The singer and the song: The neuromechanics of avian sound production

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Song is crucial to songbirds for establishing territories and signaling genetic quality and an important driver in speciation. Songbirds also have become a widely used experimental model system to study the neural basis of vocal learning, a form of imitation learning with strong parallels to human speech learning. While there is a strong focus on central processing of song production, we still have limited insights into the functional output of the motor neural circuits. This review focuses on recent developments in motor control, biomechanics and feedback mechanisms of sound production in songbirds.

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Introduction

Neuromechanicists seek to understand how muscles, sense organs, motor pattern generators, and brain interact to produce coordinated movement [1], including locomotion, eye–limb coordination and also sound production. Many vertebrates have evolved the ability to produce sounds with highly specialized organs [2], driven by complex motor patterns [3,4] and executed by exceptional muscles [5,6].

Songbirds produce among the most sophisticated communication signals in nature and song is of critical importance to them. It helps birds establish and maintain territories and to signal reproductive quality to mates [7,8]. The physical and neural mechanisms by which songs are perceived, produced, and learned are substrates chosen for and against by sexual and natural selection, and song is an important aspect driving speciation [9,10]. Songbirds and their songs have also proven an invaluable

model system to answer fundamental questions in neuroscience [3]. As a result songbirds have become a widely used experimental model system [11], especially for studies aimed at understanding the neural basis of vocal production learning, a complex form of imitation learning with strong parallels to human speech learning [12–14]. Although we have an increasing understanding of the physics [15] and sensorimotor control [16] of speech and song production in humans, there we lack the experimental manipulations to understand its learned control. In contrast, through studying songbirds, we have the unique potential to quantify the entire neuromechanical system, including neural circuitry interactions, peripheral biomechanics, and feedback mechanisms.

Vocal learning depends on integrated action of neural systems for auditory perception, song learning, and song production. The songbirds, that with over 4000 species comprise almost half of all living bird species, have a set of brain nuclei whose sole function is song learning and production and is referred to as the song system [11]. This circuitry is molecularly distinct from its immediately surrounding tissue [17] and comprises a song motor pathway, which spans from the telencephalon (nucleus HVC) to a brainstem vocal-respiratory network, and an anterior forebrain pathway traversing the telencephalon, striatum, and thalamus [18]. The vocal-respiratory network controls the three major motor systems essential to sound production: the respiratory system, vocal organ, and upper vocal tract. Our understanding of the central processing of song is advancing rapidly [11], but the output and function of these motor neural circuits is still not well understood. Here I review recent developments with a focus on the peripheral motor control and feedback mechanisms to the central control of sound production, and highlight gaps in our knowledge on how motor commands are translated into sound.

Sound production physiology

Birds have evolved a unique and complicated structure dedicated to produce sound, the syrinx, located at the bifurcation of the trachea into the bronchi [19–21] (Figure 1). This vocal organ is morphologically highly diverse between different bird taxa [22]. The songbird syrinx consists of highly modified partially ossified tracheal and bronchial (half)rings. The caudal parts are fused and form a bone cylinder, the tympanum, which is the insertion point for six to eight pairs of syringeal muscles that apply force and torque to articulate three paired bronchial bones [23]. These bones in turn modulate

