Motor control of birdsong

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One of the challenges when considering the motor control of birdsong is to understand how such a wide variety of temporally and spectrally diverse vocalizations are learned and produced. A better understanding of central neural processing, together with direct endoscopic observations and physiological studies of peripheral motor function during singing, has resulted in the formation of new theoretical models of song production. Recent work suggests that it may be more profitable to focus on the temporal relationship between control parameters than to attempt to directly correlate neural processing with details of the acoustic output.

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Abbreviations

DM	dorsomedial intercollicular nucleus
IMAN	lateral subdivision of magnocellular nucleus of the anterior neostriatum
nXIIts	tracheosyringeal motor nucleus (caudal portion of hypoglossal nucleus)
RA	nucleus robustus archistriatalis
RAm	nucleus retroambigualis

Introduction

Birdsong has provided an important animal model in which to study motor control. Its widespread importance in courtship and territorial behavior has subjected song to strong sexual and natural selection, which has presumably contributed to the striking specializations for vocal learning and vocal control in the brain of songbirds. Selection may also have favored the inclusion of a highly versatile, low mass vocal organ operating in the regulated environment of an air sac deep in the thorax. The performance of this vocal system is remarkable for the temporal dynamics, extraordinary complexity and stereotypy present in the songs of many species. As a group, the oscine songbirds provide an opportunity to study motor control at the extremes of performance.

The acoustic units of birdsong, the notes and syllables, are generated by motor patterns involving the coordinated activity of many muscle groups, most notably those of the respiratory system and vocal organ. New insights into both central and peripheral mechanisms of song production bring us closer to understanding how these vocal gestures are formed and how they may specify the acoustic output. However, the links between central processing and peripheral mechanisms are still poorly understood. New experimental findings and theoretical models of vocal control could help to bridge this gap. In this review, we focus mainly on adult song; reviews of models and mechanisms of song learning can be found elsewhere [1].

Sound production and the vocal periphery

The vocal organ of songbirds, the syrinx, is composed of modified cartilages (Figure 1) and specialized muscles that are located at the junction between the primary bronchi and the trachea. The longstanding assumption that sound resulted from vibration of the thin tympaniform membranes that form the medial wall of each bronchus has been challenged by observations that the tympaniform membranes can be destroyed with only a small effect on the bird's song. Direct endoscopic observation of the syrinx when producing sounds that were evoked by brain stimulation suggests a new mechanism. These observations show that sound is generated in songbirds by small masses of connective tissue, the medial and lateral labia, which are located at the cranial end the bronchus ([2,3]; Figure 1).

The labia on each side of the syrinx are controlled by ipsilateral members of several pairs of muscles, which are innervated by the ipsilateral tracheosyringeal branch of the hypoglossal nerve. The principal functions of these muscles in sound production have been deduced from electromyography combined with simultaneous measurements of syringeal airflow and respiratory pressure during song [4–6], and by endoscopic observation of their action in response to direct electrical stimulation in anesthetized birds [7••]. These studies indicate that the dorsal muscles (i.e. the dorsal syringeal and dorsal tracheobronchialis muscles) adduct the labia into the bronchial lumen where they form a V-shaped slit and vibrate, much like the human glottis. The frequency spectrum of the labia, measured by an optical vibration sensor, is similar to that of the vocalization [8]. The mechanical properties of the medial labium and the associated medial tympaniform membrane have also been studied in excised syrinxes [9,10].

The labia also act as a pneumatic valve that closes the ipsilateral bronchus when fully adducted, blocking airflow and preventing it from producing sound. The ventral tracheobronchialis muscle opens the syrinx by abducting the lateral labium [6,7••]. The ventral syringeal muscles control fundamental frequency, presumably by exerting tension on the labia, but have little effect on the syringeal aperture [4,6]. It is thus possible for the two sides of the syrinx to generate harmonically unrelated sounds simultaneously or for the bird to switch phonation quickly from one side to the other [11–13].

