

## REVIEW

### Integrating perspectives on vocal performance and consistency

Jon T. Sakata<sup>1,\*</sup> and Sandra L. Vehrencamp<sup>2</sup>

<sup>1</sup>Department of Biology, McGill University, Montreal, QC, Canada, H3A 1B1 and <sup>2</sup>Neurobiology & Behavior, Cornell University, Ithaca, NY 14853, USA

\*Author for correspondence (jon.sakata@mcgill.ca)

Accepted 22 October 2011

#### SUMMARY

**Recent experiments in divergent fields of birdsong have revealed that vocal performance is important for reproductive success and under active control by distinct neural circuits. Vocal consistency, the degree to which the spectral properties (e.g. dominant or fundamental frequency) of song elements are produced consistently from rendition to rendition, has been highlighted as a biologically important aspect of vocal performance. Here, we synthesize functional, developmental and mechanistic (neurophysiological) perspectives to generate an integrated understanding of this facet of vocal performance. Behavioral studies in the field and laboratory have found that vocal consistency is affected by social context, season and development, and, moreover, positively correlated with reproductive success. Mechanistic investigations have revealed a contribution of forebrain and basal ganglia circuits and sex steroid hormones to the control of vocal consistency. Across behavioral, developmental and mechanistic studies, a convergent theme regarding the importance of vocal practice in juvenile and adult songbirds emerges, providing a basis for linking these levels of analysis. By understanding vocal consistency at these levels, we gain an appreciation for the various dimensions of song control and plasticity and argue that genes regulating the function of basal ganglia circuits and sex steroid hormones could be sculpted by sexual selection.**

**Key words:** songbird, stereotypy, reproductive success, practice, performance, anterior forebrain pathway, basal ganglia, levels of analysis, behavioral evolution.

#### Introduction

In his seminal book ‘The Study of Instinct’, Nikolaas Tinbergen (Tinbergen, 1951) outlined four levels of analysis that he argued were crucial for a comprehensive analysis of behavior: adaptive significance (i.e. function), ontogeny (i.e. development), mechanism (i.e. physiology) and evolutionary history (i.e. phylogeny). While studies on these distinct levels can independently yield valuable insights, integrating findings from different levels of analysis can lead to novel interpretations, hypotheses and synergies (MacDougall-Shackleton, 2011).

Birdsong provides a rich opportunity for such integration. The vocal signals (i.e. songs) of male songbirds are important for attracting females and defending territories and, therefore, are under sexual selection pressure to provide honest information about the singer’s quality and intentions (Bradbury and Vehrencamp, 2011; Catchpole and Slater, 2008; Hauser, 1996; Nowicki and Searcy, 2004). The songs of songbirds are not innate but, like human speech, must be learned during development. Songbirds learn their vocalizations by memorizing and imitating the vocalizations of other individuals and use sensory and social feedback signals to shape their songs during development (Beecher and Brenowitz, 2005; Brainard and Doupe, 2000; Doupe and Kuhl, 1999; Goldstein and Schwade, 2010; King et al., 2005; Konishi, 2004). Songbirds have evolved specialized neural circuits that regulate the learning, control and performance of song (Bolhuis and Gahr, 2006; Brainard and Doupe, 2002; Konishi, 2004; Mooney, 2009; Nottebohm and Liu, 2010; Wild, 2008). Further, individual and species differences in the function and organization of these circuits are postulated to underlie individual and species differences

in vocal learning, control and performance. Taken together, research from these various perspectives has demonstrated that birdsong is important for reproductive fitness, influenced by developmental experiences, controlled by distinct neural circuits and shaped by evolutionary history and selection forces.

Here, we review functional, developmental and mechanistic studies pertaining to vocal consistency. We specifically define vocal consistency as the ability to consistently produce the spectral structure of a song element (‘syllable’) or phrase across renditions, including its dominant or fundamental frequency, note shape and duration. We first review recent behavioral studies on the adaptive significance of vocal consistency, and then summarize recent neurophysiological investigations into the control of vocal consistency. We concentrate on how activity in basal ganglia and vocal motor circuits influences vocal consistency, but do not describe the constraints imposed by peripheral vocal organs in detail. Subsequently, we elaborate on the role of vocal practice and propose directions for future studies. By reviewing the significance of vocal consistency to reproductive success as well as the biological control of vocal consistency, we reveal potential mechanistic substrates that have been shaped by selection pressures and, more generally, emphasize the importance and power of understanding behavior at multiple levels of analysis.

