A COMPUTATIONAL MODEL OF BIRDSONG LEARNING BY AUDITORY EXPERIENCE AND AUDITORY FEEDBACK

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INTRODUCTION

In addition to the goal of acquiring a precise description of the acoustic environment, central auditory processing also provides useful information for animal behaviors, such as navigation and communication. Singing is a learned behavior of male songbirds for protecting territories and attracting females (Konishi, 1985; Catchpole and Slater, 1995). It has been experimentally shown that singing behavior depends on auditory information in two ways. First, the phonetic features of a bird's song depends on the bird's auditory experience during a limited period after birth. Second, the development of songs of a juvenile bird depends on the auditory feedback of its own vocalization.

A young male songbird *learns* to sing by imitating the song of a *tutor*, which is usually the father or other adult males in the colony. If a young bird does not hear a tutor song during a *critical period*, it will sing short, poorly structured songs. If a bird is deafened in the period when it practices vocalization, it develops highly abnormal songs. These observations indicate that there are two phases in song learning: the sensory learning phase when a young bird memorizes song templates and the sensorimotor learning phase in which the bird establishes the motor programs using auditory feedback (Konishi, 1965). These two phases can be separated by several months in some species, implying that birds have remarkable capability for memorizing complex temporal sequences. Once a song is *crystallized*, its pattern is very stable. Even deafening the bird has little immediate effect.

In this chapter, we propose a theoretical framework for song learning based on recent experimental findings. Specifically, we focus on the function of the anterior forebrain pathway, which is not involved in song production in adult birds, but is necessary for song learning in young birds (Bottjer et al., 1984). Our main hypothesis is that the anterior forebrain

pathway works as a reinforcement learning system that is similar to the *adaptive critic* architecture proposed by Barto et al. (1983). We tested the functional plausibility of our hypothesis by implementing it as a neural network model based on anatomical and physiological constraints. In computer simulations, the network model learned to imitate syllables from natural and synthetic birdsongs within several hundred learning trials. Preliminary results of this study have been reported elsewhere (Doya and Sejnowski, 1994, 1995).

NEUROANATOMY OF BIRDSONG CONTROL SYSTEM

The brain nuclei involved in song learning are shown in Figure 1 (Nottebohm et al., 1976; Bottjer et al., 1989). The primary motor control pathway is composed of HVc, RA, DM, and nXIIts, which projects to the syrinx, the avian vocal organ. If any of these nuclei is lesioned, singing behavior is severely impaired. Experimental studies suggest that HVc is involved in generating syllable sequences whereas RA is involved in controlling finer units of vocalization, such as individual notes (Vu et al., 1994; Yu and Margoliash, 1996).

HVc receives auditory input from auditory forebrain nucleus field L. Some neurons in HVc have selective tuning to complex acoustic features, such as frequency modulation, combination of harmonics, sequence of notes and syllables (McCasland and Konishi, 1981; Margoliash, 1986; McCasland, 1987; Margoliash and Fortune, 1992; Lewicki and Konishi, 1995). Many cells are best tuned to the bird's own song (Margoliash, 1986; Volman, 1993).

In addition to the direct motor pathway from HVc to RA, there is a bypass from HVc to RA which consists of area X, DLM, and LMAN, called the *anterior forebrain pathway* (Bottjer et al., 1989; Doupe, 1993). Lesions in these nuclei in adult birds do not impair their crystallized songs. However, lesions in this pathway in young birds before completion of the motor learning phase result in song deficits (Bottjer et al., 1984; Sohrabji et al., 1990; Scharff and Nottebohm, 1991).
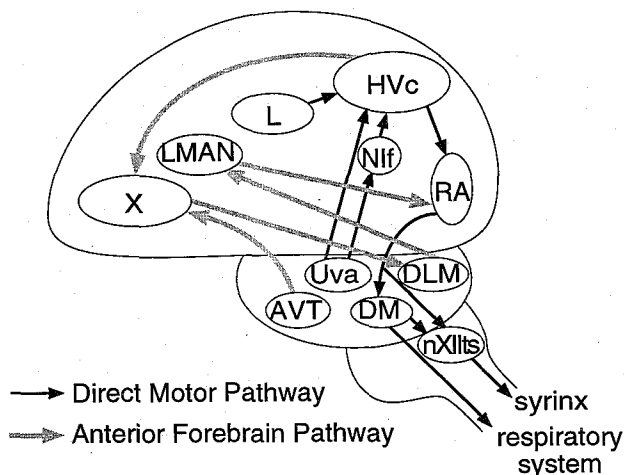
Figure 1. Schematic diagram of the major songbird brain nuclei involved in song control. The thinner arrows show the direct motor control pathway and the thicker arrows show the anterior forebrain pathway. Abbreviations: Uva, nucleus uvaeformis of thalamus; NIf, nucleus interface of neostriatum; L, field L of forebrain; HVc, high vocal center (formerly called hyperstriatum ventrale, pars caudale); RA, robust nucleus of archistriatum; DM, dorsomedial part of nucleus intercollicularis; nXIIts, tracheosyringeal part of hypoglossal nucleus; AVT, ventral area of Tsai of midbrain; X, area X of lobus parolfactorius; DLM, medial part of dorsolateral nucleus of thalamus; LMAN, lateral magnocellular nucleus of anterior neostriatum.

