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33 A Computational Model of Avian Song Learning

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ABSTRACT Oscine song learning has an auditory phase during which a tutor song is learned and a sensorimotor phase of successive improvement that leads to adult song. A theoretical framework for song learning is presented based on the hypothesis that the primary role of the *anterior forebrain pathway* of the song system is to transform an auditory template to a motor program by a form of reinforcement learning. This framework was tested by building a network model of the song-learning system including a model of the syrinx, the avian vocal organ. The model replicated the spectral envelopes of the syllables from zebra finch songs after several hundred trials of learning. The performance of the model was even better when trained on songs generated by another model having the same architecture. Experiments are proposed to further test the biological plausibility of the hypothesis, which may lead to a more detailed model of the song-learning system. Other types of sensorimotor learning based on mimicry could be implemented with a similar type of computational model.

In comparison with our understanding of the preprogrammed central pattern generators found in many invertebrates and lower vertebrates responsible for complex motor behaviors (Cohen, Rossignol, and Grillner, 1988; Harris-Warrick et al., 1992; Kristan, 1992), much less is known about the representation of motor patterns acquired through experience in humans and other vertebrates, such as walking, riding a bicycle, or talking. Singing in oscine birds is a favorable system for studying the acquisition of complex motor patterns. Much is known about the ethology of birdsong learning and the influence of early auditory learning (Marler, 1963; Konishi, 1965; Marler, 1991; Catchpole and Slater, 1995). The major brain nuclei involved in song control and learning have been identified, as schematically shown in figure 33.1 (Nottebohm, Stokes, and Leonard, 1976; Bottjer et al., 1989). New data are accumulating from lesion and recording experiments on these nuclei (for reviews, see Konishi, 1985; Doupe, 1993; Margoliash, 1997; Bottjer and Arnold, 1997).

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The primary goal of this chapter is to present a theoretical framework and a working model 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, Miesner, and Arnold, 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, Sutton, and Anderson (1983).

The song *template* is a key concept in birdsong learning. A young male bird listens to a *tutor song* during the *critical period* and memorizes a template of the song; later, the bird learns to sing the stored song by comparing its own vocalization to the song template using auditory feedback (Konishi, 1965). However, it is still an open question how the song is encoded and where in the bird's brain the song template is stored. Recent experiments in zebra finch suggest that the song control system has a hierarchical organization: HVC, the high vocal center, is involved in producing a sequence of syllables, whereas its downstream nucleus RA is responsible for the subsyllabic components (Vu, Mazurek, and Kuo, 1994; Yu and Margoliash, 1996).

If we assume that a song is learned in such a hierarchical fashion, the problem of song learning can be decomposed into the following three subproblems:

1. *Sensory encoding*: How to encode the acoustic features of syllables in such a way that they are reliably recognized.
2. *Sequential memory*: How to organize the network so that syllable sequences are stably memorized and reproduced.
3. *Motor decoding*: How to find the motor command patterns needed to replicate the acoustic features of each syllable.

Existing experimental evidence does not provide straightforward solutions to these problems. A computational approach could help in exploring the biological solutions and, in particular, in providing functional

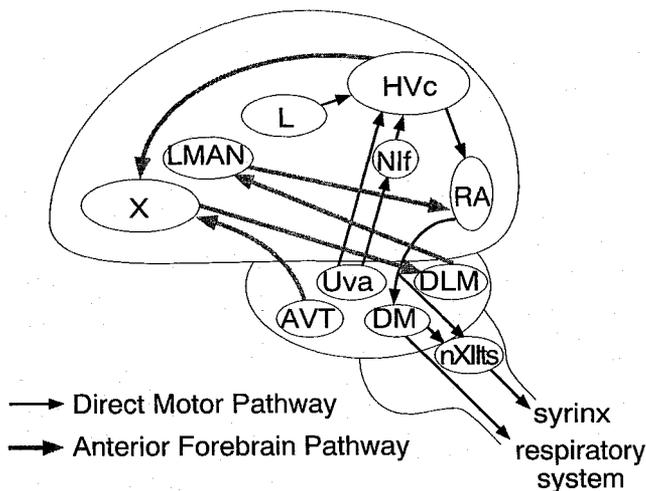


FIGURE 33.1 Schematic diagram of the major songbird brain nuclei involved in song control. The thinner arrows show the direct motor control pathway, and the thicker arrows show the anterior forebrain pathway. Abbreviations: Uva, nucleus uvaeformis of thalamus; NIf, nucleus interface of neostriatum; L, 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; nXIIIts, 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.

constraints on the organization of the learning system. For example, theories of unsupervised learning (von der Malsburg, 1973; Amari, 1977; Linsker, 1986; Bell and Sejnowski, 1995) suggest several possible solutions to sensory encoding problems. Studies of associative memory networks (Fukushima, 1973; Sompolinsky and Kanter, 1986; Dehaene, Changeux, and Nadal, 1987; Amari, 1988; Morita, 1996) provide constraints on representation and architectures that enable stable storage of temporal sequences. There have been extensive studies on the “inverse problem” of finding the control input for a nonlinear system to realize a given target output (Miller, Sutton, and Werbos, 1990; Gullapalli, 1995).

In this chapter, we propose a working hypothesis for the functions subserved by song-related brain nuclei in songbirds (figure 33.1), with an emphasis on the role of anterior forebrain pathway in solving the motor decoding problem.

Figure 33.2 illustrates various schemes for solving inverse problems using neural networks. In the first scheme (figure 33.2a), the desired output is converted to a desired motor command by an inverse model of the motor system that enables replication of the desired output in one shot. 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 33.2b) that uses a linear approximation of the inverse model to convert motor output error into the motor command error for incremental learning of the control network. The problem is that the learning schemes proposed to date either use a biologically implausible algorithm (Jordan and Rumelhart, 1992) or assume the preexistence of an approximate inverse model (Kawato, Furukawa, and Suzuki, 1987; Kawato, 1990). Furthermore, in order to calculate the error in the acoustic output, a replica of the target output, or the tutor song, has to be available.