#### The relevance of vocal performance and consistency

Historically, evolutionary and ecological studies of birdsong have focused on repertoire size (i.e. the number of distinct songs or elements in a male’s repertoire) as a marker of song and male quality (reviewed in Catchpole and Slater, 2008). This emphasis

was based on the notions that learning more song elements is difficult and that the number of song elements learned serves as an honest indicator of quality. The importance of repertoire size was supported by the fact that many species learn and produce a variety of song types and by classic studies demonstrating that females prefer males with larger song repertoires, even in species that sing only a limited number of song types (Catchpole and Slater, 2008; Searcy and Yasukawa, 1996).

However, the ubiquity and importance of female choice for large song repertoires has recently been challenged. Byers and Kroodsma (Byers and Kroodsma, 2009), for example, reviewed 47 published field and laboratory studies and did not find compelling evidence of female choice for larger repertoires. Most field studies failed to find female preference for larger repertoires, and within species that demonstrated preference for large repertoires, the strength of preference was not consistent across studies. Wiley (Wiley, 2000) and Byers and Kroodsma (Byers and Kroodsma, 2009) also review studies arguing that the method of song delivery in species with song repertoires is incongruent with female preferences for large repertoires: males tend to repeat one song type before switching to another song type ('eventual variety') instead of switching songs rapidly ('immediate variety') (e.g. Byers, 1995; Kroodsma et al., 1999). Additionally, phylogenetic studies of song evolution have found that reductions in repertoire size are not uncommon (e.g. Cardoso and Mota, 2007; de Kort and ten Cate, 2004; Irwin, 1990; Price and Lanyon, 2004; Price et al., 2007). For example, Price and Lanyon (Price and Lanyon, 2004) report that the strength of sexual selection pressure (as measured by the degree of sexual dimorphism) is correlated with a decrease, not an increase, in repertoire size for oropendolas and caciques. These studies suggest that female preference for repertoire size might not be as prevalent or important for reproductive success as previously proposed.

Recently, an increasing number of behavioral ecologists have used adult song performance as a metric for male quality (reviewed in Podos et al., 2009). For example, a number of studies illustrate that rapidly producing song elements that span a broad range of frequencies is difficult and that females prefer males that can produce such difficult vocalizations (e.g. Ballentine et al., 2004; Podos, 1997; Vallet and Kreutzer, 1995). In addition, Lambrechts and Dhondt (Lambrechts and Dhondt, 1988) highlight motor constraints on producing sequences of vocalizations in rapid succession and propose that the ability to produce song elements at a consistent rate serves as an honest indicator of a male's physical capabilities.

There are at least two reasons for this increased emphasis on the quality of vocal performance (Byers and Kroodsma, 2009; Byers et al., 2010; Gil and Gahr, 2002; Podos et al., 2009). First, an examination of vocal performance is relevant to all avian species in which song is used to assess conspecifics, not just to species that sing multiple song types. Consequently, understanding the relevance of vocal performance can lead to more general hypotheses about the evolution of birdsong. Second, from the perspective of the receiver, assessment of vocal performance requires less time and memory than assessment of repertoire size. For example, hundreds of renditions of songs are required to thoroughly assess the breadth of song types and variants in songbirds with medium to large repertoires (e.g. Botero et al., 2008; Smith et al., 1997), whereas an adequate assessment of the difficulty of syllable production, even in species with large repertoires, requires only one or a few songs (e.g. de Kort et al., 2009). Further, the repetitive nature of song delivery during social interactions in some species facilitates assessment of vocal

performance over an assessment of repertoire size (e.g. Botero and Vehrencamp, 2007; Byers and Kroodsma, 2009; Vehrencamp et al., 2007; Wiley, 2000). Accordingly, vocal performance not only has broad relevance but also is an attractive trait to study from the perspective of both the signaler and receiver.