Neurons in the anterior forebrain pathway have auditory selectivity for the bird's own song (Doupe and Konishi, 1991; Doupe 1997). Interestingly, the indirect connection from HVc to RA through the anterior forebrain pathway is established earlier than the direct axonal connection from HVc to RA (Konishi and Akutagawa, 1985). It has been shown that the synaptic input from LMAN to RA is predominantly mediated by NMDA-type glutamate receptors, whereas input from HVc to RA is mainly mediated by non-NMDA type receptors (Kubota and Saito, 1991; Mooney and Konishi, 1991).

A variety of hypotheses have been proposed for the function of this pathway: comparison of sensory and motor representations of song (Williams, 1989), reinforcement of syllable specific activation patterns within RA (Bottjer et al., 1989), processing of auditory feedback and modulation of plasticity (Scharff and Nottebohm, 1991), a measure of how well a vocalization matches a particular auditory template (Doupe, 1991), and selective reinforcement of synaptic connections from HVc to RA (Mooney, 1992).

COMPUTATIONAL ISSUES IN SONG LEARNING

The process of song learning can be explained by the "template hypothesis" (Konishi, 1965). In the sensory learning phase, a young bird hears a song of an adult bird and memorizes it as a *song template*. In the sensorimotor learning phase, the bird learns to sing a song that matches the template through repeated practice using auditory feedback. However, it is still unknown where and how template is stored in the brain and how the articulatory command that matches the template is learned.

First consider the computational problems that need to be solved in song learning. Assuming that the motor program of a song is represented in a hierarchical manner in HVc and RA there are three major issues to be addressed:

- **Encoding of syllables:** How should the syllables be encoded in HVc for efficient long-term memory?
- **Memory and production of syllable sequences:** How should a sequence of syllables be memorized and reproduced?
- **Transformation of syllable codes into muscular commands:** How should the motor command patterns needed to replicate the acoustic features of each syllable be learned?

In this study, we focus on the third issue of sensory motor mapping. Because the tutor provides only acoustic example of a song, a young bird has to determine the spatio-temporal pattern of muscular command for its vocal organ that results in the same acoustic output as the tutor's. This is an inverse problem commonly studied in motor control theory: given a motor system (articulator) and its desired output (tutor song), find an appropriate input to the system (articulatory command) that produces the desired output. Figure 2 illustrates representative schemes for solving inverse problems (Kawato, 1990; Jordan and Rumelhart, 1992; Gullapalli, 1995).

In the first scheme (Figure 2a), the desired output is converted to a desired motor command by an *inverse model* of the articulator which have been given *a priori* or acquired by learning. If a bird has a perfect inverse model of the articulator, it should be able to replicate a song in *one-shot* without repetition of trials and auditory feedback. Although attractive as a model of vocal learning in other species like humans, this is not an appropriate model for vocal learning in songbirds because they require many repetitions of singing trials with auditory feedback.