Respiratory motor programs for singing

The respiratory component of song has received less attention than its syringeal control, but is equally important in

determining the vocal output. Nearly all song is produced during expiration, although in zebra finches (*Taeniopygia guttata*) some individuals sing certain notes during the inspiration between the adjacent syllables [14]. Except at very high syllable repetition rates, a small inspiration (or minibreath), which replaces the air expelled to produce a syllable, is typically inserted between syllables [15]. Electromyography of respiratory muscles shows the alternating, non-overlapping activation of inspiratory and expiratory muscles [16]. In a small bird such as a canary (*Serinus canaria*), these alternating muscle activities may accompany syllable repetition rates as high as 30 s^{-1}. The respiratory pattern has a major role in determining the temporal properties of the song [13]. There is evidence that the syllable is a motor unit of song. When a zebra finch stops singing in mid-song it does so between syllables. If its song is interrupted by a burst of strobe light these stops also occur between syllables, with only rare exceptions [17,18•]. In both cases, the song is interrupted when the respiratory phase reverses, suggesting that the respiratory cycle may define the motor units of song production [18•].

Different syllable types in adult song are each produced by stereotypical patterns of respiratory pressure and syringeal airflow, implying the presence of well-defined respiratory, as well as syringeal, 'vocal motor gestures'. High cross-correlation values of pressure and airflow between syllables tend to be associated with similarly high correlation between spectograms of the accompanying vocalization [18•,19,20]. Different zebra finches often use similar pressure patterns to produce the same syllable. When a zebra finch copies a syllable or note from another individual it usually also copies the pattern of respiratory pressure that was used to produce it, suggesting that the adult motor pattern is shaped by motor constraints during song learning [18•]. The various theories of birdsong learning place different degrees of emphasis on the role of the environment in instructing development, and of selection during development from a pre-determined range of motor patterns [21]. Understanding the mechanisms and constraints on motor patterning and sensorimotor processing, will be important in resolving these issues at a mechanistic level.

Coordination of respiration and phonation
The dynamics of respiratory pressure and airflow during phonation depend on the activity of both the respiratory muscles that drive ventilation and the syringeal muscles that control syringeal resistance by adducting or abducting the labia. The motor programme for singing thus includes both syringeal and respiratory 'vocal gestures'. Exactly how these separate muscle groups are coordinated with near-millisecond precision during song is an important area for future research.

Auditory feedback, which is so essential during vocal learning [22], continues to have a role in maintaining adult crystallized song. When deafened as adults, songbirds show a gradual deterioration in the quality of their song.