The third scheme (figure 33.2c) is based on the paradigm of reinforcement learning (Sutton and Barto, 1998). It does not use an inverse model and 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, Sutton, and Anderson, 1983; Gullapalli, 1995). There is no need to maintain 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 33.2c) is the most likely for birdsong learning. We will 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 anatomy, physiology, and the results of lesion studies. We then describe a neural network model that replicates song learning behavior based on these constraints. Experimental tests of the model and limitations are addressed in the “Discussion.”

Earlier versions of this model have appeared elsewhere (Doya and Sejnowski, 1994, 1995).

Model of the song control system

ANATOMY OF THE SONG CONTROL SYSTEM The principal brain nuclei involved in song learning are shown in figure 33.1 (Nottebohm, Stokes, and Leonard, 1976; Bottjer et al., 1989). There are two major pathways: the direct motor pathway and the indirect, anterior forebrain pathway. The direct pathway is composed of Uva, NIf, HVC, RA, DM, and nXIIIts. Lesions to these nuclei immediately disrupt singing, although the effects of lesions in Uva and NIf are variable (Nottebohm, Stokes, and Leonard, 1976; Mc-

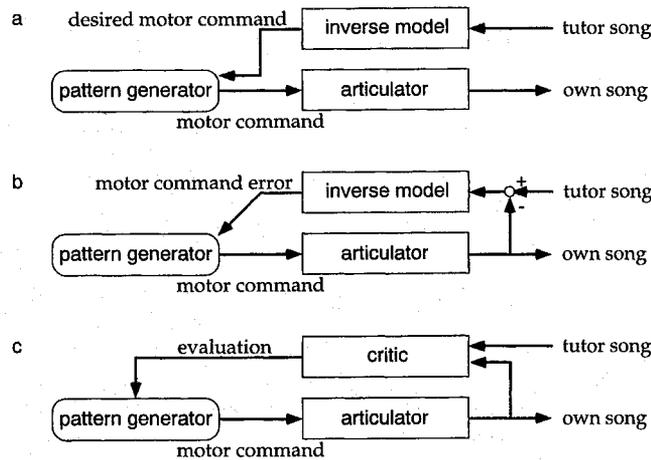


FIGURE 33.2 Different schemes for solving sensorimotor inverse problems. (a) One-shot learning by an inverse model of the motor system. (b) Error correction learning by an approxi-

mate inverse model. (c) Reinforcement learning by a stochastic controller and a critic.

Casland, 1987; Williams and Vicario, 1993; Vu, Kuo, and Chance, 1995). In a recent microstimulation experiment on singing birds, stimulation of HVC produced disruption of the sequence of syllables, whereas stimulation of RA only disrupted the pattern of individual syllables (Vu, Mazurek, and Kuo, 1994). Furthermore, recent study of extracellular recording from singing birds revealed that the activity patterns in HVC are uniquely associated with syllable identity, while precisely timed burst activities in RA are uniquely associated with subsyllabic components (A. C. Yu and Margoliash, 1996). These data suggest that HVC is a candidate site for representing sequences of syllables and that RA is a possible site where the motor patterns for each syllable are stored.

The indirect pathway consists of area X, DLM, and LMAN, forming a bypass from HVC to RA. This pathway is not directly involved in song production because lesions in this pathway in adult birds do not impair their "crystallized" songs (Nottebohm, Stokes, and Leonard, 1976). However, if a lesion is made at any point along the indirect pathway in young birds before the end of vocal learning, their songs become highly abnormal (Bottjer, Miesner, and Arnold, 1984; Sohrabji, Nordeen, and Nordeen, 1990; Scharff and Nottebohm, 1991). There have been a variety of hypotheses 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 and Konishi, 1991), and selective reinforcement of synaptic connections from HVC to RA (Mooney, 1992).

FUNCTIONS FOR COMPONENTS OF THE SONG CONTROL SYSTEM We propose a functional model of the song control system based on the following experimental evidence:

1. Sequences of syllables are produced at the level of HVC (Vu, Mazurek, and Kuo, 1994; A. C. Yu and Margoliash, 1996).
2. RA is a myotopically organized (Vicario, 1991b).
3. Both the direct and indirect pathways linking HVC and RA are unidirectional (Bottjer et al., 1989).

These facts imply the following constraints on the localization of the computational processes suggested in the preceding list:

1. The representation of syllables suitable for auditory recognition and sequential memory is constructed in the ascending auditory pathway up to the level of HVC.
2. The memory and production of syllable sequences are performed within HVC.
3. The syllable representation in HVC needs to be transformed into muscle-oriented representation in RA.

Figure 33.3 illustrates our current working hypothesis about the functions of song-related nuclei. The ascending auditory pathway from the cochlea through the auditory thalamus and the forebrain auditory nucleus field L to HVC performs hierarchical processing of auditory input, leading to some internal representation of syllables that is useful for recognition and memory. On one hand, it is known that field L has a tonotopical organization (Bonke, Scheich, and Langner, 1979) and that the neurons respond to pure tone or band-limited noises (Margoliash, 1986). On the other hand, no tonotopical organization is found in HVC, whose neurons have more

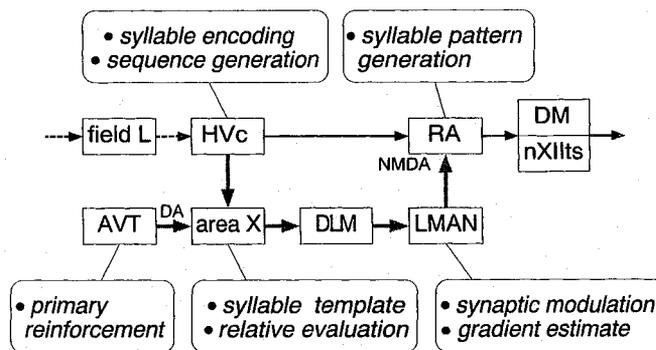


FIGURE 33.3 Schematic diagram indicating the proposed functions for each of the major nuclei of the song system. The direct pathway is shown at the top, starting with auditory input into field L. The anterior forebrain pathway starts at HVC and

makes a side loop to RA through area X and LMAN. The bullets in each balloon give the proposed function of the corresponding nucleus. See text for more details.

selective response properties to complex acoustic features, such as frequency modulation, combination of harmonics, sequence of notes, and sequence of syllables (Margoliash, 1983; Margoliash and Fortune, 1992; Lewicki and Konishi, 1995; Lewicki, 1996). Many cells are strongly tuned to the bird's own song (Margoliash, 1986). It has recently been found that the auditory responses of HVC neurons to different syllables have distributed and overlapping spatial patterns (Sutter and Margoliash, 1994), but the functional implication of such a representation remains to be studied.