Another possible scheme is error correction learning (Figure 2b) that uses a linear approximation of the inverse model to convert the error in the motor output into an error in the
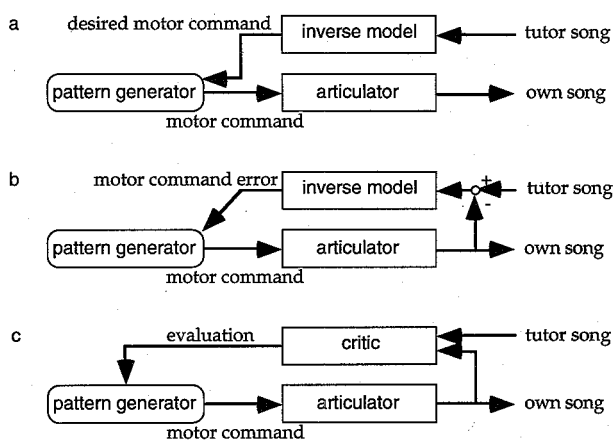
Figure 2. Different schemes for articulatory learning. **a.** One-shot learning by an inverse model of the articulator. **b.** Error correction learning by an approximate inverse model. **c.** Reinforcement learning by a stochastic controller and a critic.

motor command. In this case, learning is incremental and requires auditory feedback. However, learning of the inverse model of a nonlinear system is quite difficult, especially when the system has redundancy, as is usually the case with musculoskeletal system. The existing learning schemes either use an biologically implausible algorithm (Jordan and Rumelhart, 1992) or assume pre-existence of an approximate inverse model (Kawato, 1990). Furthermore, in order to calculate the error in the acoustic output, the bird has to maintain some form of a replica of the tutor song.

The third scheme (Figure 2c) is based on the paradigm of reinforcement learning. It does not use an inverse model but instead uses a *critic* that evaluates the motor output by comparing the present vocal output with the tutor song. Learning is based on the correlation between stochastic changes in the motor command and the increase or decrease in the evaluation (Barto et al, 1983; Gullapalli, 1990). There is no need to have a replica of the tutor song. Activation levels of auditory neurons that have selective tuning to the tutor song can be used as the evaluation signal.

Among these alternatives, we argue that the reinforcement learning scheme (Figure 2c) is the most likely for birdsong learning. We further propose a hypothesis about how this reinforcement learning scheme can be implemented in the known circuitry of the song control system with the constraints given by the anatomy, physiology, and the results of lesion studies.

REINFORCEMENT LEARNING MODEL OF THE SONG SYSTEM

Figure 3 illustrates our current working hypothesis about the functions of song-related nuclei. Discrimination of acoustic input is carried out in the ascending auditory pathway from the cochlea through the auditory thalamus and field L to HVc, resulting in a selective codes of syllables and their sequences in HVc neurons (Margoliash, 1986; Margoliash and Fortune, 1992; Sutter and Margoliash, 1994; Lewicki and Konishi, 1995).

Such encoding of syllables is then used for memory and reproduction of syllable sequence in HVc (Vu et al., 1994; Yu and Margoliash, 1996). Its output is transformed into muscle-oriented representation in RA, which has topographic connection to nXIIts, which in turn projects topographically to the muscles in the syrinx (Vicario, 1988, 1991).
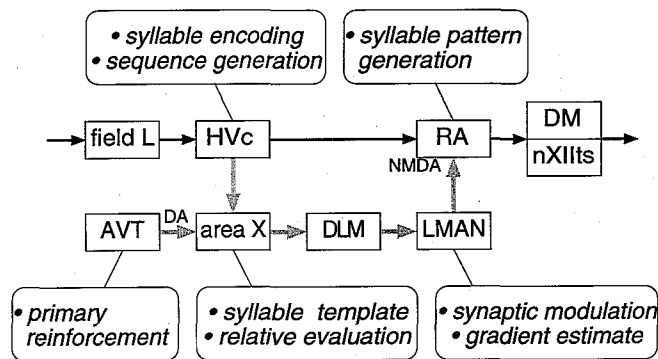
Figure 3. Schematic diagram indicating the proposed functions for each of the major nuclei of the song system. The direct pathway is shown at the top. The anterior forebrain pathway starts at HVc and makes a side loop to RA through area X and LMAN. The bullets in each balloon give the proposed function of the corresponding nucleus.