Figure 1
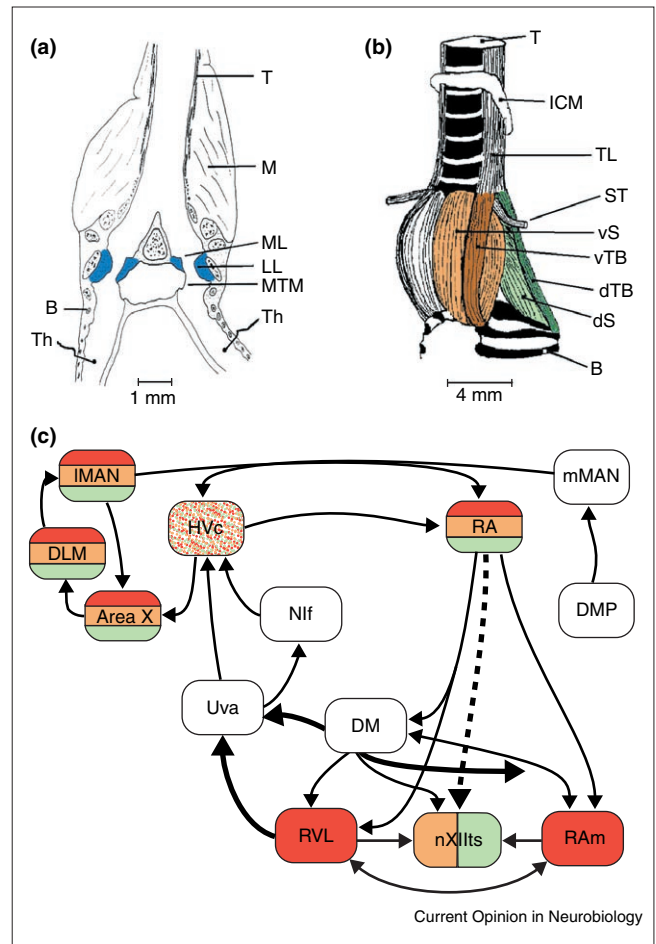
The syrinx and song system. **(a)** The oscine syrinx, shown in frontal section, is a bipartite structure that contains two sound sources, each consisting of a pair of labia (blue) at the cranial end of each bronchus. The syrinx is located in the interclavicular air sac. A microbead thermistor, (Th), in each bronchus measured the rate of airflow and sound production on each side of syrinx during song. **(b)** Ventrolateral external view of syrinx, showing the ventral (tan) and dorsal (green) syringeal muscle groups, respectively. **(c)** Connections of the song system. The syringeal muscles are represented in relatively discrete subregions of several of the central nuclei, as is a separate pathway that terminates in respiratory brainstem centers (shown in red). The schematic depiction of subregions within the song nuclei is color-coded to match the green dorsal and tan ventral syringeal muscles in (b), and is not meant to convey anatomical location. The 'red' pathway is not as well established for nuclei DLM (dorsolateral nucleus of the medial thalamus) and Area X. HVc is not regionally topographic. Bold lines indicate bilateral connections; DM projects onto its contralateral homologue; the projection of RA onto nXIIts is bilateral in some species but not others, and is represented by a dashed bold line. Abbreviations: B, bronchus; DLM, dorsolateral nucleus of the medial thalamus; dS, m. syringealis dorsalis; dTB, m. tracheobronchialis dorsalis; ICM, membrane of the interclavicular air sac; LL, lateral labium; M, syringeal muscle; ML, medial labium; mMAN, medial subdivision of magnocellular nucleus of the anterior neostriatum; MTM, medial tympaniform membrane; NIf, nucleus interfacialis; RVL, rostral ventrolateral medulla; ST, m. sternotrachealis; T, trachea; TL, m. tracheolateralis; Uva, nucleus uvaformis; vS, m. syringealis ventralis; vTB, m. tracheobronchialis ventralis. ((a) modified from [11]; (b) modified from [4].)
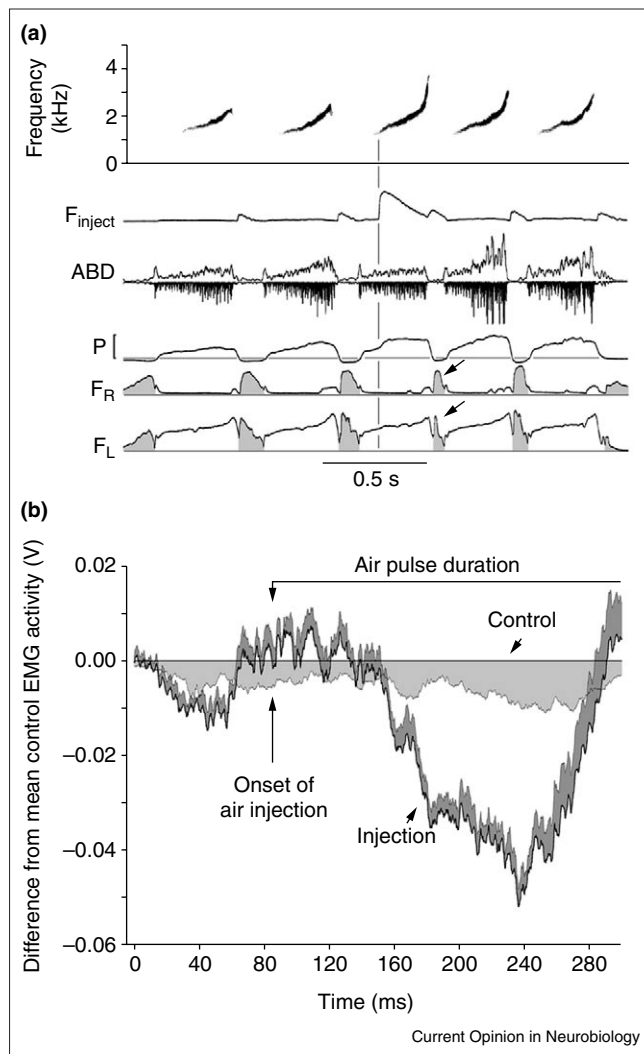
Somatosensory feedback mediates real-time compensatory adjustments in contraction of abdominal expiratory muscles in the response to increased respiratory pressure. **(a)** Phrase of cardinal song with a puff of air injected into a thoracic air sac during the third syllable. Note the reduction in amplitude of abdominal expiratory muscle (ABD) EMG and increase in air sac pressure at time of air injection. Minibreaths (shaded) are smaller after air injection (arrows). The EMG is shown rectified (time constant 0.1 ms) and integrated (time constant 5 ms) upward, and rectified downward; F_{inject}, rate of airflow into air sac; F_R and F_L, rate of airflow through right and left sides of syrinx, respectively; P, subsyringeal air sac pressure (bar = 10 cm H_2O). Horizontal lines indicate ambient (zero) pressure and zero airflow. **(b)** Relative mean amplitude of abdominal expiratory muscle EMG during syllables with air injection (injected) compared to the same syllable without air injection (control) for a bird deafened by bilateral removal of its cochleae. (From Suthers RA, Goller F, and Wild JM. *Proc Nat Acad Sci USA*. 2002.**99**:5680-5685. Copyright 2002 National Academy of Sciences, reproduced with permission [31••].)