HVC is regarded as the main center for memory and generation of syllable sequence (Vu, Mazurek, and Kuo, 1994; A. C. Yu and Margoliash, 1996). Sequence production in HVC is probably controlled by timing cues from Nif and Uva (McCasland, 1987; Williams and Vicario, 1993). Neurons in HVC show both auditory and motor responses (McCasland and Konishi, 1981; McCasland, 1987), but neither tonotopical or myotopical organization is seen in HVC. Nor has any simple correlation been reported between the auditory and motor responses for the same syllable (McCasland and Konishi, 1981; McCasland, 1987; C.-H. Yu and Margoliash, 1993). There appears to be a drastic change in the operation of HVC during singing: The spontaneous activity increases (C.-H. Yu and Margoliash, 1993; A. C. Yu and Margoliash, 1996), and the auditory response is suppressed for a few seconds afterward (McCasland and Konishi, 1981).

RA has topographic connection to nXIIts, which topographically projects to the muscles in the syrinx (Vicario, 1988; Vicario, 1991b). The dorsal part of RA projects to DM, which projects to the respiratory control system. Since no myotopical organization is apparent in HVC, the syllable representation in HVC would have to be transformed into a more muscle-oriented representation in the connection from HVC to RA. The anterior

forebrain pathway forms a side path to this motor decoding pathway. Lesions in area X or LMAN in adults do not affect crystallized songs, but disrupt song learning in young birds (Bottjer, Miesner, and Arnold, 1984; Sohrabji, Nordeen, and Nordeen, 1990; Scharff and Nottebohm, 1991). Neurons in area X, DLM, and LMAN have highly selective response to the bird's own song in adult birds (Doupe and Konishi, 1991), but some of them are selective to the tutor song in young birds (Solis and Doupe, 1995). Synaptic connections from LMAN to RA are formed prior to those from HVC (Konishi and Akutagawa, 1985) and are mediated mainly by NMDA-type glutamate receptors (Kubota and Saito, 1991; Mooney and Konishi, 1991), which are involved in development and learning in the mammalian central nervous system (Malenka and Nicoll, 1993; Fox and Zahs, 1994). These facts suggest that the function of the anterior forebrain pathway is to set up appropriate synaptic connections from HVC to RA that lead to a better match between the bird's own vocalization and the song template (Bottjer et al., 1989; Mooney, 1992; Doupe and Konishi, 1991; Doupe, 1993).

Based on these previous suggestions, we hypothesize that the anterior forebrain pathway functions to be a specific reinforcement learning system called an *adaptive critic*, as shown in figure 33.4 (Barto, Sutton, and Anderson, 1983). In a reinforcement learning paradigm, a stochastic perturbation is given to the motor commands, and if it results in better performance, the perturbed motor command is reinforced; that is, the perturbation is made permanent. In order for this learning scheme to work efficiently, it is necessary that the positive and negative reinforcement be balanced. An important role of the critic is to evaluate the present performance relative to the recent average performance, a method known as *reinforcement comparison* (Sutton and Barto, 1998). In the context of syllable vocalization learning, we propose that

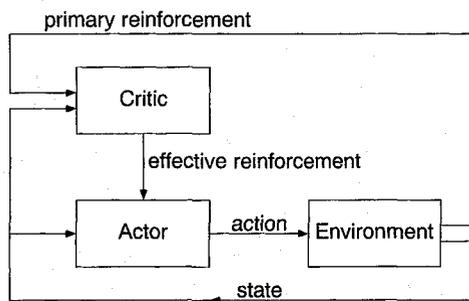


FIGURE 33.4 A block diagram showing the actor-critic architecture for a feedback control task (Barto, Sutton, and Anderson, 1983). The direct control pathway is the closed loop between the actor and the environment. The control policy is learned through interaction with the critic, which evaluates the sensory feedback caused by the action of the actor. A scalar reinforcement signal generated by the critic is used by the actor to modify its future action. The critic receives information used for the evaluation from a primary reinforcer. In the birdsong literature, the term “template” is used for the information used by the critic to perform the evaluation.

LMAN provides stochastic perturbation to the HVC-to-RA connection and that area X evaluates how well the resulting syllable matches the template. The raw similarity index is compared to the recent average similarity index for the syllable, and the relative evaluation signal then determines whether the temporary change in the HVC-to-RA connection is made permanent or not. In this scheme, the evaluation and perturbation modules are on a side path to the main motor control pathway and are not necessary for control when learning is completed.

Several lines of evidence 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 singing in the adulthood when songs are normally crystallized. This effect is similar to that of early deafening. Early lesion in LMAN results in stable but poorly structured song with fewer syllables than normal. These observations are nicely explained if we assume that area X serves as the critic, which provides evaluation of vocalization based on auditory feedback, and that LMAN modulates the connection strengths from HVC to RA and provides a random element to the controller.