One feature of vocal performance, namely vocal consistency, has recently received attention not only from ethologists and behavioral ecologists but also from neuroscientists and psychologists. Vocal consistency refers to the ability to replicate the acoustic features of song from one rendition to the next. For example, in species that produce songs containing pure tones as song elements (e.g. the whistle of a white-crowned sparrow song, the 'fee' and 'bee' elements of a chickadee song), vocal consistency can be reflected in the ability to precisely produce the same frequency across songs. The ability to produce consistent vocalizations requires the generation of consistent vocal motor commands by the nervous system, the accurate coordination of syringeal and respiratory muscles on a fine timescale, and muscular resistance to fatigue (Lambrechts and Dhondt, 1988; Suthers and Zollinger, 2008). Additionally, the right and left sides of the avian syrinx are unilaterally innervated and therefore independently controlled (e.g. Halle et al., 2003; Nottebohm et al., 1976) (reviewed in Suthers and Zollinger, 2008; Suthers et al., 2004; Williams et al., 1992; Zollinger et al., 2008), and as a result, the consistent production of song elements requires bilateral coordination, both centrally and peripherally (Ashmore et al., 2008; Schmidt, 2003; Vu et al., 1998; Wild, 2008). Because of the requirement to produce consistent vocalizations, behavioral ecologists consider vocal consistency a measure of vocal performance that could honestly signal male quality. Furthermore, given these motor demands, it is not surprising that song is not highly consistent from the outset of singing but that vocal consistency emerges across development: vocalizations of juvenile songbirds are initially 'noisy' (e.g. high spectral entropy) and variable, and subsequently become more structured and consistent with increased practice (e.g. Arnold, 1975; Clark et al., 1987; Marler and Peters, 1982; Nottebohm et al., 1986; Podos et al., 1995; Tchernichovski et al., 2001). Interestingly, this developmental change in vocal consistency in songbirds mirrors that in humans; the 'noisy' and variable babbles of infants gradually develop into structured speech phonemes with vocal practice (Doupe and Kuhl, 1999; King et al., 2005; Goldstein and Schwade, 2010).

### Functional (behavioral) studies of vocal consistency

The adaptive significance of a behavior ultimately rests in its effects on reproductive success. To assess the functional relevance of vocal consistency, researchers have analyzed how it varies across seasons, ages and social contexts as well as how it relates to dominance, female preference and the number of offspring sired. To analyze vocal consistency, researchers have measured the variability [coefficient of variation (CV) or standard deviation] of syllable structure (e.g. fundamental or dominant frequency) or calculated cross-correlations of the spectrogram of different renditions of a syllable.

A number of studies have demonstrated that the consistency with which song syllables are produced changes across season. For example, male canaries, *Serinus canaria*, produce syllables that are spectrally variable from one rendition to the next outside the breeding season but perform syllables with greater consistency across renditions during the breeding season (Nottebohm et al., 1986). Smith and colleagues (Smith et al., 1995; Smith et al., 1997) provide comprehensive analyses of vocal consistency in Gambel's white-crowned sparrows, *Zonotrichia leucophrys gambelii*, and

song sparrows, *Melospiza melodia*, and illustrate similar increases in vocal consistency from non-breeding periods to the breeding season. For example, the consistency with which song sparrows produce syllables (i.e. spectral cross-correlation) is ~10% higher during the spring than the autumn (Smith et al., 1997).

Similar increases in vocal consistency have been found with age in adult songbirds. For example, in adult banded wrens, *Thryothorus pleurostictus*, tropical mockingbirds, *Mimus gilvus*, and great tits, *Parus major*, syllable consistency increases by ~3% over 1 year (Botero et al., 2009; de Kort et al., 2009; Rivera-Gutierrez et al., 2010). In zebra finches, *Taeniopygia guttata*, the consistency of syllable structure is ~40% higher for adult males 4 years and older than for adult males less than 6 months old (Kao and Brainard, 2006). A number of studies have found that females preferentially mate with older males, possibly because older individuals have demonstrated viability (by surviving) and are often able to outcompete younger individuals (e.g. Hegyi et al., 2006; Hyman et al., 2004). The fact that older males produce more consistent songs suggests that females can gather information about the age of a male by assessing his vocal consistency and use this information to select potential mates.

In addition to gradual changes across seasons and with age, vocal consistency can rapidly change depending on the social context. In adult zebra and Bengalese finches, the structure of syllables is significantly more consistent when males produce courtship song to females than when males produce interleaved renditions of non-courtship song in isolation (Fig. 1) (Kao et al., 2005; Kao and Brainard, 2006; Leblois et al., 2010; Ölveczky et al., 2005; Sakata et al., 2008; Teramitsu and White, 2006). For example, the trial-by-trial variability in fundamental frequency is ~30% lower for courtship song than for non-courtship song in the Bengalese finch, *Lonchura striata* var. *domestica* (Sakata et al., 2008). Because the quality of courtship song is important for securing mating opportunities, these data provide indirect evidence that vocal consistency could be important for male reproductive success.