Previously, it was thought that this effect was limited to birds that change their songs seasonally in adulthood, after song has crystallized at the end of juvenile development, but important exceptions are now known [23,24]. Further experiments are needed to determine which species require auditory feedback to maintain their adult songs, and what rules govern the extent to which song mainte-nance requires auditory feedback. Such studies may also breathe life into attempts to answer the difficult question of how differences in song behavior relate to other ecological aspects of behavior.

Changes in the song of deafened adults may first be detected within days or may not be evident until months after hearing is impaired, depending on the species [23,24]. Perturbed auditory feedback also causes adult zebra finches to sing abnormally, and the initial effects of auditory feedback perturbation on song may appear more rapidly than those of deafening [25]. In zebra finches, songs may deteriorate after deafening, but this degeneration may not be noticeable for up to two months [23]. Interestingly, the effects of deafening change with the age of the adult bird, which would suggest that over time auditory feedback has less influence in maintaining the ongoing motor program [26].

When the tracheosyringeal nerve is severed in adult zebra finches, their song is highly disrupted but recovers over several weeks as the nerve grows back. In birds with lesions of the anterior forebrain nucleus lMAN (that is, lateral subdivision of the magnocellular nucleus of the anterior neostriatum), the effects of tracheosyringeal nerve damage on song are greatly reduced [27•]. This supports the model in which the lMAN is part of an error-generating or error-correcting pathway [1]. Sectioning the tracheo-syringeal nerve may cause changes in both auditory and somatosen-sory feedback. When deafening is combined with lesions of lMAN, there is no deterioration in song. In some cases, zebra finches with lMAN lesions sing normal songs one year after they have been deafened [28•], demonstrating that auditory feedback interacts with the activity of lMAN to modify forebrain circuits for song. The locus of these effects presumably includes the telencephalic nucleus robustus archistriatalis (RA), which receives input from lMAN and HVc, used as a proper name, and sends major projections to the midbrain and brainstem. Preliminary results indicate that stimulating lMAN during singing may alter the song pattern [29], and lesioning lMAN may release or uncover auditory responses in RA that are not otherwise observed [30]. The strength and phasic/tonic form of these RA auditory responses appear to depend on the age of the adult bird when the lMAN lesion was performed, suggesting a connection to the diminishing role of auditory feedback throughout adulthood. It could be that these preliminary studies are converging on components of the neural repre-sentation of errors that are mediated by auditory feedback during singing.

Non-auditory, somatosensory feedback also influences song production and provides on-line modulation of both the respiratory and the syringeal vocal gestures. The extent to which it plays a role in maintaining normal adult song in the absence of auditory feedback is not known.