Figure 1
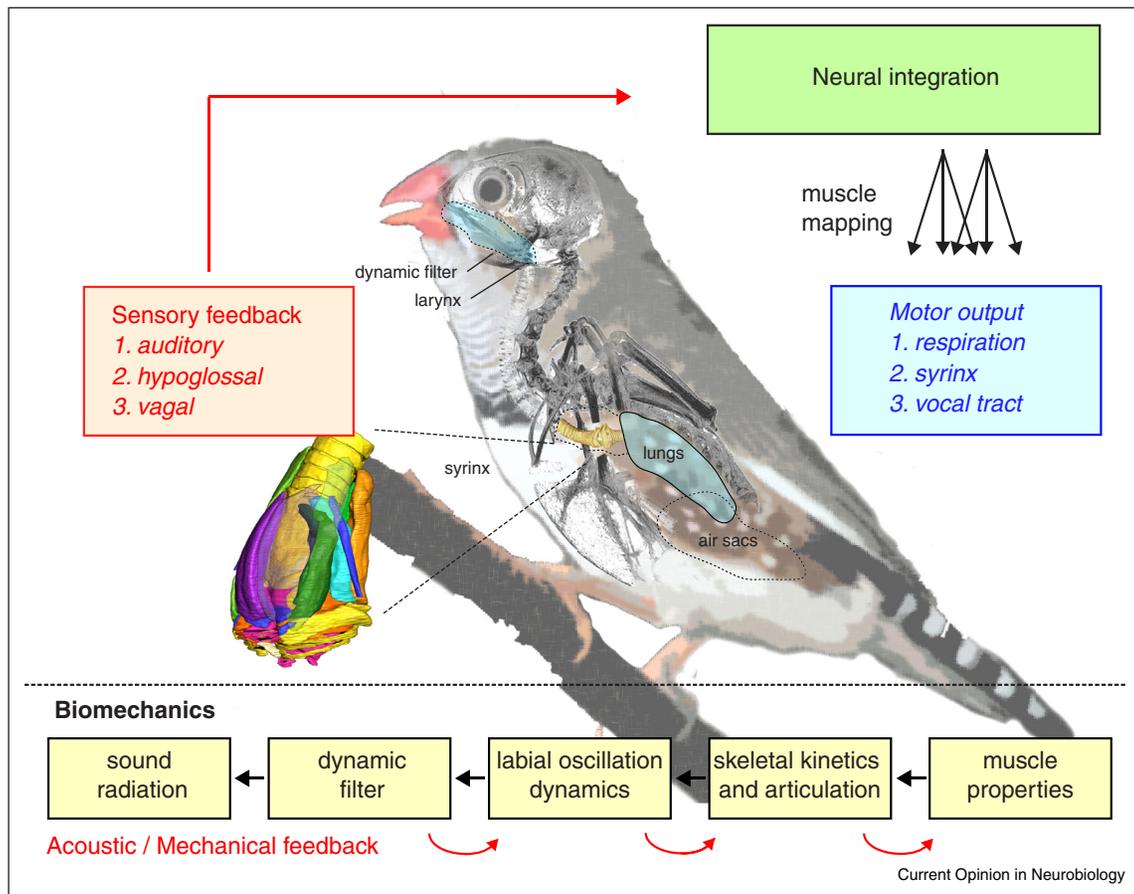
The main motor, biomechanical and feedback mechanisms involved in sound production and control.

the position and tension of sound producing labia. Compared to the larynx, the limited accessibility and small size of the syrinx makes it difficult to study in freely moving birds. Therefore, we currently have no quantitative information on the kinematics (motion), kinetics (forces associated with motion) and control of the syringeal skeleton.

Sound is produced by airflow-induced vibrations of tissue powered by subsyringeal pressure from the respiratory system [24•,25,26]. Songbirds have one pair of oscillating labia (a medial and lateral labium) in each bronchus and are capable of singing two independent tones simultaneously [27•]. These labia consist of extracellular matrix containing elastin and collagen fibers that form different layers due to orientation and composition differences [28]. The fundamental frequency (F0) of labial oscillation dictates the F0 of sound [29] and material properties play an important role in setting the boundaries of oscillation frequencies [28]. Across songbird species the labia are assumed to vibrate in the wide range of 100–12 000 Hz [30]. For comparison, in

mammals the F0 correlates to vocal fold size and ranges from about 15 Hz in elephants to over 100 kHz in some bats [31]. The normal human vocal range is 80–1100 Hz for both sexes combined.

Most of what is currently known about the physics of vocal production is based on the human voice [15,32]. Vocal folds in the larynx exhibit self-sustaining, flow-driven lateral oscillations, powered by expiratory pressure of the lungs, which cause pressure fluctuations in the vocal tract, that is, sound. Energy transfer from respiratory airflow to oscillating tissue is made possible by a configuration change in the shape of the vocal folds. That is, during the opening phase within an oscillation the shape is divergent and during the closing phase convergent [15]. The lateral oscillation and a configuration change are core concepts of the myoelastic-aerodynamic theory of sound production [32]. Detailed quantification of temporal and spatial dynamics of labial oscillation in birds is therefore critical to our understanding of the physics of sound production, but still lacking. Additionally, labial shape configuration changes are assumed to occur in all current

mathematical birdsong models [33[•],34–37], but have yet to be empirically demonstrated in birds.

Sounds produced by vocal fold oscillation in the mammalian larynx contain multiple integer multiples of the F0, called harmonics or overtones, when measured close to the source. At first approximation, the spectrum of the radiated sound is a linear superposition of the spectral content at the source and the filter properties of the vocal tract (the source-filter theory) [32]. By changing the position of for example, our tongue, lips and jaw, we alter the filter properties of our vocal tract and suppress certain harmonics independently of the F0. In speech, much information is contained in the relative spacing of the remaining peaks in frequency distribution called formants. However birdsong contains few or strongly suppressed harmonics. Recent research has shown that the pressure modulations produced by the syrinx are filtered by an effective, actively controlled upper vocal tract filter [38[•]]. This filter consists of beak and hyoid movements, that change the volume of the oropharyngeal–esophageal cavity (OEC), glottal movements and tracheal length changes [38[•],39], but also lingual articulation [40]. Zebra finches can use vocal tract length, beak gape, and OEC expansion as vocal articulators to filter the sound produced by the syrinx [41]. This research firmly establishes that the source-filter theory of human speech production also applies to songbird vocal communication. Although the larynx is not known to contribute to sound generation in birds, it may have a role in tuning acoustic power output [42].