More direct evidence for the adaptive significance of vocal consistency comes from recent field studies. In the chestnut-sided warbler, *Dendroica pensylvanica*, males that produce more consistent songs sire more extra-pair offspring than males that produce less consistent songs (Byers, 2007). Specifically, Byers (Byers, 2007) measured the highest and lowest frequencies, frequency of peak power, and start and end times for each song bout (in addition to other song features such as the number of syllables, singing rate and song duration), then analyzed the degree to which the mean and CV of these measures explained variation in reproductive success (number of genetic offspring outside the male's own nest). He found that males that sired more extra-pair offspring produced songs with less variation in the frequency of peak power and lowest frequency. In contrast, features like the number of syllables, total song and syllable repertoire size, frequency bandwidth and song duration did not significantly explain variation in reproductive success. Similarly, male banded wrens that produce more consistent song (based on spectral cross-correlations) are more likely to secure extra-pair copulations than males that produce less consistent song (Cramer et al., 2011). In a number of songbird species, dominant males, which enjoy greater reproductive success, produce more consistent songs. Dominant male tropical mockingbirds produce more consistent syllable structure than subordinate males (Botero et al., 2009); dominant black-capped chickadees, *Poecile atricapillus*, maintain a more consistent frequency ratio and relative amplitude between the fee and bee notes of their songs compared with subordinates (Christie

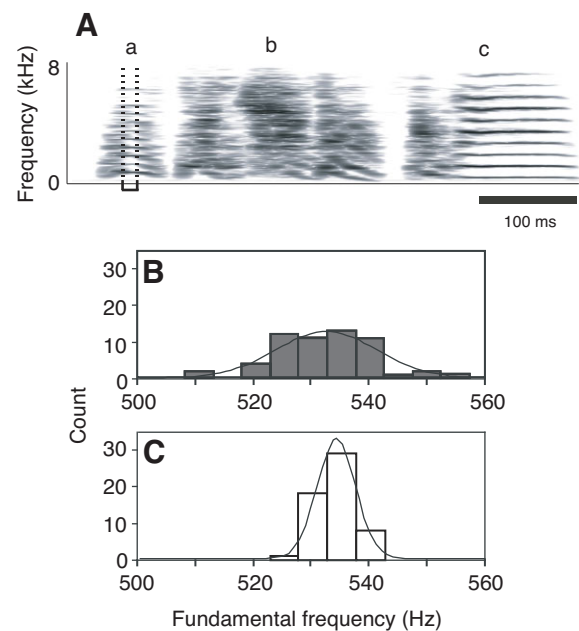


Fig. 1. The structure of song syllables is more consistent when male zebra finches produce courtship song to females than when they produce non-courtship song in isolation. (A) A spectrographic representation (intensity as a function of frequency and time) of a zebra finch song, with unique labels above each unique song element ('syllable'). Dashed lines indicate the time window in which fundamental frequency (FF) was measured for the syllable 'a'. (B,C) Two histograms displaying the distribution of FF for the syllable 'a' when this bird produced non-courtship (B) and courtship song (C; line indicates Gaussian fit to data). In this example, there was a significant decrease in the variability of FF when the bird produced courtship song relative to when he produced non-courtship song. However, there was no significant change in the mean FF across contexts. Redrawn and adapted from Kao and Brainard (Kao and Brainard, 2006).

et al., 2004; Hoeschele et al., 2010); and dominant great tits show less drift in inter-phrase interval during song strophes (Lambrechts and Dhondt, 1986). Finally, male great reed warblers, *Acrocephalus arundinaceus*, with more consistent (and longer) whistle note durations have larger harems (Węgrzyn et al., 2010). These studies provide strong support for the notion that vocal consistency influences reproductive success.

A laboratory study in the zebra finch suggests that female preference for more consistent syllable production could contribute to the increased reproductive success of males with more consistent syllable production. Using a phonotaxis assay, Woolley and Doupe (Woolley and Doupe, 2008) demonstrate that females strongly prefer the more consistent courtship song to the less consistent non-courtship song. Additionally, they found that the strength of preference for courtship song over non-courtship song correlated with the magnitude of difference between courtship and non-courtship song in the consistency of syllable structure. The degree to which mate choice in a more naturalistic setting depends on vocal consistency is unknown, but this study warrants further investigation into female preferences for consistent songs.

Taken together, these findings are compatible with the notion that the consistency of syllable production influences reproductive success and could play an important role in the evolution of birdsong. Differences in vocal consistency across males could signal information about ability, age and quality, and females could use this information to select mating partners.



