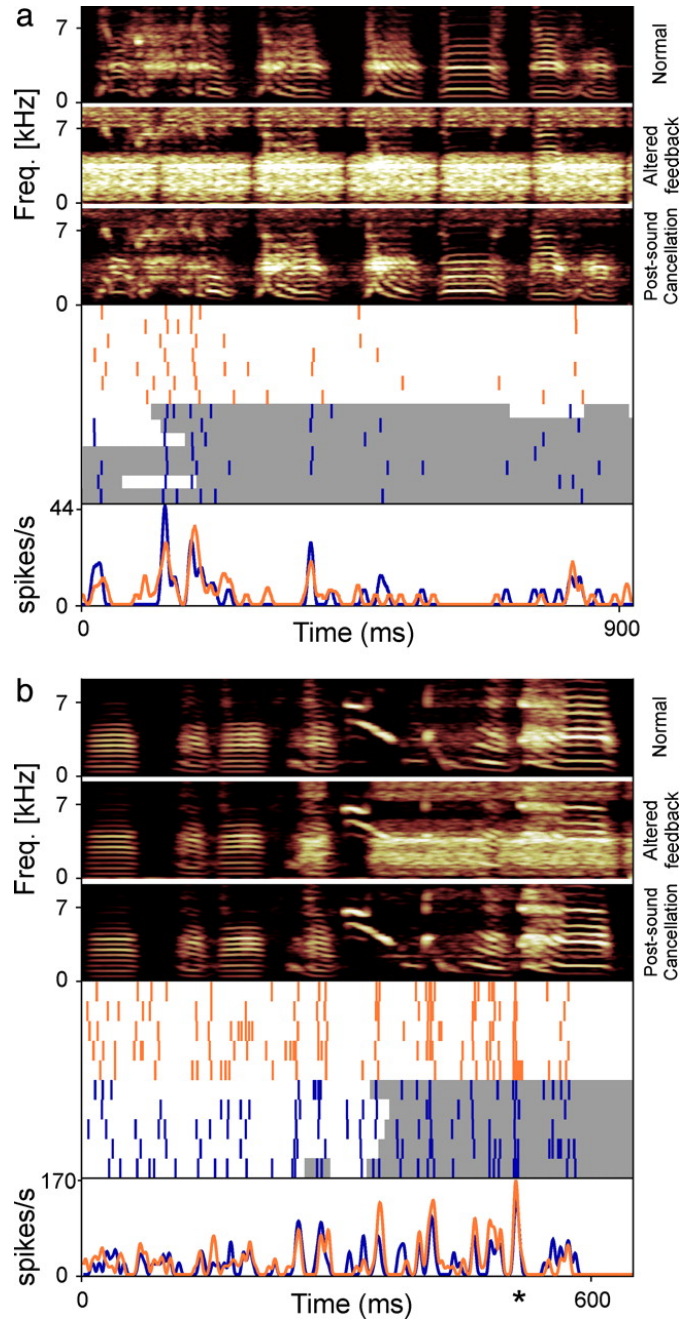
Finally, insofar as such information is relevant for providing constraints to our computational model, we note that the electrophysiology, cytology, and microcircuitry

of the neurons and nuclei in the song system have not been sufficiently explored. Not surprisingly, HVC is the best studied [71, 72, 110, 111, 113, 128, 129], with some detail on RA [71, 77, 79, 130] and LMAN [73, 80, 95].

### **The disputed role of LMAN in song learning**

Leonardo, making single-unit recordings from LMAN neurons of adult zebra finches, observed that a considerable fraction of activity in LMAN is time-locked to the progression of the bird's song (Figure 7). Leonardo stated that, "remarkably, 30% of the spike events generated by LMAN neurons had a precision of <2 ms, indicating that LMAN neurons produce spikes locked with millisecond precision to acoustic structure in the bird's song even when that acoustic structure was entirely masked by noise." [2] Of course, the converse of the proposition that 30% of spikes in LMAN are time locked to the bird's song is that 70% of spikes—the great majority—are not. In recent years there has been considerable debate over what function LMAN serves in song learning, and this debate hinges largely on the questions of how or if this time-locked activity would be present in juveniles and how, or even whether, such time-locked activity in LMAN might affect juvenile song production and learning. There are three main possibilities that have been examined: that the time-locked activity is not important, and that LMAN's function is to create variability in the bird's song; that the time-locked activity represents an immediate error signal; and that the time-locked activity represents a bias signal that is directing the output of the motor pathway.

Arguments in favor of the first possibility tend to focus primarily on the role that LMAN may play in providing variability in the bird's song. The non-time-locked portion



**Figure 7** LMAN neurons exhibit a mix of timing-locked and timing-independent activity. From Leonardo [2]. Neurons were recorded during singing; panels (A) and (B) represent recordings from single neurons in two different birds. Raster plots showing LMAN neural activity over multiple motif performances are in the middle segment of each panel. Each neuron displays time points in the song at which it fires with a high degree of regularity.

of LMAN's output appears to drive the motor pathway to produce transient variations during singing; these variations may enable the bird to perform a trial-and-error search on possible improvements to its song [131]. A line of evidence in favor of this hypothesis comes from the previously mentioned LMAN lesioning studies [3, 92], which can be interpreted as suggesting that variability from LMAN is a prerequisite for song learning.

The second possibility, that LMAN sends an immediate error signal to the motor pathway, has not held up to experimental testing. An immediate error signal should change in response to feedback from the bird's singing; Leonardo was able to show that the time-locked component of LMAN's activity was insensitive to manipulation of auditory feedback [2]. The third possibility, that LMAN produces a biasing signal that changes the bird's song, is supported primarily by the work of Andalman and Fee [132], who demonstrated that the biasing signal in LMAN could be error-reducing, as suggested by others [98, 133].

### **Reinforcement learning as a model for song learning**

Reinforcement learning (RL) is a formal model of learning in which the learner must learn to map circumstances to actions in order to maximize favorable outcomes [134]. RL derived in part from ideas about operant conditioning [135] and is often used to describe a song learning process in which a vocal output that matches a previously heard and memorized model is, supposedly, reinforcing [38, 132, 133, 136-138]. This is a form of unsupervised learning [139], in which the learner does not receive any advance information about what actions lead to the best outcomes; instead the learner

must discover this mapping between actions and outcomes itself. It has been suggested that basal ganglia-cortical loops, like the AFP, support a kind of reinforcement learning [140, 141].

Reinforcement learning takes a number of forms, with parallels in many classic optimization algorithms, such as random search [142] and simulated annealing [143]. Typically, but not exclusively, reinforcement learning is considered to be a form of trial-and-error learning [144]. For song learning, the form of RL most often discussed is that of the actor-critic-experimenter architecture [145], as it maps fairly easily onto the components of the song learning system. The actor has a sequence of motor commands that it knows, and the experimenter proposes a variation to that sequence. The actor then performs the variation, and the critic decides whether or not this was an improvement over the existing motor command sequence. If it was an improvement, the critic sends a reinforcement signal to the actor, the actor makes its sequence of motor commands more like the good variation, and the song the actor produces should be a little bit better than it was before. After a large number of iterations of this process, the song should be much more like the bird's memory of the model it is trying to imitate, often referred to as the bird's "template."

How well does the reinforcement learning paradigm map onto the avian brain? Two of the three components in the architecture have identifiable analogs in the oscine brain. The actor is the HVC+RA component of the motor pathway, which is responsible for producing the motor commands that cause the bird to sing its song. The work of Aronov, Andalman, and Fee, in which HVC lesioning eliminated song but not song-like vocalization [146], strongly implicate the MCP as a primary locus of song motor

memory. The experimenter also has a fairly clear analog in LMAN: lesions to LMAN result in a loss of vocal variability [3, 92], as does temporary inactivation of LMAN [131].

The largest remaining piece of the puzzle then is the critic. Doya and Sejnowski suggested that Area X might be the locus of the critic [147], based on observations that lesioning Area X prevents song crystallization [3], although this suggestion is only a hypothesis. Wherever or whatever the critic is, however, it does not seem to have much direct influence on the HVC+RA motor pathway; despite years of research, no suitable immediate feedback signal acting on HVC and/or RA has been identified.

### **Computational models of the song learning and song motor control systems**

The striking organizational clarity of the core of the song system has made it a popular subject of study for theoretical and computational modelers. Over the years a number of relevant models have been produced; we examine them here and compare them against the structure of our own model. In general, most models can be broken down into two distinct categories: those that attempt to model the song learning process, and those that attempt to model the ultra-sparse firing patterns observed in HVC.

The models attempting to model HVC's firing patterns tend to be primarily concerned with either the process of creating sparse firing chains, such as the model of Li and Greenside [148], or of considering the neuronal properties necessary to make such firing chains possible, such as the models of Ju and Jin [149]; Jin, Ramazanoglu, and Seung [150]; and Gibb, Gentner, and Abarbanel [151]. One particular model of interest

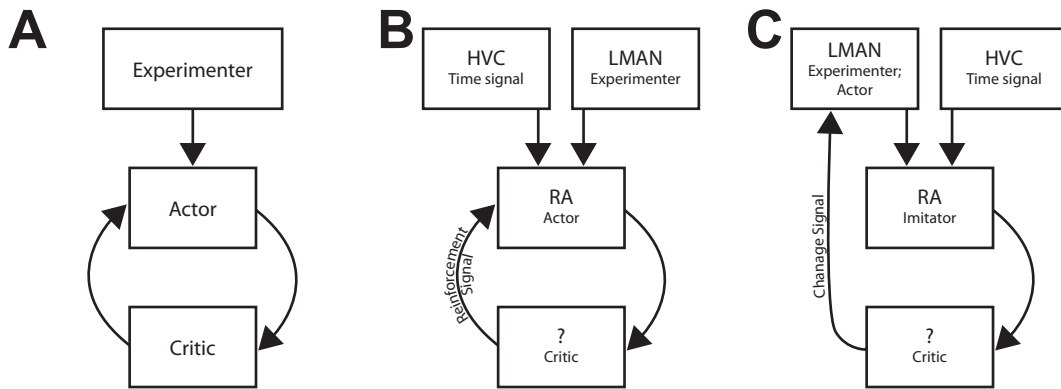
in this category is that of Fiete, Hahnloser, Fee, and Seung [152]. In their model, they considered what would happen if HVC did not have a sparse firing pattern. Their conclusion was that for every doubling of the number of firing times an HVC neuron had during song, the learning time necessary to learn the correct HVC→RA synaptic weights would double as well, and predicted that this would necessitate juveniles having a sparse firing pattern in HVC as well as adults.

The models that are primarily concerned with song learning are surprisingly varied, with each making a different set of underlying assumptions about the connectivity and function of nuclei in the song system (Figure 8).

The model of Doya and Sejnowski was arguably the first major attempt to formalize ideas about song learning into a computational model, and an early proponent of the idea of song learning as an instance of reinforcement learning [147]. In this model, output from RA is fed through a sound synthesizer and into a critic module, presumed here to be Area X, and this reinforcement signal is then sent through the AFP to LMAN. LMAN serves to introduce both noise and a bias signal that persistently modifies synaptic weights. In doing so, this model presaged the idea that LMAN could provide both variability and a persistent teaching signal to the motor pathway, although through mechanisms that may not be biologically feasible [155].

Drew and Abbott produced a model of birdsong learning that focused primarily on HVC; in particular they were interested in how HVC could develop responses selective to the bird's own song [156]. Within the model, the primary forebrain auditory receptive field (Field L) was modeled as a set of spectrotemporal receptive field filter





**Figure 8 Comparison of connectivity in published models. Schematics of various models: (A) Basic schematic of the reinforcement learning with random search paradigm. (B) Schematic of the models proposed by Troyer and Doupe [138, 153] and by Fiete et al. [154]. In these models, LMAN serves as a source of random variation, and RA receives the immediate reinforcement signal. (C) Schematic of the model proposed by Doya and Sejnowski [147] as well as the model presented in this thesis. In this model, LMAN provides a “working copy” of a motor program, and RA learns whatever patterns LMAN is presenting.**

functions and HVC was modeled as a homogeneous set of integrate-and-fire neurons. The model highlights the role of NMDA-type receptors in learning, and demonstrates how after the neurons of HVC have learned sensitivity for a sequence of input from Field L, the same neurons can then reproduce this pattern when stimulated.

Gibb, Gentner, and Abarbanel [151, 157] and Abarbanel *et al.* [158] produced several models of the song learning system, with each model focusing on a different issue. These models explored the possible role of inhibitory interneurons in creating HVC's sparse bursting behavior [151], ideas about how HVC could drive syllable sequencing [157], and a detailed study of how time delay between premotor activity in the motor pathway and activity in the AFP could be used to drive learning, depending on the details of the synaptic plasticity model used.

The model of Troyer and Doupe encompasses a very large number of ideas [138, 153]. One of the issues it considered was the problem of time delay in transmitting feedback about singing performance to the motor pathway; the length of time necessary for the bird to sing, hear himself singing, evaluate his performance, and transmit this via the AFP to RA seemed far larger than the window of opportunity for Hebbian-like synaptic plasticity to occur in RA neurons after firing. As a solution to this problem the model proposed that HVC provided an efference copy of the song being sung to the AFP, the presumed pathway for the transmission of feedback signal, and explored how HVC could develop such an efference copy through inputs from a BOS-responsive brain nucleus such as Field L.

The model also considered at some length the problem of how birds learn to produce a fixed sequence of syllables, given that the presumed generator of syllable

sequence (HVC) has no direct inputs from the presumed generator of feedback (AFP). Again, the model drew upon the efference copy from HVC to create an associative chain of operations that would produce a sequence of syllables in HVC, and showed how the AFP, acting through RA, could change this sequence of syllables.

The more recent model of Fiete, Fee, and Seung assumes that LMAN does not carry a biasing signal to the motor pathway but serves exclusively as a source of variability [154, 159]. This model posits a neurotransmitter-based reward signal that is released in RA, providing a different kind of feedback loop. Although this seems entirely plausible, and RA neurons have receptors for modulatory neurotransmitters such as dopamine [160], at the time of writing this thesis no direct evidence of such a neurotransmitter-based mechanism had been published.

Several of these models either explicitly or implicitly support an actor-critic-experimenter learning mechanism. These models differ primarily in terms of what they propose the reinforcement signal is and when and where it is delivered. The models of Fiete, Seung, and Fee [154, 159] and Troyer and Doupe [138, 153] hew closely to the actor-critic-experimenter paradigm, although they do not agree as to what these parts might be. Fiete *et al.* identify LMAN as the experimenter, and posit an unspecified reward signal targeted at RA. Troyer and Doupe identify LMAN as the source of the reward signal, and posit an unspecified or endemic experimenter. Although the model of Doya and Sejnowski is explicitly described in terms of RL, it does not precisely follow the actor-critic-experimenter paradigm [147]. In their model LMAN is the experimenter, but also a teacher, providing a signal to the motor pathway that the motor pathway can then learn. This teaching signal is not given to the model *a priori*;

instead the teaching signal is constantly being updated by feedback from the model's critic unit.

## CHAPTER 2: CHRONIC REPETITIVENESS IN THE JUVENILE ZEBRA FINCH

The phenomenon of vocal repetitiveness during sensorimotor learning in the zebra finch was first reported on by Tchernichovski *et al.* [20], who noted that the juvenile zebra finches in their experiment “tend to produce back-to-back repetitions of similar sounds,” and was followed up on by Liu, Gardner and Nottebohm [1] who elaborated on the complex dynamics of the phenomenon. Intrigued by the reported ability of birds to develop songs in two distinct ways, I sought to learn more about what external factors drive birds to vocal repetitiveness, and in so doing, perhaps to shed some light on what purpose this behavior could have.

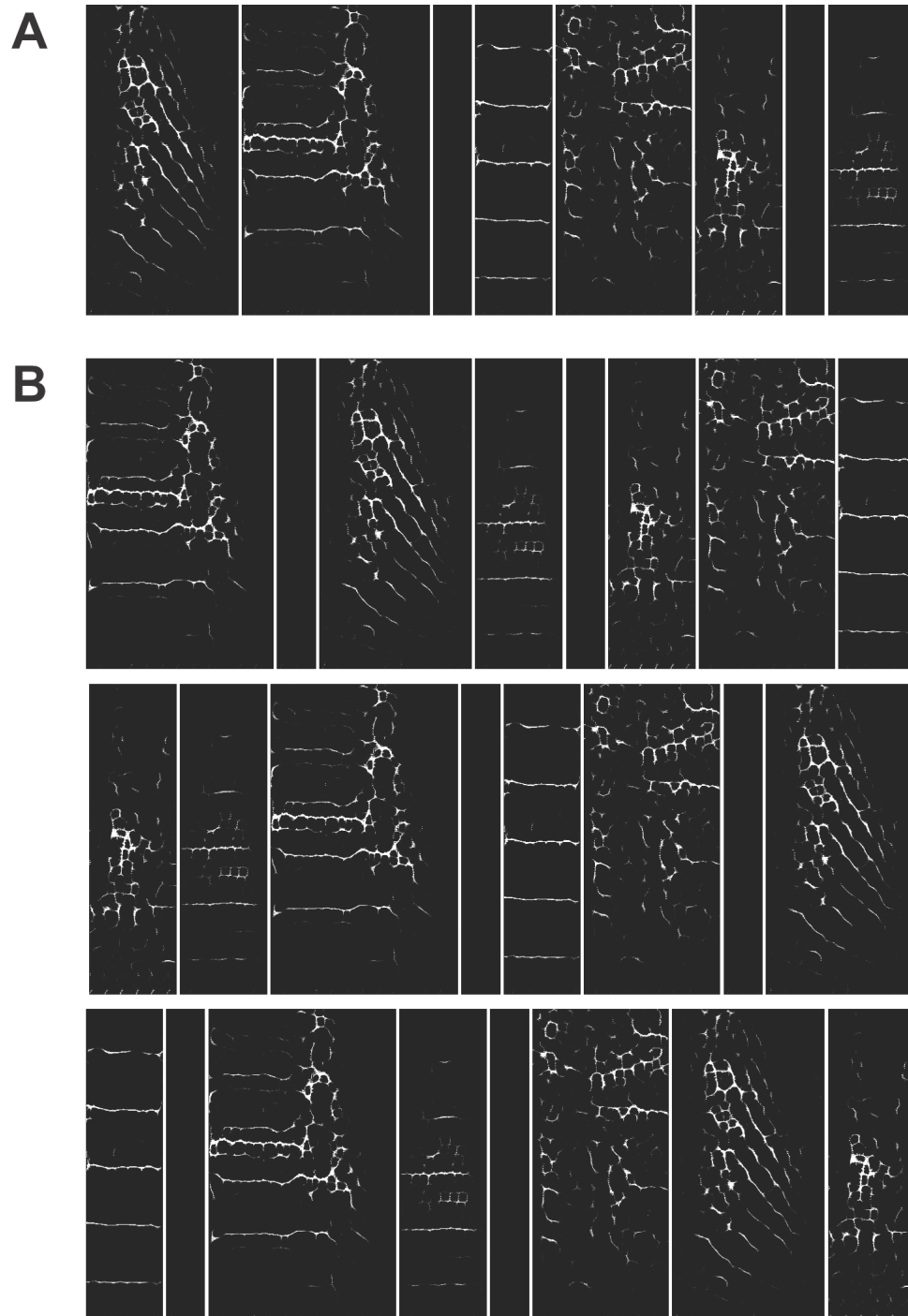
Tchernichovski *et al.* [20], in their original description of the phenomenon, wrote that serial repetitiveness was an apparently normal part of song learning, at least as demonstrated in their experiment, although they conceded that by denying the subjects exposure to a song model until late in the sensorimotor learning phase they may have created an abnormal situation. Liu *et al.* [1] hypothesized that serial repetitiveness was a strategy for learning, along with a non-repetitive learning strategy, and suggested that the ability to follow different learning strategies may help juveniles in their learning process.

The idea that this phenomenon is beneficial and perhaps purposeful is appealing, but it opens the question of what that purpose might be. Our original thoughts on the matter were social in nature: are cohabiting birds attempting to avoid occupying the same “song space,” for example? Could repetitiveness be a way for young birds to avoid interfering with each other as they learn their songs?

A social perspective may not be sufficient to understand this phenomenon, however. We turn instead to the formalism often used to describe the song learning process, reinforcement learning [134, 147, 154], which posits that song learning is a trial-and-error process in which variability is used to discover improvements to the bird's song. If song variability is an essential part of the song learning process, then a reduction in variability should not be beneficial. Instead of serving as a strategy for learning or serving some useful purpose, repetitiveness may instead be an inconsequential byproduct of other mechanisms or possibly even deleterious to learning.

If we are willing to consider that repetitiveness may not be beneficial, we can look at a new set of reasons why this behavior might exist. The results of Tchernichovski *et al.* [20] may provide a clue: birds without tutoring until very late develop into repetitive birds. Clearly a bird that has never had a tutor cannot have developed a strong song template, and as such, cannot judge the extent to which its song is improving. If the song learning process is effectively an ongoing search for improvements to the song, then chronic repetition may be an indication that the bird has stopped searching because it does not know what it is searching for. This idea led to our ultimate hypothesis: that repetitiveness can be caused by confusion about the song model the bird is attempting to emulate.

To test this hypothesis, an experimental protocol was developed that could provide a bird with a song model that it cannot learn. This was accomplished by taking the song of a normal adult zebra finch and dividing it into a set of notes and then recombining these notes in every possible way (Figure 9). Birds were played



**Figure 9** Permuting a bird's song. (A) Spectrogram of the normal motif, divided into segments. (B) Sample permutations of the motif. There were 20 160 permutations in total.

these recombined songs randomly so that even though the parts of the song were always the same, the bird would not be able to learn any larger pattern; and to the extent that the bird had already learned a song template, these permutations might disrupt that model. The young birds subjected to this scrambled song were then recorded from as they learned to sing.

Our results appear to support our hypothesis: birds subjected to scrambled song are more repetitive, on average, than birds that hear normal (unscrambled) song or no song; overall repetitiveness correlates with the length of time a bird is repetitive; and the syllable being repeated does not generally change over time. New details about the distribution of repetitiveness and the extent to which birds can be classified as repetitive or not are also examined. The rest of this chapter describes these results in detail and presents further ideas about the causes of repetitiveness.

## **METHODS**

### **Bird rearing and care**

Nineteen birds in total were used in this experiment. From hatching until 25 days post-hatch, juvenile zebra finches were housed with their mothers, fathers, and clutch-mates in a family setting. From 25 days to 35 days, the juveniles were housed in small cohorts of 2-4 individuals along with one of two adult tutors. A single male was used to raise these tutors, and they were judged by ear to have similar songs. Juveniles that were tutored by a single individual were distributed evenly between treatment groups. On day 35, the juveniles were housed singly in auditory isolation chambers; the duration of auditory isolation was variable, with a mean of 28 days. After the end of



isolation, juveniles were placed in a colony setting. At all times the juveniles were given food and water *ad libitum*. The juveniles were cared for in accordance with the standards set by the American Association of Laboratory Animal Care and Rockefeller University's Animal Care and Use Committee.

### **Song playback**

During isolation, birds were divided into three groups. Each group heard different kinds of sound played back at random intervals. The first group (“silence”) heard only ambient background noises, such as the sounds of other birds shuffling their feathers, or recordings of dead air. The second group (“normal”) heard a recording of the song of an adult tutor played back, in addition to ambient noises. The third group (“scrambled”) heard the same adult tutor’s song, however the song was scrambled so that the notes appeared in a random order rather than the original order. These scrambled songs were derived by manually segmenting a sample of the adult's song into eight components, including two "gap" components that were effectively silent, and computing every possible permutation of these components. This resulted in a set of 20 160 permutations, with the consideration that the two “gap” components were essentially interchangeable; by our estimate, at the rate of playback used, a juvenile would hear any given permutation an average of 1.6 times over a seven-day period.

Sounds were played to birds via a software player, designed to emulate an adult bird’s vocalizations through a Markov chain-based probabilistic mechanism. The sound player had three states: singing, calling, or silent. In each state the player would wait a randomly chosen period of time and then play a randomly selected sound. After playing

a sound, the player could remain in the same state or randomly transition to another state. For calls and songs, the time to next sound was calculated from a Poisson distribution with a mean sound interval of 2 seconds; for silence, the time to next sound had a mean sound interval of 20 seconds. These time constants were arrived at by observing the inter-song intervals of a live adult zebra finch. Transition parameters were fit by numerical simulation so that the model played approximately the same amount, as measured in seconds, of songs and calls in a day as did the adult male used to generate the statistical model (38 minutes total over a twelve-hour period, or about 5% of the time). Songs were from either the permuted set or the non-permuted original (20 160 samples and 1 sample, respectively), calls were taken from a fixed set of call samples (503 samples total), and “silent sounds” were taken from a fixed set of non-vocal sounds, including feather shuffles, metal "clanking", and background hiss (300 samples total).

### **Audio recording of birds**

Continuous recordings were made of the juvenile male zebra finches from 35 days post-hatch to 50+ days post-hatch with Behringer ECM-8000 measurement microphones (Behringer International GmbH, Willich, Germany) and Rolls MP13 preamplifiers (Rolls Corporation, Murray, UT). A MCC PCI-DAS6013 digital acquisition card (Measurement Computing Corporation, Norton, MA) was used to digitize the audio inputs. Recordings were made at 44.1kHz, 16 bits/sample, and stored as lossless FLAC [161] files.

All birds were recorded at 90 days post-hatch or later by placing them in an isolation chamber with one or two females until they sang, which required anywhere from five seconds to two days. Recording conditions and equipment were as before.

### **Extraction of song samples**

Bird sounds were extracted as follows: (1) denoising and bandpass filtering using a “noisered” filter (proper name) and “sinc” filter in the 100 Hz-8 kHz range, respectively, of the “sox” sound processing tool [162]; (2) audio event extraction using a custom software tool; (3) manual selection of extracted events to eliminate erroneous samples.

The custom extraction tool searched for time points in recordings with amplitude maxima (peaks) above a certain threshold (“events”) and then extracted all audio up to the nearest amplitude minima before and after the event to create an audio sample. Events that overlapped or occurred within 0.2 seconds of each other were combined into a single sample and samples less than 0.3 seconds long were excluded from consideration.

Samples were extracted from every day for each bird and filtered using the WSPR tool [163] to identify samples typical of juvenile vocalizations. A minimum of fifteen samples comprising at least five seconds total time for each day were manually selected, eliminating samples of spurious audio events and samples with high levels of interference (human activity, banging on cage, etc.). Days on which less total sound than this was extracted were excluded from analysis. Approximately 15 000 samples were used for the data set on which our observations are based.