Our specific hypothesis is that the anterior forebrain pathway functions as a reinforcement learning system that is similar to the *adaptive critic* architecture proposed by Barto et al. (1983). The adaptive critic system is composed of a *search* element that produces stochastic perturbations of motor command and a *critic* element that specifies whether the motor command should be reinforced or not. An important function of the critic is to provide *relative evaluation* of performance by subtracting the expected level of performance from the raw performance index. We propose that area X works as the critic, evaluating relative goodness of the preceding vocal output, and that LMAN works as the search element that induces exploration of the motor command.

Several lines of evidences support this hypothesis. Lesions in area X and LMAN in young birds result in contrasting deficits (Scharff and Nottebohm, 1991). Early area X lesion results in unstable song patterns in the adulthood when songs are normally crystallized. Early lesion in LMAN results in stable but poorly structured song with fewer syllables than normal. These observations are neatly explained if we assume that area X serves as the critic, which provide evaluation of vocalization based on auditory feedback, and that LMAN provides perturbation to the output of RA and induces plasticity of the HVc-RA connection with its NMDA-type synaptic input to RA.

In accordance with the hypothesis that area X functions as a critic, it was recently shown that some of the area X neurons in young birds are selective to the tutor song (Solis and Doupe, 1995). Although many neurons in area X and LMAN are tuned to the bird's own developing song, such activity may reflect the relative evaluation of a song compared to recent performance.

Furthermore, area X receives dopaminergic input from a midbrain nucleus AVT, the avian homologue of the mammalian ventral tegmental area (Lewis et al., 1981, Casto and Ball, 1994). Activity of dopamine neurons represents reinforcement signals in many species (e.g. Schultz et al., 1997). We hypothesize that the selection of auditory input that is to be memorized as song template happens in area X by association of auditory input from HVc and reinforcing input from AVT. In other words, whereas the auditory tuning of HVc cells simply reflect auditory inputs, responses of area X cells are tuned to the specific songs to be learned.

COMPUTER SIMULATION OF VOCALIZATION LEARNING

In order to test whether the reinforcement learning scheme outlined above could be implemented within the known biological constraints and if such a system can perform song learning within a realistic number of trials, we constructed computer model of the entire song control system including the vocal organ. Since it was beyond the scope of the present investigation to model detailed mechanisms of auditory encoding and sequential memory, we used simplified mechanisms that were not necessarily biologically realistic.

Syrinx: Sound Synthesizer

The avian vocal organ syrinx is located near the junction of the trachea and the bronchi (Brackenbury, 1982). The sound is generated with the oscillation of a pair of tympaniform membranes. Activation of the dorsal syringeal muscles coincides with the air flow in the bronchus and that activation of the ventral syringeal muscles correlates well with the fundamental oscillation frequency of the sound (Goller and Suthers, 1995). The spectral profile of the sound is also affected by the resonance property of the vocal tract (Nowicki, 1987).

A simple model of the syrinx, shown in Figure 4, consisted of a variable-frequency sound source, a bandpass filter and an amplifier. A triangular wave form was used for the sound source because it includes all the integer harmonic components. The output of this sound synthesizer was controlled by the following four variables: the fundamental frequency of the harmonic sound source (F), the peak frequency (P) the sharpness (S) of the bandpass filter, and the gain of the amplifier (A). The output sound waveform was calculated from the time course of the variables (A(t), F(t), P(t), S(t)). The model could produce bird-like chirps and warbles with the time courses of the input variables chosen appropriately.
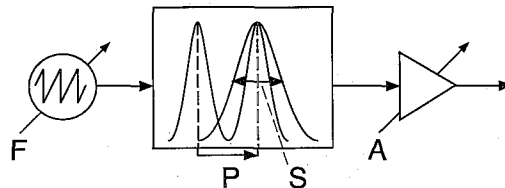

Figure 4. The model of the syrinx used in the song learning model. The sound output was controlled by four input variables: A, gain of the amplifier; F, fundamental frequency of the sound source; P, peak frequency, and S, sharpness of the band-pass filter.

RA: Syllable Pattern Generator

HVc input to RA evokes fast non-NMDA-type, slower NMDA-type, and delayed polysynaptic inhibitory responses (Mooney, 1992). Neurotransmitters mediated by second-messenger systems such as norepinephrine and GABA-B agonists, also have effects on neurons in RA on slower time scales (Perkel, 1994). Although the details of the local circuits in RA are not yet known, the observed cellular and synaptic time courses could produce the complex temporal responses needed to produce syllables in response to command inputs from HVc.