### Mechanistic (neurophysiological) studies of vocal consistency

Mechanistic investigations have capitalized on the finding that vocal consistency gradually changes across development and rapidly changes across social contexts to identify pertinent neurobiological processes. Changes in activity within the neural circuits controlling song are likely to contribute to both gradual and rapid changes in vocal consistency. There are two main neural circuits regulating song production, control and plasticity: the vocal motor pathway (VMP) and anterior forebrain pathway (AFP; Fig. 2A). The VMP, which includes the forebrain nuclei HVC (proper name) and RA (robust nucleus of the arcopallium), is directly responsible for producing the motor commands for song (Fee et al., 2004; Mooney, 2009; Reiner et al., 2004). Neurons in HVC and RA show patterned activity during song production (reviewed in Fee et al., 2004; Hahnloser et al., 2002; McCasland, 1987; Ölveczky et al., 2011; Prather et al., 2008; Sakata and Brainard, 2008; Sober et al., 2008; Yu and Margoliash, 1996), and perturbations of activity in HVC and RA lead to acute vocal motor changes (Ashmore et al., 2005; Long et al., 2010; Vu et al., 1994; Wang et al., 2008). Of particular interest here is the finding that the activity of RA neurons, which project to brainstem nuclei that control vocal and respiratory musculature, encodes and controls the spectral composition of syllables (Ashmore et al., 2005; Leonardo and Fee, 2005; Sober et al., 2008; Vu et al., 1994; Wohlgemuth et al., 2010; Yu and Margoliash, 1996). For example, in adult Bengalese finches, variation in the premotor activity of RA neurons correlates with variation in the fundamental frequency of syllables (Sober et al., 2008). Therefore, changes in the activity of neurons in the VMP, especially in RA, contribute to changes in vocal performance.

The AFP is an avian basal ganglia–thalamic–forebrain circuit that shares many properties with mammalian basal ganglia–thalamic–cortical loops, including a central role in vocal learning and control (Brainard, 2004; Doupe et al., 2005; Graybiel, 2005). The output nucleus of the AFP, the lateral nucleus of the anterior nidopallium (LMAN), sends glutamatergic projections to RA and, thus can influence activity and plasticity in the VMP as well as vocal performance and plasticity. Classic studies demonstrate that LMAN is crucial for the development of accurate and stereotyped imitations of tutor songs (Basham et al., 1996; Bottjer et al., 1984; Scharff and Nottebohm, 1991; Sohrabji et al., 1990). Syllable structure is initially variable when juvenile birds start vocalizing but becomes progressively more consistent as song develops (e.g. Arnold, 1975; Clark et al., 1987; Marler and Peters, 1982; Nottebohm et al., 1986; Podos et al., 1995; Tchernichovski et al., 2001). Correspondingly, the premotor activity of LMAN neurons is more variable across renditions when juveniles produce their variable songs than when adults produce their consistent songs (Kao et al., 2008; Ölveczky et al., 2005). This suggests that LMAN introduces more variable activity into the VMP when juveniles produce song than when adults produce song, thereby making juvenile vocalizations more variable. The causal contribution of LMAN to vocal consistency is underscored by the finding that inactivation of LMAN neurons in juvenile zebra finches acutely increases the consistency of syllable structure and RA premotor activity (Ölveczky et al., 2005; Ölveczky et al., 2011) and that lesions of LMAN cause song to prematurely ‘crystallize’ on an immature version of song (Scharff and Nottebohm, 1991). These data illustrate the importance of the AFP to developmental changes in vocal consistency.

The precise mechanisms underlying developmental changes in the consistency of song and neural activity remain unclear. It is likely that feedback and reinforcement mechanisms play a major role in shaping firing patterns in the AFP and VMP (see below)

(reviewed in Brainard and Doupe, 2000; Konishi, 2004; Mooney, 2009; Ölveczky et al., 2011). In addition, developmental changes in sex steroid hormone concentrations could contribute to developmental changes in vocal consistency and neural activity in song circuitry. Neurons in the AFP and VMP are replete with sex steroid hormone receptors, in particular androgen receptors (Ball et al., 2003; Brenowitz, 2004). Androgen levels surge at sexual maturity (reviewed in Adkins-Regan, 2010), a time when song becomes crystallized, and androgen manipulations affect the development of vocal consistency. For example, Marler and colleagues (Marler et al., 1988) castrated male swamp and song sparrows within a month of hatching and found that only after testosterone administration did adult castrates produce songs with adult-typical levels of consistency. Similarly, in zebra finches, castration and antisteroid treatment prevent or slow down the maturation of song consistency (Arnold, 1975; Bottjer and Hewer, 1992), and androgen administration to juveniles prematurely crystallizes song (Korsia and Bottjer, 1991; White et al., 1999). While the precise mechanisms by which sex steroid hormones affect the development of vocal consistency are unknown (but see Livingston and Mooney, 2001; White et al., 1999), we hypothesize that developmental steroid effects are mediated, in part, by changes to the variability of activity in the AFP.