Small, externally imposed, abrupt increases in air-sac pressure during a syllable cause adult northern cardinals (*Cardinalis cardinalis*) to reduce the contraction of their abdominal expiratory muscles, thus reducing the pressure change ([31••]; Figure 2). This compensatory muscle response is greatly reduced or absent during silent respiration and is not affected by deafening. This indicates that the response is specifically related to song production and is mediated by proprioceptive or mechanoreceptive feedback, although the receptors have not yet been identified. The muscle response is of sufficiently short latency (35–70 ms) that the bird can make real-time adjustments in the respiratory song motor programme, often re-adjusting pressure and syringeal airflow within the syllable in which the pressure perturbation occurs [31••]. Syringeal muscles exhibit similar responses to a sudden increase in respiratory pressure, but compensate by increasing, rather than decreasing, their contraction [32]. The rapid nature of these somatosensory responses suggests that the compensatory mechanisms involve reflex-like arcs and brainstem nuclei. It is credible to surmise that these pathways are adjusted during song learning to the specific dynamics of the bird's song. If so, this would imply that song learning modifies brainstem structures in relation to afferent feedback.

Two of the nuclei for song control project to respiratory nuclei. The RA of the song motor pathway projects to premotor expiratory neurons in nucleus retroambigualis (RAm) and to the inspiratory ventrolateral nucleus of the rostral medulla (RVL), as well as to syringeal motor neurons in the hypoglossal nucleus (nXIIts). RAm also receives input from the dorsomedial intercollicular nucleus (DM) in the midbrain ([33–36]; Figure 1). DM and especially RAm and other brainstem respiratory nuclei have strong bilateral projections onto nXIIts [37], even though there are no lateral pressure differences between the air sacs, whereas the projection of nXIIts to the syrinx is strictly ipsilateral in songbirds [38]. DM and RVL of the brainstem project bilaterally onto the uvaeform nucleus (Uva), which projects onto nucleus interfacialis (NIf) and HVc ([39]; Figure 1). For a system in which exquisite bilateral coordination is essential, it is noteworthy that the forebrain components are not bilaterally connected.

Tonic activity of XIIts motor neurons but not of RA neurons is modulated by the respiratory rhythm, so that activity is strongest during expiration [40–42]. Consistent with a respiratory gating mechanism, the strength of the action potential volleys in the tracheosyringeal nerve that are elicited by electrical stimulation of HVc depends on the respiratory cycle, achieving their maximal value during expiration. Recent *in vivo* intracellular recordings show that the XIIts respiratory rhythm is largely due to expiratory-linked synaptic excitation, and brain-slice preparations show that this excitation most likely arises from synaptic inputs originating in RAm [43]. This suggests that RAm neurons excite XIIts motor neurons during normal respiration, and may serve as an 'AND' gate for RA inputs onto the

vocal motor neurons. RAm also gives rise to a potent glycinergic inhibitory input onto nXIIts. Song playback, which in anesthetized birds excites RA neurons to fire in a pattern somewhat akin to the pattern during singing [44], also evokes hyperpolarizing responses in XIIts motor neurons that are immediately followed by strong excitation and can sometimes entrain the expiratory EMG [43]. Therefore, RA may be able act through RAm to inhibit XIIts and excite expiratory motor neurons. This feature could be important for establishing appropriate phase delays between abdominal expiratory and syringeal muscles, which may be of critical importance in determining the acoustic properties of the song (see song models below).

Forebrain representations of song

If RA encodes phase relations between respiration and phonation, then RA neurons should exhibit precise timing in their activity patterns. Indeed, the temporal precision of neural activity that is observed in the brainstem is also observed in the forebrain. For example, when zebra finch males direct their songs towards females, there is sub-millisecond precision in the control of spike-burst timing in RA, and in the order of millisecond timing that relates spike bursts to acoustic features of song [45•]. It was possible to observe the timing of these features at such high resolution by taking advantage of the precision and accuracy in the time-of-occurrence of individual spikes and spike bursts to accurately locate acoustic features. This suggests the possibility that precise timing that is hard detect or interpret could also exist in other systems, in which the behavior is difficult to precisely measure. Remarkably, during directed singing, syllable duration is regulated to around 1 ms or a variation of <1%. The duration of syllables at the beginning of a song is regulated better than those that follow, suggesting a minute loss in motor control over the course of each song. This has the intriguing implication, as yet untested, that female zebra finches can detect these fine differences in temporal patterning, which must be at the extreme of their predicted psychophysical capability [46]. If so, improved temporal auditory resolution in female songbirds may be one of the factors driving the evolution of male vocal performance [45•].