Muscle function in motor control

While the respiratory system controls 'slow' pressure variations (~10 Hz) driving sound production, the spectral modulation and fine-temporal structure of song are under direct motor control of highly specialized superfast syringeal muscles, capable of power production at cycle frequencies up to 250 Hz [6]. Songbirds have typically 2 pairs of extrinsic (one insertion site on the syrinx and one elsewhere) and 5 pairs of intrinsic (both insertions sites on the syrinx) syringeal muscles, of which in zebra finches two are further divided in two and three subparts, adding up to 10 functional muscle pairs directly affecting the syrinx skeleton. We currently lack crucial mechanistic insights into the function of most syringeal muscles [19,43]. However, we have obtained insight in the effects of specific syringeal muscles by either correlating electromyogram (EMG) amplitude with acoustic features of song in singing birds [44,45[•],46[•],47[•]] or by studying labial ad/abduction caused by electrical stimulation of syringeal muscles or premotor nuclei [48]. Together these and other studies have provided evidence to assign specific functions, such as labial adductors, abductors or muscles affecting pitch [19]. However a recent high-resolution examination of muscle insertion showed that even physically close muscles can have insertion sites on different skeletal elements, implying differential mechanical effects [23].

Research to date has mostly focused on F0 control of sound, a parameter that is easy to extract. A seminal EMG study [46[•]] demonstrated a correlation between F0 and activity of the *m. syringealis ventralis* (VS), the largest syringeal muscle, suggesting the VS as the main F0 modulator. This was supported by a recent study that inhibited muscle activation by botulinum toxin injections in (predominantly) VS resulting in the absence of frequency modulation [49]. One dorsal muscle is also in a morphological position to alter pitch [23] and was shown to increase F0 by manual manipulation [26]. By analogy to humans, F0 is assumed to be affected by several other factors besides syringeal muscle forces [30], such as the driving pressure, which was recently shown in birds [50], and the pressure difference between driving pressure and the air sac in which the syrinx is suspended [35].

Muscle stimulation studies provide causal functional relationships. The effect of syringeal muscles on the position of the labia has been imaged during respiration in anesthetized animals [48]. Because of the large amplitude vibrations, the relationship between adduction/abduction and sound amplitude can be expected to be highly nonlinear [26]. One study quantified effects of muscle stimulation on airflow and sound amplitude modulation [6]. Because radiated sound intensity depends on syringeal modulations, vocal tract filtering and emission directionality, sound amplitude is a more difficult parameter to interpret in freely singing birds. Dissecting the motor control parameters underlying sound amplitude, and other behaviorally relevant sound qualities, remains a challenge.

Synergistic motor control

From locomotion studies we know that while muscles are often viewed as motors that produce movement by shortening to perform mechanical work, they may serve a variety of other functions in a dynamical context. They may stabilize motion at joints, store elastic energy in connective tissues, and absorb work as well as perform it [51]. The function of a muscle is therefore impossible to assess without biomechanical context. For example, especially during fast motion, the time at which peak forces occur may not correspond to the time at which peak motion (speed or position) occurs, and delays occur due to excitation-contraction coupling and the dynamic behavior of damping and inertial components. A single neural signal can therefore produce variable mechanical outputs depending on the biomechanical context, and the function of motor neurons depends upon the mechanical configuration of the periphery [1].

Additionally, the nervous system does often not control individual muscles, but instead activates flexible

combinations of so-called muscle synergies to produce a wide repertoire of movements [52–54]. Instead of controlling each muscle individually, muscle synergies work like building blocks, defining characteristic patterns of activation across multiple muscles. Muscle synergies therefore reduce the dimensionality of control and may be individually unique, but with similar robust task-level functions. They have been shown to underlie arm reaching [54] and finger movement control [53], and because central pattern generator networks for patterning of locomotion and vocal production share a common developmental and evolutionary origin [55,56], this raises the question whether birdsong may also be controlled with muscle synergies. If true, this would have significant implications for models of motor control, because single neural premotor activity will not directly correlate with an acoustic parameter (e.g. sound frequency or amplitude), but to the underlying muscle synergy. Because even close to the terminus of the premotor pathway the correlation with sound parameters is relatively weak [57], control may be effected using muscle synergies. The presence of muscle synergies is tested by recording simultaneous EMGs in many muscles under a range of behavioral conditions, followed by computational analysis such as non-negative matrix factorization or independent components analysis to identify synergies from the EMGs [53,54]. The wider the range of behavioral conditions that can be explained by muscle synergies, the more support there is for such an explanation. To date, this remains untested for birdsong: no study has reported having recorded activity in all or sufficient syringeal muscles simultaneously. If present, muscle mapping of synergies to muscles may occur in the premotor pathway either in between or within nucleus HVC and RA. A course myotopic representation of syringeal muscles is present in premotor nuclei nXIIts and RA [58]. However, to localize where muscle mapping occurs, we need a more detailed analysis to resolve the connectivity of the neural circuitry in the premotor pathway HVC–RA–nXII.