Traditionally, the AFP was thought to specifically regulate song learning and plasticity in juvenile songbirds. However, more recent investigations into the rapid change in vocal consistency across social contexts have documented a real-time contribution of LMAN to vocal consistency in adults. Congruent with a role of RA in vocal control, the premotor activity of RA neurons is more consistent during the production of the more consistent courtship song than during the production of the less consistent non-courtship song in adult Bengalese finches (Sober et al., 2008). Similarly, the activity of Area X and LMAN neurons is more consistent during the production of the more consistent courtship song in adult zebra finches (Fig. 2B) (Hessler and Doupe, 1999; Kao et al., 2005; Kao et al., 2008). The importance of the AFP to the social modulation of vocal consistency and neural activity in the VMP is underscored by studies demonstrating that inactivation of LMAN decreases the variability of RA activity during singing (Ölveczky et al., 2011) and that lesions and inactivation of LMAN eliminate the difference in consistency between courtship and non-courtship song in adult zebra and Bengalese finches (Fig. 2C) (Hampton et al., 2009; Kao et al., 2005; Kao and Brainard, 2006; Ölveczky et al., 2005; Stepanek and Doupe, 2010). Importantly, lesions and inactivation of LMAN eliminate the social modulation of vocal consistency by increasing the consistency of non-courtship song to the level of courtship song. Therefore, LMAN modulates vocal consistency across social contexts by injecting higher levels of variability into the VMP when birds produce non-courtship song than when they produce courtship song.

Collectively, these mechanistic studies highlight the contribution of avian basal ganglia–forebrain circuits to vocal consistency. In particular, LMAN, the output of the AFP, contributes not only to the development of vocal consistency in juvenile songbirds but also to the rapid social modulation of vocal consistency in adults. Neurons in LMAN introduce varying levels of excitatory activity into the VMP, thereby affecting the variability of motor commands and the degree of vocal consistency. This, in turn, affects the attractiveness of song. Given the importance of vocal consistency to reproductive success, these data suggest that sexual selection could sculpt heritable factors that influence the development and activity of LMAN neurons.

### Bridging perspectives: the importance of vocal practice

In reviewing functional, developmental and mechanistic studies, one can highlight common themes that bridge the levels of analysis. One such theme for vocal consistency is the importance of vocal practice.

The notion of vocal practice was formalized in pioneering studies of song learning and development (for reviews, see

Brainard and Doupe, 2000; Konishi, 2004; Marler, 1997; Nottebohm and Liu, 2010; Mooney, 2009). In the sensorimotor phase of song development, juveniles engage in vocal practice to hone their vocalizations into songs that closely match those memorized during the sensory period. As juveniles first begin to vocalize and practice, the sounds they produce are highly variable.