To mimic the myotopical organization (Vicario, 1991), the model of RA had four sub-networks, each of which could exert control on of the four output motor command variables (A, F, P, S). Within each subnetwork, there were five temporal response kernels, where each unit had a different time course, as shown in Figure 5. The temporal responses of the 20 RA units were determined by the inputs from HVc units and a set of connection weights W.
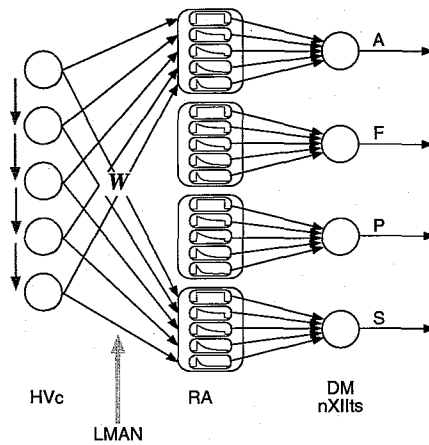
Figure 5. Model of the direct motor pathway. Syllables were unary-coded in HVc, and their sequential activation triggered syllable pattern generation networks in RA. The RA units were divided into four groups corresponding to the four motor command variables (A,F,P,S). Within each group, there were five exponential temporal kernels with different time constants. The sum of their response profiles served as the motor command for the syrinx model.

HVc: Syllable Sequence Generator

Recorded data from HVc in awake birds suggest that each syllable in a song is encoded by a specific pattern of activities of HVc neurons (Yu and Margoliash, 1996). Although there is evidence showing that both auditory (Sutter and Margoliash, 1994) and motor (Yu and Margoliash, 1996) encoding of syllables are distributed and overlapped, we adopted a simple syllable coding in which all the neurons that become active for one syllable were aggregated as the state of a single *unit*. The onset and offset of each syllable in a tutor song was detected by thresholding the sound amplitude. During the course of a singing trial, each syllable coding unit was turned on and off at the stored onset and offset time.

LMAN and Area X: Stochastic Gradient Ascent

Once the output of HVc is given, the vocal output is determined by the connection weight vector W. The goal of motor learning then is to find a weight vector that produces a vocalization which maximizes the evaluation of the template-matching measure. We took a reinforcement learning algorithm as follows, in which T denotes the trial number:

1) A stochastic perturbation $\delta W(T)$ is added to the connection weight $W(T)$.
2) Let the model produce a song with perturbed weight $W(T)+\delta W(T)$ and measure its raw evaluation $r(T)$, as described below.
3) Compute the relative evaluation $\hat{r}(T) = r(T) - \bar{r}(T)$, where $\bar{r}(T)$ is the running average given below
4) Update the weight depending on the relative evaluation:
   $W(T+1) := W(T) + \delta W(T)$ if $\hat{r}(T) > 0$
5) Update the running average of evaluation: $\bar{r}(T+1) = \beta r(T) + (1-\beta)\bar{r}(T)$
6) Update a trend in synaptic change G:
   $G(T+1) = \alpha\, s(\hat{r}(T))\delta W(T) + (1-\alpha)G(T)$, where s( ) is a sigmoid function.
7) Generate the next perturbation based on the trend and Gaussian noise $N(T)$:
   $\delta W(T+1) = G(T+1) + \eta N(T)$
8) Increment T and go to 1)

The evaluation for each syllable was given by the correlation between the spectrographic patterns (80 frequency bins x 20 temporal bins) of the tutor syllable and the generated syllable. The parameters used in the simulations were $\alpha=0.2$, $\beta=0.1$, $\eta=0.02$, and $s(r)=\tanh(r/0.1)$.