The hypothesis that area X functions as a critic is supported by the fact that it receives dopaminergic input from a midbrain nucleus AVT, the avian homologue of mammalian ventral tegmental area (Lewis et al., 1981; Casto and Ball, 1994). Activity of the dopamine system is related to reward in many species (Schultz, Apicella, and Ljungberg, 1993). During auditory learning, this dopaminergic input can be used for selection of auditory input that is to be memorized as song template. It has been shown that a young bird does not indiscriminately

memorize all of its auditory experience as its song template. When a young zebra finch is caged with several adult birds, it selects most of its song syllables from the adult that had most frequent interaction with the bird, especially feeding interactions (Williams, 1990). We postulate that this selection of auditory input that is to be memorized as song template happens in area X by association of auditory input from HVC and reward input from AVT. In other words, whereas the auditory tuning of HVC cells should simply reflect auditory experience, responses of area X cells are tuned to the specific songs to be learned. Although the majority of neurons in both HVC and area X in young birds are tuned to the bird's own developing song rather than to the tutor song (Volman, 1993; Doupe, 1993), some of the neurons in area X have preferred tuning to the tutor song (Solis and Doupe, 1995). During the sensorimotor learning phase, the activation level of those neurons could be used to evaluate the match between the vocalization of the bird and that of the tutor. Furthermore, if the function of area X is not simply to detect a match to the stored template but also to provide “relative” evaluation based on recent level of performance, then there should be many cells that are tuned more to the bird's current song than to the tutor song.

As mentioned earlier, 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). The NMDA-type input from LMAN may enable both short-term and long-term changes in the HVC-to-RA synaptic efficacy during sensorimotor learning. It has been observed in slice preparations that simultaneous stimulation of both HVC and fibers originating in LMAN results in a response larger than the linear summation of individual responses (Mooney, 1992), consistent with some nonlinear interaction between these two inputs. For example, when there is a tonic NMDA-type input, the postsynaptic response to the same non-NMDA-type input is amplified, which effectively modulates the synaptic conductance of the non-NMDA inputs (Thomson and Deuchars, 1994). Although long-term changes of synaptic strengths have not yet been found in RA, activation of NMDA-type receptors triggers plastic synaptic change in many other central nervous systems (Malenka and Nicoll, 1993).

Computer simulations of vocalization learning

We focus on only one of the three computational problems in song learning, namely that of finding the motor commands needed to produce a desired auditory

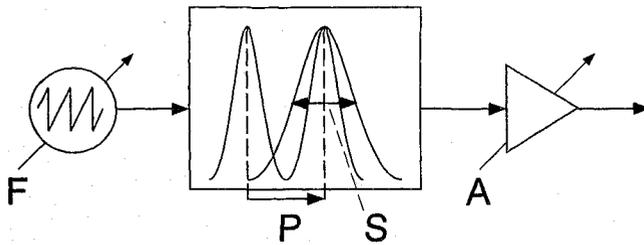


FIGURE 33.5 The model of the syrinx used in the song learning model. The sound output was controlled by four input variables: *A*, gain of the amplifier; *F*, fundamental frequency of the sound source; *P*, peak frequency; and *S*, sharpness of the band-pass filter. In addition to these parameters, the output was governed by units with a range of temporal responses (see figure 33.6).

impression. The question we asked is whether the reinforcement learning scheme that we have outlined can be implemented within the known biological constraints and whether such a system can perform sensorimotor learning within a realistic number of trials. We required the model to produce sound that could be compared to real birdsong.

The outline of the simulation system is as follows. We built a simple model of the syrinx, the avian vocal organ, and then constructed a neural network model of RA and HVc that sends a series of motor commands to the syrinx model. We implemented the adaptive critic learning system by assigning the stochastic perturbation to LMAN and the syllable evaluation to area X. Since it was beyond the scope of the present investigation to model the detailed mechanisms of auditory encoding and sequential memory, we used simplified spectrographic template matching for syllable templates and unary encoding of syllables in HVc, which are not necessarily biologically realistic.

SYRINX: SOUND SYNTHESIZER In order to test the performance of the model of the vocal control system, we designed a computer program that mimics the function of the syrinx, the avian vocal organ located near the junction of the trachea and the bronchi (Brackenbury, 1982; Vicario, 1991a). The sound source for the syrinx is the oscillation of a pair of tympaniform membranes on the medial side of the bronchi. Depending on the tension of the membrane and the airflow around it, which are controlled by the activity of six pairs of syringeal muscles, the syrinx can produce pure tones, harmonic sounds, and nonharmonic sounds with complex frequency modulation (Casey and Gaunt, 1985). Activation of the dorsal syringeal muscles coincides with the air flow in the bronchus, and 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 33.5, consisted of a variable-frequency sound source, a band-pass 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 band-pass filter, and the gain of the amplifier *A*. The output sound waveform $x(t)$ was calculated from the time course of the variables $(A(t), F(t), P(t), S(t))$, which had values between zero and one:

$$\dot{\phi}(t) = f_0 + (f_1 - f_0)F(t)$$

$$z(t) = [\phi(t) \bmod 1] \times 2 - 1$$

$$\omega(t) = 2\pi[f_2 + (f_3 - f_2)P(t)]$$

$$\mu(t) = \mu_0 + (\mu_1 - \mu_0)S(t)$$

$$\dot{u}(t) = \omega(t)[z(t) - u(t)] - \mu v(t)$$

$$\dot{v}(t) = \mu u(t) - \omega(t)v(t)$$

$$x(t) = A(t)u(t)$$

where $\phi(t)$ and $z(t)$ are the phase and the output of the harmonic oscillator, and $\omega(t)$ and $\mu(t)$ are the angular frequency and damping factor of the band-pass filter, respectively. The values of the parameters were $f_0 = 0.4$ kHz, $f_1 = 1.2$ kHz, $f_2 = 2$ kHz, $f_3 = 8$ kHz, $\mu_0 = 1.0$ ms⁻¹, and $\mu_1 = 0.1$ ms⁻¹. The system was numerically integrated by the Euler method using a time step of 1/32 ms. The model could produce "birdlike" chirps and warbles with the time courses of the input variables chosen appropriately (figure 33.9).