Mechanisms of feedback

Just as for human speech, zebra finches require auditory feedback to learn and maintain song [11]. In contrast to locomotory control, neural feedback to the song motor system during sound production does not occur within labial oscillation cycles, because these are too fast (typically ranging from 0.4 to 4 kHz), but still can occur as fast as tens of milliseconds [59]. Several studies have used different online perturbation paradigms, such as altered auditory feedback [60–62] or reinforcement learning by white noise bursts, to drive changes of acoustic target parameters, such as F0 [60,61,63•] or syllable duration [63•] over successive song iterations. There is also mounting evidence for fast somatosensory feedback (tens of ms) affecting song due to integration of song and respiratory systems [64,65•]. Air injections in the respiratory system during song have resulted in a compensatory reduction of

expiratory muscle activity [65•]. Although conventional vertebrate muscle spindles have not been observed in syringeal muscles, the hypoglossal (syrinx, upper vocal tract, and tongue) nerve includes afferent sensory neurons [66,67]. The vagus nerve includes afferents that contain information from receptors sensitive to changes in the inflation of air sacs [68]. Disruption of somatosensory feedback induced by vagal [68] and hypoglossal [67] lesions causes changes in the motor patterns of song [67,68] and this feedback is thus likely to be functionally important to vocal learning.

On a faster timescale, the intrinsic properties of striated muscle play important self-stabilizing roles during movement, particularly immediately after perturbations [1,51]. The force output of skeletal muscle increases automatically when subjected to a higher force to resist the imposed load. As the muscles that articulate the syringeal skeleton induce length changes, the intrinsic self-stabilizing behavior of the syringeal sternotrachealis muscle may aid to increase the mechanical stability of the entire syrinx and hence reduce acoustic variance.

Neuromechanical modelling

To better understand complex motor systems with many degrees of freedom, two types of neuromechanical models can help lead to testable hypotheses [69]. The 'template' model describes and predicts the behavior of the body as a target for control (hereon referred to as 'toy' model to avoid confusion with the term 'song template', which refers to the perceptual target to which juvenile birds match the developing vocalizations during sensorimotor learning). Toy models do not incorporate detailed mechanisms, and omit all complexity of joints, muscles and neurons, therefore collapsing the system's dimensionality. However the diversity of nature's mechanisms can be the very focus of study, and not a detail to be removed. Consequently, the 'anchor' model includes more degrees of freedom, such as more realistic geometry, more muscles, and is a more representative model of the biological system of interest. By adding degrees of freedom, neuromechanical hypotheses can be tested at the desired level of detail.

While 'anchor' models have not yet been used in birdsong research, several 'toy' models have been developed to describe the dynamics of respiration [70•,71] and sound production in doves [35] and songbirds [33•,36,37,50,72]. Recently, models were developed to acoustically synthesize zebra finch song based on a single sound source driven by only two physiological driving parameters: (subsyringeal) pressure, and (labial) tension. Physiological parameters (named 'gestures') driving these models were fitted to sound recordings of an individual [33•,34,73], followed by additional fitting and noise addition procedures to generate a synthetic copy of the recorded song. We currently do not know how these gestures relate

to physiologically realistic neural control signals and if they present unique solutions. Because of the simplified approach, these gestures do for example, not exclude the possibility that motor control is encoded as muscle synergies, as the focus is mostly on gesture extremes (e.g. onsets and offsets). Discussing the potential implications of these models on the central mechanism of birdsong control is unfortunately beyond the scope of this review. Nevertheless it is evident that neuromechanical 'toy' models can provide exciting new hypotheses and aid in closing the gap between central and peripheral control of birdsong.

Conclusions

Neuromechanics provides a solid framework to study avian and mammalian sound production control. The source-filter theory for human voice production has been shown to applicable to songbirds and several mechanisms of sensorimotor feedback have been detected in songbirds. In spite of significant progress many questions remain unanswered or at least partially so. Principal among these are observations establishing physical mechanisms of sound production under controlled conditions, biomechanics of syringeal skeleton articulation in comparative contexts, and the establishment of synergistic or direct muscle recruitment. Mathematical models based on neuromechanical principles aid in explaining complex dynamics of respiration and song production.

Conflict of interest statement

Nothing declared.

Acknowledgements

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- •• of outstanding interest

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