RESULTS

Computer simulation was performed on Sparc Station 10 (Sun Micro Systems) with an audio interface to facilitate evaluation of songs by human ears. The simulation system was programmed in the C language and took approximately 30 minutes to simulate 500 learning trials. The results reported below were confirmed in at least five simulation runs using different random seeds for the stochastic learning.
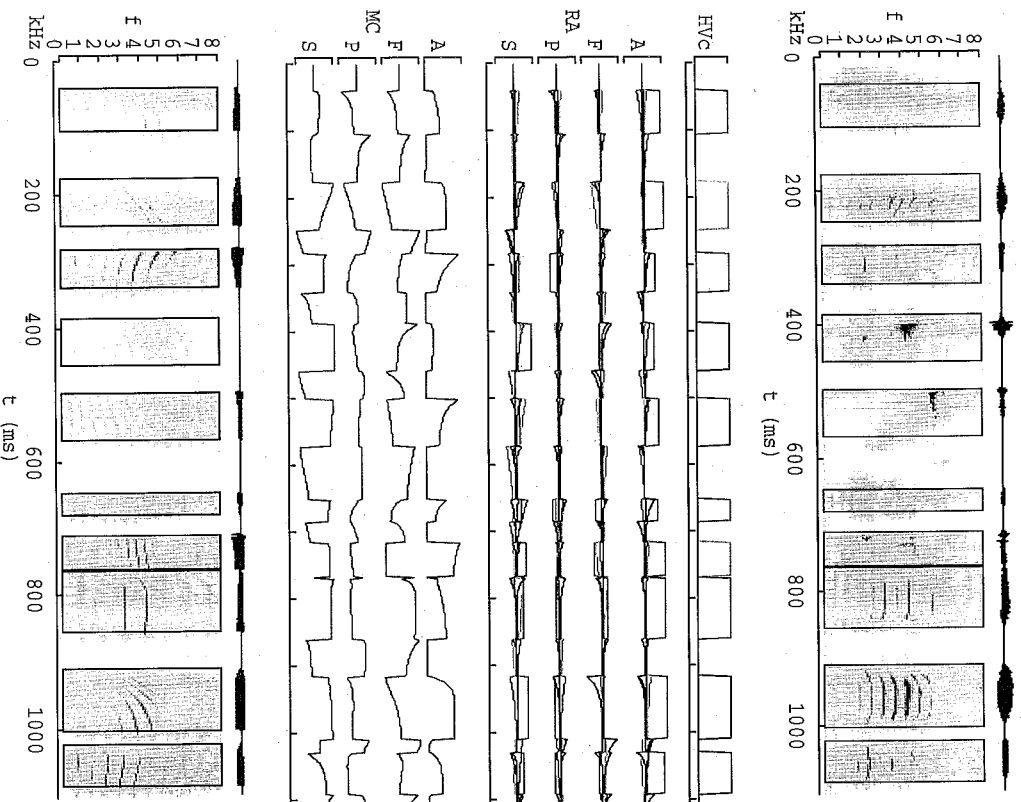
Figure 6. Input and output of the song learning model. Top panel: spectrogram of the tutor song motif. Upper middle panel: activation pattern of HVc units. Middle panel: responses of the units in RA. Lower middle panel: four motor command variables. Bottom panel: spectrogram of the song produced by the model.
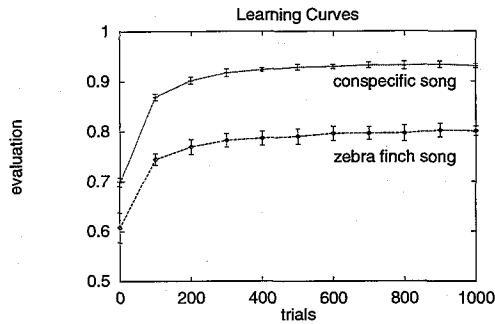
Figure 7. Learning curves for the song learning model. Two different learning curves are shown, one using a zebra finch song as the tutor (dashed line) and the second using a 'conspecific' song synthesized by another model as the tutor (dotted line). On each trial, a new set of weight perturbations was chosen, and a song was produced, and evaluated as described in the text. The evaluation shown here is the correlation between the syllable and its corresponding template. The curves represent the average evaluation of 50 syllables (10 syllables per song; 5 simulation runs).

Initially, the connection weights W were set to small random values, so the syllables did not resemble the original song. After about 500 trials, the average correlation between the original and synthesized syllables reached about 0.8 (dashed line in Figure 7). The final synthesized song motif sounded more similar to the tutor song than the random initial song.

Learning a Synthesized Song

One possible reason for the imperfect reproduction of the zebra finch song was that our model of the syrinx and the motor command production network were more primitive than those of a real zebra finch. In order to check the performance of the model when the target song can be exactly reproduced, we took a set of syllable templates from a synthesized song motif and trained another model from a random start. The correlation after 500 trials was 0.94 (dotted line in Figure 7) and the song sounded quite similar to the synthetic tutor song as judged by human ears.