### **Measuring repetitiveness for juvenile vocalizations**

A novel method of measuring repetitiveness (referred to hereafter as “R”) was developed for this work; it shares some similarities with the measure of rhythmicity developed by Saar and Mitra [164]. The measure finds the point of best overlap between a sample and itself, time-shifted by a small amount. A typical “repeating” bird was observed to have a rhythm in the 150-millisecond to 200-millisecond range, so the time-shift window used was 100-300 milliseconds. The overlap is calculated as one minus the cosine distance between the unraveled (vectorized) spectrograms of the audio sample and its time-shifted partner, bandpass filtered in the 500-8000 Hz range. Spectrograms were calculated with a rectangular window 10 milliseconds wide and an overlap of 5 milliseconds between each neighboring spectra. The measure produces a score between zero and one, with zero indicating absolutely no overlap between the spectrogram and itself for any time shift, and one indicating a perfect overlap between the spectrogram and itself for some time shift in the 100-300 millisecond time window. The time shifting was performed in 10 millisecond increments.

### **Measuring similarity of juvenile vocalizations to a reference syllable**

To find the extent to which a single syllable was repeated across multiple days, a single reference syllable was taken for each bird. To find this reference syllable, a set of samples from each bird in the 2-8 days after the onset of subsong was taken and a dominant repeating syllable was identified and extracted by manually examining samples with high repetitiveness scores. In the case that no obvious dominant syllable

could be identified, a syllable that seemed typical of the examined samples was used instead.

The reference syllable was compared to a test sample by a sliding-window method similar to that used for repetitiveness. The similarity (referred to hereafter as “S”) is calculated as one minus the cosine distance between the unraveled (vectorized) spectrograms of the two audio samples, bandpass filtered in the 500-8000 Hz range. The reference sample is time-shifted over the entire test sample via a sliding window method, and the maximum similarity across all time points is taken as the similarity score for the test sample.

### **Determination of onset of subsong**

The day of onset of subsong was taken as the first day in which the bird produced any amount of distinctively subsong-like vocalization, as identified by ear: relatively low-amplitude vocalizations with low stereotypy that were distinctly different from typical calls. Birds that began singing immediately upon isolation on day 35 were considered for calculations to have begun subsong on that day.

### **Spectrograms**

All spectrograms in this chapter were produced using either the Praat software package [165] or the method of Gardner and Magnasco [166].

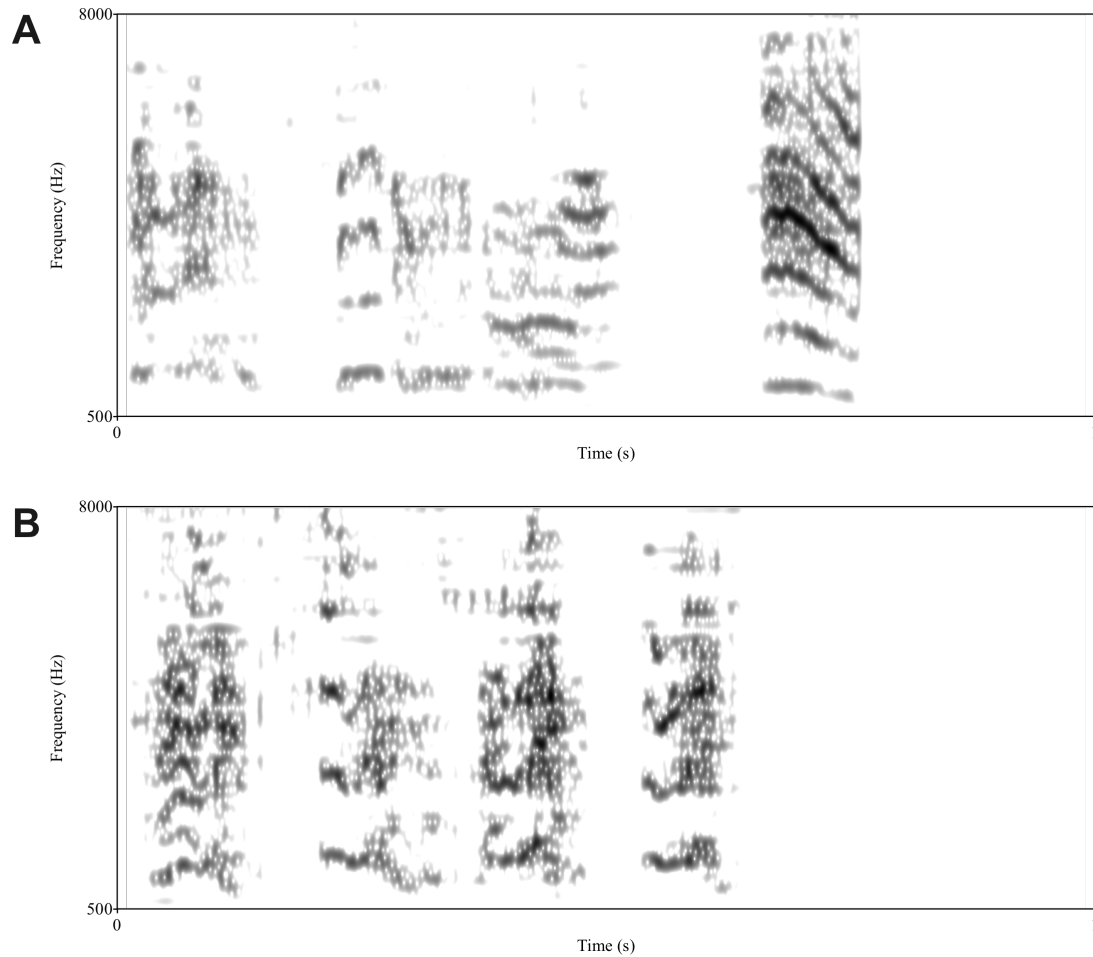
## **RESULTS**

This research broadly confirms earlier reports that juvenile zebra finches can adopt a repetitive singing behavior during the plastic song phase; indeed every bird

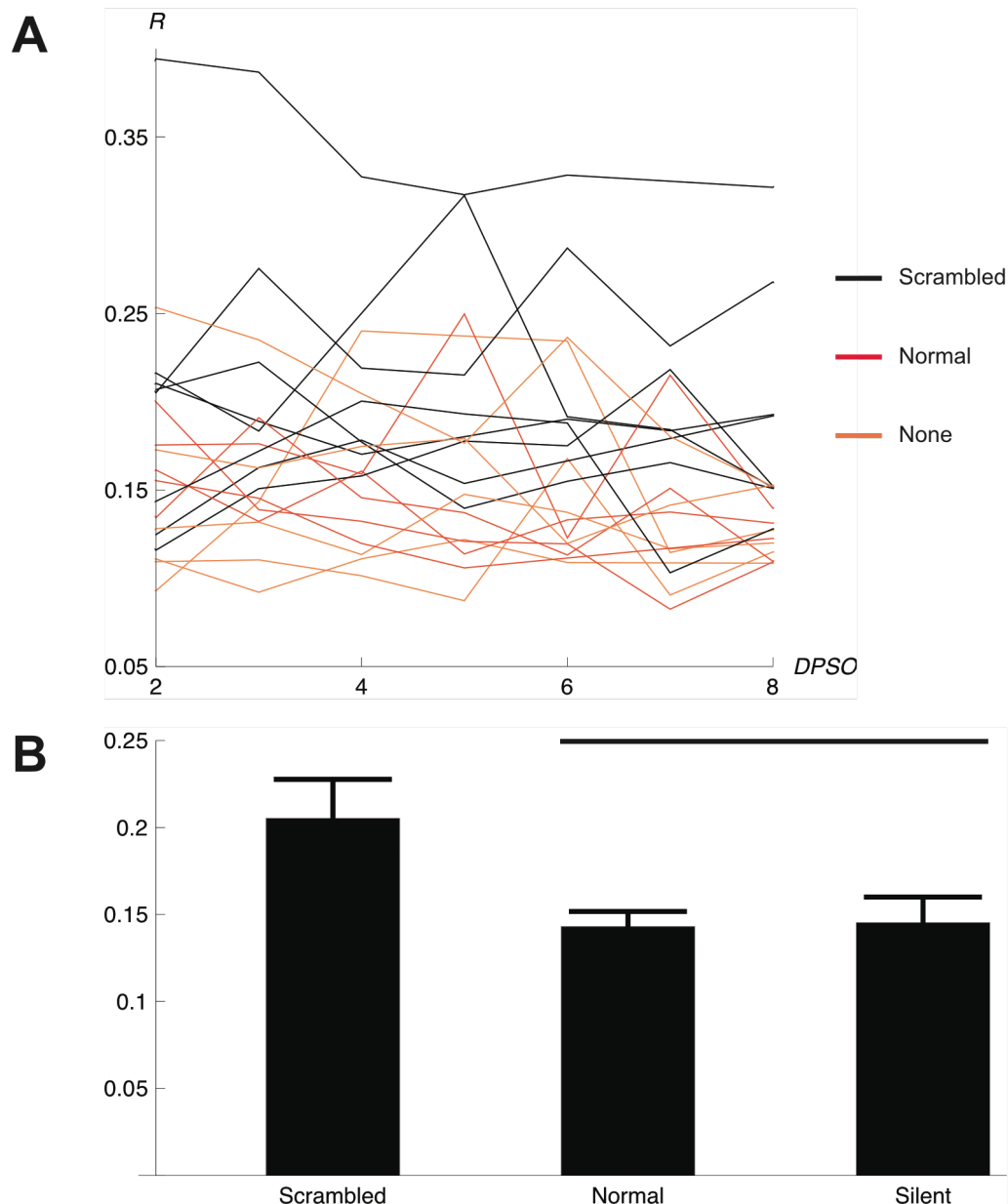
examined produced vocalizations that scored very highly against the repetitiveness measure (repetitiveness score  $>0.35$ ), although some birds did so only infrequently, as illustrated in Figure 10. Other individuals tended to repeat more often, and generally at greater length.

Birds could vary considerably from day to day in terms of their repetitiveness, but overall the repetitiveness of a bird in the one-week period from 2 to 8 days after the onset of subsong (DPSO, days post subsong onset, approximately days 37-43 post-hatch) provided the best timeframe to examine this behavior. In days 0-2, many birds sang very little, and after day 8 some birds began developing motif-like vocalizations of multiple syllables that were under 300 milliseconds long—within the time window examined by the repetitiveness measure—and hence scored highly as repetitions even though they did not accurately represent the characteristic repetitive behavior of a single syllable being repeated.

Figure 11A illustrates the evolution of repetitiveness that was observed. Generally, there was not evidence for a distinct categorization of repeaters vs. non-repeaters, but a continuous distribution of repetitiveness. Furthermore, birds could change their repetitiveness from day to day, sometimes substantially. There was a notable peak in the repetitiveness around five to six DPSO. There was also one individual (“the outlier”) whose scores were uniformly higher than all others; manual examination indicated that the animal was—as his scores suggested—highly repetitive; this repetitiveness manifested itself as soon as he began singing, and remained so throughout the seven-day window.



**Figure 10** Most birds studied repeat occasionally. Spectrograms of vocalizations from a single individual, taken on the same day (44 days post-hatch). This individual was not generally prone to repetitions, as illustrated in (A); however on occasion this individual would produce repetitive vocalizations as well, as illustrated in (B).



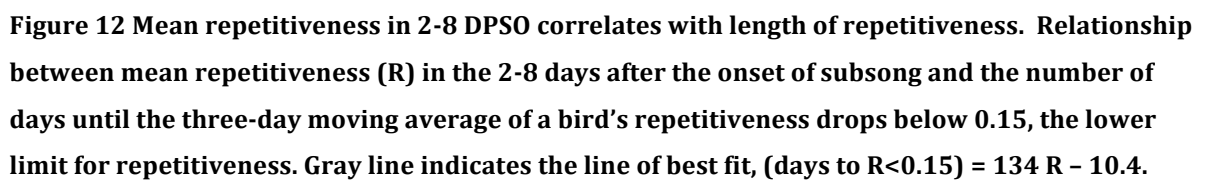
**Figure 11** Repetitiveness was higher for birds that heard scrambled song. **(A)** Repetitiveness (“ $R$ ”) trajectories during a critical development period, from two to eight days after the onset of subsong. Although there was considerable overlap between groups, the birds that heard the scrambled song had higher mean repetitiveness scores during this period than either the group that heard normal song or no song. **(B)** Mean repetitiveness scores for each treatment group during the same time period. Error bars indicate standard error of the means. The difference between the scrambled group and the other two groups was statistically significant (Kruskal-Wallis,  $P=0.024$ ).



Despite the chaotic set of trajectories in Figure 11A, there was a measurable difference between treatment groups with regard the mean repetitiveness of a bird in the 2-8 DPSO range. Birds who heard no songs and birds that heard normal song were, on average, less prone to repetitiveness than those that heard scrambled songs (Figure 11B). This difference was found to be statistically significant (Kruskal-Wallis,  $X^2=7.4$ ,  $P=0.024$ ). Even without the very highly repetitive individual, the result remained significant ( $P<0.05$ ).

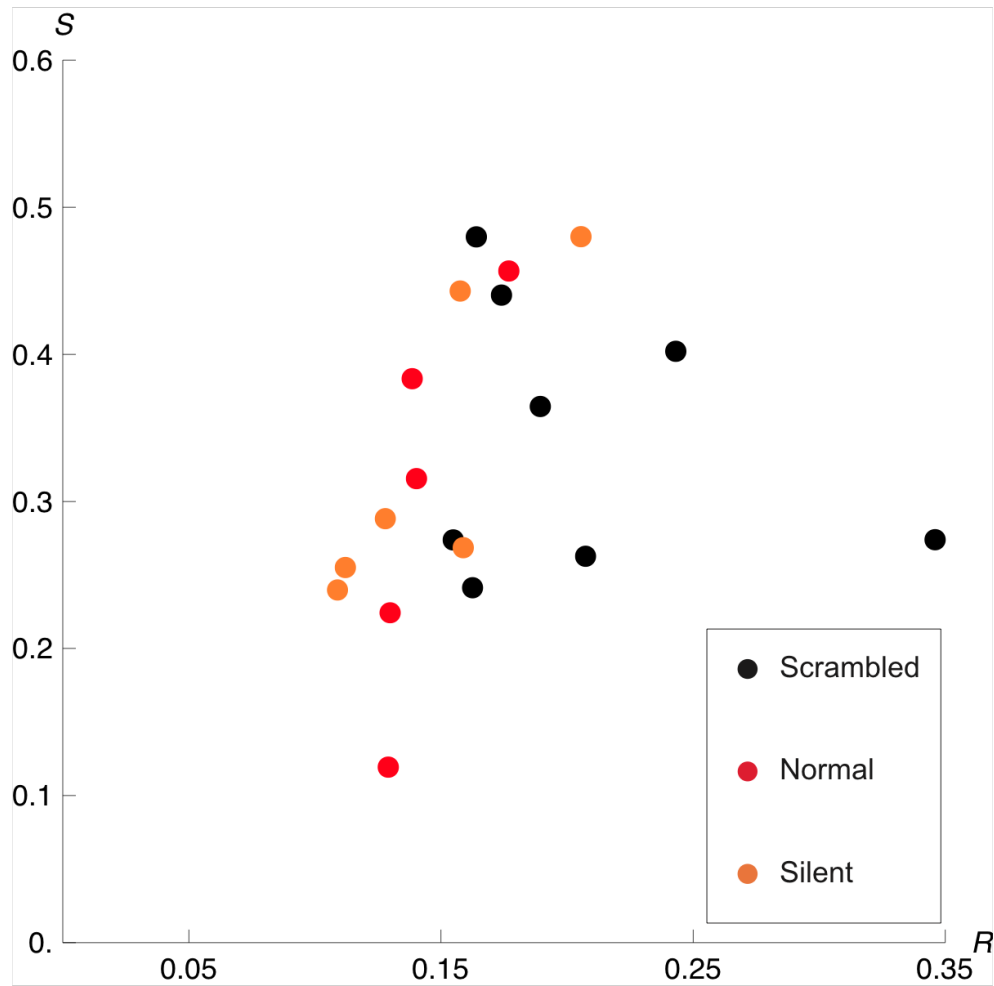
While the experiment was being conducted it became apparent that some birds that heard scrambled song seemed to exhibit repetitive behavior for an extended period of time. This was examined further by looking at how many days each bird took to get a repetitiveness score below 0.15, the lower cutoff for repetitiveness. This was calculated as the moving average of the repetitiveness score over three days, beginning five days after subsong onset. One individual, whose song did not fall below the cutoff before recording ended, was excluded from this analysis. Once again there was a significant difference between groups (Kruskal-Wallis,  $X^2=6.5$ ,  $P=0.038$ ), with birds that heard scrambled song taking longer on average than birds that heard normal song or nothing. Two birds that heard scrambled song took over thirty days to move past this threshold, substantially higher than the 9.5-day average of all other birds. There was a correlation between repetitiveness in the 40-50 day window and time to move past repetitions (Figure 12), with a Spearman rank correlation of 0.78; this correlation was statistically significant (Spearman rank test,  $P=0.00010$ ).

In addition to measuring overall repetitiveness, there was a need to measure the extent to which a bird's repetitions persisted over time: a bird could, conceivably, be

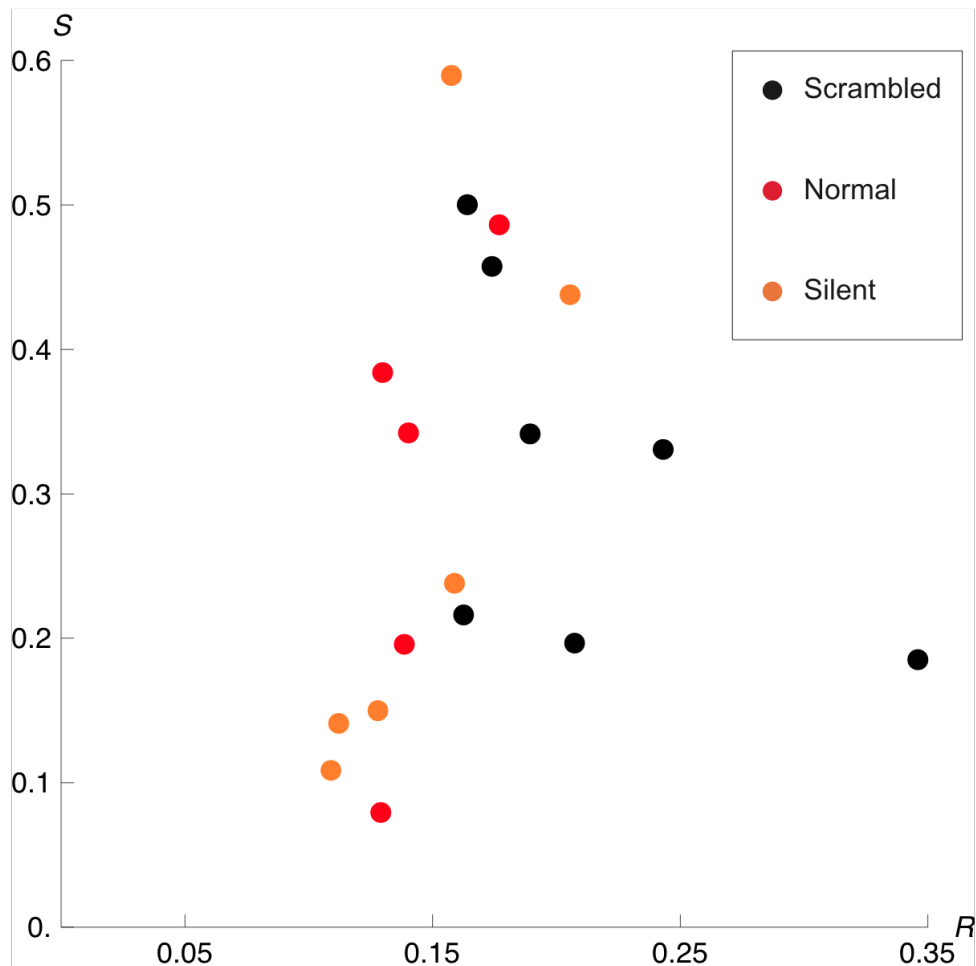


highly repetitive and yet vary what it was repeating from day to day, for example. Using the similarity measure described earlier, each bird's vocalizations were compared to a manually extracted sample (the reference sample) of a frequently repeated syllable taken from the 2-8 DPSO window. There was a significant correlation between overall repetitiveness in the 2-8 DPSO window and the mean similarity of all vocalizations in the same time period to the reference sample (Spearman's rank test,  $\rho=0.51$ ,  $p=0.027$ ), indicating that birds do in fact tend to repeat the same syllable over a period of time (Figure 13). The single outlier seen to the far right of Figure 13 was the same "outlier" described previously; a careful examination of his samples suggested that while highly repetitive within samples, the syllable he was predominantly repeating changed slowly over time. The extent to which this syllable persisted over a longer period of time was also examined; each bird's reference sample was compared to the set of samples from the day that the bird's repetitiveness level fell below the minimum threshold ( $R<0.15$ ), calculated in the same fashion as described previously. In this case there was not a statistically significant correlation, although the correlation approached significance (Spearman's rank test,  $p=0.089$ ) and would have been significant in the absence of the outlier (Figure 14).

A quantitative comparison of the reference syllables against the syllables of the tutor song was also intended, however this presented a considerable technical challenge. The juvenile syllables differed significantly from the tutor's syllables in terms of pitch, entropy, and timing, and given the very short length of these syllables quantitative comparison was found to be essentially impossible. For five of the nineteen birds, spectrograms of the reference syllable took the form of a downward harmonic



**Figure 13 Repetitiveness 2-8 DPSO correlates with a dominant syllable during that period. Relationship between repetitiveness (R) in the 2-8 days after the onset of subsong and mean similarity (S) of a manually selected reference syllable to all samples in the same time period. The relationship between repetitiveness and similarity to the reference syllable is statistically significant (Spearman's rank test,  $P=0.027$ ).**

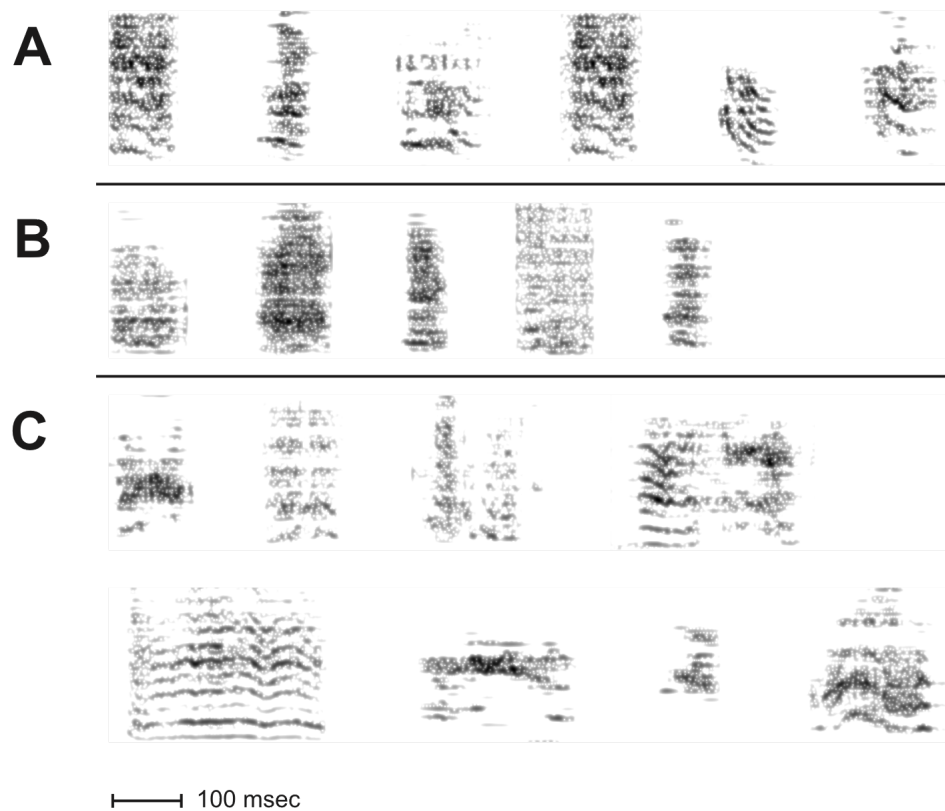


**Figure 14 Longevity of the reference syllable. Relationship between repetitiveness (R) in the 2-8 days after the onset of subsong and mean similarity (S) between the reference syllable and the bird's song on the day it falls below the minimum threshold for repetitiveness ( $R < 0.15$ ).**

sweep, the same basic pattern as seen in the first syllable of the tutor's song. For five additional birds, the spectrogram of the reference syllable took the form of a noisy burst, with spectral density spread fairly evenly across a large range of frequencies. There were no significant groupings or points of reference with the tutor's song for the remaining nine birds. Spectrograms of the reference syllable for each bird, organized by apparent type, are found in Figure 15.

Finally, the learning trajectories of several individual birds were examined in greater detail, as illustrated in Figures 16-18. Figure 16 shows a series of spectrograms illustrating the song development of a single bird in the 2-8 DPSO window; this bird had a low mean repetitiveness score ( $R < 0.15$ ) and never clearly evinced a single dominant syllable during plastic song. By day 6 a multi-syllable motif had already begin to take shape. Figure 17 illustrates the song development of a bird that had an intermediate repetitiveness score ( $R > 0.15$ ); this bird had a dominant syllable that persisted as part of its singing until day 12. In addition to its dominant syllable, this bird continued to produce other syllables as well; in many cases, pairs or triplets of sequential syllables appear similar even if they are not the dominant syllable. Finally Figure 18 provides the same development history for a bird with a high mean repetitiveness score ( $R > 0.2$ ).

For this bird, a dominant syllable appeared on day 4, and this syllable quickly came to dominate the bird's singing, to the exclusion of almost all else. This syllable persisted in the bird's song for an extended period: it is still clearly visible in the bird's singing 37 days after the onset of subsong, when the bird's mean repetitiveness score dropped below 0.15.



**Figure 15 Reference syllables grouped by type. Spectrograms illustrate reference syllables grouped by apparent type: (A) harmonic down-sweeps; (B) noisy bursts; (C) Uncategorized. All spectrograms have a frequency range of 500 Hz – 8 kHz.**



**Figure 16 Song development of a non-repetitive bird. Spectrograms illustrating song ontogeny of a bird with a low mean repetitiveness score ( $<0.15$ ) in the 2-8 DPSO window. Each spectrogram is 500 Hz to 8 kHz and 1.25 seconds long. By day 6 a precursor to a larger motif has appeared, highlighted with a red underline; this motif continues to develop in days 7 and 8. All spectrograms have a frequency range of 500 Hz – 8000 kHz.**





**Figure 17 Song development of a moderately repetitive bird. Spectrograms illustrating song ontogeny of a bird with moderate repetitiveness ( $0.15 < R < 0.2$ ) in the 2-8 DPSO range, and at day 12, the day its 3-day moving average repetitiveness dropped below 0.15. By day 5 a dominant repetitive syllable has appeared (underlined in red) and there is in many cases a high degree of similarity between sequential syllables whether or not they resemble the dominant syllable. The dominant syllable persists in the bird's singing at least until day 12. All spectrograms have a frequency range of 500 Hz - 8000 kHz.**



**Figure 18 Song development of a strongly repetitive bird. Spectrograms illustrating song ontogeny of a bird classified as strongly repetitive ( $R > 0.2$ ). Samples are shown for every day in the 2-8 DPSO window, day 20, and day 37, the day the bird's three-day moving average repetitiveness score dropped below 0.15. The syllable the bird repeated primarily, a harmonic downsweep, appeared clearly on day 4 (underlined in red) and by day 8 had come to dominate the bird's singing. This harmonic downsweep persisted as part of the bird's singing until day 37. All spectrograms have a frequency range of 500 Hz – 8000 kHz.**

## DISCUSSION

These results validate the work of Tchernichovski *et al.* [20] and Liu *et al.* [1] insofar as repetitiveness is a behavioral feature of song development in the zebra finch; this study marks the first attempt I am aware of to deliberately manipulate this behavior. These results suggest that, at least under some conditions, the occurrence of repetitiveness is much less clearly defined than was reported by either Tchernichovski *et al.* or Liu *et al.* however; repetitiveness affects almost all birds to some extent, with considerable day-to-day variability in some instances and a continuous distribution in a bird's average degree of repetitiveness.