RA: SYLLABLE PATTERN GENERATOR RA is capable of producing a variety of temporal responses in order to produce command outputs for syllables with various spectral features. Several constraints are available from experimental studies. First, RA has a myotopical organization (Vicario, 1991b). Second, in slice preparations, HVc input to RA evokes fast non-NMDA-type, slower NMDA-type, and delayed polysynaptic inhibitory responses (Mooney, 1992). Third, 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 myotopical organization, the model of RA had four subnetworks, each of which could exert control

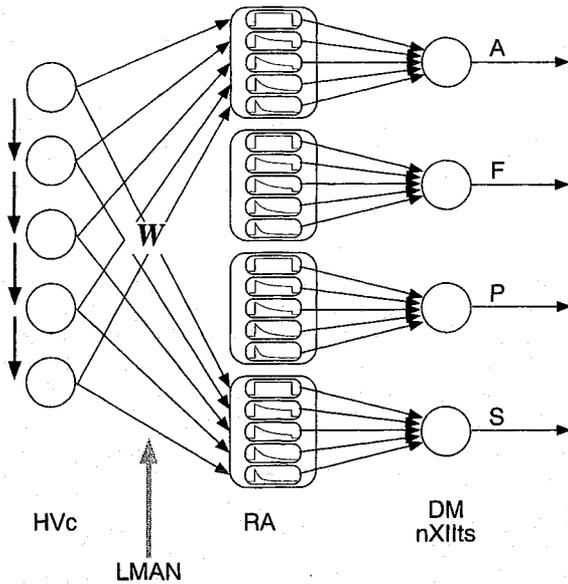


FIGURE 33.6 Model of the direct motor pathway. Syllables were unary coded in HVC, and their sequential activation triggered syllable pattern generation networks in RA. The RA units were divided into four groups corresponding to the four motor command variables (A , F , P , S). Within each group, there were k exponential temporal kernels with different time constants. The sum of their response profiles served as the motor command for the syrinx model.

on one of the four output motor command variables (A , F , P , S). Within each subnetwork, there were $k=5$ “temporal response kernels,” where each unit had a different time course, as shown in figure 33.6. The temporal response of an RA unit $r_j(t)$ to the input from HVC $s_i(t)$ ($i=1, \dots, n$) was

$$p_j(t) = \sum_{i=1}^n w_{ji} s_i(t)$$

$$\tau_j \dot{q}_j(t) = p_j(t) - q_j(t)$$

$$r_j(t) = p_j(t) - q_j(t)$$

where $p_j(t)$ is the input sum, $q_j(t)$ is delayed inhibition or adaptation, and τ_j is the time constant of the j th unit. The motor command output was synthesized from a combination of these responses:

$$m^C(t) = f \left[\sum_{j=1}^k r_j^C(t) + b^C \right]$$

where index C denotes one of the command variables (A , F , P , S), f is a sigmoid function $f(x) = 1/[1 + \exp(-4x)]$, and b is the bias. The time constants of the $k=5$ kernels were $\tau_1 = \infty$ [i.e., $r_j(t) = p_j(t)$], $\tau_2 = 80$, $\tau_3 =$

40 , $\tau_4 = 20$, and $\tau_5 = 10$ (ms). In order to assure clear syllable onset and offset, the bias for the sound amplitude was $b^A = -1$, and the weight for the first kernel was initially set as $w_{11}^A = 1$. Other biases and initial weights were set to zero. The weights w_{ji} were initialized at the beginning of learning to random values generated with a Gaussian distribution having a standard deviation of 0.1. The reinforcement learning algorithm given in the next subsection incrementally changed the weights corresponding to each syllable.

HVC: SEQUENCE GENERATOR In recordings from HVC in awake birds, some neurons became activated preceding specific syllables (McCasland, 1987; A. C. Yu and Margoliash, 1996). A simple syllable coding was adopted in which all the neurons that become active for the i th syllable were aggregated as the state of a single “unit,” s_i . The onset and offset of each syllable in a tutor song was detected by thresholding the sound amplitude and storing the interval in an event table. During the course of a song, each syllable coding unit s_i was turned on ($s_i = 1$) and off ($s_i = 0$) at the stored onset and offset time. This “unary encoding” scheme is oversimplified, and there is evidence that the motor encoding of syllables has overlaps, so that a single HVC unit would be active during more than one syllable (A. C. Yu and Margoliash, 1996), as in the case of auditory encoding (Sutter and Margoliash, 1994). A distributed encoding could have been used to model HVC, but this was not included in the present model for simplicity.

LMAN: STOCHASTIC GRADIENT ASCENT The vocal output is determined by the connection weight matrix $W = \{w_{jv}^A, w_{jv}^F, w_{jv}^P, w_{jv}^S\}$ based on the preceding models of HVC, RA, and the syrinx. The goal of motor learning then is to find a point in this $4kn$ -dimensional weight space that produces a vocalization that maximizes the evaluation of the template-matching measure. In the reinforcement learning algorithm used here, this goal was accomplished by a stochastic method for optimizing the evaluation function.

In the first step of the learning algorithm, the output motor command from RA was stochastically perturbed by temporarily changing the input connection strengths from HVC. Such perturbations in the output of RA units could be produced by the modulation of the HVC-to-RA connection weights by NMDA-type synaptic input from LMAN. The perturbation of the weights was implemented as a static weight change δw_{ji} during each song trial. This produces a perturbation in the RA:

$$\delta p_j(t) = \sum_{i=1}^n \delta w_{ji} s_i(t)$$

The second step was to evaluate this perturbed song by comparing it with the song template. By the procedure mentioned in the next section (on area X), a syllable-specific value \hat{r} , the “effective” reinforcement, was derived. Finally, the weights were permanently changed based on correlations among the inputs, outputs, and the evaluation (Barto and Jordan, 1987; Barto, 1995):

$$\Delta w_{ji} \propto \hat{r} \times \delta p_j(t) \times s_i(t)$$

With the unary encoding scheme of HVc adopted here, this expression reduces to

$$\Delta w_{ji} \propto \hat{r} \times \delta w_{ji}$$

since only one syllable unit i is active ($s_i = 1$). In other words, the temporary synaptic modulation δw_{ji} persists as a plastic change Δw_{ji} if the effective evaluation is positive, which is a kind of “weight perturbation” optimization algorithm (Alspector et al., 1993; Unnikrishnan and Venugopal, 1994).