Learning a Zebra Finch Song

Figure 6 shows an example of how the song learning simulator was performed. The spectrogram of a song motif of a zebra finch is displayed in the top row. Ten syllables in the motif were identified (shown in boxes) and their spectrographic patterns were stored as syllable templates. Ten syllable-coding HVc units were alternately turned on and off at the syllable onset and offset times of the original song motif (upper-middle rows). RA units in the model were driven by the HVc output through the synaptic connection weights W. For each of the four motor command variables (A, F, P, S), there were five units with different time constants (middle rows). The sum of the different temporal response profiles determines the time course of the motor command output (lower-middle rows), which was sent to the syrinx model. The waveform of the synthesized song was then converted into a spectrogram (bottom row). The spectrographic patterns of syllables (marked by boxes) were sampled and compared to the templates, yielding an evaluation r for each syllable which were then used for changing the weights W.

DISCUSSION

The primary question addressed in our simulation of song learning was whether a relatively simple reinforcement learning system could converge to a tutor song within the number of trials that are available to a real zebra finch. The model is based on specific hypotheses for how the computational problems could be solved in a way that is consistent with the neural responses that have been observed in song control nuclei. The simulations demonstrate that the proposed learning system can satisfy these constraints and imitate birdsong.

Many simplifying assumptions were made in the present network model: syllables were unitary coded in HVc; the sound synthesizer was much simpler than a real syrinx; simple spectrographic template matching was used for syllable evaluation. However, it is possible to replace these simplified modules with more biologically accurate ones as warranted by further experimental data. Since the number of learning trials needed to reach convergence in the present model was many fewer than the number of vocalization that occurs during real birdsong learning, which has not been counted in the zebra finch but number many thousand, there is adequate margin for elaboration.

In the following, we consider further experimental tests of our specific hypothesis that the anterior forebrain pathway works as a reinforcement learning system and some open problems that were not covered in the present work.

Effect of Dopaminergic Input to Area X

We have suggested that dopaminergic input from AVT to area X could be used for selection of a particular auditory input as a song template. Lesion or reversible block of dopaminergic system in AVT should disrupt memory of tutor syllables if this hypothesis is true. Injection of dopaminergic agonist or antagonist into area X during tutor song presentation should affect selection of songs to be learned. If confirmed, this would provide strong evidence that the song templates are stored in the anterior forebrain pathway.

Analysis of the Time Course of Syllable Development

The basic assumption behind the model is that vocal learning is a process driven by stochastic gradient ascent. Careful examination of trial-by-trial changes in syllable morphology would allow this assumption to be refined. The patterns of changes might reveal a more complex method for choosing the next vocalization based on previous experience.

Delay in Auditory Feedback

We assumed that each vocalized syllable was evaluated separately. The auditory response latency is about 30 msec in HVc and 50 msec in LMAN in anesthetized birds (Williams, 1989). If the latency is similar in awake birds, by the time the anterior forebrain pathway processes the auditory feedback, the motor units in HVc and RA should be generating the next syllable. Some form of "eligibility trace" in each synapse (Barto et al., 1983; Schweighofer et al., 1996) might be sufficient for accommodating this delay in learning signal. However, a structural mechanism for avoiding temporal crosstalk might be necessary for efficient learning.

Feedback Connection within the Anterior Forebrain Pathway

Recently, novel axonal connections were found from RA to DLM (Wild, 1993) and from LMAN to area X (Vates and Nottebohm, 1995; Nixdorf et al., 1995). Although the new

findings are still consistent with our basic assumption that the connection from HVc to RA is one-way, the feedback loop within the anterior forebrain pathway raises a possibility of different learning schemes. For example, the connection from LMAN to area X makes it possible that the correlation between perturbation and evaluation, which is the main factor of stochastic learning, is taken at the level of area X instead of in LMAN as we assumed.

CONCLUSION

The current theory and simulation results given here could be regarded as an "existence proof" for one solution to the song learning problem, but it does not exclude other possible solutions. Experimental tests of the proposed model would provide a better understanding of the mechanisms of song learning and, more generally, the neural principles underlying the acquisition of novel motor patterns based on sensory experience.

ACKNOWLEDGMENTS

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