The temporal scale that RA activity encodes during singing is similar to the temporal scale of activity observed at the vocal periphery. Birds tend to use the same pattern of respiratory activity for the same vocal gesture even if it is embedded in different larger units of vocal production, such as different syllables [18•]. Similarly, when RA neurons burst, different burst patterns are associated with different notes of a syllable, and the same notes embedded into different syllables will yield the same RA burst patterns [47]. Separate pathways representing respiration and phonation are also maintained in RA. A dorsal subdivision of RA preferentially projects to RAm and DM, and the ventral/medial and middle/ventrolateral regions of RA preferentially project to the caudal and rostral regions, respectively, of nXIIts. In turn, the caudal and rostral

Figure 3
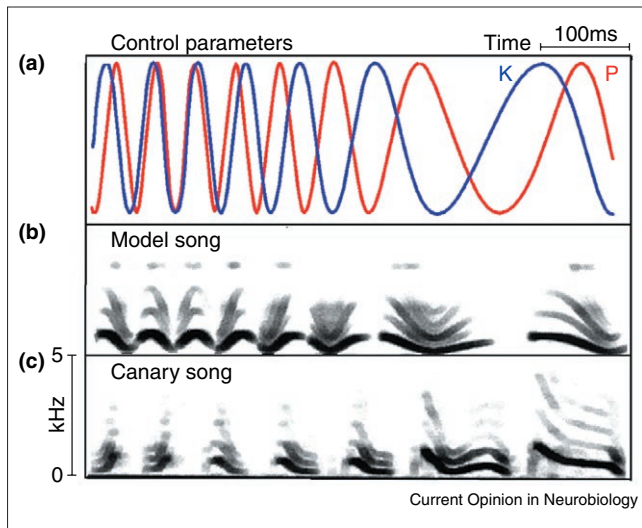
Many properties of canary syllables can be reproduced by varying the phase lag between cyclical changes in respiratory pressure and the tension of the vibrating labia. **(a)** Synthetic signals (control parameters) that represent slow modulations of respiratory pressure (P) between 0 and 2 kPa and labial tension (K) between 0 and 7 N/cm^3. **(b)** Model song syllables were produced by changes in phase lag between control parameters. This song model does not include muscle activity. **(c)** Natural canary song. (From Gardner T, Cecchi G, Magnasco M, Laje R and Mindlin GB. *Phys Rev Lett*. 2001. **87**: 208101. Copyright 2001 by the American Physical Society, reproduced with permission [55•].)

regions of nXIIts project to the dorsal and ventral muscle groups of the syrinx, which are associated with the control of syringeal aperture and fundamental frequency, respectively, of the sound (see above; Figure 1). The relative separation of pathways coordinating different attributes of the syringeal and respiratory patterns suggests that these features of song are represented separately in the forebrain (RA). The projection of HVc onto RA appears not to be topographically organized and is highly divergent [48], implying that separate representations for respiration, syringeal aperture, and sound frequency emerge in the HVc-to-RA projection (see song models below).

The distinction between RA as being closely tied to the demands of peripheral motor patterns and HVc as having "higher-level" functions was first suggested in electrical perturbation studies during singing. Stimulating HVc at low intensities causes zebra finches to stop singing and re-set to the beginning of a motif, whereas similarly stimulating RA only results in local distortion of the vocalization and does not disrupt the temporal pattern of song [49]. However, it is not known if electrical stimulation of the RA recruited neurons in the dorsal, respiratory subdivision, which might affect temporal patterning. Furthermore, in contrast to RA, HVc neurons (now presumed to be interneurons) exhibit tonic activity during singing that depends on the syllable identity and is less strongly influenced than RA neurons by the constituent notes of the

syllable [47]. The interpretation of HVc as representing more global features of song is also supported by recent elegant experiments showing that RA-projecting HVc neurons only emit brief (~10 ms) and infrequent bursts of spikes during singing. There is typically only one spike burst per song motif, that is, a repeated sequence of syllables [50••]. Thus, timing at the level of whole motifs is represented in the activity of these HVc neurons.