A refinement of this basic reinforcement algorithm was used that improved the convergence of the learning. For each trial T , the temporary weight perturbation $\delta w_{ji}(T)$ was the sum of the evaluation gradient estimate $G_{ji}(T)$ defined subsequently and a random perturbation $N_{ji}(T)$ of size η :

$$\delta w_{ji}(T) = G_{ji}(T) + \eta N_{ji}(T)$$

The network with perturbed weights $w_{ji}(T) + \delta w_{ji}(T)$ was used to produce a vocal output, and its evaluation $\hat{r}(T)$ was given by the model of area X described in the next subsection. The weights were then permanently changed only if the trial was successful:

$$w_{ji}(T+1) = w_{ji}(T) + \delta w_{ji}(T) \quad \text{if } \hat{r}(T) > 0$$

The estimate of gradient in the weight space $G_{ji}(T)$ was updated by the sum of the perturbations $\delta w_{ji}(T)$ multiplied by the effective evaluation:

$$G_{ji}(T) = \alpha \hat{r}(T) \delta w_{ji}(T) + (1 - \alpha) G_{ji}(T)$$

where the constant $0 < \alpha < 1$ controls the influence of the new trial on the running average over trials. A geometrical interpretation of this learning algorithm is illustrated in figure 33.7. The weighted running average of the weight change is like the “momentum” that is commonly used in other neural network learning algorithms (Rumelhart, Hinton, and Williams, 1986). We used $\alpha = 0.2$ and $\eta = 0.02$ in all the simulations reported here.

AREA X: EVALUATION BY SPECTROGRAPHIC TEMPLATE MATCHING The activation levels of the neurons selective for the tutor song that have been observed in area X

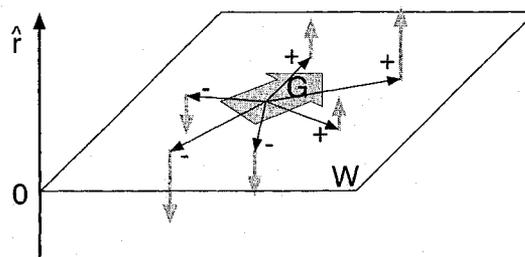


FIGURE 33.7 Estimate of evaluation gradient G from weighted summation of perturbation vectors. The vertical axis is the evaluation \hat{r} , and each point in the W plane represents a choice for two of the weights (there were many more in the actual model). The gradient G (central arrow) gives the running average of the evaluation function over the recent history of stochastically chosen weights, represented by the thin vectors from the central thick arrow.

(Solis and Doupe, 1995) could represent the similarity of the recently produced syllable to the corresponding tutor syllable (Doupe and Konishi, 1991). The evaluation of each syllable was assumed to be available separately, and a simple spectrographic template-matching method was used for evaluating its similarity to the tutor syllable, as follows.

First, the sound waveform from the bird was transformed into a spectrogram, which had 80 frequency channels in steps of 100 Hz, sampled every 1 ms. The onset and offset of the syllable were detected by appropriately setting a threshold for the sound amplitude. The spectrographic pattern of each syllable was down-sampled with a Gaussian filter having 40 frequency bins and 20 temporal bins, to accommodate slight variations in both frequency and time domains. The resulting 800-dimensional vector was normalized and then stored as the template vector for each syllable. A sample vector for a synthesized syllable was made in the same way. The correlation $0 \leq r \leq 1$ between the template and sample vector was used as the raw evaluation score.

We further assumed that area X functions as an “adaptive” critic that provides the evaluation in a form relative to currently expected level of performance. The running average \bar{r} of the evaluation r was updated at each time step:

$$\bar{r}(T+1) = \beta r(T) + (1 - \beta) \bar{r}(T)$$

where $0 < \beta < 1$ is the smoothing constant for the averaging. The “effective evaluation” \hat{r} that was used for learning in LMAN was given by

$$\hat{r}(T) = \tanh\{[r(T) - \bar{r}(T)]/\gamma\}$$

The squashing function \tanh was used to regulate the learning process. We used $\beta = 0.1$ and $\gamma = 0.1$ in all simulations.

ZEBRA FINCH SONG SAMPLES Songs of male adult zebra finches were recorded and digitized at 12 bits and with a 32-kHz sampling rate by Michael Lewicki at the California Institute of Technology.

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 in the next subsection were confirmed in at least five simulation runs using different random seeds for the stochastic learning.

LEARNING A ZEBRA FINCH SONG Figure 33.8 shows an example of how the song learning simulator 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 panel). RA units in the model were driven by the HVC output through the synaptic connection strengths w_{ji} . For each of the four motor command variables (A, F, P, S), there were five units with different time constants (middle panel). The sum of the different temporal response profiles determines the time course of the motor command output (lower middle panel), which was sent to the syrinx model. The waveform of the synthesized song was then converted into a spectrogram (bottom panel). The spectrographic patterns of syllables (marked by boxes) were sampled and compared to the templates, yielding an evaluation r for each syllable that was then used for changing the weights w_{ji} .

Initially, the connection weights w_{ji} were set to small random values, so the syllables did not resemble the original song. After about 500 trials, the average correlation