Provision of an unlearnable song for the juveniles to hear induced an overall increase in repetitive behavior, in some cases to a large degree. On average, birds exposed to the scrambled song were more repetitive, and for a longer time period, than birds that heard the unscrambled song or no song, and the dominant syllable they repeated persisted for an extended period of time; this syllable could persist as part of a bird's singing even as overall repetitiveness declined.

While Liu *et al.* [1] hypothesized that repetitiveness represented a strategy for learning, in light of these results one might suggest that chronic repetitive behavior may represent a "failure mode" of sorts for juveniles, one that at least temporarily retards song development; as a counterpoint to this idea however, Liu *et al.* have suggested that this temporary delay may itself be advantageous, allowing the juveniles to delay committing to a song model until conditions for learning improve.

Liu *et al.* [1] reported on several phenomena that our results did not reproduce: the bimodality of repetitiveness, and the rapid and highly synchronous start and end of repetitiveness. These differences may be due to experimental conditions, and perhaps to some extent to differences in how repetitiveness is measured.

The results presented here are consistent with the hypothesis, and the results of Tchernichovski *et al.* [20] and Liu *et al.* [1] can be understood in light of this hypothesis as well. Those of Tchernichovski *et al.* need little additional explanation, but those of Liu *et al.* require closer inspection. At no point were the animals in that study denied a tutor to learn from, and yet many of the birds developed repetitive behavior. The birds in that study were raised in a family setting with parents and siblings, and other juveniles could themselves be a confounding influence on template learning, as juvenile zebra finches have been shown to learn from other juveniles [167], and hearing other juveniles while learning to sing has been shown to decrease learning accuracy [168].

There is an open question as to how common this phenomenon would be in wild zebra finches in a natural setting. In the wild, finches fledge by day 21 or so [9, 169] and are no longer effectively confined in the company of other finches, juvenile or adults. To the extent that chronic repetition may be caused by confusing stimuli, wild birds may be able to avoid such issues simply by moving a few meters away.

My results can be interpreted as evidence in favor of the reinforcement learning model [134]. Repetitiveness is fundamentally a lack of variability in singing, and if the reinforcement learning model is correct, then variability is required for vocal exploration so that the bird can discover improvements to its song. The observation

that chronic repetitiveness in an early stage of plastic song is associated with extended periods of repetitiveness suggest that this may indeed be the case.

When comparing juveniles' reference syllables to the tutor's song, the results are ambiguous at best. While ten birds produced reference syllables that broadly resemble syllables in the tutor's song—those that produced harmonic down-sweeps and those that produced noisy bursts—the fact that so many other birds had reference syllables without obvious points of even broad similarity with the tutor's song suggests that the similarities might be due to chance as much as learning. Although it was not possible due to time constraints to house birds in isolation until reaching maturity, and hence their song as adults cannot be considered for experimental purposes, these birds were nonetheless recorded from after 90 days post-hatch. Of all 19 birds, only six developed reasonable facsimiles of the unscrambled tutor's song, as judged by ear, with many poor imitations across all treatment groups. Despite this poor imitation, most birds examined (15/19) had first song syllables featuring harmonic down-sweeps, as did the tutor's song. This may have been a result of partial learning, or it may simply be a common pattern amongst zebra finches; see the spectrograms of birdsong found in Williams [47], Eales [21], and Zann [41] for examples of this.

I close with a bit of speculation on the neurological basis of repetitiveness and its possible importance. The AFP, through LMAN, is generally thought to drive variability during singing [98, 131]. Chronic repetitiveness—a decline in variability during singing—might then correspond with a change in activity within LMAN or with a change in the extent to which LMAN transmits this variability to the motor pathway. Troyer and Bottjer, based on the results of lesioning and deafening studies [170, 171],

suggested that LMAN may provide variability to the motor system when the bird detects an error between its song and its template, in order to facilitate vocal exploration [172]. The phenomenon of chronic juvenile repetitiveness may represent a corollary to this hypothesis: that LMAN does not provide as much variability to the motor system when the bird does not detect an error, even in juveniles. This should be experimentally testable, as electrophysiology studies in LMAN have been performed on awake animals [2, 146], and the methods presented here provide a tool for exploring this possibility. Such studies may help to provide valuable insight into the nature of the “error signal” that has been suggested to exist but not yet identified [33].

## **CHAPTER 3: A SPIKING NEURON MODEL OF SONG LEARNING WITH BIASING**

### **ACTIVITY IN THE AFP**

The songs of the true oscine songbirds are not innate; instead these songs must be learned. This learning process has two parts: the sensory learning component, in which a bird somehow internalizes a model song, its template; and the sensorimotor learning component, in which a bird learns how to produce this internalized song. Many lines of evidence suggest that the sensorimotor learning component is a kind of trial-and-error process [26, 98, 131, 133, 136, 138, 147, 153, 154, 173-178] in which the bird must try variations of the song it has learned so far in order to discover improvements. This trial-and-error process is often described within the context of reinforcement learning (RL), particularly through the actor-critic-experimenter framework. This framework divides the sensorimotor learning process into three distinct tasks: performing the bird's song that has been learned so far (actor), evaluating how that performance compares to the bird's internal template (critic), and creating variations of the song to perform (experimenter). During song learning, the experimenter produces a modified version of the bird's song, which is performed by the actor; the critic then determines whether this modified version represents an improvement to the song. If it is, the critic sends a reinforcement signal to the actor, and the song of the actor is updated to make it more like the modified version. Over a large number of trials, the bird's song will come to resemble the template version.

How is this trial-and-error learning process implemented in the oscine brain, and are there candidates to fill the roles of actor, critic, and experimenter? Singing and sensorimotor learning are supported in the brain by a set of dedicated nuclei organized

into two main pathways: the motor control pathway (MCP), which is needed for song production and consists of two pallidal nuclei with descending projections to motor control nuclei in the brainstem, and the anterior forebrain pathway (AFP), a basal ganglia-thalamocortical loop that has been implicated in the song learning process. These pathways connect at the robust nucleus of the arcopallium (RA), a nucleus of the MCP. RA receives input from HVC, another nucleus of the MCP, and from the lateral magnocellular nucleus of the nidopallium (LMAN), part of the AFP. To some extent these pathways and nuclei can be fit within the actor-critic-experimenter framework: HVC and RA are natural matches for the actor, as they are required for singing [3]; the location of critic is currently unknown, although possibilities have been suggested [133, 147]; and the experimenter is best matched to LMAN, as experimental results have demonstrated that LMAN produces variability in song [3, 92, 131].

Recently, however, a string of experimental results has clouded the picture of LMAN as experimenter. In addition to providing variability to song, and whatever effect LMAN's signal to Area X might be, there is evidence that LMAN may transmit a signal about the song to the motor control pathway [92, 173, 178]. Leonardo [2] and Kao *et al.* [179] showed through electrophysiological studies that at least some of the activity in LMAN during singing is time-locked to specific points in the song, and Andalman and Fee [180] have demonstrated that LMAN can bias MCP output to reduce errors in singing.

How is this bias created, and could it have a role in the song learning process? We can imagine three broad possibilities for the origin of this bias. First, it may be that the bias is an error signal that indicates the set of corrections necessary to produce a



song that matches the template. This would then represent a form of error-directed learning [172]. However the hypothesis that this bias could carry an error signal was disputed by Leonardo who demonstrated that the time-locked signal in LMAN was insensitive to immediate changes in song feedback [2], as an error signal presumably would be.

The second possibility is that the biasing signal is a complete representation of the motor program needed to emulate the template, produced through an inverse mapping between song output and motor commands. If this is the case, the biasing signal might not change immediately, or ever, in response to feedback manipulation, until such time as the bird's inverse mapping changes.

The third possibility is that this biasing signal is itself a subject of search in which the bird is actively testing variations of this bias signal in order to discover improvements to its song. This was proposed in the model of Doya and Sejnowski [147] and more recently by Goldberg and Fee [133]. Troyer and Doupe [138] suggested that LMAN may be biasing RA's activity to produce the correct syllable sequence, but it seems just as plausible that LMAN may be biasing RA's activity to produce the fine structure of the syllables themselves.

Which of these possibilities, if any, is correct? The patterns of activity seen in LMAN may provide a clue. In trial-and-error learning there is a conflict between the need to search for improvements and the desire to take advantage of what has already been discovered; this is commonly known as the exploitation vs. exploration tradeoff [181]. For song learning to progress optimally, a balance must be established between vocal exploration and consolidating what's been learned within the motor control

pathway. Perhaps the mixture of timing-locked and timing-independent signal that has been observed [2, 98] represents this balance at work. This leads to the hypothesis that in the situation where the bias signal is a subject of search, a mixture of timing-locked activity and timing-independent activity will produce optimal learning results; conversely, if the bias signal is not a subject of search, a mixture of timing-locked activity and timing-independent activity will produce suboptimal learning results.

To explore this hypothesis, a computational model has been developed in which the possibility of LMAN as a source of bias can be explored. The model contains analogs of key components of the motor control pathway (RA and HVC) and of the anterior forebrain pathway (LMAN). Within this model, LMAN can produce a mixture of timing-locked and timing-independent activity with an arbitrary ratio between the two; the timing-locked signal produced by LMAN is presumed to be the biasing signal from LMAN that affects the output of the motor pathway, as observed by Andalman and Fee [180].

This model is an abstraction in several key ways. Firstly, the trial-and-error learning process, as defined, is algorithmic in nature and likely to be substantially different in a biological system. This algorithmic approach was used to avoid overspecifying a poorly-understood system and to create a mechanism in which the ratio of timing-locked signal to timing-independent signal can be easily modified. The model does not have any auditory output, instead treating the output of RA as a proxy for the bird's singing. The model is also circumscribed in terms of how much of the song learning process it describes; the model covers only the learning of syllables, not the sequencing of those syllables, which is likely to involve other processes.

The model, like all models, makes a number of assumptions. These assumptions and their justifications are discussed below.

*1. The timing-locked signal is being actively remodeled as part of the song learning process, and this remodeling takes the form of a trial-and-error search in which variations on the biasing signal are tested and improvements are reinforced.* This is the central, novel assumption made and the basis for the model. This idea is supported by the simultaneous presence of a biasing signal in LMAN as well as highly variable activity. If the biasing signal were simply an error-correcting signal, the bird would presumably have no need for vocal variability. In addition, there is some experimental evidence that can be considered favorably in light of our hypothesis: Sober and Brainard [182], like Andalman and Fee [132], have used vocal feedback manipulation to study song adaptation. The learning trajectories shown by Sober and Brainard, notably in their Figures 2 and 4, display the constantly changing direction characteristic of a blind search. If improvements to song were computed as error signals, one might expect smooth learning trajectories, rather than the back-and-forth patterns seen.

*2. The biasing signal can permanently modify HVC→RA synapses to encourage RA neurons to fire at a time in the song specified by the LMAN neuron.* LMAN may serve directly as a “teacher” to the motor control pathway. Previous conceptual models have highlighted the idea of reinforcing coincident LMAN and HVC inputs to RA neurons as the basis for permanent learning; in that sense this model is no different. Possibly the simplest mechanism for this is to have LMAN inputs to RA directly induce plasticity—as recent evidence suggests may be the case [176]—but this is not a prerequisite for our model to work. Andalman and Fee, in their work, used auditory feedback manipulation

to induce changes in adult birds' songs, and observed the birds' adaptation to this manipulation over a series of days [132]. By temporarily inactivating LMAN while the birds were adapting, they were able to show that only part of the accumulated adaptation could be attributed directly to the biasing signal. This supports the idea of LMAN as teacher: the results of Andalman and Fee would suggest that some part of the bias signal's content had been retained by the motor control pathway even after abolishing the bias signal itself.

*3. The myotopic mapping from LMAN to RA is fine-grained enough to support targeting at least as precise as the number of effective RA output targets.* For the bias in LMAN to be meaningful in song production, the myotopic mapping from LMAN to RA must be reasonably accurate. Miller-Sims and Bottjer [84] have studied these mappings and made measurements of their accuracy. Dividing LMAN and RA into thirds, they concluded that approximately 70% of LMAN's projections to RA terminated in the corresponding third in RA as they originated from in LMAN. At first this might seem like a very rough mapping, but some consideration of how they measured it is in order.

With the assumption that LMAN's projections to RA target the same relative position in RA, with a Gaussian-distributed random error added, one can estimate the standard deviation of the position error needed to reproduce Miller-Sims and Bottjer's results [84]. Our calculations suggest that with these assumptions, the standard deviation of the position error would be only about 16% of the overall size of RA. Given that there are only six pairs of muscles in the syrinx [50], this may be sufficient precision, although vocal control involves tracheal and respiratory muscles as well. Additionally, Miller-Sims and Bottjer observed this topographic mapping becoming

more refined over time, from 20 to 35 days post-hatch, at which time their observations ended. There is no reason to believe this refinement could not continue beyond this time.

*4. The critic can target specific parts of the motor command pattern for change.*

The basis for this assumption is based both on physiology and experimental results. The physiological argument is that if the critic is found within the AFP, then the topographic mapping seen throughout the AFP could support such specific targeting. The experimental results come from Ravbar, Lipkind, Parra, and Tchernichovski, who have recently demonstrated that vocal exploration and learning can in fact be localized to specific parts of the song [183].

The rest of this chapter describes in detail the computational model, demonstrates that it can train the HVC/RA part of the MCP to generate repeatable firing patterns corresponding to motor control sequences in a manner consistent with known experimental results, and explores how the mixture of timing-locked and timing-independent activity within LMAN affects learning. Also considered is the possibility that the signal from the critic to LMAN could be destabilizing rather than reinforcing, and the effects of search size and plasticity models on the behavior of the simulations are examined.

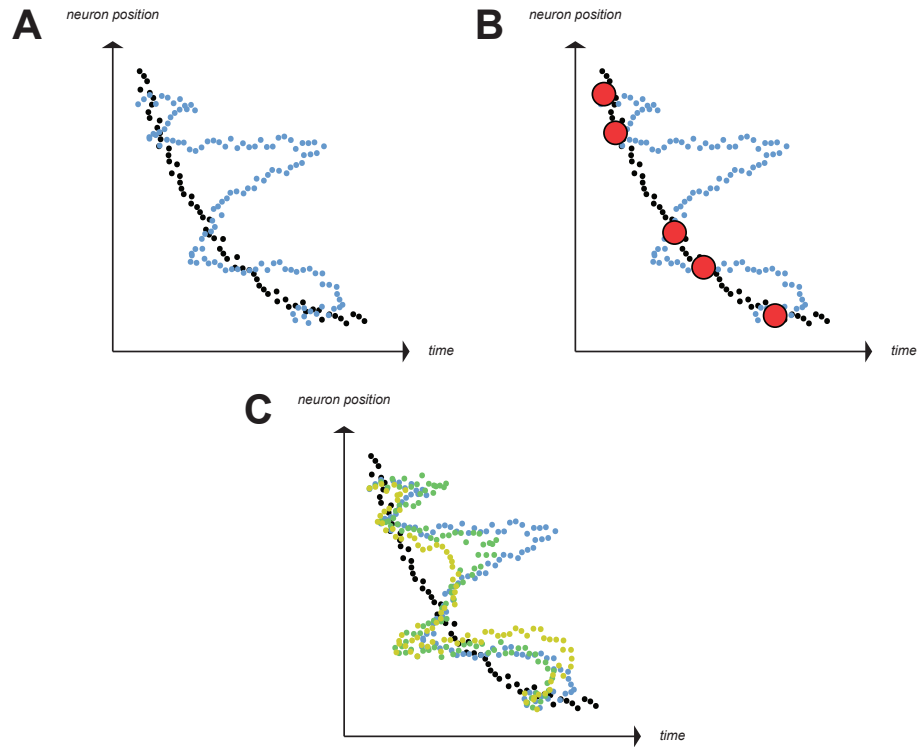
## **METHODS**

A computer model was developed in C++ and Python. The model contains structures analogous to the three nuclei at the junction of the AFP and MCP: HVC,

LMAN, and RA. The model also contains additional putative structures that are not analogous to any specific brain nucleus, as described below.

The model features two learning processes at work simultaneously. The first is the process by which the motor control pathway learns a motor command sequence provided to it by LMAN. The output of LMAN potentiates HVC→RA connections that are triggered coincidentally; for time-locked output from LMAN these potentiation events will occur repeatedly, strengthening the relevant HVC→RA connections until the HVC input alone is sufficient to trigger firing in the postsynaptic RA neurons. Within the model the primary role of RA is to learn a mapping from times (provided by HVC) to motor actions (provided by LMAN).

The second process at work in the model is that by which LMAN acquires its timing-locked activity pattern, illustrated in Figure 19. LMAN has a time-locked firing pattern that it must discover through trial and error, via a form of blind search. LMAN begins the simulation with a purely random firing pattern; as the simulation runs, this pattern is output indirectly through RA, and is compared against the template by the critic. The critic sends a reinforcement signal to the parts of LMAN that are closest to the template's reference pattern, and those parts of LMAN's firing pattern are temporarily stabilized, becoming LMAN's "working copy" of the motor control program. The parts of LMAN's firing pattern that are not stabilized are subject to random change. As the simulation progresses, LMAN discovers better firing patterns for parts of the motor control program that are incorporated into the working copy. Eventually this working copy comes to resemble the template firing pattern. By varying the proportion



**Figure 19 Trial-and-error learning in the model. Schematic illustrating the trial-and-error learning process within LMAN. Each subplot represents a raster plot of neuron firing times, with time along the X-axis and an arbitrary ordering on the Y-axis; all nuclei in this plot share a topographic mapping such that the Y-orderings are equivalent across all subplots. (A) LMAN produces a firing pattern (blue) which differs substantially from the ideal firing pattern as defined by the critic (black). (B) The critic sends reinforcement signals to targeted parts of LMAN (red dots), preventing the firing pattern in these parts from changing in the next iteration of the simulation. Parts not reinforced will change randomly. (C) Subsequent iterations of the simulation will show different firing patterns from LMAN (green, yellow) which change randomly over time, although reinforced parts of the pattern will not change.**

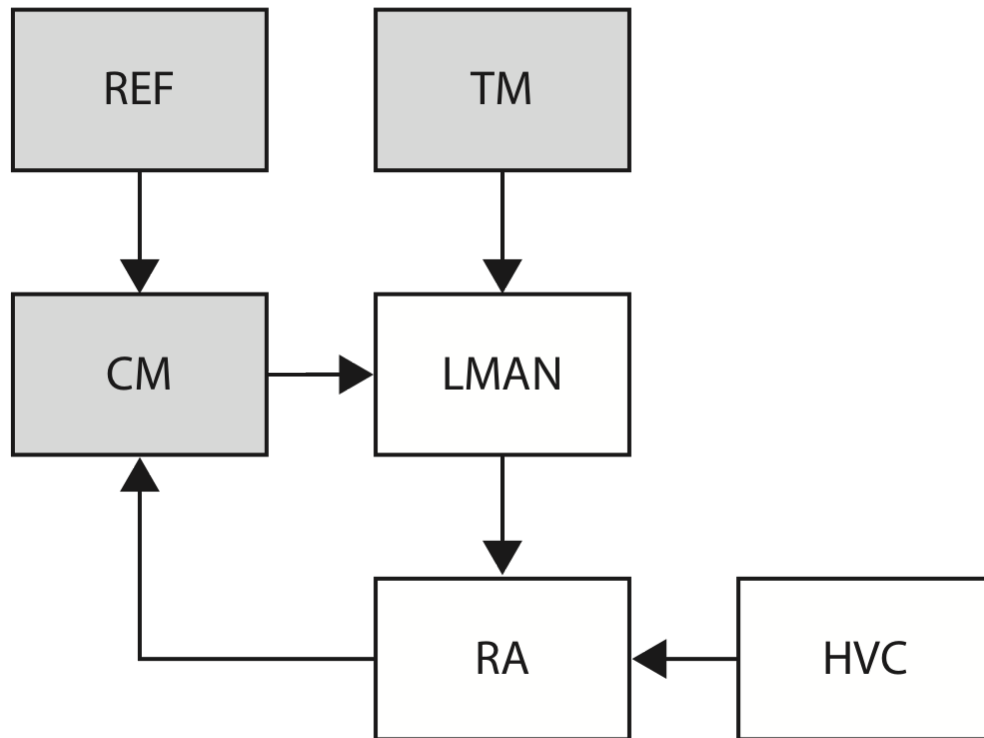
of the motor control program that stabilized, the ratio of timing--locked to non--timing--independent activity in LMAN can be precisely controlled.

In addition to HVC, RA, and LMAN, the model contains a number of other functional units: a reference pattern generator module (REF), the source of the bird's "template" pattern; a critic module (CM), that compares the firing patterns generated by RA to those from REF; and a timing module (TM) that provides LMAN with reliable time information during singing. All structures take the form of one- or two-dimensional arrays of simulated neurons. A schematic illustrating the model's components and their connections can be seen in Figure 20. During simulation runs, the model evolves using a fixed time step ( $\Delta$ ) of 0.0005 seconds. The population counts for each structure are summarized in Table 1 and the connection densities between structures are summarized in Table 2.

### **Simulated neurons**

The neurons in RA and LMAN are simulated as two-compartment neurons with an adaptive integrate-and-fire type somatic compartment and a separate dendritic compartment. A summary of all variables and parameters used for the simulated neurons can be found in Table 3.





**Figure 20 Full structure of the computational model. Structures in gray are putative and do not have a direct physiological analogue. Known structures include RA and HVC, components of the song motor control pathway, and LMAN, a component of the anterior forebrain pathway. Putative components include REF, a reference signal that specifies the ideal firing pattern for RA; CM, the comparison module, which compares the reference pattern to RA's output and sends error signals to LMAN; and TM, a timing module that provides LMAN with a reliable measure of time during singing.**

**Table 1 Neuron counts in the model.**

| <b>Structure</b> | <b>Neuron count</b>                                  |
|------------------|--|
| RA               | $300 \times 0.968$ RAP, $300 \times (1 - 0.968)$ RAI |
| HVC              | 300  |
| LMAN             | 60   |
| TM               | 25   |
| CM               | 30   |
| REF              | 300  |

**Note:** RAP=RA projection neurons, RAI=RA inhibitory interneurons.

**Table 2 Connectivity densities in the model.**

| <b>Source</b> | <b>Target</b> | <b>Connections per target</b> | <b>Topographically organized?</b> |
|---------------|---------------|-------------------------------|-----------------------------------|
| HVC           | RA            | 150                           | No                                |
| LMAN          | RA            | 1                             | Yes                               |
| RAI           | RAP           | 15                            | No                                |
| RAP           | CM            | 10                            | Yes                               |
| REF           | CM            | 10                            | Yes                               |
| CM            | LMAN          | 2                             | Yes                               |
| TM            | LMAN          | 25                            | No                                |

**Note:** RAP=RA projection neurons, RAI=RA inhibitory interneurons.

**Table 3 Summary of variables and parameters used in the simulated model neurons.**

| Value                       | Meaning   | Units           |
|-----------------------------|---|-----------------|
| <i>Soma</i>                 |   |                 |
| $v$                         | Somatic membrane voltage                            | V               |
| $u$                         | Recovery variable                                   | A               |
| $E_L$                       | Leak reversal potential                             | V               |
| $E_R$                       | Voltage reversal potential (may differ from $E_L$ ) | V               |
| $g_{leak}$                  | Leak conductance                                    | S               |
| $\Delta_T$                  | Slope factor  | V               |
| $V_t$                       | Spike initiation threshold                          | V               |
| $V_F$                       | Peak firing voltage                                 | V               |
| $C$                         | Membrane capacitance                                | F               |
| $\tau_w$                    | Recovery time constant                              | A <sup>-1</sup> |
| $v_r$                       | Reset voltage                                       | V               |
| $a$                         | Subthreshold adaptation                             | S               |
| $b$                         | Spike-triggered adaptation                          | A               |
| <i>Dendrites</i>            |   |                 |
| $g_{dend}$                  | Dendritic conductance                               | S               |
| $h$                         | Open ion channel quantity equivalent                | S               |
| $A$                         | Time constant                                       | S <sup>-1</sup> |
| $B$                         | Time constant                                       | S <sup>-1</sup> |
| <i>Synaptic plasticity</i>  |   |                 |
| $w$                         | Synaptic weight                                     | S               |
| $\bar{x}$                   | General neurotransmitter trace                      | -               |
| $\bar{n}$                   | NMDA-specific neurotransmitter trace                | -               |
| $\bar{v}_+$                 | Membrane voltage trace                              | V               |
| $\bar{v}_-$                 | Membrane voltage trace                              | V               |
| $\tau_{\bar{x}}$            | Time constant                                       | S <sup>-1</sup> |
| $\tau_{nmda}$               | Time constant                                       | S <sup>-1</sup> |
| $\tau_{\bar{v}_+}$          | Time constant                                       | S <sup>-1</sup> |
| $\tau_{\bar{v}_-}$          | Time constant                                       | S <sup>-1</sup> |
| $\Theta_+$                  | LTP voltage threshold                               | V               |
| $\Theta_-$                  | LTD voltage threshold                               | V               |
| $A_+$                       | LTP adjustment rate                                 | -               |
| $A_-$                       | LTD adjustment rate                                 | -               |
| <i>Synaptic competition</i> |   |                 |
| $w_{tot}$                   | Ideal total synaptic input                          | S               |

The somatic compartment is governed by the neuron model of Brette and Gerstner [184], defined as follows:

$$\begin{aligned}\frac{1}{C} \frac{dv}{dt} &= -g_{leak}(v - E_L) - g_{dend}(v - E_R) + g_{leak} \Delta_T e^{(v-V_t)/\Delta_T} - u \\ \frac{1}{\tau_w} \frac{du}{dt} &= a(v - E_L) - u \\ \text{if } v &\geq V_F, \\ v &\leftarrow v_r \\ u &\leftarrow u + b\end{aligned}$$

In these equations, a neuron is considered to have fired if its membrane voltage reaches or exceeds  $V_F$ . The dendritic compartments are governed by the following set of equations:

$$\begin{aligned}\frac{dg}{dt} &= h - Bg \\ \frac{dh}{dt} &= -Ah \\ \text{on synaptic input,} \\ h &\leftarrow h + w(B - A)\end{aligned}$$

For a single synaptic input, this system of differential equations along with the update rule is exactly equivalent to a double-exponential curve, which is a commonly used way of fitting postsynaptic response data. For multiple inputs it behaves as a sum of constituent double-exponential curves.