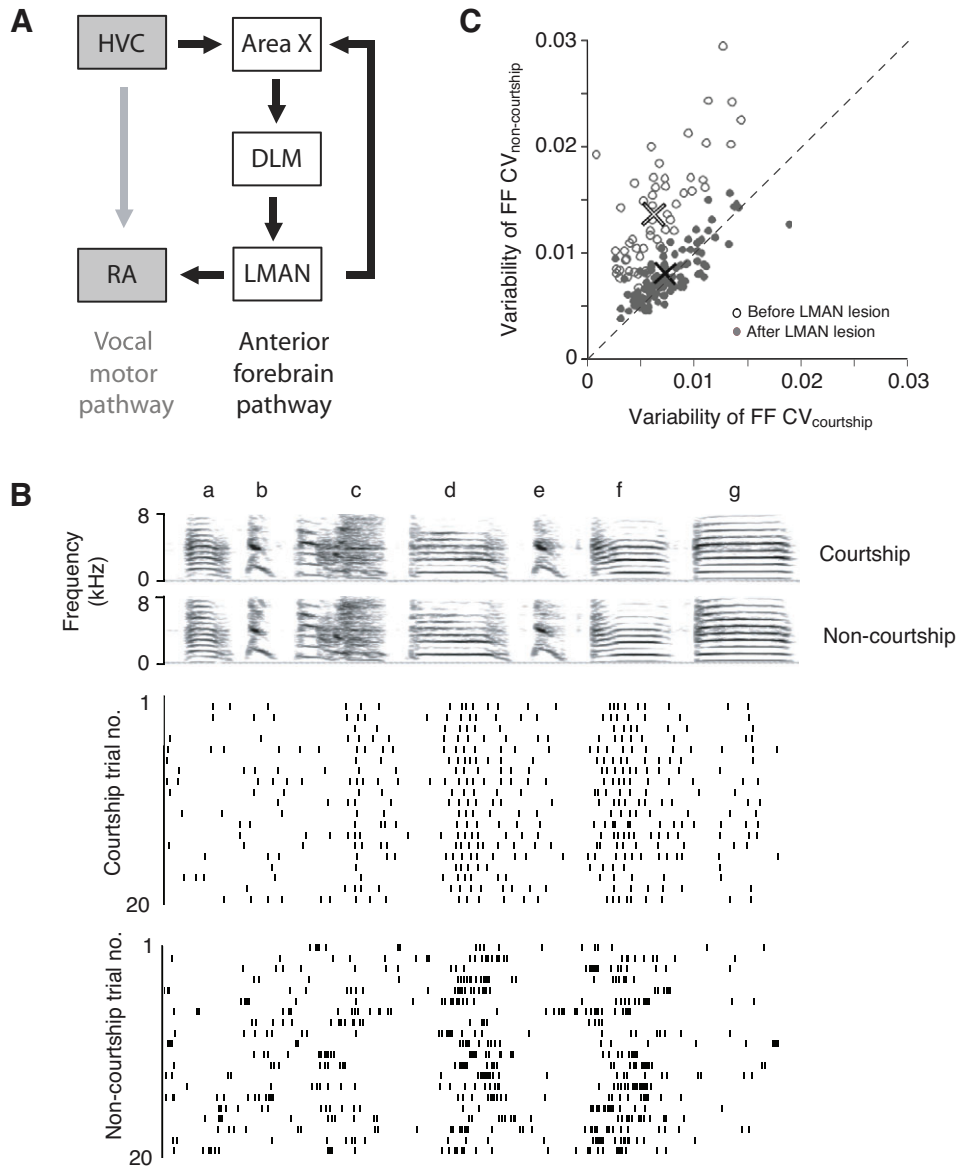


Fig. 2. The importance of the lateral nucleus of the anterior nidopallium (LMAN) to vocal consistency. (A) Schematic diagram of the song system. The song system of songbirds consists of two main pathways. The vocal motor pathway (VMP; grey) consists of brain nuclei such as HVC (proper name) and RA (robust nucleus of the arcopallium), and neurons in the VMP encode the motor commands for song. The anterior forebrain pathway (AFP; white) is an avian forebrain-basal ganglia circuit that is important for song learning and plasticity. The AFP consists of the avian basal ganglia nucleus Area X, the thalamic nucleus DLM (medial dorsolateral nucleus of the thalamus) and the cortical-like nucleus LMAN. LMAN is the output of the AFP and can influence activity in the VMP via its projections to RA. (B) LMAN neurons show patterned activity during singing and different levels of trial-by-trial variability across social contexts. Plotted from top to bottom are spectrograms of the sequence 'abcdefg' for courtship and non-courtship song and raster plots summarizing the spiking activity of a single LMAN neuron across different renditions during courtship and non-courtship song. Each tick in the raster plot represents a single spike, and each row represents a single rendition of the sequence 'abcdefg'. Importantly, the activity of this LMAN neuron is more consistent across renditions when the bird produces courtship song than when he produces non-courtship song. This suggests that LMAN could introduce less variability into the VMP when birds produce courtship song, thereby reducing the variability in VMP activity and vocal motor output. Redrawn and adapted from Kao et al. (Kao et al., 2008). (C) Lesions of LMAN eliminate the social modulation of vocal consistency. Plotted are the coefficients of variation (CV), a measure of variability (inverse of consistency), of fundamental frequency (FF) for individual zebra finch syllables. Open circles refer to data collected before LMAN lesions whereas filled circles refer to data collected after LMAN lesions. There was a significant effect of social context on syllable consistency before LMAN lesion (white cross), with CV being higher for non-courtship song than for courtship song, but no effect of social context following LMAN lesion (black cross). Redrawn and adapted from Kao and Brainard (Kao and Brainard, 2006).

Empirical, theoretical and computational studies of reinforcement and motor learning (including song learning) emphasize that this variability serves as the substrate upon which feedback and reinforcement signals act to improve motor function (Doya and Sejnowski, 1998; Liu and Nottebohm, 2007; Margoliash et al., 1991; Sutton and Barto, 1998; Troyer and Doupe, 2000). In particular, the nervous system uses information from motor variability to reinforce motor commands that produce desired outcomes and weaken motor commands that produce undesired outcomes. This leads to the development of more accurate and consistent motor commands. With regard to song development, the variable vocalizations of juveniles are shaped by sensory feedback, in particular auditory feedback, as well as behavioral feedback from conspecifics to form a song that resembles the memorized song and is effective at eliciting responses from conspecifics (Doupe and Kuhl, 1999; Goldstein and Schwade, 2010; King et al., 2005; Marler, 1997; West and King, 1988). Consequently, feedback and reinforcement signals during vocal practice hone the nervous system (and vocal periphery) and allow for the development of communication signals that are refined and consistent in structure.