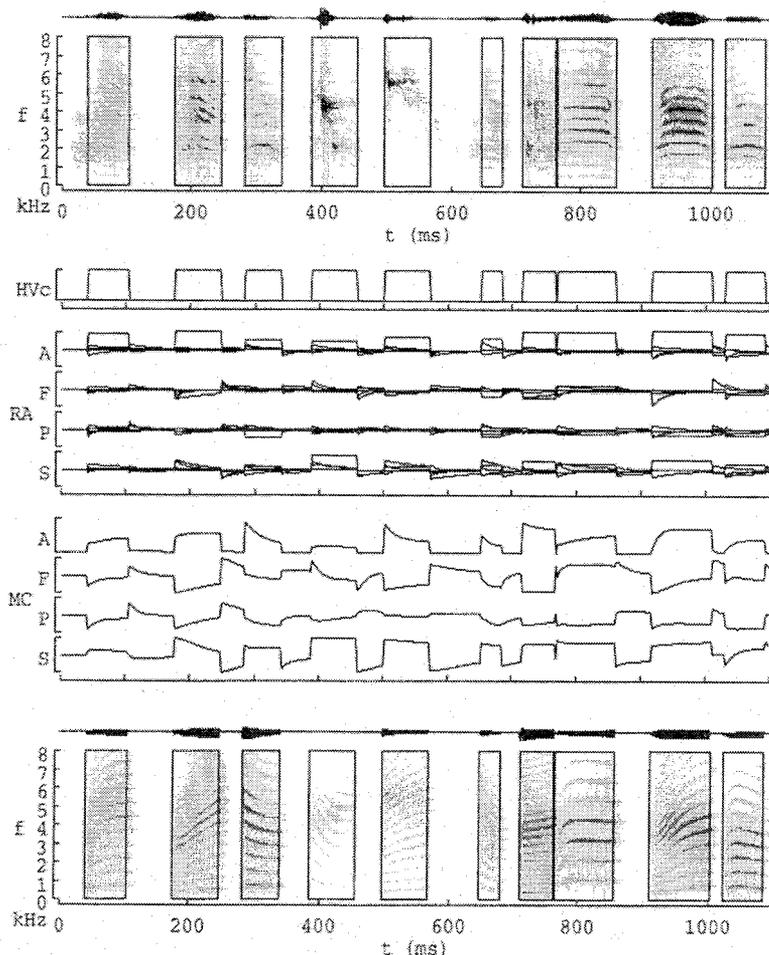


FIGURE 33.8 Input and outputs of the song learning model. (top panel) Spectrogram of the tutor song motif, which consisted of five syllables. (upper middle panel) Activation pattern of

HVC units. (middle panel) Responses of the units in RA. (lower middle panel) Four motor command variables. (bottom panel) Spectrogram of the synthesized song produced by the network.

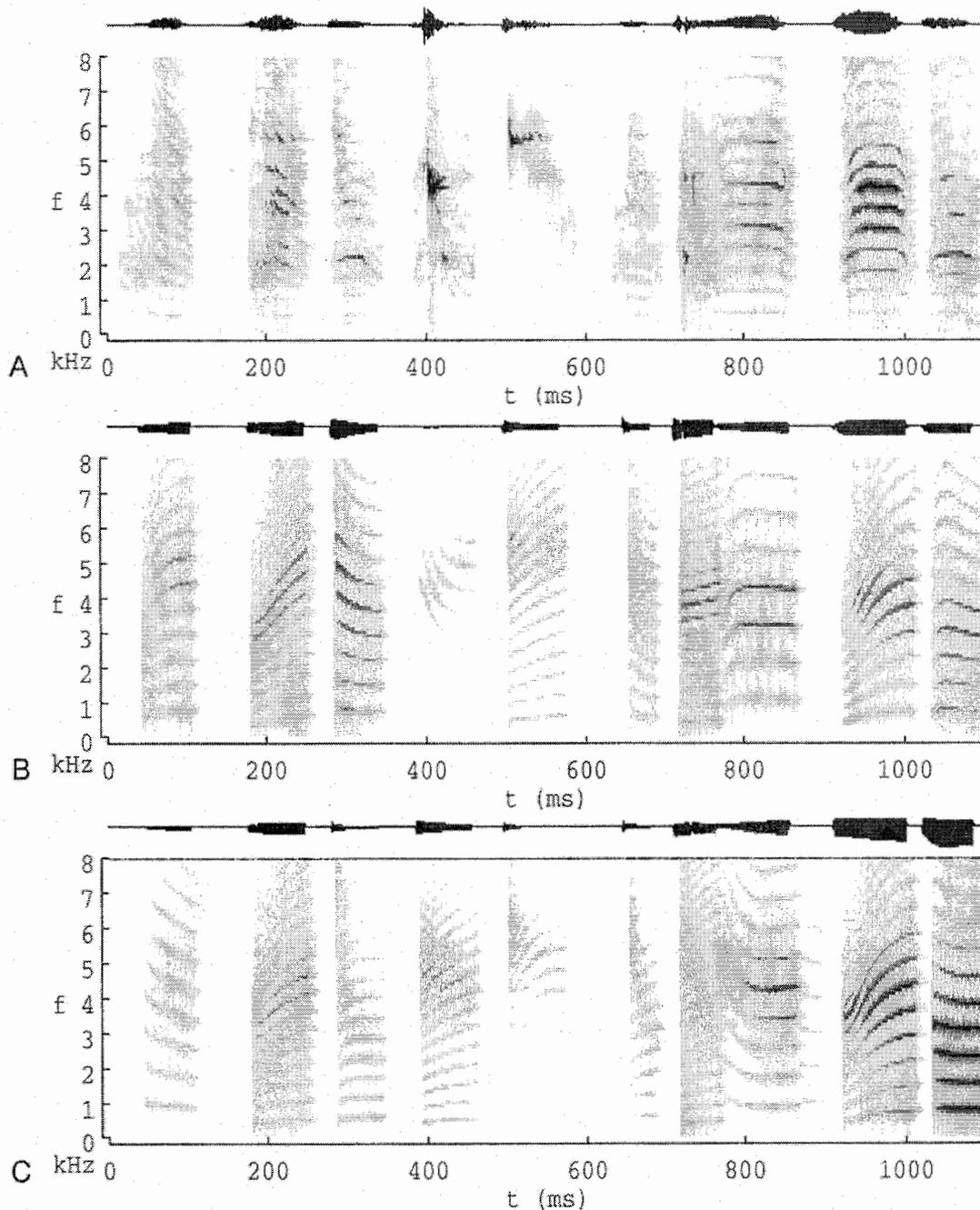


FIGURE 33.9 Sonograms. (A) The original zebra finch song motif. (B) A song produced by the model after 500 trials using

the zebra finch song A as the template. (C) A song produced after 500 trials using the model song B as the template.

between the original and synthesized syllables reached about 0.8 (figure 33.10). The final synthesized song motif sounded more similar to the tutor song than the random initial song. As shown in the spectrograms (figure 33.9), the overall frequency profiles of the syllables were similar, although the detailed features in the spectrogram, such as harmonic structures and frequency modulation patterns, were not accurately reproduced.