It has been suggested in a different context (reinforcement learning in macaque monkeys) that spike-timing dependent plasticity [185] can provide an implementation of reinforcement learning, specifically, temporal-difference learning in neuronal systems [186]. In concordance with this idea, synaptic plasticity for RA neurons is provided via a modified form of the plasticity model of Clopath, Busing, Vasilaki, and

Gerstner [187], a form of spike-timing dependent plasticity (STDP) [188]. In general STDP models account for both long-term potentiation (LTP) and long-term depression (LTD) by strengthening synapses whose presynaptic input times predict postsynaptic firing, and attenuating synapses whose presynaptic input times are predicted by postsynaptic firing. The model of Clopath *et al.* was chosen for its relative computational simplicity and its biological plausibility compared to many other STDP models. The equations governing this model are as follows:

$$\begin{aligned}\frac{d\bar{x}}{dt} &= \frac{-\bar{x}}{\tau_{\bar{x}}} \\ \frac{d\bar{v}_-}{dt} &= \frac{-\bar{v}_- + v}{\tau_{\bar{v}_-}} \\ \frac{d\bar{v}_+}{dt} &= \frac{-\bar{v}_+ + v}{\tau_{\bar{v}_+}} \\ \frac{d\bar{n}}{dt} &= \frac{-\bar{n}}{\tau_{nmda}} \\ \text{if } v > \Theta_+ \text{ and } \bar{v}_+ > \Theta_+, \\ w &\leftarrow \min(w + A_+ \bar{n} \bar{x} (v - \Theta_+) (\bar{v}_+ - \Theta_+), 0) \\ \text{on synaptic input,} \\ \bar{x} &\leftarrow 1 \\ \text{if } \bar{v}_- > \Theta_-, \\ w &\leftarrow \min(w - A_- \bar{n} (\bar{v}_- - \Theta_-), 0)\end{aligned}$$

Finally a synaptic competition mechanism was added to simplify balancing LTP and LTD. If a neuron has  $k$  inputs in total, then

$$\begin{aligned}w_{tot} &= \sum_{i=1}^k w_i \\ \frac{dw_i}{dt} &= \frac{w_{max} - w_{tot}}{k \tau_{comp}} \quad \forall i = 1..k \\ \text{if } w_i < 0, w_i &\leftarrow 0 \\ \text{if } w_i > 1, w_i &\leftarrow 1\end{aligned}$$

Here  $w_{tot}$  is the ideal total weight of all synapses for the neuron, and  $\tau_{comp}$  is the time constant with which the total weight is adjusted. The competition system, as defined, works to gradually push the total weight of all synaptic inputs towards this ideal total weight.

For the alternative “coincident” model of synaptic plasticity, the following equations are used. Variables and constants have the same meanings as for the equations of the model of Clopath *et al.* [187]:

$$\frac{d\bar{x}}{dt} = \frac{-\bar{x}}{\tau_{\bar{x}}}$$

$$\frac{d\bar{v}_+}{dt} = \frac{-\bar{v}_+ + v}{\tau_{\bar{v}_+}}$$

$$\frac{d\bar{n}}{dt} = \frac{-\bar{n}}{\tau_{nmda}}$$

if  $v > \Theta_+$  and  $\bar{v}_+ > \Theta_+$ ,

$$w \leftarrow \min(w + A_+ \bar{n} \bar{x} (v_+ - \Theta_+), 0)$$

on synaptic input,

$$\bar{x} \leftarrow 1$$

When employed, this model is used in conjunction with the synaptic competition mechanism described previously.

The version of the model of Clopath *et al.* [186] that was used to examine the effects of postsynaptic bursting on plasticity differed somewhat. The plasticity model there is not associated to any kind of model neuron; instead it receives a signal when a postsynaptic spike is arbitrarily created. The equations used are as follows:

$$\begin{aligned}
\frac{d\bar{x}}{dt} &= \frac{X(t) - \bar{x}}{0.006} \\
\frac{d\bar{u}_-}{dt} &= \frac{V(t) - \bar{u}_-}{0.006} \\
\frac{d\bar{u}_+}{dt} &= \frac{V(t) - \bar{u}_+}{0.007} \\
w_+ &= 720 \times (V(t) + 0.006)_+ (\bar{u}_+ + 0.0066)_+ \\
w_- &= 7.2 X(t) (\bar{u}_- + 0.0066)_+ \\
w &\leftarrow w + w_+ - w_-
\end{aligned}$$

Where  $(z)_+$  is the rectification of  $z$  (0 if  $z < 0$  and  $z$  otherwise);  $X(t)=1$  if a presynaptic input occurs at time  $t$  and 0 otherwise; and  $V(t)=0.1$  if a postsynaptic input occurs at time  $t$  and -0.0067 otherwise. A similarly simplified version of the coincident plasticity model was also used:

$$\begin{aligned}
\frac{d\bar{x}}{dt} &= \frac{X(t) - \bar{x}}{0.006} \\
\frac{d\bar{u}_+}{dt} &= \frac{V(t) - \bar{u}_+}{0.007} \\
w &\leftarrow w + 16.8 \bar{x} (\bar{u}_+ + 0.0066)_+
\end{aligned}$$

Both models were subjected to precomputed pre/post spike trains, consisting of a single presynaptic spike and either one or five postsynaptic spikes. The relative timing of the presynaptic spike was shifted from -20 milliseconds to +20 milliseconds relative to the time of the first postsynaptic spike, and the net effect on the synaptic weight ( $w$ ) was measured.

## HVC and REF

Within the model, HVC primarily serves as a source of timing information to RA, and REF serves as the neural instantiation of the template. Neurons in HVC and REF fire according to preprogrammed schedules and have no capacity to respond to inputs. The



firing pattern in HVC is designed to emulate the firing pattern of RA-projecting neurons in HVC as described in the literature [77]: every neuron fires at a single specific time within each performance of the motor program. HVC neurons are grouped into “teams” of six neurons that are programmed to fire at the same time. Each HVC neuron fires a burst of 5 spikes with an inter-spike interval of 1.6 milliseconds. The firing of teams is overlapping so that after one team fires, the subsequent team begins firing 1.6 milliseconds later. Although HVC undergoes changes during song learning [187], it is not clear whether or how this affects HVC’s firing sequence, and so in the model HVC’s firing sequence is assumed to be effectively constant for the duration of a simulation.

In REF, each neuron fires with a single spike per production of the motor program. REF, like LMAN and RA, is given a topological organization in order to facilitate comparisons between RA and REF. This topological organization extends in a single dimension within the structure; when raster plots from REF are organized along this axis, the firing pattern is made readily apparent. REF is programmed to produce five distinct firing patterns: a forward sweep, a reverse sweep, a forward slide, a sine curve, and a series of separate bars. These patterns are arbitrary targets to be learned, and do not represent songs, spectrograms, or estimates based on electrophysiological recordings from the song system.

## **CM**

The CM neurons comprise the critic module, and function by comparing the reference pattern from REF to the output of RA and providing an all-or-nothing error signal to a targeted region in LMAN. Each CM neuron connects to a small group of 2-5

LMAN neurons. CM neurons take inputs from REF and RA and compare their activity. This comparison is facilitated by the topological mappings shared by REF and RA: each REF neuron is compared to a single corresponding RA neuron. The CM neuron records the firing times of its input RA and REF neurons, and after a specified number of iterations of the motor program, calculates an error measure as follows:

$$err = \text{mean}\left(\left|X_{i,j} - Y_i\right|\right) \quad \forall i \in 1..I, j \in 1..J \quad \textbf{(Equation 1)}$$

Here,  $I$  is the number of (RA, REF) input pairs into the CM neuron,  $J$  is the number of recorded RA firing times since the last error calculation,  $X_{i,j}$  is the  $j$ th recorded firing time of the  $i$ th RA neuron, and  $Y_i$  is the closest firing time of the  $i$ th REF neuron in the same iteration of the motor program as  $X_{i,j}$ . This is the same error measure used to evaluate RA's output accuracy in the results, and it represents the mean difference between the ideal firing time and actual firing time; as such it is itself in units of time (milliseconds).

After all CM neurons have calculated their error measures, the CM neurons with the highest errors fire, sending an error signal to their recipient LMAN neurons. In this way, CM neurons provide a relative error measure to LMAN: even as the overall pattern produced by the model improves, the relatively worst-performing parts of LMAN receive error signals. The exact proportion of CM neurons that fire upon evaluation is 30% by default, although this value was changed in some experiments.

## **LMAN**

Within the model, LMAN provides both variability and an estimate of the ideal motor control program to RA. LMAN neurons are simulated using the expanded Brette-Gerstner model described earlier, but without plasticity or synaptic competition. The neurons are homogeneous in their parameter values, differing only in connectivity. In the absence of detailed electrophysiology information about LMAN neurons, the parameters for these neurons were chosen by hand so that each neuron, once triggered, fires a rapid burst of 3-6 spikes, consistent with the literature [2, 179]. The exact values for these parameters can be found in Table 4. Each LMAN neuron receives inputs from the full set of TM neurons and one single CM neuron.

The LMAN neurons preferentially tune to input from a single timing neuron, causing them to fire at a single specific time during singing. When a critic neuron in the CM sends an error signal to an LMAN neuron, the LMAN neuron randomly selects a new TM input to respond to. In this way, CM firing causes connected LMAN neurons to randomly produce a new firing pattern.

## **RA Neurons**

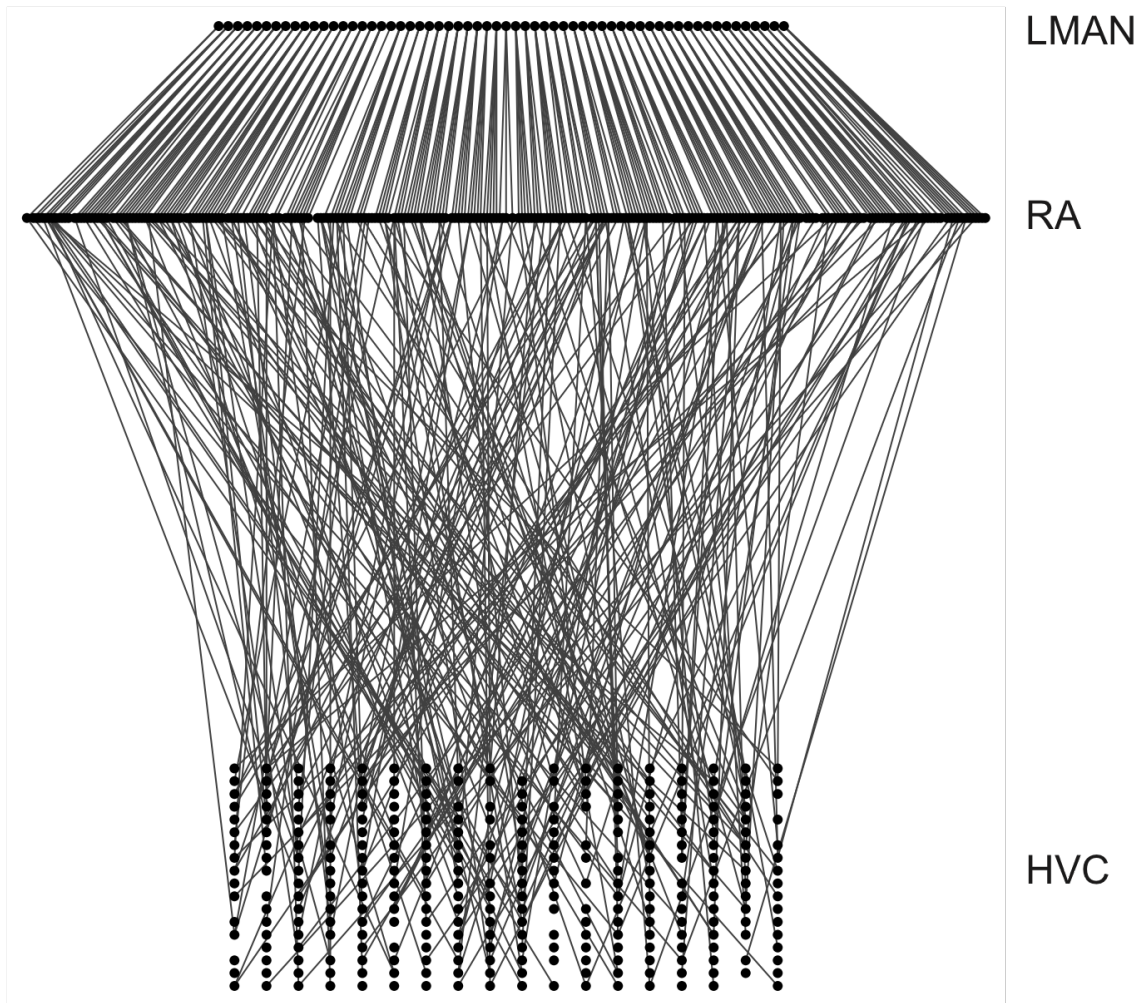
RA neurons produce the motor control program that represents the output of the simulation. RA neurons, like LMAN neurons, are simulated using the expanded Brette-Gerstner model described earlier, including plasticity and synaptic competition. Two classes of neurons are included in RA: excitatory projection neurons (RAP), and inhibitory interneurons (RAI). These classes differ both in connectivity and in parameter values.

**Table 4** Parameter values for LMAN neurons.

| Parameter                        | Value                 |
|----------------------------------|-----------------------|
| Neuron count                     | 60                    |
| Structure length                 | 0.35 mm               |
| <i>Soma</i>                      |                       |
| $E_L$                            | -70.6 mV              |
| $E_R$                            | -66.8 mV              |
| $g$                              | 30 nS                 |
| $\Delta_T$                       | 2 mV                  |
| $V_T$                            | -43 mV                |
| $V_F$                            | 20 mV                 |
| $C$                              | 281 pF                |
| $a$                              | 4 nS                  |
| $b$                              | 0.0805 nS             |
| $\tau_w$                         | 0.144 s <sup>-1</sup> |
| <i>TM</i> → <i>LMAN</i> synapses |                       |
| $A$                              | 100 s <sup>-1</sup>   |
| $B$                              | 200 s <sup>-1</sup>   |
| $k$                              | 35E-9                 |

The excitatory projection neurons, which in the zebra finch project to brainstem motor control nuclei, are the proxy output for the model, and also feed into the CM neurons. The inhibitory interneurons connect only to the excitatory projection neurons. Both classes receive inputs from HVC and LMAN (Figure 21).

For both classes of neurons, the two-equation Brette-Gerstner model used at the somatic compartment is effectively reduced to a single equation (for voltage) in order to improve computational speed and reduce the risk of parameter overfitting; the simplification eliminates firing-rate adaptation, however RA neurons do not generally exhibit a high degree of adaptation [79]. Remaining somatic parameters were chosen using numerical optimization techniques followed by manual adjustment in order to fit the neuron's behavior to the known behavior of RA neurons, namely the spike rate vs. current injection responses and the hyperpolarization responses following negative current injection as seen in the work of Spiro, Dalva, and Mooney [79]. Parameters for the time constants  $A$  and  $B$  in the dendritic compartment were arrived at similarly, by fitting a double-exponential curve to RA neurons' synaptic responses as described by Mooney and Konishi [81]. The dynamics of LTP and LTD for RA neurons have not been published, and so there was no guide for how these should be treated in the model. Parameters were thus chosen by beginning with the parameters used in Clopath *et al.* [187] and were adjusted by hand to produce results that provide a reasonable balance of LTP and LTD in the simulation. The final parameters for RA neurons used in the model are found in Table 5.



**Figure 21 Connectivity in the model. Connections between LMAN, RA, and HVC within the model. Connections shown are a random sample of the complete set. Both LMAN and HVC project to RA. Note the topological mapping between LMAN and RA, and the lack of topological mapping between HVC and RA.**

**Table 5 RA neuron parameters.**

| <i>Parameter</i>        | <i>Value</i>                 |
|-------------------------|------------------------------|
| RAP neuron count        | $0.968 \times 300$           |
| RAI neuron count        | $(1 - 0.968) \times 300$     |
| Structure length        | 0.5 mm                       |
| <i>Soma</i>             |                              |
| $E_L$                   | -67 mV                       |
| $E_R$                   | -67 mV                       |
| $g$                     | 32 nS                        |
| $\Delta_T$              | 4 mV                         |
| $V_T$                   | -60 mV                       |
| $V_F$                   | 20 mV                        |
| $C$                     | 200 pF                       |
| <i>HVC→RA synapses</i>  |                              |
| $A$                     | 700                          |
| $B$                     | 1000                         |
| $k$                     | 30E-9                        |
| $\tau_{\bar{x}}$        | 0.006 s <sup>-1</sup>        |
| $\tau_{nmda}$           | 0.1 s <sup>-1</sup>          |
| $\tau_{\bar{v}_+}$      | 0.006 s <sup>-1</sup>        |
| $\tau_{\bar{v}_-}$      | 0.007 s <sup>-1</sup>        |
| $\Theta_+$              | -67 mV                       |
| $\Theta_-$              | -45.3 mV                     |
| $A_+$                   | 7200                         |
| $A_-$                   | 3.5                          |
| <i>LMAN→RA synapses</i> |                              |
| $A$                     | 100 s <sup>-1</sup>          |
| $B$                     | 200 s <sup>-1</sup>          |
| $k$                     | 50E-9 for RAP, 30E-9 for RAI |
| <i>RAI→RAP synapses</i> |                              |
| $A$                     | 100 s <sup>-1</sup>          |
| $B$                     | 200 s <sup>-1</sup>          |
| $k$                     | -15E-9                       |

## **Generating the motor program and timing**

HVC, TM, and REF, whose firing patterns are scripted, drive singing in the model by producing their firing patterns in a synchronized manner. The length of the motor program is determined as a function of the number of teams of neurons in HVC and the firing rate of HVC neurons:

$$(\text{motor program length}) = (\text{HVC size}) \div (\text{HVC team size}) \times (\text{HVC firing interval})$$

This maximizes the length of the motor program while ensuring that there are no gaps in which no HVC neurons will be bursting. The above formula results in a motor program that is 0.08 seconds long. A pause of 0.1 seconds is inserted between iterations to simplify analysis and allow neurons to settle.

## **Variations on the model**

One major variation of the model is used in this chapter to test learning dynamics in the case where LMAN's biasing signal is precomputed rather than discovered through trial-and-error learning. In this variant of the model, the firing pattern for LMAN's timing-locked signal is provided to the model at the beginning of the run. During the run, LMAN neurons will fire either at their ideal time (from the time-locked pattern) or at another time, randomly chosen, with the probability depending on the ratio of timing-locked to timing-independent activity. In all other ways this version of LMAN is designed to emulate the behavior of the learning version of LMAN as closely as possible, changing firing times at the same intervals and firing with the same overall firing rate.



Because the biasing signal is provided to LMAN at the start of these runs, the simulation tends to produce a reasonable imitation of the reference pattern much faster. Subsequently, the rates of change for synapses in STDP were reduced and run length was reduced as well; these changes are seen in Table 6.

## RESULTS

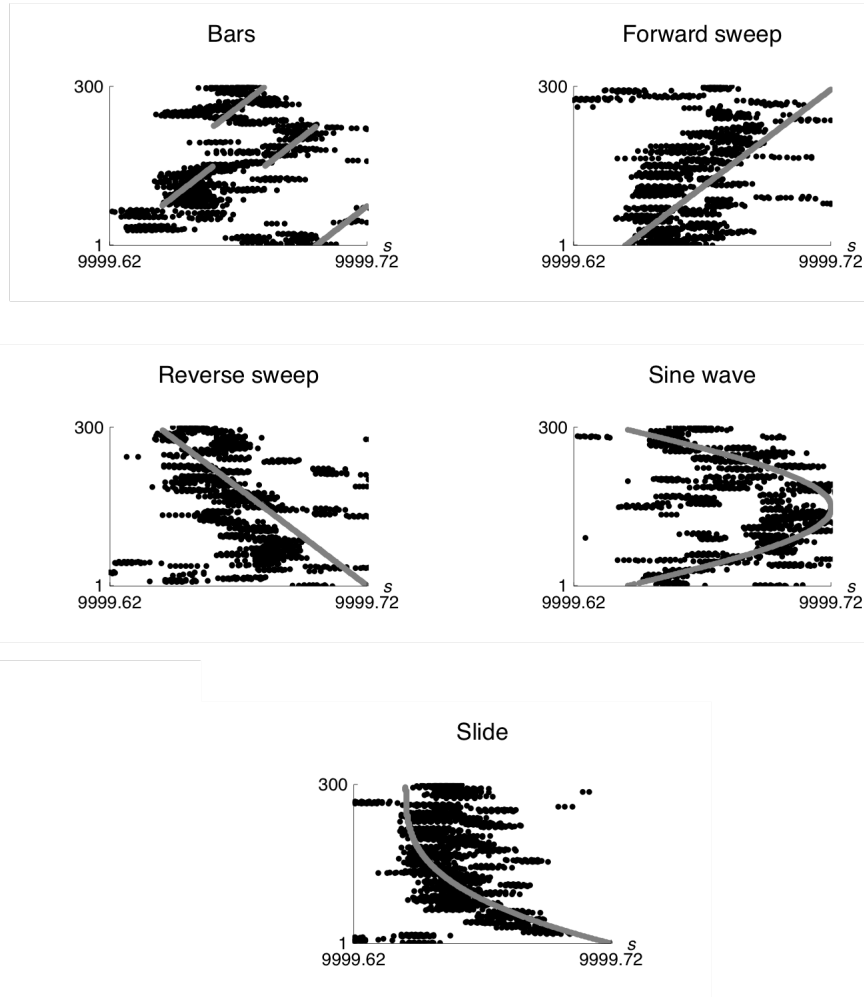
A critical test of our model, in which LMAN rather than the MCP is the recipient of the critic's output, is whether or not RA can be trained to emulate the template pattern generated by REF. To test this the model was run for 10 000 simulated seconds and the pattern produced by RA at the end of the run was evaluated. Because the length of the motor program is very short, 10 000 seconds of simulated time amounts to approximately 54 000 iterations. One 10 000-second run was performed for each of the five patterns that REF produces. As shown in Figure 22, by 10 000 seconds of simulated time, RA produces a reasonable approximation of REF's pattern in all five cases, although some patterns were better learned than others: the "sine wave" was the best-learned (error=16.1 milliseconds), and the "forward sweep" pattern was the worst-learned (error=24.0 milliseconds), with a mean error of 19.1 milliseconds. The error measure used here is the same as that defined in Equation 1.

Looking in more detail at the run from the "slide" pattern, we can see how the model improves its performance over time. At the beginning of the run the firing pattern produced by RA is effectively unrelated to the reference pattern. After 500-1500 iterations, an identifiable pattern has formed, albeit one not much like the

**Table 6 Modified RA neuron parameters.**

| <b>Parameter</b>                | <b>Value</b> |
|---------------------------------|--------------|
| Simulation run time             | 250 seconds  |
| <i>HVC</i> → <i>RA</i> synapses |              |
| $A_+$                           | 720          |
| $A_-$                           | 0.35         |

**These parameters are used for simulation runs in which LMAN is provided with the ideal firing pattern at the beginning of the run.**

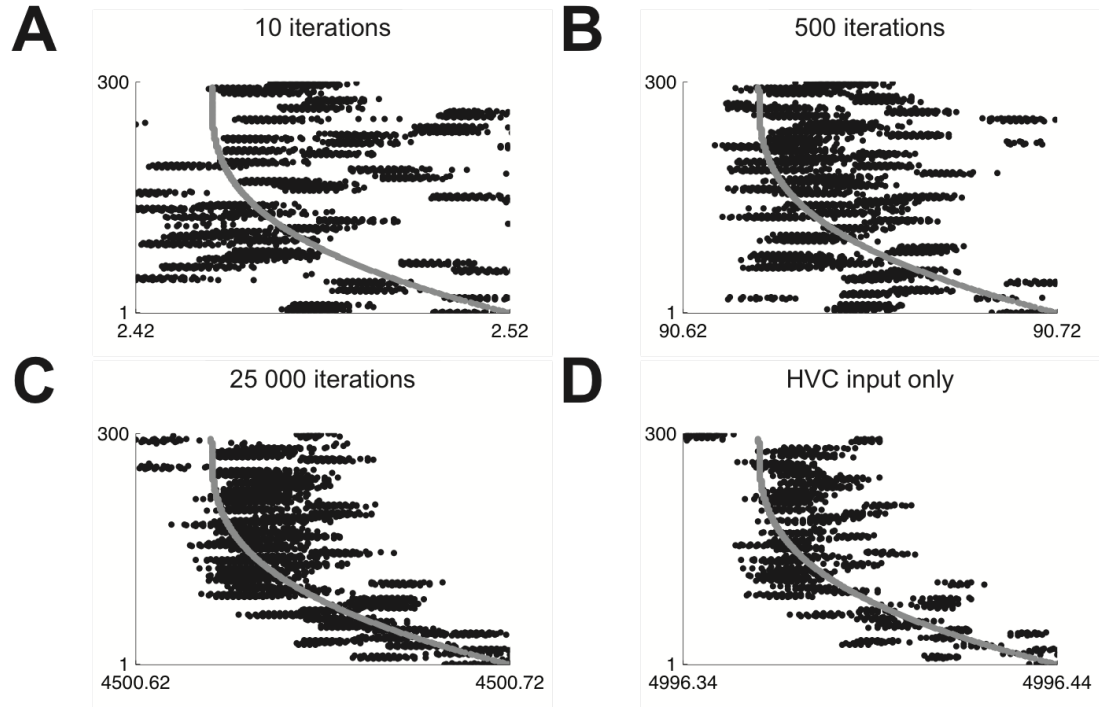


**Figure 22** The model can learn various reference patterns. Raster plots of the model after being trained on various reference patterns. Black points indicate RA firing times; gray points (appear as gray lines) indicate REF firing times. In this and following raster plot figures, the horizontal axis is time and the vertical axis is cell number.