One of the fundamental problems in learning to sing is the need to modify ongoing premotor activity on the basis of evaluation of auditory feedback from earlier events. In RA, there is a precise match in burst patterns and burst timing between auditory and premotor patterns of activity. RA auditory activity depends on the prior sequence of sounds. As zebra finches repeat the same song motifs, RA auditory activity during the prior sequence of syllables can potentially predict with high reliability the subsequent pre-motor activity [51••]. How pre-motor and auditory activity is represented in the RA of birds that sing more variable songs (e.g. song repertoires) is an important avenue of future research. One noteworthy question is when is a particular motor sequence specified during a bird's singing performance, and how is the RA informed of or how does it contribute to that aspect of motor programming? It will also be valuable to test whether RA-projecting HVc neurons exhibit a match between auditory and premotor activity patterns. The sparse firing of RA-projecting HVc neurons may be part of a mechanism that resolves the feedback timing problem, in the sense that any given neuron is typically not firing when the feedback could be evaluated [50••]. Further study is needed to understand how the relevant component of the error signal that is derived from sensory feedback reaches the appropriate RA-projecting HVc neuron, and how synapses are modified during a period when the RA-projecting HVc neurons are completely inactive. Either there exists in HVc a feed-forward mechanism similar to that which has been described for RA [51••], or the RA-projecting HVc neurons as described are active during singing independent of auditory feedback.

Curiously, auditory activity in the song system is expressed most strongly during sleep [51••]. This has stimulated hypotheses on the role of sleep in consolidating song motor programs, and suggests that sleep may function as an 'off-line' component of vocal learning [44,52]. Subsequent experiments have provided some support for this hypothesis. A recent study of juvenile song learning provides the first quantitative description of the detailed dynamics of vocal learning [53••]. In one experiment, the first changes observed in juvenile song following exposure to tutor songs were delayed until after a period of sleep; however, this *post hoc* observation of a single bird needs to be repeated. Another study indicates that RA burst patterns can change following a period of sleep [54]. It will be important to associate such variability with changes in singing behavior.

Models of song production

A recent theoretical model of song production proposes that a significant portion of syllable diversity might be achieved by varying the temporal relationship between the respiratory and syringeal components of the song motor programme. Gardener *et al.* [55•] suggested that a simplified model for sound generation by human vocal folds may also apply to the labia of songbirds. They demonstrated that many of the basic temporal and spectral features of canary syllables could be reproduced by simple oscillations of bronchial pressure and labial tension, similar to the observed cyclical changes in sub-syringeal air pressure and contraction of the ventral syringeal muscles, which are thought to control labial tension. Synthetic signals that are qualitatively similar to a variety of natural syllable types could be generated by varying the frequency and relative phase of these two parameters (Figure 3). Laje *et al.* [56••] have simplified this model and modified it to include the action of syringeal muscles that gate phonation by adducting or abducting the syringeal labia. This new model indicates that a bird could produce a variety of syllable types simply by controlling smooth oscillations of three parameters corresponding to respiratory pressure, the position of the labia (syringeal muscles adducting or abducting the labia), and the tension of the labia (the ventral syringeal muscles).

An implication of this model, if correct, is that if we are to map central neural activity onto peripheral motor action during song, it may be necessary to correlate activity in the central motor pathway with the proposed control parameters — that is respiratory pressure and the activity of syringeal muscles controlling the position and tension of the labia — rather than with the acoustic properties of the emitted vocalization. Given its close association with peripheral patterns of activity, the activity of RA neurons during singing might be particularly amenable to such modeling.

Conclusions

Our knowledge of how birds produce their song has been furthered by recent advances on three fronts: a better understanding of the peripheral mechanisms of song production, new insights into the processing and timing of neural activity in the motor pathway of the central song control system, and the development of a physiologically based theoretical model that suggests specific control parameters. The combination of these experimental and theoretical approaches is bringing us closer to understanding how neural activity in the brain is shaped by learning and transformed into song.

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