LEARNING A SYNTHESIZED SONG There are two possible reasons for the imperfect replication of the zebra finch song syllables. One is that our model of the syrinx and the motor control network were much more primitive than those of a real zebra finch, and therefore precise mimicry was impossible. Another is that the reinforcement learning procedure converged to a suboptimal solution. In order to differentiate these possibilities,

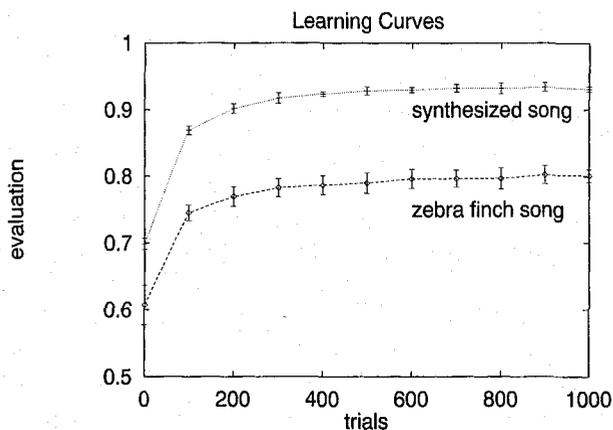


FIGURE 33.10 Learning curves for the song learning model. Two different learning curves are shown, one using a zebra finch song as the tutor (dashed line) and the second using a synthesized song generated by another model as the tutor (dotted line). On each trial, a new set of weight perturbations was chosen, a song produced, and an evaluation carried out 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).

we tested the performance of the model when the target song could be exactly reproduced by taking a set of syllable templates from a synthesized song motif and training another model from a random start. The correlation after 500 trials was 0.94 (dotted line in figure 33.10) and the song sounded quite similar to the tutor model as judged by human ears (see figure 33.9B,C). This result implies that the relatively low performance using a real zebra finch song as a template was mainly due to the differences between the vocal system of the real bird and that of the model. However, even with the synthesized song, the reinforcement learning algorithm did not converge to the optimal solution with a correlation of 1.0. Note that imperfect replication of syllables and the resulting individual variability of songs are also seen in real birds.

Discussion

The primary question addressed by our model of song learning is 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 unary 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 vocalizations that occur during real birdsong learning, which have not been counted in the zebra finch but number many thousand, there is adequate margin for elaboration.

Additional experiments are needed to test and improve the model, as outlined in the following subsections.

BLOCKING DA INPUT FROM AVT 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 the 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 method would provide strong evidence that the song templates are stored in the anterior forebrain pathway.

TEST OF MODULATION AND PLASTICITY INDUCED BY LMAN We assumed that NMDA-type synaptic input from LMAN to RA modulated the non-NMDA-type synaptic input from HVC to RA. There has been no direct experimental evidence for plastic changes in RA synapses induced by input from LMAN. Further experiments in slice preparations could reveal when and how such plasticity is induced, or could indicate that such plasticity is not plausible. Another approach is electric stimulation of LMAN in young, singing birds. If altered activity in LMAN results in perturbation of ongoing song or plastic change in the song after perturbation, that would suggest the existence of modulatory or plastic mechanisms *in vivo*.

SUPPRESSION OF AUDITORY RESPONSE IN HVC DURING SINGING In HVC neurons that have both auditory and motor responses, the auditory responses are suppressed during and soon after the bird is singing (McCasland and Konishi, 1981; McCasland, 1987). If the suppression is complete and occurs in young birds, we would have to reconsider the use of auditory feedback in the model. One possibility is that the suppression is due to the same mechanisms that induce hyperpolarization in

HVc neurons with the auditory stimulus of the bird's own song (Lewicki, 1996). This may help in narrowing the auditory selectivity of the HVc neurons.

DELAY IN AUDITORY FEEDBACK We assumed that each vocalized syllable was evaluated separately, but this approach may not be possible if there is significant overlap in the motor and auditory responses to adjacent syllables. The auditory response latency is about 30 ms in HVc and 50 ms 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. In order to utilize the delayed evaluation signal, the synapses from HVc to RA have to use an "eligibility trace" for plasticity (Barto, Sutton, and Anderson, 1983). Examples of possible biological implementation of eligibility traces can be seen in Houk, Adams, and Barto, (1994), and Schweighofer, Arbib, and Dominey (1996).

Recently, a new hypothesis was proposed for a "forward model" within HVc that predicts the auditory outcome from the HVc motor output. The predicted auditory outcome is then used for immediate reinforcement of ongoing motor activity instead of the actual auditory feedback (Troyer, Doupe, and Miller, 1996). However, it may be difficult for such prediction of auditory outcome to be reliably performed within HVc while the connection from HVc to RA is changed by learning.

FEEDBACK CONNECTION IN 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-Bergweiler, Lips, and Heinemann, 1995). Although we did not take into account these possible feedback connections within the AFP, they are still consistent with our basic assumption that there is no feedback connection back to HVc in the AFP.

The finding of the novel connection from LMAN to area X raises a possibility that 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. It has been shown that the connections from LMAN through area X to DLM (Vates and Nottebohm, 1995) and from DLM through LMAN to RA (Johnson, Sablan, and Bottjer, 1995) are topographically organized. This organization would enable the activity pattern in LMAN to be correlated with the syllable evaluation in area X and then sent back to LMAN through DLM to alter the next activity pattern in LMAN. Together with the finding that the ventral and

middle parts of RA differentially control the dorsal and ventral syringeal muscles and that these muscles control the air flow and the fundamental frequency, respectively (Goller and Suthers, 1995), it is possible that there are distinct channels within the AFP that are involved in evaluation and modulation of different aspects of vocalization. However, data on the activity of AFP neurons during singing would be necessary to test these possibilities.

Conclusions

In this chapter, we have identified computational mechanisms that could account for birdsong learning and shown how these mechanisms could be supported by the known anatomy of the avian brain. We then focused on the issue of sensorimotor learning and tested our specific hypothesis that the anterior forebrain pathway works as a reinforcement learning system. 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. Nevertheless, this is the first computational model of the entire song-learning system that is able to replicate realistic birdsongs. Because the model was based on the recent experimental findings, especially those from the anterior forebrain pathway, experimental tests of the proposed model should 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.

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