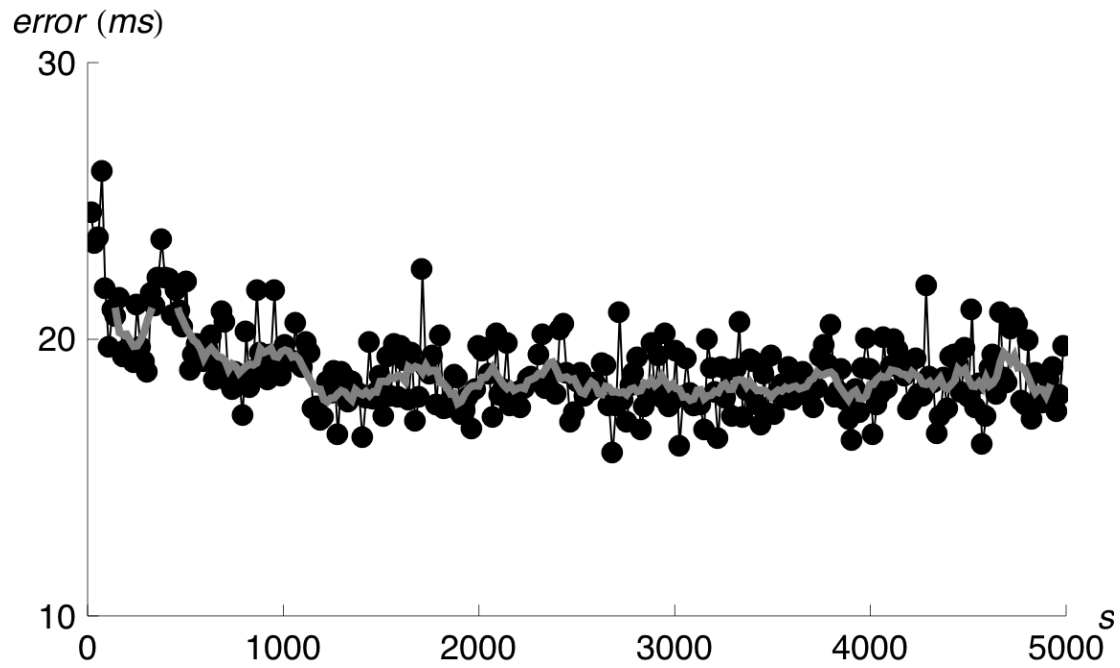
reference pattern. After 25 000 iterations, RA's firing pattern is a good approximation of the reference pattern. Figure 23 illustrates the patterns produced by RA at various time points, and Figure 24 shows how the error measure evolves over time. In general, the error declines rapidly at the beginning of the simulation, and then much more slowly past roughly 500 seconds; error does not decline monotonically however—there are many notable points in which error increases before decreasing again, as illustrated by the moving average curve shown in Figure 24.

How does the model learn? A key idea within the model is that repetitive signals from LMAN enable RA neurons to “pick and choose” amongst their inputs from HVC, strengthening those whose timing matches LMAN's input and attenuating the rest. A demonstration of this process can be found in Figure 25. At the beginning of the simulation run, all synapses for a neuron are weighted equally. Fairly quickly however, LMAN's inputs drive the RA neuron to focus on a very limited set of inputs: Figure 25A shows how a single RA neuron's synaptic weights begin evenly weighted but quickly become tuned to a very limited set of inputs. Figure 25B shows the synaptic evolution for a single RA neuron over a whole 5000-second run; because of the way the model works, synapses tend to stay stable for long periods, with interim periods of rapid synaptic change as the model repeatedly modifies the firing pattern of the connected LMAN neuron.

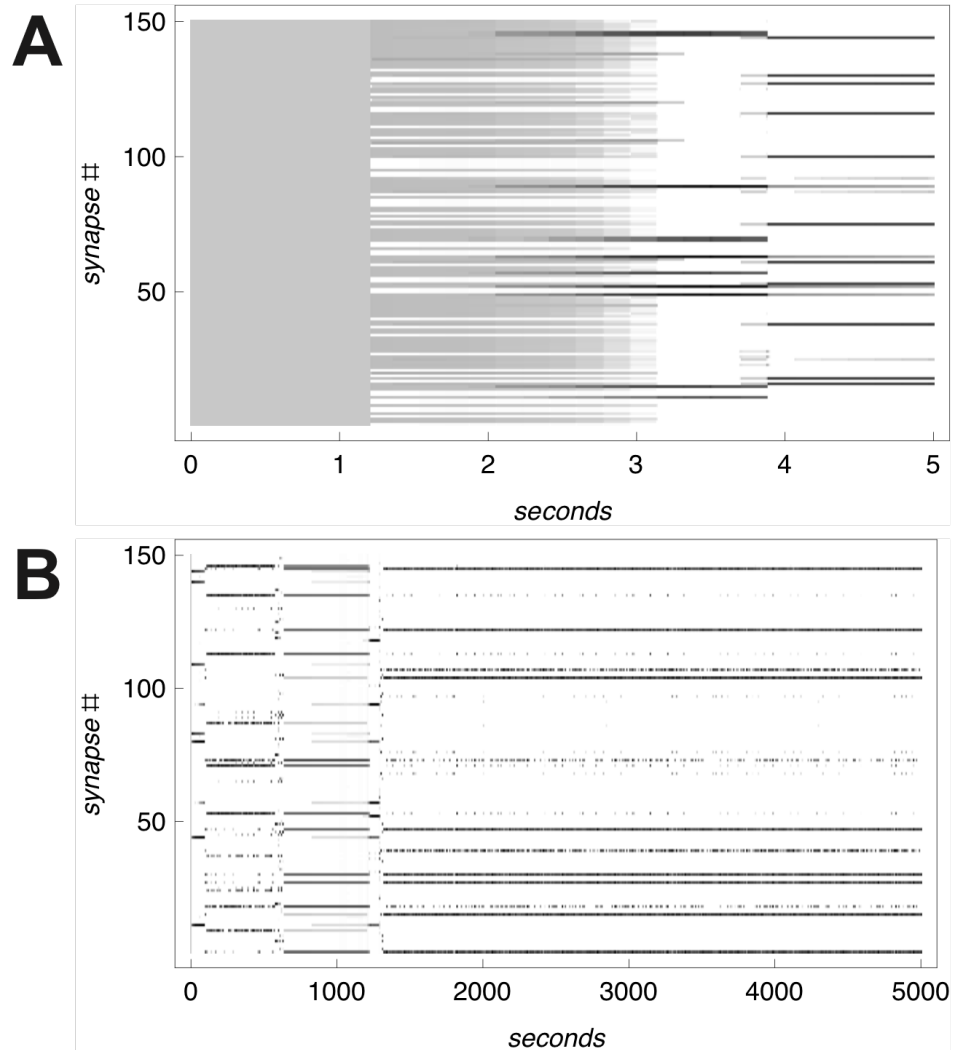
In mature birds, LMAN appears to have a greatly diminished role in driving song production [74], and studies indicate that in adults LMAN can be lesioned without severely impairing song production [98]. One test of the model then is the extent to which MCP can produce a learned pattern in the absence of LMAN.



**Figure 23** Details of learning progression in the model. X-axis in all plots is in seconds of simulation time. (A) Near the beginning of the run, the output pattern of RA (black points) is essentially unrelated to the reference pattern (gray points). (B) After several hundred iterations, there is evidence of consolidation but RA's firing pattern is still a poor match for the reference pattern. (C) After 25 000 iterations, RA generates a reasonable match for the reference pattern. (D) After more than 25 000 iterations RA is able to generate a reasonable match for the reference pattern even in the absence of input from LMAN, using only input from HVC.



**Figure 24 Evolution of error in the simulation. Error gradually decreases as the simulation learns to emulate the reference pattern. Black points indicate error of output pattern as evaluated at specific time, gray curve indicates moving average of error (10 samples/point).**



**Figure 25 Synapse evolution in the model.** Synapse evolution of HVC→RA synapses for two RA neurons, with one single neuron represented in each plot. Darkness at a point indicates synaptic strength, with white being minimal synaptic strength and black being maximal. Synapses are ordered arbitrarily along the Y-axis. (A) At the beginning of the simulation, all synapses are weighted equally; fairly quickly however, some synapses begin to be strengthened due to coincident LMAN inputs and the other synapses are weakened. (B) Over the course of an entire simulation run, the neuron's synapses experience long periods of relative stability with intermittent periods of instability. These periods of instability are caused by CM/LMAN targeting the relevant part of the song for improvement by testing alternatives.

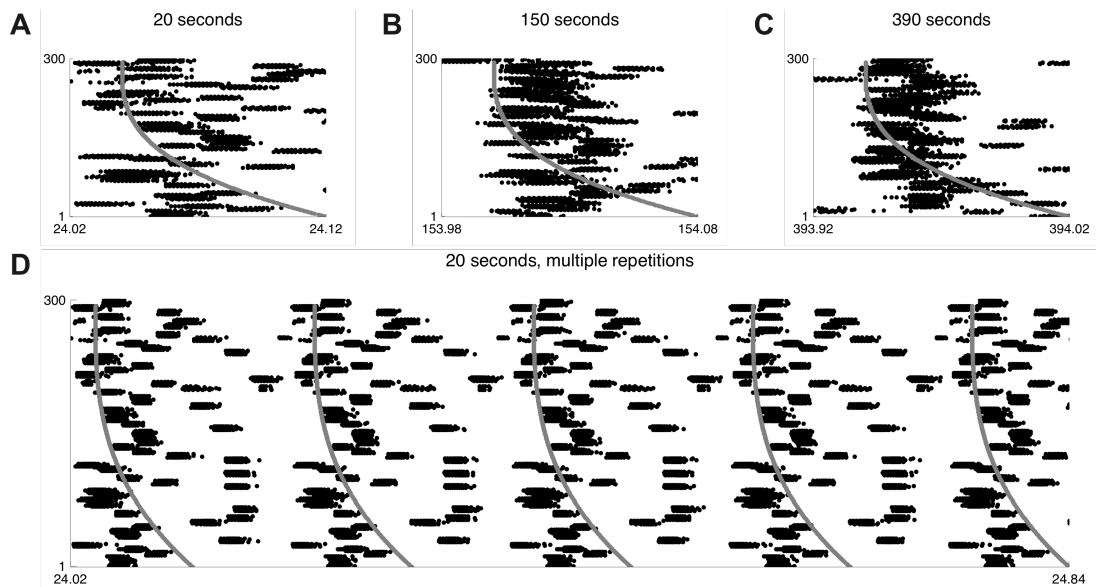
Multiple simulation runs were performed in which LMAN is shut off, by turning off TM, before the end of the run. The simulator was run for 2500 seconds, and LMAN was shut off five seconds before the simulation ended. This was equivalent to lesioning LMAN after approximately 14 000 iterations of the motor program. The resulting firing pattern is shown in Figure 23D, next to the firing pattern just before shutoff as seen in Figure 23C. The MCP clearly continues to produce a firing pattern very similar to the one it produced just before LMAN's shutoff. There is a notable reduction in RA activity, which is to be expected, as LMAN is no longer present to drive firing activity, but otherwise the pattern is still being generated; the pre-lesioning error was 17.9 milliseconds and the post-lesioning error was 19.2 milliseconds.

Simulated lesionings at other time points are shown in Figure 26. Generally, the later the lesioning, the better the firing pattern produced by RA. A very early lesion (20 seconds simulation time) resulted in a firing pattern that bore almost no resemblance to the reference pattern (error=24.4 milliseconds). As previously, consolidation of the firing pattern can be seen progressing over time (error=21.6 milliseconds at 150 seconds, error=17.1 milliseconds at 400 seconds). In each case, simulated lesionings resulted in the immediate fixation of the firing pattern produced by RA, as shown in Figure 26D.

### **Pattern stability in LMAN**

As noted by Leonardo [2] and by Kao *et al.* [179], a large percentage of activity in LMAN is independent of song timing. In our model timing-independent activity is created in parts of LMAN that are not temporarily stabilized, and by changing the

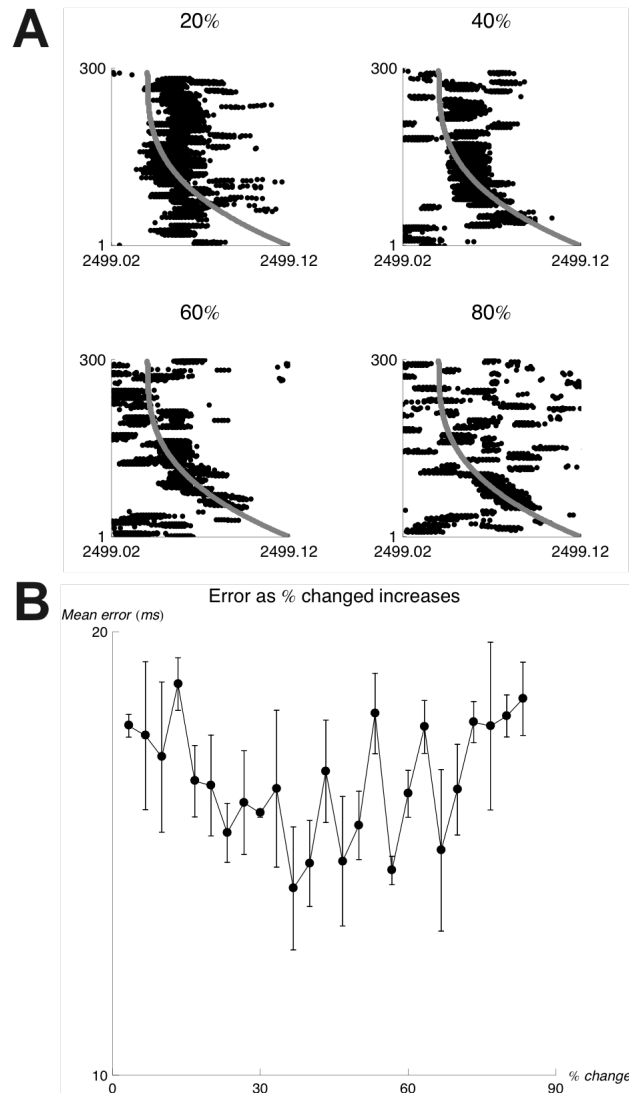




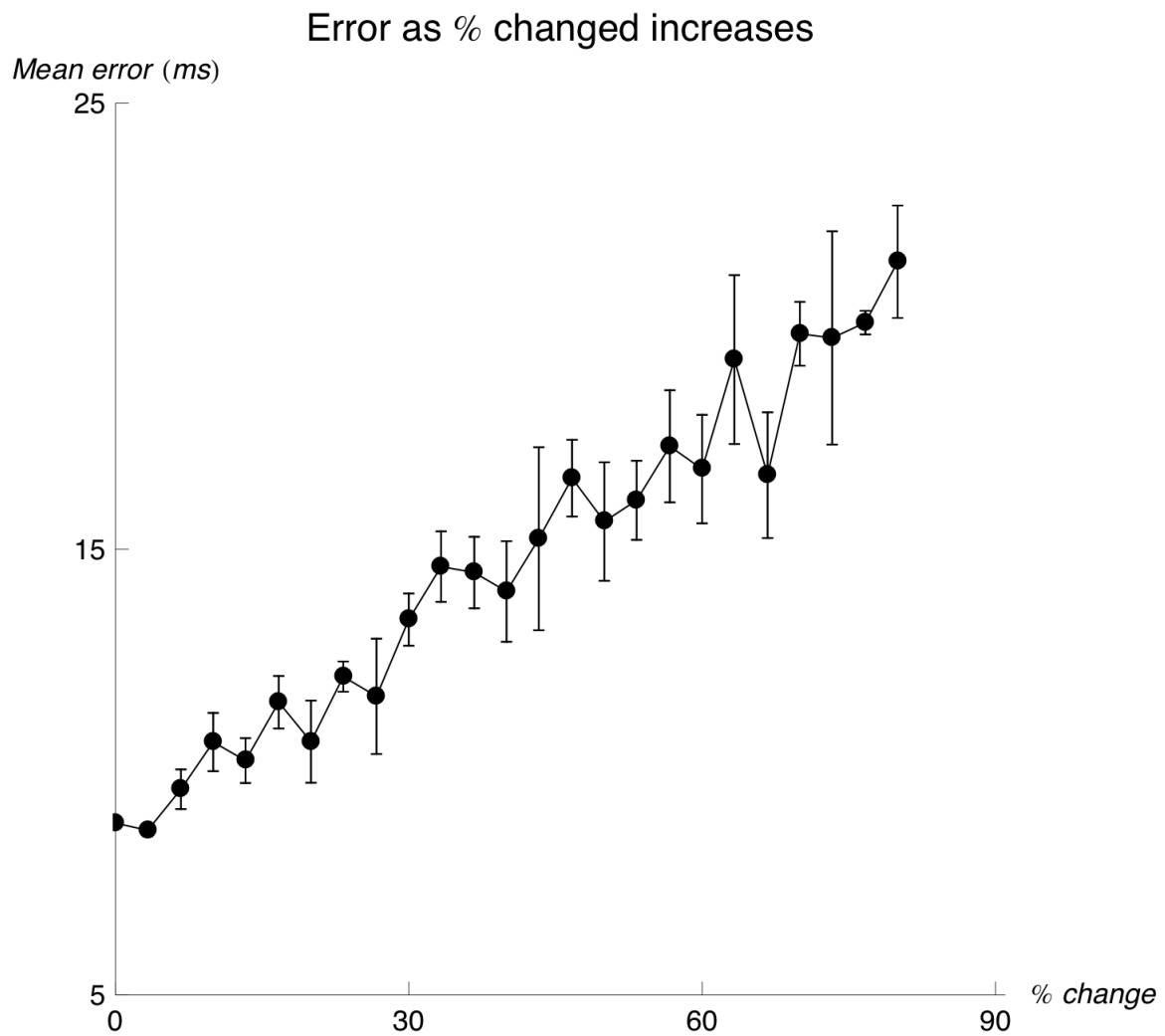
**Figure 26 Results of simulated lesioning experiments. Raster plots of RA cell activity after simulated lesioning. (A) If LMAN is lesioned very early, RA becomes stuck producing an essentially random firing pattern. (B-C) If LMAN is lesioned at later time points but before learning is complete, RA becomes stuck producing suboptimal firing patterns that are not good matches for the reference pattern. (D) After LMAN is lesioned, RA's firing pattern immediately becomes highly stereotyped, with little variability between iterations.**

percentage of CM neurons that fire at each evaluation the level of timing-independent activity (noise) in the model can be easily adjusted. The trivial edge cases, 0% noise and 100% noise, are obviously poor choices: 0% noise will result in an immediately fixed firing pattern in LMAN, preventing the pattern from ever improving, and 100% noise will prevent any pattern from ever forming. Somewhere in between these two points then there must be an optimal noise level or range of optimal noise levels for LMAN.

In the model, noise levels were adjusted in 3.3% increments, from 0% to 100%, and for each noise level the simulation was run for 2500 seconds. The patterns produced at the ends of these runs, after LMAN had been shut off, were evaluated. Figure 27A shows the effect of noise on the pattern produced by RA at selected noise levels. At 20%, the pattern is not well-learned although a definite consolidation of firing times has taken place. At 40% and 60%, the pattern produced is a good match for the reference pattern. At 80% noise, the pattern shows significant degradation. Figure 27B shows the error of RA's output as a function of noise level. There is what appears to be a wide "valley" of acceptable noise levels, between roughly 30%-60%; after 60% the error level begins rising, and below 20% there is a sharp increase in error. Results were substantially different in the case where the biasing signal in LMAN was not discovered through trial-and-error search, but was somehow computed directly. In this case, LMAN was given the correct firing pattern at the beginning of the run; during the run neurons would fire either at their ideal time or at another time, with the relative probabilities dependent on the ratio of timing-locked to timing-independent activity. This version of the model was tested over the same range of noise levels as above (Figure 28). Here



**Figure 27 Effect of noise in LMAN on learning. (A) Too little noise (20%) or too much noise (80%) both result in suboptimal learned patterns; however noise levels for a range of values (40%, 60%) all produce reasonably good learned patterns. (B) Error of learned pattern as a function of noise level. Noise levels above 60% or below 30% result in suboptimal learning; noise levels in the range of 20%-60% all produce roughly equivalent outcomes. Each point is the mean of 3 trials; error bars represent standard error.**



**Figure 28** Error of a learned pattern as a function of noise level. For these simulations LMAN was provided its firing pattern at the beginning of the run, representative of scenarios in which the biasing pattern in LMAN is computed directly rather than discovered through trial-and-error learning.

there was a strong inverse relationship between noise level and error in the learned motor pattern, with no or very little noise resulting in the best overall match with the reference pattern.

### **Offline learning and update frequency**

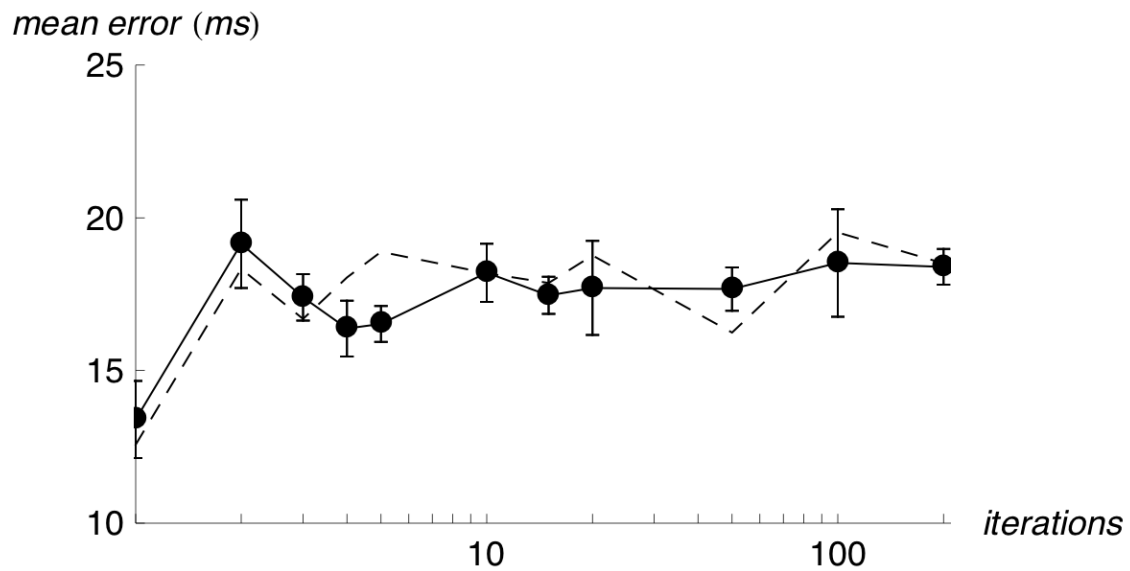
So far, the operation of the model has been framed in terms of a reinforcement signal stabilizing parts of the firing pattern of LMAN; an alternative would be to have a signal that actively destabilized LMAN's firing pattern. Although these two options are effectively equivalent within our model, in a real animal they could have substantially different implications. Because activity patterns could persist over longer time frames, such a mechanism could support a form of "offline" learning in which no immediate feedback into the song system during singing would be necessary for learning. One possible time for such offline learning would be during sleep: a considerable amount of activity takes place in the song system during sleep, including in HVC [123], RA [124, 126, 127, 189], and LMAN [117, 190-193], and according to one published result, a juvenile's song can degrade overnight [194], which is what one might expect if one were in fact destabilizing connections. An important question in a system that permits offline learning is how long the system can wait before evaluating performance. One would expect that updating LMAN's firing pattern could be done after almost any number of iterations, although in the extreme limit (i.e. never) this would end pattern improvement, and needlessly long delays before evaluating would slow learning. There may also be a lower limit on how often evaluation can take place—if it occurs more rapidly than the MCP has time to incorporate changes from LMAN's new firing pattern,

the output from the MCP may not reflect the pattern in LMAN and the critic would be unable to accurately evaluate the MCP's output. To test these ideas in the model, the interval between output evaluations was changed. Instead of the default (one evaluation per ten iterations of the motor program), other intervals were chosen, from 1 to 200. Models were run for 5000 seconds, and the output patterns after LMAN shutoff were evaluated. Results are summarized in Figure 29.

In practice, there was little apparent difference to be seen by changing update frequency, up to a very large update interval: above intervals of 150 or so iterations, a noticeable increase in both error and variability could be seen. The only update interval with a substantially different outcome was updating every single iteration, which resulted in noticeably lower error levels.

### **Search complexity**

One can consider each RA neuron, and therefore each LMAN neuron that influences it, to be randomly searching for its best possible firing time within the song; each neuron has a “search space” of all the  $n$  possible firing times it can choose from. Two neurons would have a search space of  $n^2$  possible configurations, three neurons would have a search space of  $n^3$  configurations, etc. As the size of the neuron group increases, the search space increases very rapidly. In the model this is dealt with in a divide-and-conquer fashion through a set of critic neurons, each of which governs the search for a small set of LMAN neurons, allowing a search on small subsets of the pattern rather than having to stumble across the whole pattern in one step. One would expect that as the number of critic neurons decreases, the speed of learning would also decrease, as



**Figure 29** Effect of critic evaluation frequency on learning. In general, extending the evaluation interval has little effect on learning efficiency. Solid line represents error at the end of each run (5000 seconds) with error bars indicating standard error; dashed line represents error at a mid-run time point (1500 seconds). Scale is logarithmic on the x-axis.

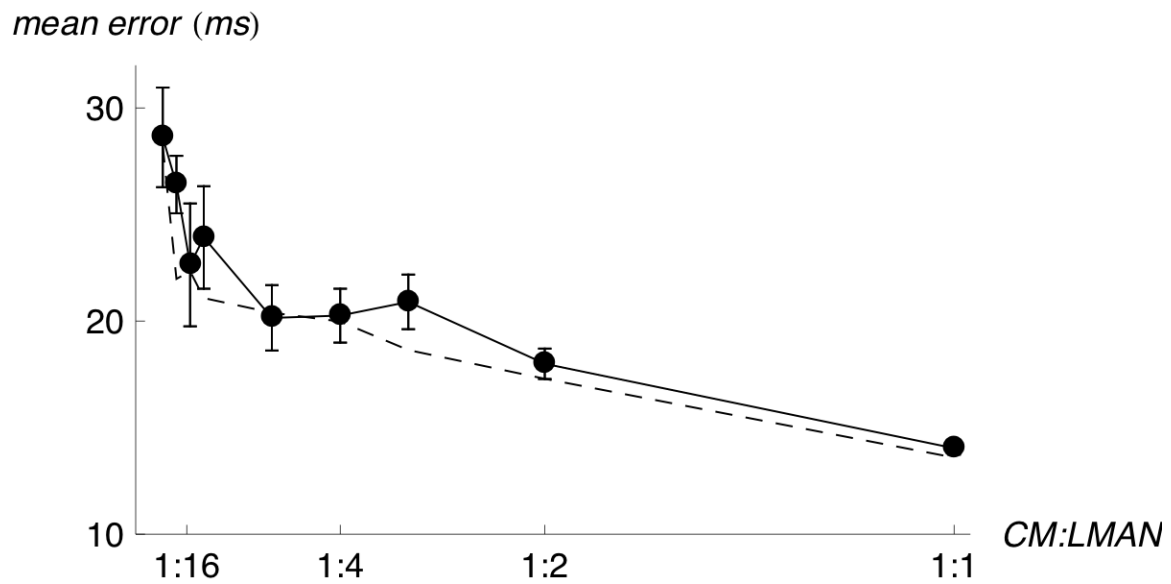
the search space for the set of LMAN neurons governed by each critic neuron increases. Is this so? To test this, the ratio of critic neurons to LMAN neurons was changed from 1:1 to 1:30. The results are shown in Figure 30 and indicate, as expected, that error declines as the ratio of CM:LMAN neurons approaches 1:1. Ratios of 1:5 or higher produce results that would generally be considered unacceptable (error > 20 milliseconds).

### **Alternate models of plasticity**

Within the model I have elected to use the synaptic plasticity model of Clopath *et al.* [187] although other choices exist, and the bursting behavior of RA neurons needed to be considered. LMAN, RA, and HVC all fire in bursts, and *in vitro* experiments suggest that postsynaptic bursting can change the dynamics of LTP/LTD. Two possible cases in the literature that dealt with plasticity and postsynaptic bursting were identified, albeit not in the avian song system. In one case, the authors described a general “LTP always wins” outcome [195]; in the other case, the authors described a more complex scenario in which high-frequency postsynaptic bursting resulted in an “LTP wins” outcome and lower-frequency bursting resulted in a “1<sup>st</sup> pair wins” outcome [196].

Because RA neurons are known to fire in rapid bursts, there is the possibility that a LTP-dominated plasticity mechanism may be at work at the MCP-AFP junction, instead of a STDP-type model that balances both LTP and LTD. One question was how the plasticity model of Clopath *et al.* [187] would respond to postsynaptic bursting. A simplified model composed of one RA neuron and one HVC neuron was set up, and the HVC neuron was scheduled to fire regularly. The RA neuron was also scheduled to fire

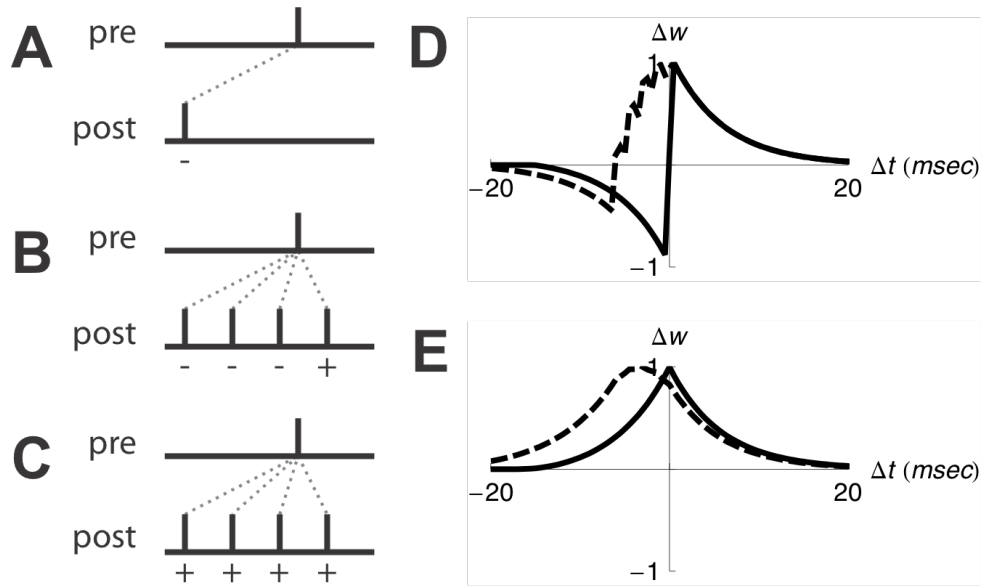




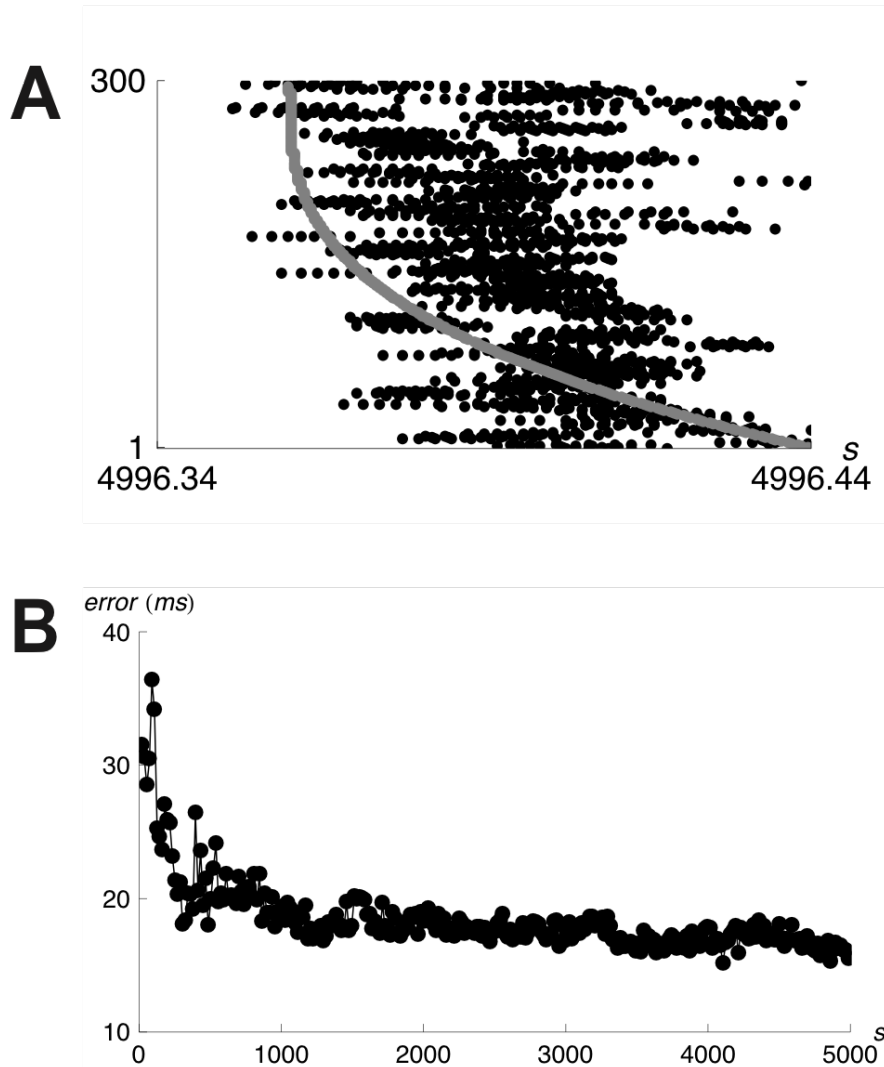
**Figure 30** Effect of changing the number of discrete critic modules on learning. Learning efficiency is reduced as the number of critic modules is reduced. Error bars indicate standard error, dashed line indicates error at a mid-run time point (1500 seconds).

regularly, anywhere from -20 to +20 milliseconds relative to the HVC neuron, with either a single spike or a rapid burst of five spikes. The relative synaptic weight change under various time differences for either single-spike or bursting postsynaptic responses was measured. The results are shown in Figure 31. With a single postsynaptic spike, the model of Clopath *et al.* performs exactly as a canonical STDP model would: strengthening HVC inputs that come before the postsynaptic firing, and weakening HVC inputs that come after the postsynaptic firing. With a postsynaptic burst however the model of Clopath *et al.* changes somewhat, so that in many cases there is still a strengthening of the HVC input even when it arrives after the RA neuron fires. In broadest terms, postsynaptic bursting has changed the behavior of the model of Clopath *et al.* from one that rewards predictions to one that rewards coincidence, and pushed the model towards a “LTP wins” outcome.

Despite this result, there was still concern that the Clopath *et al.* [187] model may not adequately capture the effects of a LTP-dominated plasticity model. An alternate model was tested, described in the methods, which was similar in spirit to the model of Clopath *et al.* but which implemented a “LTP wins” policy. Running the same simulation but with this alternative model produced results that were different from those produced via the model of Clopath *et al.*: the reference pattern was not learned particularly well (error=22.8 milliseconds), as shown in Figure 32A. The learning trajectory was also substantially different, with improvements in the score occurring in significant “leaps” rather than gradually, as shown in Figure 32B.



**Figure 31** Alternative possibilities of how plasticity handles postsynaptic bursting. (A) Single presynaptic spike follows postsynaptic spike, triggering LTD in the typical logic of STDP. (B) Single presynaptic spike is preceded by three out of four spikes of a postsynaptic burst. Under standard STDP logic, the three preceding postsynaptic spikes would result in LTD, and the one following postsynaptic spike would result in LTP. (C) Experimental results [195, 196] have indicated that in some circumstances postsynaptic bursting can result in a "LTP dominates" outcome. (D) Clopath model response to single pre-post pair (solid line) and postsynaptic burst of five spikes (dashed line). Postsynaptic bursting partially, but not fully, moves the model's response from standard STDP logic towards a "LTP dominates" logic. (E) Coincident model response to single pre-post pair (solid line) and postsynaptic burst of five spikes (dashed line). This model has been designed to result in "LTP dominates" logic under all circumstances. In (D) and (E), each curve has been scaled to reach a maximum value of 1.0, and time is relative to the first spike in the postsynaptic burst; the first postsynaptic spike is at  $\Delta t=0$ .



**Figure 32** Model performance using the “coincident” plasticity model. (A) Learned pattern in RA at 5000 seconds, after LMAN output to RA has been shut off. (B) Learning trajectory is considerably different from that seen with the plasticity model of Clopath *et al.*

## **DISCUSSION**

This chapter presented a computational model of part of the song learning process that can account for observations about the oscine song learning system that no previous model has: namely, the lack of an apparent reinforcement signal in RA/HVC, and the intriguing observation that some, but not all, of LMAN's activity is time-locked to the bird's song.

Computational simulations performed with the model demonstrate that, in principle at least, such a system can learn to produce a desired pattern; that after a sufficient learning period the pattern can be produced without input from the AFP, in accordance with existing lesioning studies; and that the pattern can be learned even in the face of considerable random activity within LMAN.

### **Noise and pattern stability within LMAN**

One interesting result of the model, and its key prediction, is that there is a range of timing-locked levels in LMAN that are better for learning: our model predicts an ideal noise level of 20%-60%, in contrast with Leonardo's ~70% noise level [2]. Why the discrepancy between our model's predictions and observed results? The age of the bird may be relevant. While the nonrandom activity in LMAN may be very low in young juveniles, who have not begun producing syllable-like sounds, and low again in adults, who may no longer be using this mechanism extensively, there may be a peak age during song learning when this nonrandom activity would be measurably higher. In contrast, the birds studied by Leonardo were fully grown adults and had already learned their songs [2]. Another possibility is that a larger number of neurons

in LMAN and/or RA would mitigate some of the effects of noise, as some noise could be averaged out across a larger number of synaptic inputs. Regardless, the actual proportion of timing-locked activity in LMAN should be directly observable in juveniles using the same methods Leonardo [2] and Kao *et al.* [98] used in adults.

Two related predictions of the model may be more difficult to test experimentally. The first prediction is that the timing-locked signal should be remodeled over time, but not immediately, in response to vocal errors. It is difficult to see how this could be tested with current tools, as it would require monitoring the activity of single neurons or small groups of neurons within LMAN over a period of multiple days. It's possible however that localized groups of neurons within LMAN may share timing-locked activity patterns, in which case feedback-manipulation experiments may be able to examine this. The second prediction is that the maintenance of the bias signal in LMAN is dependent on vocal variability. Assuming the previous experiment was possible, this prediction should be testable through feedback manipulation also. A possible experiment might take the following form: a bird would be recorded singing and then surgically silenced. A modified version of its recorded song would be played to the bird whenever it attempted to initiate singing. Because this modified song would lack any variability, the bird could be effectively denied feedback about variations without direct interference (e.g. lesioning or drugs) with the function of the song system. I would hypothesize that in such a situation the timing-locked firing pattern in LMAN would not change to reduce errors in singing, although it may change in other ways.

In versions of the model in which the timing-locked pattern in LMAN was precomputed the variability produced by LMAN was strictly deleterious to the learning process; in such a system the optimal strategy would be to eliminate all variability as soon as the biasing pattern in LMAN had been established. As both the timing-locked and timing-independent components of LMAN's activity persist into adulthood [2, 98], it would appear that the version of the model that is most parsimonious with LMAN's known behavior would be that in which the biasing signal is established through trial-and-error learning.

### **Offline learning**

The idea of a destabilizing signal that permits offline learning, rather than a stabilizing (reinforcement) signal, has considerable appeal, but it also comes with some significant drawbacks. In its favor, it provides an explanation for why an immediate auditory feedback mechanism in the song system has never been clearly identified; it also provides a compelling explanation for why neural activity during sleep should change activity patterns and even degrade song. Against this hypothesis however is the fact that neural firing patterns observed by Kao *et al.* [98] and Leonardo [2] appear largely unstable over short timescales. One possibility is that this stability is not on-off but a matter of degree; in such an instance intermediate stability would be difficult to measure and might not be apparent in the way Leonardo measured the proportion of timing-locked activity. It may also be the case that both stabilizing and destabilizing mechanisms may be at work.

The other major hurdle with a destabilization mechanism is to then explain how things become stabilized in the first place. One can imagine at least one mechanism by which such a random selection takes place, in which an LMAN neuron receiving a randomly-timed plasticity-inducing signal, along with a number of time-locked inputs, would rapidly adjust its synaptic weights among the time-locked inputs to match the timing of the random input. This random signal could be external to LMAN, or internal to it, as suggested by recent experiments [197].

### **Search complexity**

A consequence of the model's structure, as presented here, is the need for a fairly fine-grained critic that can analyze the performance for specific parts of the motor program, rather than the song as a whole. As shown in the results, the less granularity the critic has and the greater the size of the search space, the longer it will take the system to learn. This may be essentially correct: perhaps the critic, whatever it is, does have a fine-grained evaluation ability; some evidence exists to support this hypothesis [185]. Another possibility is that the number of degrees of freedom in the search space may actually be fairly low. Although our model makes no attempt to “sing”, models that have, such as that of Fiete *et al.* [154] and Doya and Sejnowski [147] have singing systems with a very low number of parameters, typically about four or so. While these singing systems seem somewhat unrealistic in their details, the fact that they can emulate a bird's song with so few parameters suggests the possibility that the bird's own singing system (i.e. its syrinx) has relatively few “parameters”—indeed, the oscine syrinx has only six pairs of lateralized muscles [50], although tracheal and respiratory



coordination would also be necessary. If the effective number of degrees of freedom for producing song is small enough then the search space may still be small enough to explore efficiently, even if the critic's signal is not very fine-grained. There is also the possibility that the search is not actually random, but may be directed or constrained in some way—for example, the timing window that each LMAN neuron can explore may shrink over time, thus helping to “focus” the search, in a manner analogous to simulated annealing.

### **Alternate models of plasticity**

As mentioned in the introduction, the LTP and LTD dynamics of RA neurons has not been adequately studied, so choosing a plasticity model is essentially a guessing game. While the model of Clopath *et al.* [187] provides a Hebbian-like logic using what I feel is a plausible abstraction of biological processes, it may be substantially different from what occurs at RA's synapses. There was particular concern about possible LTP-dominated effects of postsynaptic bursting that would substantially change the logic of synaptic plasticity. What was discovered is that an alternate model of plasticity, the rules of which were quite different from traditional STDP, was also broadly usable in the model: although the “coincident” model as tested did not perform as well as the model of Clopath *et al.*, it clearly made progress on learning the reference pattern, and minor adjustments to parameters or to the model itself might have resulted in improved performance. Many specific Hebbian-like models of plasticity may be workable within the larger model, and the exact choice of model may not be critical. To

the extent then that RA synapses are governed by Hebbian-like logic, the results shown here should not be overly dependent on the plasticity model used.

### **Limitations of the model**

How plausible is this model? Obviously its implementation represents an abstraction. In several key ways, the model takes “shortcuts” in order allow direct manipulation of key variables and, just as importantly, to avoid overspecifying structures and processes that are not well understood. The four primary abstractions in the model are: the source of the critic’s performance information, the ability of LMAN neurons to randomly tune to specific inputs, the algorithmic manner in which CM changes LMAN’s firing pattern, and the sources of timing and random information that LMAN uses.

One major simplification is direct RA→critic feedback loop. While there is almost certainly an analog to the reference signal (see Adret [27] for a review of current hypotheses), it is almost certainly not the case that RA’s output is being evaluated directly; instead it seems clear that the bird should ultimately be evaluating its own singing, and studies in which birds are deafened indicate that hearing one’s own performance is essential for song learning [39]. Within the model, the recurrent loop from RA to the critic neurons should not be taken literally, but as a representation of a singing-hearing loop that eventually delivers a signal to the critic.

The method used by CM/LMAN to selectively stabilize and destabilize parts of LMAN is also very simplistic. The method is algorithmic in flavor, maintaining a constant proportion of stable activity in LMAN and destabilizing the parts of LMAN with

the highest errors; as currently realized in the model, the selective stabilization mechanism requires that each LMAN neuron can have only one correct firing time during the motor program. It is unlikely that such a mechanistic method would be realized within an avian brain, the essential feature of the method—selective stabilization of LMAN's activity—could be realized through localized targeting of plasticity-regulating neuromodulators such as serotonin or dopamine. Such a mechanism would overcome the limitations of our method and be preferable in practice, although for our purposes it could also make setting arbitrary ratios of timing-locked and timing-independent activity difficult.

While I feel the “working copy” hypothesis has merit, and can explain the apparent mixture of timing-locked and timing-independent activity in LMAN, other possibilities cannot be ruled out. It is possible, for example, that the timing-independent activity seen in LMAN is used to generate a reverse mapping between vocal output and motor commands, which is then used to directly generate the optimal pattern of biasing activity in LMAN. The results presented here suggest that in such a case it would be counterproductive to continue producing noise once this bias has been established, but limitations may require it: LMAN may be unable to stop producing noise, for example. I also feel that the observed dynamics of syllable development, in which syllables are actively remodeled in small, local time changes [20, 183], is consistent with our idea of an actively changing “working copy” although considering the vast numbers of unknowns involved this could probably support any number of hypotheses.

## **On the utility of computational models**

This chapter has presented a model that attempts to link established observations about neurophysiology and animal behavior to a possible mechanism for song learning. Other models, from other researchers, have been discussed that make different assumptions and have different mechanisms but which also seem plausible. Which of these models is right, or at least less wrong? To quote George Box, “all models are wrong but some are useful.” Each of these models tries to explain a particular set of phenomenological details, and each comes to different conclusions about the likely circuitry and processes involved in singing.

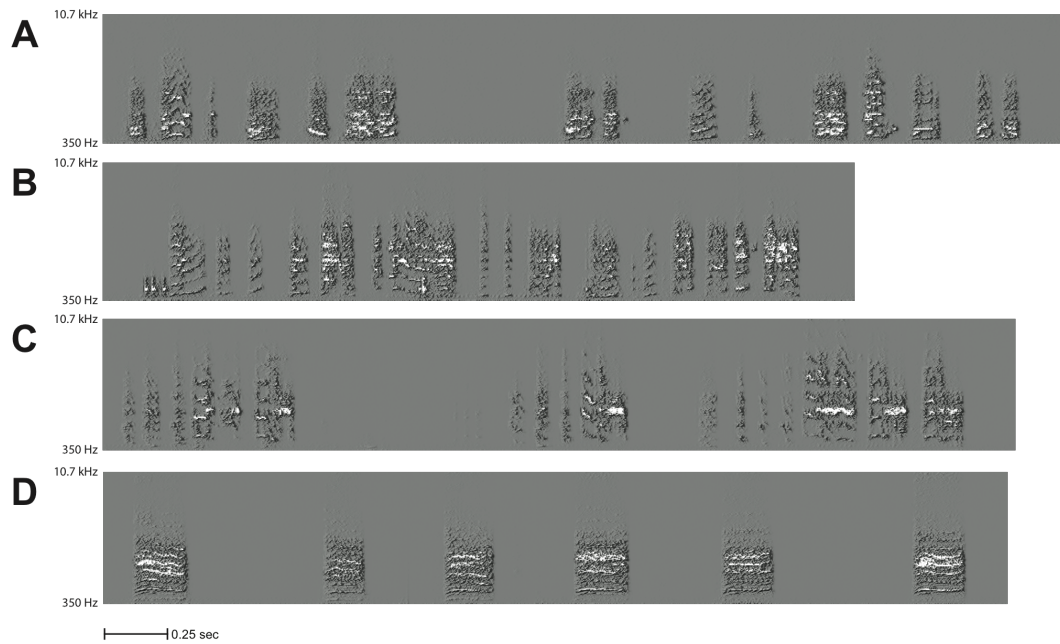
At the very least, this should be a humbling reminder of how little is understood about a process that would seem on the surface to be as well suited for study as one could reasonably hope. Somewhat more usefully, one would hope that this proliferation of models would serve as a guide and source of ideas for researchers studying the song learning system: finding the source and nature of the feedback mechanism, be it error signal [34], reinforcement signal, or another form, would be a boon not just for the birdsong community, but for those studying the neurological bases of learning in general.

## **CHAPTER 4: QUANTITATIVE TOOLS FOR EXAMINING THE VOCALIZATIONS OF JUVENILE SONGBIRDS**

In the course of our research, we have at times wanted a tool to identify and compare juvenile vocalizations, primarily to assist in the sorting of large numbers of recorded samples. Although a number of tools exist to compare the songs of adult birds, we have found that due to the low stereotypy of juvenile singing these tools do not perform well on samples from juveniles (Figure 33).

The simplest method of comparing song samples is to calculate some measure of correlation between samples, either on their waveforms or spectrograms. This method is employed by several popular tools [198, 199], but works adequately only if the sounds being compared are very similar in timing, ordering, and tone. A related technique is Dynamic Time Warping (DTW) [200], which can compensate for differences in timing but not ordering. Another strategy, used by at least one popular tool [201], might be described as heuristic feature analysis. A set of measures (e.g. peak frequency, frequency modulation, spectral entropy) is used to characterise a sample, and these measures are used to compare two samples according to some set of criteria. Although these tools typically do not require the samples being compared to be highly similar, it has been our experience that with juvenile vocalizations these methods can produce similarity scores that vary greatly between pairs of samples that, to a human observer, appear more or less equally similar.

The key feature that all these existing methods have in common is that they are designed to compare one single sample against another single sample. For highly stereotyped adult birdsong, this approach makes perfect sense, but for juveniles it may



**Figure 33 Lack of stereotypy in juvenile song. (A) Spectrogram of a juvenile's vocalizations produced during the babbling phase, at approximately 36 days post-hatch. Note the general lack of stereotypy. (B) Spectrogram of a juvenile's vocalizations produced during the early plastic song phase, at 41 days post-hatch. (C) Spectrogram of a juvenile's vocalizations produced during the plastic song phase, at 47 days post-hatch. Although the sounds are more adult-like in terms of spectral profile, they still lack the stereotypy of adult birds. (D) Composite spectrogram of a series of calls from a juvenile zebra finch (40 days post-hatch). By eye and by ear these are easily differentiated from adult song.**

not be appropriate: the high variability of juvenile song means that two samples from the same bird, taken seconds apart, may not be "similar" in any reasonable sense, and yet both are representative of that animal. With a large enough sample set, however, we should be able to identify all the characteristic sounds produced by a bird and be able to describe new samples in terms of how typical they are, even if the new sample does not seem particularly similar to any other sample.

In this chapter we present a new method for comparing a sample of juvenile birdsong against a model built from a set of training samples. We call this method Windowed Spectral Pattern Recognition (WSPR). This method provides a measure of typicality for comparing test samples to the training samples. We show that WSPR is effective as a classifier, and may be better suited to this task than another popular tool. We also show that WSPR is relatively robust to changes in a key parameter. Lastly we demonstrate that the models produced by WSPR can be used to provide measures of song ontogeny, stereotypy, and complexity.

## **METHODS**

### **Housing and care of juvenile zebra finches**

Audio recordings from three juvenile male zebra finches provided the data used in this chapter. From hatching until 25 days post-hatch, the juveniles were housed with their mothers, fathers, and clutch-mates in a family setting. From 25 days to 35 days, the juveniles were housed in small cohorts of 2-4 individuals along with an adult tutor. From 35 days to between 50 and 60 days, the juveniles were housed singly in auditory isolation chambers. At all times the juveniles were given food and water *ad libitum*. The

juveniles were cared for in accordance with the standards set by the American Association of Laboratory Animal Care and Rockefeller University's Animal Care and Use Committee.

### **Recording of juvenile birds and manual identification of samples**

Continuous recordings were made of three isolated juvenile male zebra finches from 35 days post-hatch to 60 days post-hatch with Behringer ECM-8000 measurement microphones (Behringer International GmbH, Willich, Germany) and Rolls MP13 preamplifiers (Rolls Corporation, Murray, UT). A MCC PCI-DAS6013 digital acquisition card (Measurement Computing Corporation, Norton, MA) was used to digitise the audio inputs. Recordings were made at 44.1kHz, 16 bits/sample, and stored as lossless FLAC [161] files.

We examined recordings with Audacity sound editing software [202] and manually identified vocalization bouts as being calls, song, or neither. Vocalization bouts identified as calls or song were eliminated if they contained excessive levels of spurious noise—flapping of wings, footfalls on metal bars, and the like—or if they were less than one second long. 2026 samples were taken from the three birds. Each bird's samples were assigned to one of four different sample sets: song training, song testing, call training, and call testing.

### **Binary classification of juvenile vocalization samples**

For each bird, a binary classifier was constructed using the WSPR algorithm for classifiers described in the appendix. The classifier contained one model for song, built



from the song training samples, and one for calls, built from the call training samples. The parameters used in the construction of these models are found in Table 7.

All testing samples were presented to the classifier. Samples were assigned to a group by the classifier, and the Matthews correlation coefficient (MCC) [203] was used to assess the accuracy of the assignments. The number of samples used as training and testing data for each bird, as well as mean sample lengths, are given in Table 8.

For comparison, Sound Analysis Pro (SAP) [201] was also used to classify samples from the first bird. From the 466 original samples, two hundred were randomly chosen, with fifty from each of the four sample sets (song training, song testing, call training, call testing). The samples were loaded into the SAP software and run in a series of pairwise comparisons using SAP's "batch similarity" tool, so that each test sample was compared against one training sample from the "call" set and one training sample from the "song" set. SAP's volume threshold was reduced but otherwise was run with all settings at their default values. The calculated similarity scores were then exported from SAP for statistical analysis.

When used as a classifier, the same classification method described in the appendix ("Classification using multiple models") was used on the SAP scores, with the exception that the SAP-generated scores were used in place of the algorithm's raw scores.

### **Measuring song ontogeny and stereotypy**

Recordings from the juveniles examined previously were taken and for each bird two models were made: an early model, consisting of the earliest 100 song samples; and

**Table 7 Parameters used in all examples, unless specified otherwise.**

| <b>Parameter</b>                  | <b>Value</b>            |
|-----------------------------------|-------------------------|
| STFT window width                 | 500 samples (11.6 msec) |
| STFT step size                    | 100 samples (2.9 msec)  |
| STFT bandpass cutoffs             | 500 Hz – 7500 Hz        |
| Model window width                | 11 symbols (34.0 msec)  |
| Number of power spectra clustered | 7 500                   |
| Number of prototypes generated    | 120                     |
| Silence cutoff level              | 0.01 (arbitrary units)  |

**Table 8 Summary of sample set sizes used to build and test models.**

|                                     | <b>Bird 1</b> | <b>Bird 2</b> | <b>Bird 3</b> |
|-------------------------------------|---------------|---------------|---------------|
| <b>Total samples</b>                | 466           | 569           | 991           |
| <b>Manually classified as song</b>  | 166           | 150           | 500           |
| <b>Manually classified as calls</b> | 300           | 419           | 491           |
| <b>Used as song training data</b>   | 50            | 100           | 150           |
| <b>Used as call training data</b>   | 100           | 150           | 150           |
| <b>Used as song testing data</b>    | 116           | 50            | 350           |
| <b>Used as call testing data</b>    | 200           | 269           | 341           |
| <b>Average sample length, song</b>  | 4.5 seconds   | 1.1 seconds   | 0.4 seconds   |
| <b>Average sample length, call</b>  | 1.8 seconds   | 1.1 seconds   | 0.8 seconds   |

**a late model, consisting of the latest 100 song samples. The remaining samples from each bird were grouped by day and scored against the models.**

For one juvenile, all samples were grouped into blocks of five consecutive days each and models were generated for each group, and the standard error of the non-standardized scores samples used to build the model against the model were calculated.

### **Testing the effects of parameter selection on score distributions**

Fifteen models were built with varying numbers of prototypes: 10, 20, ..., 150. All models were built using the same set of song training data for the first bird as described previously. Except as noted in the results, the WSPR parameters are found in Table 7. Each sample from the first bird's song test data was scored against all 15 models. Means and standard deviations were calculated for the scores from each model.

### **Estimating the stereotypy and complexity of sample sets**

Additional recordings were made of an adult zebra finch, over 100 days old, with equipment and conditions identical to those used for the juvenile recordings, except that the DAQ digitiser was bypassed and the computer's built-in audio input was used instead. One hundred samples of adult song were manually identified and extracted from the recordings. For each of the three juvenile birds, the WSPR algorithm was used to generate separate models for song and calls on all available samples, including both training and testing data from the earlier experiments. For the adult bird a model was generated for its song on the 100 collected samples. For all models, all samples were concatenated and the combined samples were truncated to a length of exactly two million audio samplings (approx. 45 seconds); each model was built from its corresponding concatenated sample. All samples were scored against the models they

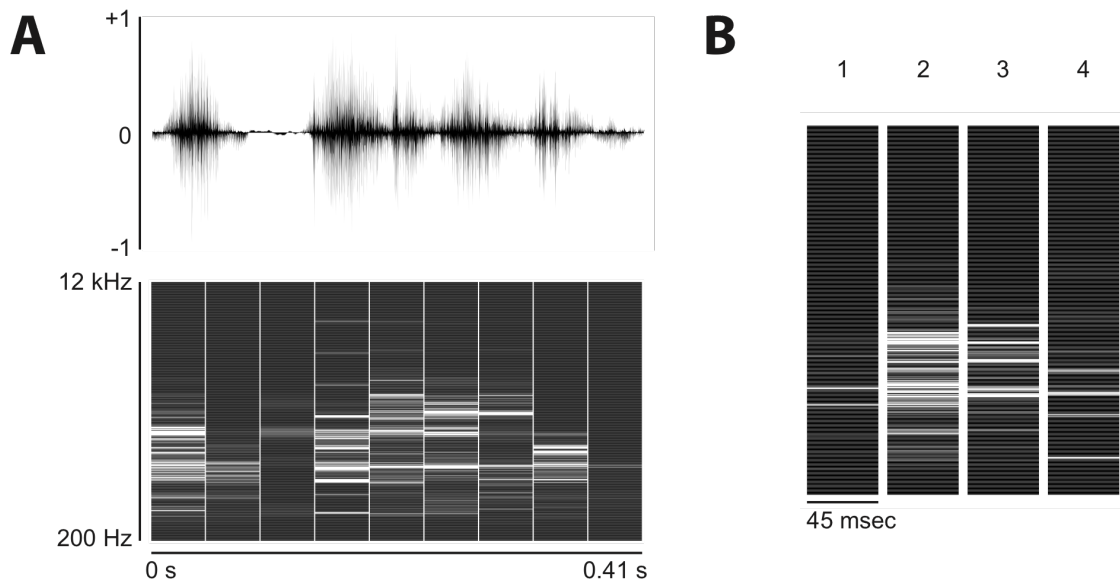
were used to train, and the standard deviations of all scores against each model were calculated. The models were generated using the parameters found in Table 7, with the following exceptions: STFT window width, 4096 samples; STFT step size, 1024 samples; model prototypes, 50; model window width, 25. The WSPR complexity of each model was also calculated according to the algorithm found in the appendix (“Calculating the complexity of a model”).

## **RESULTS**

### **Building a model using the WSPR algorithm**

Model building is composed of two discrete steps: creating an encoding, and producing the tables of observed frequencies of patterns. To create an encoding, a set of 100 samples of juvenile plastic song was taken from a single individual. Samples were converted from digitized waveforms into a frequency-vs-time representation (a spectrogram) using a discrete-time Fourier transform (DTFT), as illustrated in Figure 34A. The DTFT used a Gaussian window with a width of 88 milliseconds and a 75% overlap between one window and the next; the spectra were subsequently bandpass-filtered so that energy at frequencies below 500 Hz or above 7500 Hz was excluded from analysis.

From the set of all samples, 7 500 unique spectra were chosen without replacement. These were clustered using a *k*-means clustering algorithm [204] into 120 clusters. The *k*-means clustering algorithm works to divide the 7 500 spectra into *k* clusters, with all the items in each cluster more similar to each other than to the



**Figure 34 Converting sound to prototypes. (A)** Using a discrete Fourier transform, sounds are converted from waveform (top pane) to a sequence of frequency spectra (bottom pane)—in essence, a spectrogram. Note that each discrete frequency spectrum accounts for a period of time much larger than the sampling rate; the effect is exaggerated here to make this clear. **(B)** Examples of possible prototypes. In the WSPR algorithm, every segment of sound will be matched to a similar prototype, and coded as the prototype’s index number (1, 2, 3, 4, etc.)

members of any other cluster. Each cluster represents a single kind of "sound" that the bird makes: clusters may represent single notes, harmonic stacks, staccato bursts, or other types of sound. The members of each cluster were averaged to produce a set of prototypical sounds, one prototype per cluster, and each prototype was assigned a unique index number (its "symbol"); these prototypes formed the basis for the encoding. Sample prototypes can be found in Figure 34B.

Sounds were encoded by first converting from waveform to frequency-vs-time representation, as before. Each discrete frequency spectrum was compared to the full set of prototypes, and the spectrum was encoded as the index number of the prototype it was most similar to (determined by root mean square deviation). Each sample was thus converted from a waveform, to sequence of frequency spectra, to a sequence of symbols. With this, the encoding step of building a model was completed. The average sample was 2.42 seconds long; once encoded, the average sample was 1063 symbols long.

The second part of the model-building process is where patterns in the bird's song are identified. A window width ( $w$ ) of 11 was set, and an anchor position ( $a$ ) of 6 was set at the center of each window. An array of dimension  $120 \times 11 \times 120$  was created; all values in the array were set to zero. A count was tallied of the number of times symbol  $y$  was seen at position  $z$ , given that symbol  $x$  was seen at position  $a$ , for all  $x$ ,  $y$ , and  $z$ , by scanning each sample and tallying the observed symbols. This array contained a representation of all the distributions of all patterns seen in the data, and was subsequently used to score a test sample by comparing patterns found within it to the patterns seen in the data as represented by the array.

## Scoring a sample

A single test sample was first encoded using the same encoding method described for model building. After encoding, the sample was scanned over in a manner very similar to how the frequency array was built; however, instead of modifying the array, the values in the array were incorporated into a score, so that more common sequences of symbols will score higher than less common ones. The exact formula used is described in the appendix. Once the non-normalized (raw) score was generated, it was standardized (as a  $z$ -score) in order to make the scores easier to interpret: the score was scaled and translated relative to the standard deviation and mean of the scores of the training data; as a result, a score of zero would indicate a sample exactly as “typical” as the scores of the training data, and a score of 1.0 would indicate a sample enriched with typically observed patterns such that it scored higher than approximately 84% of all training samples (one standard deviation greater than the mean). The full details of the standardization procedure are described in the appendix. A single arbitrary sample produced a raw score of 0.34, a  $z$ -score of 0.45, and a  $p$ -value of 0.32, implying that the sample was fairly typical of the model’s training data—which in this case was to be expected, as the test sample was identified by the author as being qualitatively “of a kind” with the training data.

## Binary classification

The motivation for developing this method was to quickly classify very large sets of recorded samples, so it seemed fitting to examine its fitness for this purpose.

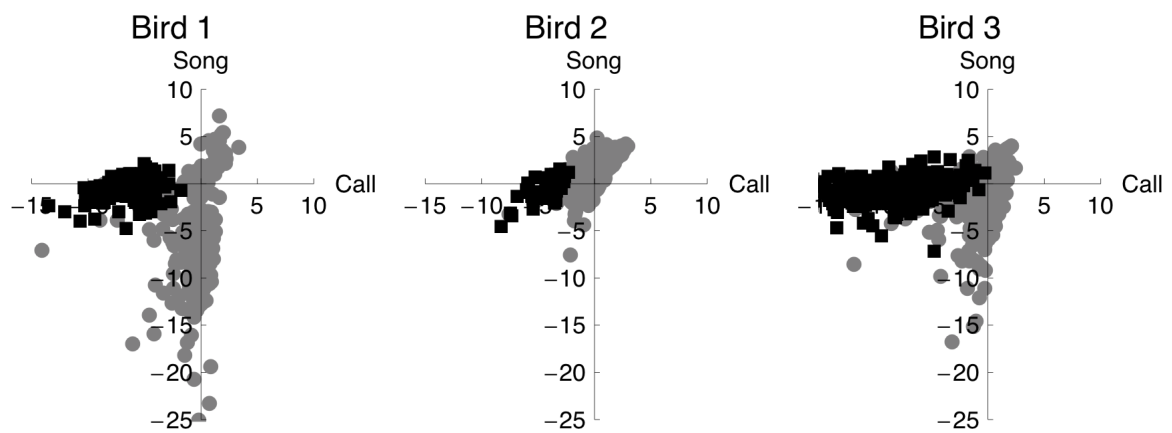


In the author's recording setup, juveniles were recorded continuously, twenty-four hours a day. It was not possible to listen to all of this audio—indeed, for months, recordings were being accumulated much faster than a single person could listen to them, even if that person listened to them every minute of every day.

A simple amplitude threshold check was able to eliminate most of the recordings, however this still left tens of thousands of audio events—samples—that needed to be examined. One of the primary goals in developing the WSPR tool was to create a reasonably robust tool that could sort through such large sample sets in minutes or hours, rather than days, and further reduce the amount of work that would need to be done manually.

A timing test was able to show that the WSPR algorithm was indeed suitable for use with such large datasets. A model was built from 200 samples; on a reasonably fast machine (Intel Core i7, 2.67 GHz clock speed), the model-building process took 12.1 seconds. Scoring 200 samples against that model took only 1.6 seconds. Assuming those 200 samples are representative of a larger set, it would take about 15 minutes to score 100 000 samples. By contrast, 200 pairwise comparisons were done using the SAP program with the same sample set. These 200 comparisons took 593 minutes to complete on the same machine. Scaling up, comparing 100 000 sample pairs would take about 200 days to complete.

While speed is important, it is of little use if the results are inaccurate. To test WSPR's accuracy, a WSPR classifier was built comprised of two models, one of "call" samples, and one of "song" samples. Figure 35 shows the raw scores against both "call"



**Figure 35** Performance on a classification task. Scores used are standardized z-scores. Each test sample was scored against both “song” and “call” models. Gray points were manually assigned to the “call” class, while black points were manually assigned to the “song” class. For all birds, the two classes of sounds are well separated.

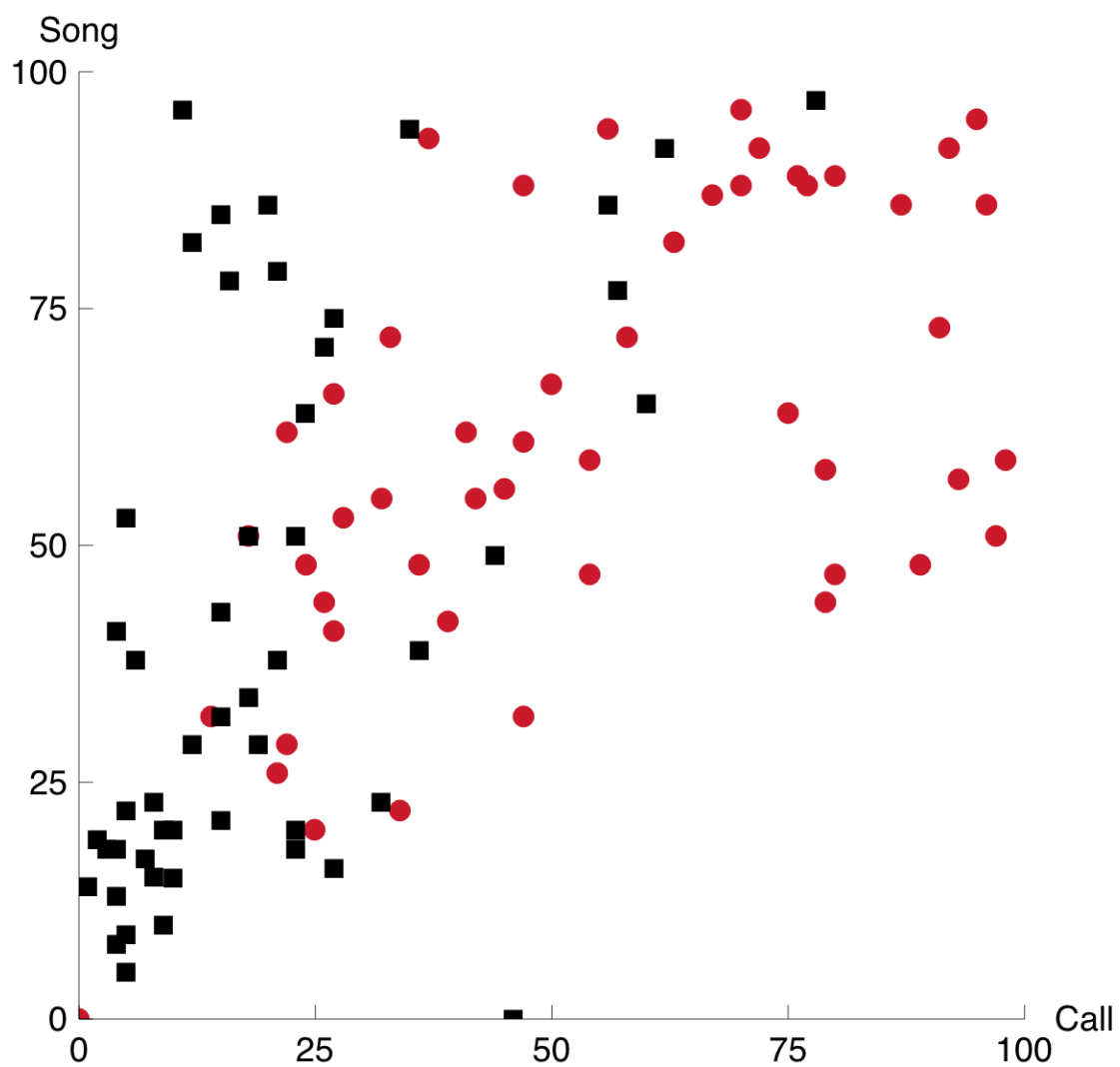
and “song” models for the test data in scatter plots. The MCCs for the classifications of each bird's samples were 0.93, 0.75, and 0.65, with a cumulative MCC of 0.78.

It is also worth comparing the accuracy of WSPR classifications to SAP scores. Figure 36 shows the raw scores produced by the SAP program. The MCC for the SAP-based classifier was 0.57, somewhat less than that for the WSPR classifier. On this task, WSPR made about 1/3 as many classification errors as SAP, although both algorithms produced fairly good results.

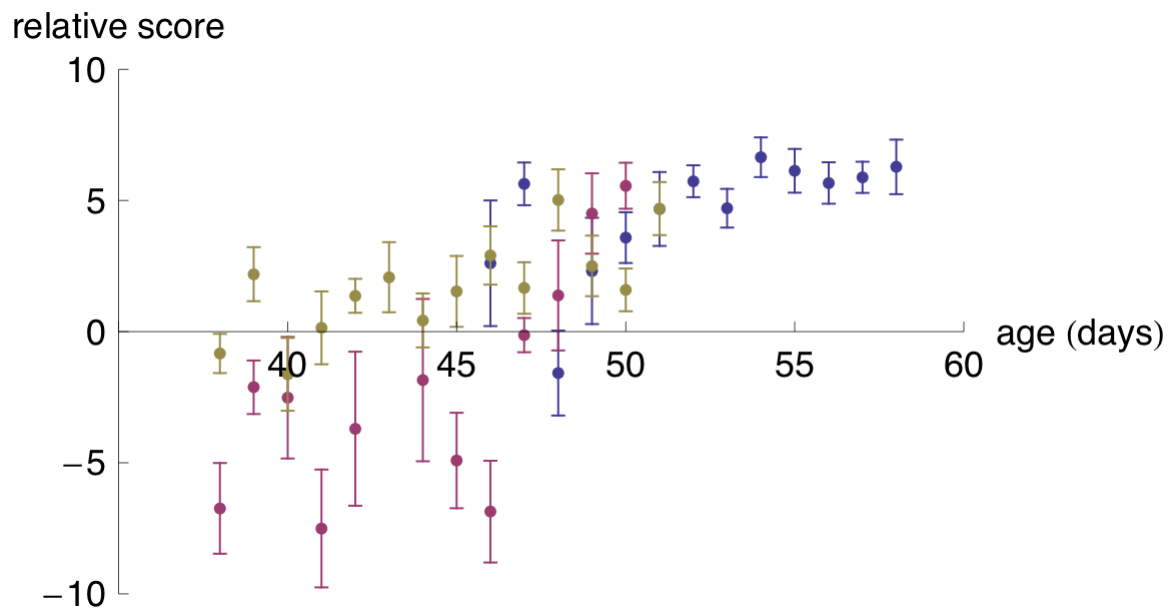
### **Song ontogeny**

In addition to its use as a classifier, the WSPR tool may also be useful for more analytical tasks. To that end, a test was devised in which WSPR was used to track the ontogenic development of the songs of three juvenile zebra finches. To do this, once again two models were created for each finch, one from a set of early samples, near day 35, and one from a set of later samples, near day 50. Sets of intermediate samples were then taken, organized by day, and scored against each model. The difference between these two scores, specifically the late-model score less the early-model score, indicates the extent to which the test sample was more typical of the late model than the early model.

Figure 37 shows that the bird's songs do progress over time towards similarity with each bird's late model. According to the scores, the birds' songs develop unevenly at times and at different rates, an observation in accord with the authors' personal experiences.



**Figure 36** SAP scores, performance on a classification task. Black points were manually assigned to the “song” class, and red points were manually assigned to the “call” class.



**Figure 37 Measuring progress in song development. Each colour represents a different bird. For each bird, an early model and late model were built of the first and last 100 samples available; all other samples were compared against both models and their difference calculated, so that negative scores suggest a sample was more typical of the early model, and positive scores suggest a sample was more typical of the late model. Each point is the mean of all samples for that day, and error bars indicate standard error. All birds progress from being essentially early-like to being late-like, but unevenly and at different rates.**

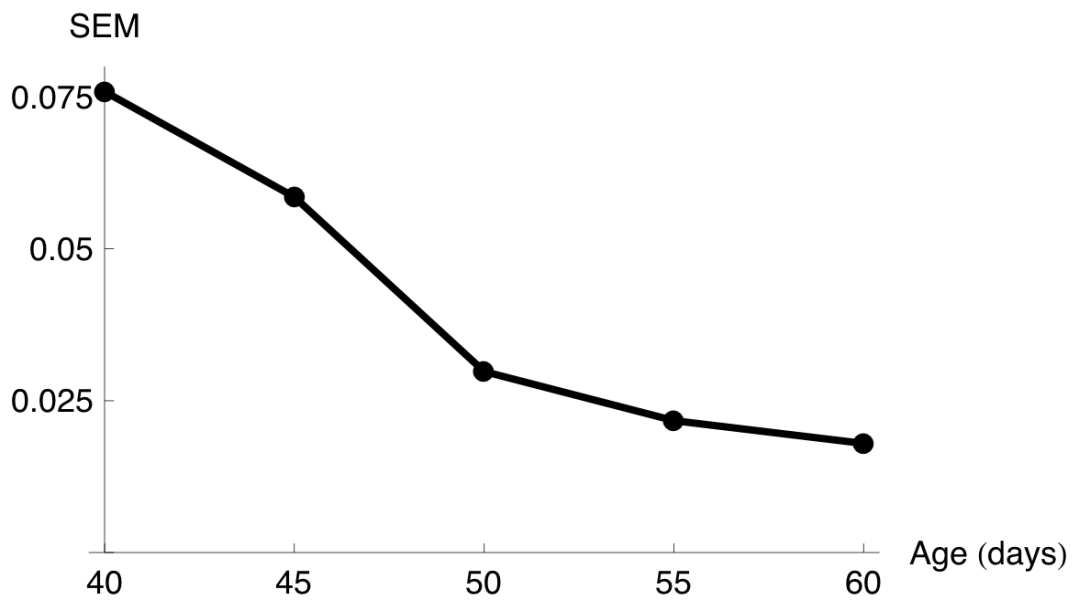
WSPR might also be used to measure stereotypy, a task it seems well suited for given its emphasis on large sample sets. One simple and intuitive measure of stereotypy using WSPR would be the standard deviation or standard error of a sample set against a model; this is the measure used here. This measure is essentially one of variability: the lower the standard error, the greater the stereotypy.

The samples from one bird were grouped into five-day periods, and a model was built for each period. The samples were then scored against their models, and the standard error of the scores was used as a measure of apparent stereotypy. Figure 38 shows the change in standard error for scores as a bird's song develops. As one would expect, variability decreases and stereotypy increases as the bird ages. There is a noticeable decrease in the rate at which variability declines around day 50.

### **Effect of parameter selection on scores**

It is important to know how sensitive the WSPR algorithm is to changes in parameters. There is a possibility that small changes in parameters might lead to large changes in scoring accuracy, a situation that would pose a practical problem for the use of the algorithm. There are three key parameters in the model that can be manipulated: the width of the STFT window, the number of prototypes, and the width of the model window.

Two of these parameters, the width of the STFT window and the width of the model window, are determined by the data being analyzed: for the width of the STFT window, the expected maximum length of time over which a sound would be



**Figure 38** Non-standardized score standard error as a bird develops its song. As the bird matures, the variability in its singing decreases.

approximately constant; and for the width of the model window, the expected length over which patterns would be identifiable. As such, one would expect the scores to vary considerably as these parameters are changed; furthermore, the structure of the data should suggest ranges for these parameters.

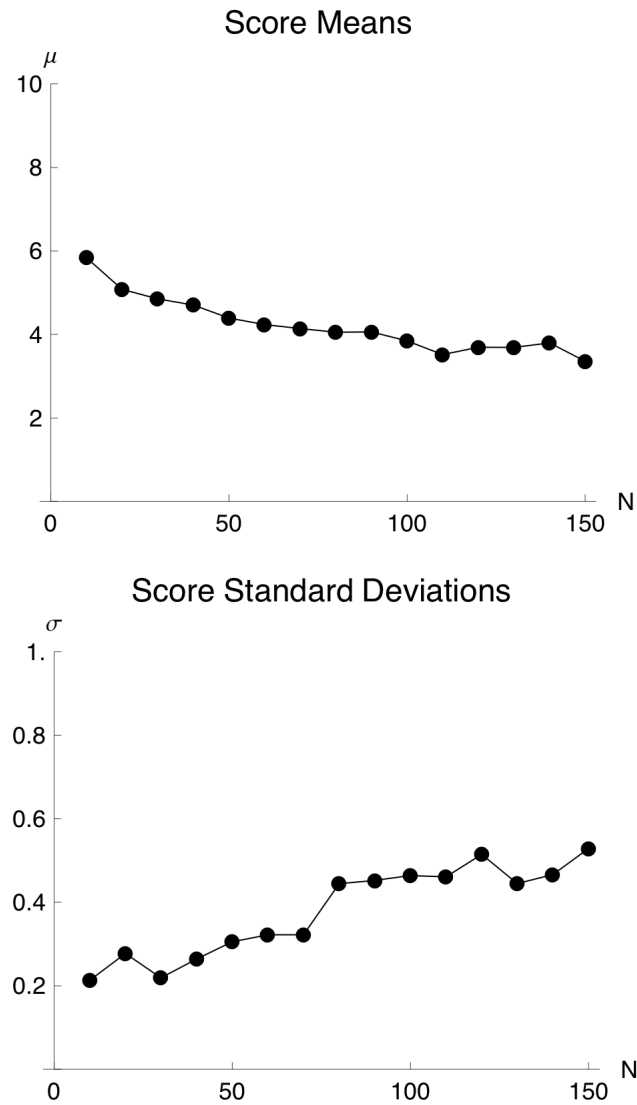
There is therefore only one major parameter remaining that must be set in an ad hoc fashion: the number of prototypes. There are potential problems with having either too few or too many prototypes. If there are too few prototypes, sounds with qualitatively different spectral profiles will be assigned to the same prototype, the specificity of the encodings will fall, and the model may produce additional false positives. If there are too many prototypes, sounds that are qualitatively similar will be assigned to different prototypes and the number of false negatives produced will rise.

Figure 39 shows how the mean score and standard deviation of scores change in relation to the number of prototypes used to build the model. It can be seen that both the score means, and to a lesser extent, the standard deviations, level off when more than roughly 100 prototypes are used. This suggests that the method is insensitive to this parameter as long as sufficiently large set of prototypes is used.

### **Stereotypy and complexity**

Finally, there is the possibility of using the WSPR algorithm as a basis for measuring the complexity of a bird's song. Exactly what is meant by "complexity" in the context of birdsong is open to debate, but most researchers would probably agree it involves the number of distinct sounds an animal makes, as well as the patterns of those sounds. For many years people have used informal measures of song complexity, such





**Figure 39 Scores and standard deviations as a function of the number of prototypes used (N). Scores were raw (non-standardized). Neither scores nor standard deviations change abruptly in the face of small changes to the number of parameters.**

as the number of distinct notes or syllables in a song [205]. In addition to a high degree of subjectivity these measures can be difficult to apply to birds with variable songs, such as juveniles or species that improvise when singing. As an alternative, WSPR can be used to generate a measure of complexity based on ideas from statistical complexity theory and information theory.

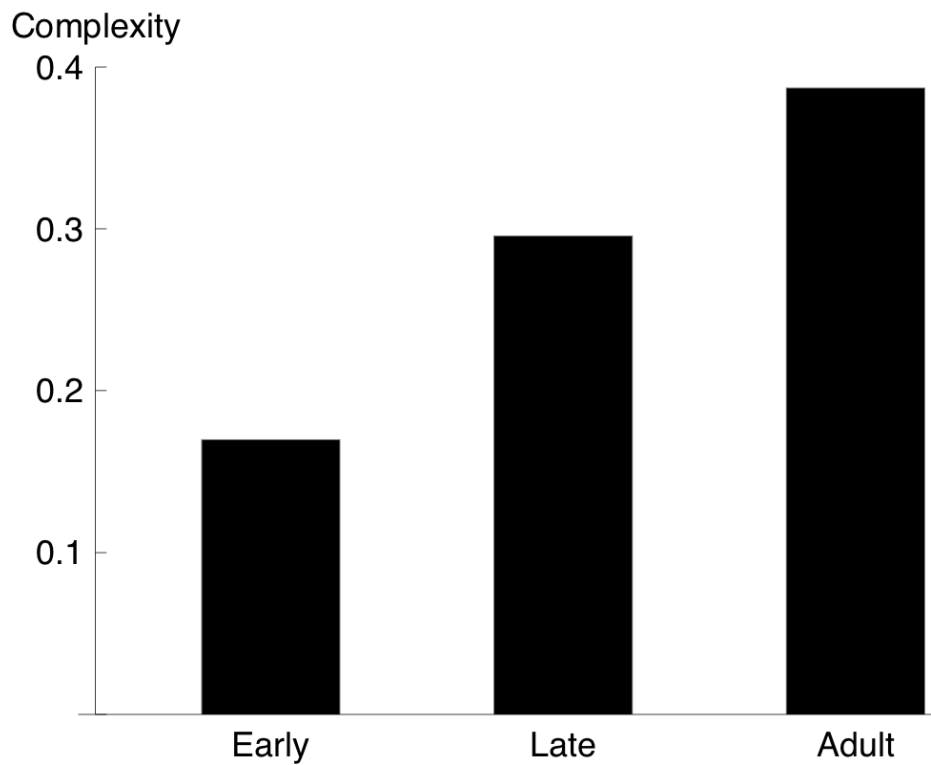
A WSPR model contains a considerable amount of information about the sounds in a bird's repertoire and the likely sequences of sound it will produce—exactly the kind of information needed to measure complexity. Our method, described in the appendix, mines a WSPR model to produce a measure of the model's complexity, which is in turn a reflection of the complexity of the sample set used to build the model. This method was tested against vocalizations from a single bird as it learned to produce its song.

Figure 40 shows complexity scores for models built on early juvenile, late juvenile, and adult models. There is a marked rise in complexity as the bird's song develops, which coincides with intuitive expectations.

## **DISCUSSION**

### **About the method**

The WSPR algorithm attempts to identify recurring patterns in the vocalization samples submitted as training data. It does not need a high degree of top-level similarity, nor does it look for any particular features. At its heart, the algorithm is built upon a simple expression of conditional probability: given that at this moment the



**Figure 40 Song complexity. Complexity was measured for early juvenile, late juvenile, and adult. As birds age, the apparent complexity of their song increases.**

sample sounds like  $x$ , what are the probabilities of the sounds heard in the preceding and following moments?

WSPR breaks the sample into short segments, and using spectral analysis techniques identifies the significant frequency components of each segment. It then estimates how probable such a frequency profile might be, and how probable its neighbouring profiles are. The probability estimates are based on the distributions observed in the training data.

### **On the meaning of scores**

Scores are best thought of as a quantitative measure of how typical each segment of the sample is and how typical its surrounding segments are as compared to the training data. Raw scores exist on a scale that is unique to the model that produces them, and so raw scores cannot be compared across models. As a result, it will generally be preferable to use standardized  $z$ -scores. These are standardized against the distribution of scores from the training data: a  $z$ -score of 0.0 means that a sample scored as highly as the average sample from the training data; a  $z$ -score of 1.0 means that a sample scored one standard deviation higher than the average sample from the training data; and a  $z$ -score of -1.0 means that a sample scored one standard deviation lower than the average sample from the training data. It is important to note that although scores are related to probabilities, they are not and cannot be used as expressions of probability. Estimated  $p$ -values, however, can also be calculated. These  $p$ -value estimates are for the two-sided hypothesis that a random score for a sample from a pool like the training data would be more extreme than the current score,

assuming a normal distribution of scores: users should verify that the scores produced by a model are approximately normally distributed before accepting the  $p$ -value estimates. About the performance of the algorithm as a classifier

On the data sets used in this chapter, the algorithm categorises samples as song or call correctly relative to human assignments about 92% of the time. Compared to SAP, the algorithm makes about 1/3 as many assignment errors, a substantial improvement.

There are some caveats in the use of SAP as a classifier, and some details that must be discussed regarding how it was used in this chapter. SAP was used to compare one single test sample against two single training samples, one from each category. In contrast, the algorithm described here compares a test sample against a digest of dozens or hundreds of training samples. A fairer comparison would involve using SAP to compare a test sample against a large set of training samples, and then using some averaging function to generate a score against each category. This is not typically how SAP is used however, and SAP's computationally intense method makes this infeasible: on a fast computer (2.6 GHz), comparing a one-second sample against 100 would take about 40 minutes. To classify a large group of samples in this manner, say 10 000, would take an unreasonable amount of time; hence we consider that the way in which SAP was used here as a classifier is a fair reflection of how it would be used in practice.

## Using models to estimate stereotypy and complexity

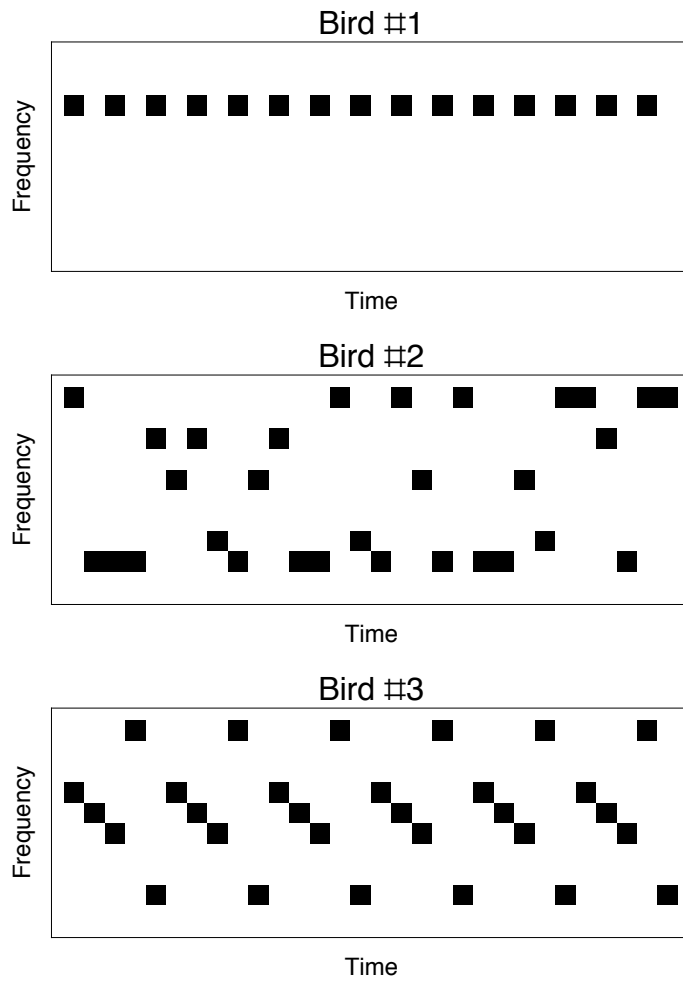
Aside from classification and general scoring tasks, the models produced by the WSPR algorithm can also be used to provide two measurements about the training data that may be of interest: stereotypy and complexity.

We propose that stereotypy can be thought of as a low degree of variance between samples. A low standard deviation of the scores of a sample set against a model provides the most direct measure based on this idea.

We can also define a measure of song repertoire complexity, by looking to the field of statistical complexity for inspiration. Measures of statistical complexity attempt to quantify the "structuredness" of a system or process. There is no consensus as to what exactly this means or how it could be best measured, but most proposals generally consider the number of parts in a system as well as the relationships between those parts.

Let us consider this idea of complexity using several examples involving birdsong, illustrated with artificial examples in Figure 41. Bird #1 has a one-note repertoire, and his song consists of repetitions of this note. He has a highly regular song, but it is very simple. His "system" has only a single "part" and we would suggest that his song is not complex.

Bird #2 has a five-note repertoire; he sings randomly and each note is sung about 20% of the time. Although the song of bird #2 has many parts, there are no relationships between these parts—each part is independent of the others, and no patterns emerge from his song beyond the individual notes. Under some measures of complexity, such as Kolmogorov complexity [206], this song would be highly complex,



**Figure 41 Hypothetical spectrograms for three birds. Bird #1 has a song with a single note, bird #2 has five notes but no pattern, and bird #3 has five notes and a clear recurrent pattern.**

as there would be no way to represent the song more concisely than its full form.

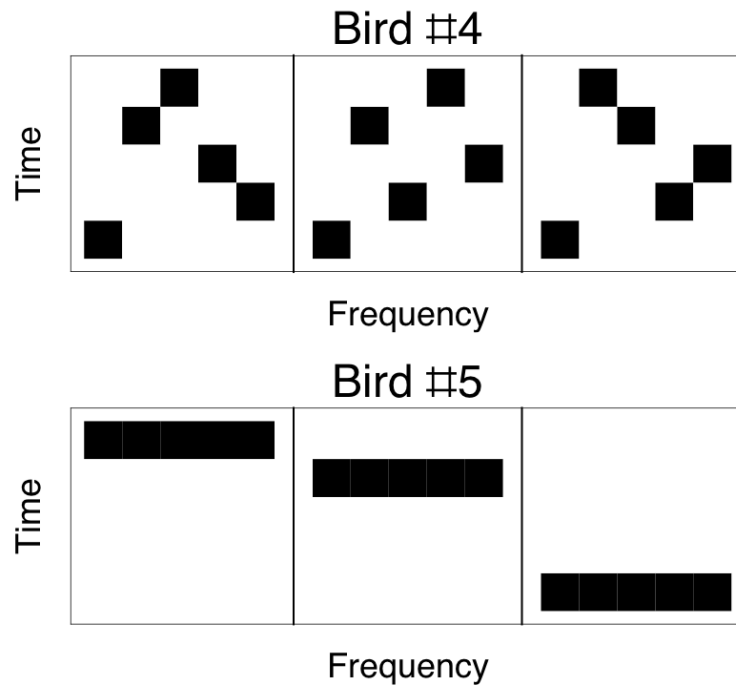
Nonetheless we would argue that, although the five notes make this bird's song more complex than bird #1, he also has a fundamentally simple song structure.

Bird #3 also has a five-note repertoire, but he sings with sequences of notes that appear regularly. Here there are meaningful relationships between parts: some notes follow others at rates much higher than random chance. We would argue that this bird has what most observers would agree is a more complex song structure.

Is there an existing measure that could be used for the purpose of measuring song complexity? Several measures of statistical complexity exist, for various problem domains [207-209], but the one that seems most relevant to birdsong is the measure of predictive information described by Bialek *et al.* [210]. To paraphrase, predictive information is how much more you know about the future states of a system upon learning about its past states. If combined with a measure of the number of different states (to prevent bird #1 from receiving a high complexity score due to the high predictability of his song), predictive information is in accord with our intuitive ideas about birdsong complexity, wherein birds with regular patterns of notes make it possible to predict the note sequence, and the more extensive the patterns are, the more that can be predicted. This measure would also be in accordance with our intuitive notions about the complexity of the songs of the three birds discussed above.

While predictive information seems like a good fit, Bialek *et al.* use mutual information [211] as their underlying measure, and under some circumstances this may lead to counterintuitive results. As an example, mutual information would consider a bird with five songs, each containing a different order of five different notes (bird #4 in





**Figure 42 Mutual information may not adequately capture intuitive notions of song complexity. Although the authors believe most people would agree that bird #4 has a more complex song than bird #5, the songs of both birds can have equal mutual information.**

Figure 42), just as simple as a bird with five songs of one different note each (bird #5 in Figure 42): both are equally predictable. For birdsong a more appropriate underlying measure might be the Kullback-Leibler divergence [212], a measure of the difference between two probability distributions; here we would use the Kullback-Leibler divergence (KL divergence) to measure the difference between the distribution of observed symbols at different times relative to our model's anchor position. The KL divergence would identify the former bird's repertoire as being more complex than the latter's. By using the KL divergence, we are subtly exchanging the idea of predictive information for a related but different one: the extent to which the past predicts changes in the future. It is our opinion that of all the measures considered, the KL divergence most closely reflects intuitive ideas about song complexity. The measure we propose uses the data about sound distributions contained in the WSPR models to estimate the structural complexity of a sample set. It is essentially a mean of multiple KL divergences of distributions at different time intervals in the model. The exact formula can be found in the appendix.

An important consideration is that for any measure, timing and the rate at which song features change are crucially important. On very short timescales, such as microseconds, a bird's song does not change much at all, and the correlation between past and present is total. On very long timescales, such as hours, the correlation between past and present singing behaviour is essentially zero. In between these extremes is a narrow range of timescales that optimally reveal the structure of the bird's song. We have not devised a satisfactory method for automatically identifying these optimal timescales, and so can only recommend that care be taken in choosing

timing parameters when attempting to measure song complexity using the method we propose.

### **Known issues**

One consideration when using WSPR is that background noise in recordings can be problematic: the algorithm does not distinguish background noise from vocalizations or any other noise of interest, and the background noise profile becomes built into the model. In the worst case, models built from samples with significant background noise may assign low scores to test samples simply because the background noise is different. To avoid this problem, noisy recordings should be denoised before either building a model or scoring against an existing model, or recording conditions should be managed to ensure a consistent level of background noise between training samples and test samples.

There are several important points to consider when using the measure of complexity we've provided. The measure is highly sensitive to the size of the sample set, so to make scores comparable across models, we recommend using exactly the same total length of sound to build each model. The measure can also be misled by extended periods of silence, especially if these frequently appear at the beginning or end of samples. To avoid this we recommend trimming silent intervals from the ends of all samples. The model will also add implicit silence to the beginnings and endings of samples as necessary to make them at least as long as the window size of the model, so if your samples are typically less than twice as long as the window size, we recommend that you concatenate all samples in advance of building your model.

## **CONCLUSIONS**

In this chapter, we have presented a novel method for comparing samples of birdsong against a larger set of samples, WSPR. WSPR is designed to cope with sample sets with low levels of stereotypy, an application that we feel no existing tool adequately addresses. We then extended this method to demonstrate a number of applications: classification problems, the original motivation behind the method's development; tracking song ontogeny; and measuring song variability and complexity. We believe that the measure of birdsong complexity presented here represents the first effort of its kind.

Although the methods described in this chapter are useable as they are, it is our hope that they may also serve as starting points for further discussion: in general, discussions about analyzing animal vocalizations and algorithms for doing so; and in particular, discussions about what complexity means in the context of animal vocalization and how best to measure it.

### **Availability of tools implementing the WSPR algorithm**

Implementations of the WSPR algorithm in C++ and Mathematica are available for download; a web-based front end has also been developed to facilitate easy access to the WSPR tool. These can all be found at <http://wspr.rockefeller.edu/wspr/>.

## CONCLUSIONS

In our work we have made a series of small but concrete steps towards a better understanding of the oscine song-learning process. Our experimental work with juvenile zebra finches has added new detail to our understanding of the song learning process, by demonstrating that strategy choice can be influenced by auditory stimulus, that strategy choice has a demonstrable effect on song learning, and by illustrating that at least under some conditions strategy choice is not an either-or phenomenon but a continuum. This work, we feel, is worthwhile in its own right; however it also has practical implications. Because chronic repetitiveness does seem to affect the song learning process, researchers working with juvenile zebra finches may need to be aware of this behavior and possibly factor it into their analyses. Secondly, because variability in singing has an apparent neural basis [131], the ability to manipulate vocal variability through protocols like ours may enable researchers to uncover new details about the song learning process, perhaps including how information about the bird's performance is communicated to the AFP and sensorimotor pathways.

The work involving computational simulations of the oscine brain has helped to identify possible origins and roles for the timing-locked signal that has been observed in LMAN, and we believe our model lends support to the possibility that LMAN and the AFP may be the true locus of the trial-and-error learning process that songbirds appear to engage in. Our model also opens up interesting questions, notably: assuming that the avian brain would choose a near-optimal ratio of timing-locked and timing-independent activity, why is our estimate of the optimal ratio so different from what has been observed?

Finally, in working to solve a practical problem involving handling very large numbers of birdsong samples, we have developed new methods for analyzing the songs of juvenile songbirds. Given that a good deal of study in this field is with juvenile songbirds, this seems like a very useful set of methods, and our aggregate approach to analyzing birdsong presents researchers with ways to measure things that have not been possible with other approaches.

There are many directions that could be taken with this research going forward. On the topic of chronic repetitiveness in juveniles, there are two primary issues: understanding more about this phenomenon, and leveraging it to discover more about the song learning process. As a practical matter, it might be good to do some “calibration curves” to find the ages for beginning treatment, the playback rates and conditions, and the auditory stimuli that maximally induce chronic repetitiveness. It would certainly be interesting to see whether very extensive repetitiveness leads to permanent changes in adult song after crystallization, and the extent to which restoration of the “proper” tutor song could rescue a bird from chronic repetitiveness.

If our hypothesis is right, and chronic repetitiveness is caused by a lack of feedback about song performance, then electrophysiological experiments may help to identify the source of feedback about song performance. In terms of understanding how song is learned, this is probably the most important contribution that could be made at this time.

Within the model there are a number of other experiments that could be run which would help to elucidate the results we have observed, including exploring the effects of other parameters on the model’s behavior, such as the absolute level of

activity in LMAN, the precision of time-locked activity, the precision of the topographic mapping from LMAN to RA, and total model size. There are also a number of variations on the model that may provide additional insights, for example, variations on the model in which the timing-locked signal could be slowly constrained over time, or variations in which the nature of the critic's signal were different, for example by giving the critic a timing-locked signal as well. From an experimental perspective, the model makes some key predictions that could be tested, most notably that there may be higher levels of timing-locked signal in juveniles. In adults, it would be interesting, albeit difficult, to test to see whether the biasing signal would evolve over time, or whether it would remain essentially static.

As regards the song analysis tools, there are an almost infinite number of improvements, changes, and alternative methods that could be developed; the analysis of birdsong and animal vocalization in general are areas where new ideas could be enormously beneficial to research. One possible variation would be to stop using power spectra as the underlying characterization of birdsong, and move instead to a set of derived measures like those used in SAP [201]; this may make the method less sensitive to relative differences in frequency. Another variation would be to explore alternate methods of building prototypes and models, for example by letting the algorithm choose the best model size. Finally, it would be helpful if the methods could be extended to support smaller datasets, by computing parametric estimates of distributions of song features rather than needing sufficient data to make these estimates directly. Lastly, it would be very interesting to see how well methods such as this could be applied to other domains such as primate vocalization.

## APPENDIX: DETAILS OF THE WSPR ALGORITHM

The preliminary step in building a model is to produce an encoding scheme for the sounds to be considered by the model. This is a form of Vector Quantization [213], in which the infinite variety of sounds is reduced to a finite set, or codebook, of representative sounds.

To generate a codebook of size  $n$  from a sample set of sounds:

- Convert each sample into power spectra via short-time Fourier transform
- Take  $100n$  random samples of power spectra from all spectrograms
- Cluster into  $n$  groups using  $k$ -means clustering
- For each group:
- Find the geometric mean of each frequency band across all samples in the cluster
- Normalise so that the mean spectrum has a total power of 1
- The result is the prototypical spectral profile for the group
- Prepend a “null” spectrum of zeros to the beginning of the prototypes

All samples must be transformed into a frequency-versus-time representation (a spectrogram) using a discrete-time short-time Fourier transform (STFT) [214].

Variations on the classical STFT are also acceptable; a STFT using a Gaussian window is used in our implementation of the algorithm. Depending on the underlying data, different STFT parameters may be used; we typically use a STFT window width of  $\sim 100$  milliseconds with either a 50% or 75% overlap between neighboring windows. Phase information is discarded, as well as parts of the spectra outside a specific band of interest, i.e. below 500 Hz or above 7500 Hz.

In cases where one wants to build two or more models from the same underlying encoding, the samples used to generate the codebook should be taken from the joint sample set of the two models.



## Encoding samples

Having constructed a codebook, all samples must now be encoded. To encode a sample:

- Convert via STFT to power spectra.
- For each power spectrum  $s$  in the spectrogram:
- If the total power in  $s$  is below the cutoff threshold, emit a zero (the null spectrum)
- Otherwise, examine the codebook,  $P$ , to find the spectrum,  $p$ , where the root mean square deviation between  $s$  and  $p$  is minimized.
- Emit the index number of  $p$ , i.e. if  $p$  is the 3<sup>rd</sup> spectrum in the codebook, then emit a 3.
- The sequence of emitted numbers is the encoding of the sound.

## Constructing the model

Perform the following steps to construct a model using the encoded samples:

- Choose a sliding window length,  $w$ . Define  $a$  as the middle (“anchor”) position of the window:  

$$a = \left\lfloor \frac{w+1}{2} \right\rfloor$$
- Create an array  $M$  of dimension  $n \times w \times n$ , and a vector  $T$  of length  $n$ . Initialise all values in  $M$  and  $T$  to 0. For every encoded sample  $e$ , create a set  $R$  of all possible subsequences of  $e$  of length  $w$ .
- For each  $r$  in  $R$ , perform the following:  

$$T_{r_a} \leftarrow T_{r_a} + 1$$

$$M_{r_a, j, r_j} \leftarrow M_{r_a, j, r_j} + 1 \quad \forall j \in \{1, \dots, w\}$$

where  $r_a$  is the symbol at the anchor position in  $r$ .
- Create an array  $M^*$ , same size as  $M$ ; and vector  $T^*$ , same size as  $T$ .
- For  $i$  in  $1, \dots, n$ , perform the following computation:  

$$T_i = \frac{T_i}{\sum_{j=1}^n T_j}$$
- For  $j$  in  $1, \dots, w$ ,  $k$  in  $1, \dots, n$ , perform the following computation:  

$$M_{i, j, k} = \frac{M_{i, j, k}^*}{\sum_{l=1}^n M_{i, j, l}^*}$$

The tuple of  $W = (P, T^*, M^*)$  constitutes the constructed model.

## Scoring a sample against the model

Finally, we must be able to compute a score of a test sample against a model.

Perform the following steps to score a test sample against a model  $W$  :

- Convert the sample to a spectrogram via STFT.
- Encode the sample as described previously, creating encoding  $e$ .
- Create a set  $Q$ , containing every subsequence of  $e$  of length  $w$ .
- For each  $q$  in  $Q$ , calculate the following:

$$\xi(q, M^*) = T_{q_a} \left( \left( \prod_{j=1}^w M_{q_a, j, q_j}^* \right)^{\frac{1}{w}} \right)$$

- The score of the sample is:

$$Z(Q; W) = \ln \left( \left( \prod_{i=1}^{\text{length}(Q)} \xi(q_i, M^*) \right)^{\frac{1}{\text{length}(Q)}} \right)$$

$Z(Q; W)$  is the non-standardized (“raw”) score of  $Q$  against the model  $W$ .

## Standardization of scores and estimation of $p$ -values

After the model is built, every sample in the training set is scored against the model. The mean ( $\mu$ ) and standard deviation ( $\sigma$ ) of these raw scores are calculated and stored along with the model. When a test sample is scored against the model, its normalised z-score can be computed as

$$Z^*(Q; W) = \frac{\mu - Z(Q; W)}{\sigma}$$

To calculate an estimated  $p$ -value, the CDF of a normal distribution with mean  $\mu$  and standard deviation  $\sigma$  is used to determine the proportion of the distribution that is more extreme than the test score.

## Classification using multiple models

Suppose we have  $x$  known classes (1, 2, 3,...) we wish to assign samples to, and training data sets  $\{S_1, S_2, \dots, S_x\}$ . We begin by building a joint set of prototypes for all samples from  $\{S_1, S_2, \dots, S_x\}$  as described previously. Then, for each set of samples  $S_i$ , we build a model  $W_i$  using the algorithm described previously

We calculate the means and standard deviations for each sample set against each model, producing a  $x \times x$  table for each statistic:

$$\begin{aligned}\mu_{i,j} &= \text{mean}(Z(s; W_j)), \\ \sigma_{i,j} &= \text{sd}(Z(s; W_j)) \\ \forall s \in S_i, j \in \{1, \dots, x\}\end{aligned}$$

The tuple  $(P, \{W_1, W_2, \dots\}, \mu, \sigma)$  constitutes the classifier.

When a sample  $Q$  is submitted for classification, we calculate the raw score  $Z(Q; W_j)$  for all  $W_j$ . Then we calculate the typicality of  $Z(Q; W_j)$  relative to each training set  $S_i$ :

$$Y(Q, i, j) = \frac{Z(Q; W_j) - \mu_{i,j}}{\sigma_{i,j}} \quad \forall j \in \{1, \dots, x\}$$

Finally, we calculate the "atypicality" (or deviation of typicality) for each class as

$$A(Q, j) = \sqrt{\sum_{i=1}^x Y(Q, i, j)^2}$$

The  $i$  for which  $A(Q, i)$  is lowest is the class to which  $Q$  is assigned. This method works not by assigning a sample to the model for which it is most typical, but by assigning a sample to the class of samples whose scores are most similar across all the models; in practice this seems to provide an improvement in accuracy.

## Calculating the complexity of a model

Take  $T^*$  and  $M^*$  from a model  $W$ . Recall that  $T^*$  is of length  $n$  and  $M^*$  is of dimension  $n \times w \times n$ . Then

$$\Gamma(T^*, M^*, k) = \left\{ T_i^*, M_{i,k,j}^* \right\} = \left\{ \gamma_1, \gamma_2, \dots, \gamma_{n \times n} \right\} \forall i \in \{1, \dots, n\}, j \in \{1, \dots, n\}$$

That is, if  $M_{i,j,k}^*$  is the probability of seeing symbol  $j$  at position  $k$  given that symbol  $i$  is at the anchor position, then  $\Gamma(T^*, M^*, k)$  is the set of every element of  $M_{i,j,k}^*$  for some value  $k$  multiplied by the probability of seeing symbol  $i$ .

If the Kullback-Leibler divergence is defined as

$$D_{KL}(P, Q) = \sum_i P(i) \log_2 \frac{P(i)}{Q(i)},$$

then our measure of song complexity is calculated as follows:

$$C_{song}(T^*, M^*, x, y) = \frac{1}{y - x + 1} \sum_{i=x}^y D_{KL}(\Gamma(T^*, M^*, a + 1), \Gamma(T^*, M^*, a + i + 1))$$

Where  $M^*$  and  $T^*$  are the components of a model  $W$ , and  $a$  is the anchor position of that model, and  $x$  and  $y$  are the range of positions in the model forward of the anchor position for which we wish to calculate the complexity.

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