Traditionally, vocal practice was thought to no longer be important following sexual maturation and song crystallization. This idea was based on studies demonstrating that the removal of auditory feedback did not significantly affect adult song performance in emberzine sparrows (e.g. Konishi, 1965). However, more recent studies in estrildid finches and other songbird species demonstrate that auditory feedback is crucial for the maintenance of consistent adult song and suggest that vocal practice continues to be important in adult songbirds (reviewed in Brainard and Doupe, 2000; Konishi, 2004; Leonardo and Konishi, 1999; Mooney, 2009). For example, syllable structure and sequencing rapidly degrade and become less consistent following deafening in adult zebra and Bengalese finches (Brainard and Doupe, 2001; Horita et al., 2008; Nordeen and Nordeen, 1992; Okanoya and Yamaguchi, 1997; Sakata and Brainard, 2006; Woolley and Rubel, 1997). Manipulation of auditory feedback and reinforcement signals can drive adaptive changes to song structure (Andalman and Fee, 2009; Charlesworth et al., 2011; Tumer and Brainard, 2007; Sober and Brainard, 2009; Warren et al., 2011), and urban noise alters vocal performance in numerous populations of adult songbirds (reviewed in Slabbekoom and Ripmeester, 2008). Additionally, auditory feedback likely contributes to the recovery of consistent song structure following peripheral injury in adult zebra finches (Bhama et al., 2011). These data illustrate that adult song continues to represent a state of vocal practice and plasticity in which feedback and reinforcement mechanisms are engaged to refine and maintain consistent vocal performance.

Given the importance of motor variability and feedback to vocal practice, the degree to which adult song is considered vocal practice should depend on the amount of motor variability and magnitude of auditory feedback contributions. As mentioned previously, the level of vocal motor variability is greater during the production of non-courtship song than courtship song in finches (Kao and Brainard, 2006; Sakata et al., 2008). Furthermore, auditory feedback contributes more to the control of non-courtship song than to courtship song (Kobayashi and Okanoya, 2003; Sakata and Brainard, 2009). These behavioral studies indicate not only that there is greater opportunity for reinforcement and motor learning during non-courtship song but also that feedback mechanisms are more engaged during non-courtship song. Neurobiological studies are consistent with these findings and suggest that neural plasticity mechanisms are more engaged during non-courtship song. In

particular, in song system nuclei, immediate early gene expression and bursting activity, both of which correlate with increased plasticity, are greater when birds produce non-courtship song than when they produce courtship song (Hessler and Doupe, 1999; Jarvis et al., 1998; Kao and Brainard, 2006; Kao et al., 2008). Collectively, these studies have led to the framework that non-courtship song represents a heightened state of vocal practice relative to courtship song, whereas courtship song represents a heightened state of vocal performance. Thus, this 'practice *versus* performance' framework postulates that non-courtship and courtship songs serve distinct purposes, and this framework hypothesizes that reinforcement and feedback signals should have greater effects on vocal plasticity when birds produce non-courtship song than when they produce courtship song.

Vocal practice has also been discussed in the context of age- and season-dependent changes in vocal consistency. In a number of songbirds, including tropical mockingbirds, banded wrens, great tits and zebra finches, vocal consistency increases with age, and it has been proposed that older males have more consistent songs because of increased opportunity for vocal practice and refinement (Botero et al., 2008; de Kort et al., 2009; Kao and Brainard, 2006; Pytte et al., 2007; Rivera-Gutierrez et al., 2010). Similarly, it has been proposed that vocal practice contributes to the higher levels of vocal consistency during the breeding season than during the non-breeding season. Generally speaking, birds produce fewer songs outside the breeding season, when song is less consistent (e.g. Nottebohm et al., 1986; Smith et al., 1995; Smith et al., 1997). As testicular hormone levels increase at the onset of the breeding season, males engage in more singing. This increased singing provides more opportunities for vocal practice, and birds can more readily hone their vocalizations and test their potency against rivals as they establish their territories. Indeed, testosterone-induced increases in singing rate precede the increase in syllable consistency in white-crowned sparrows, suggesting that increased practice causes improvements in vocal performance (Meitzen et al., 2009a). As the breeding season comes to an end, physiological changes (including photorefractoriness and a decrease in androgen levels) cause singing rate to decrease, which could, in turn, contribute to the decline in vocal consistency during the non-breeding season (e.g. Ball et al., 2003; Smith et al., 1995; Smith et al., 1997). Just as athletes become 'rusty' after periods without practice, the decrease in singing outside the breeding season could make song less consistent.

The potential role of vocal practice in age-dependent and seasonal changes to vocal consistency suggests another interpretation of the contribution of singing rate to reproductive success. Numerous studies document that singing rate (i.e. the number of songs per unit time) correlates with reproductive success and that females prefer males that are more active singers (reviewed in Catchpole and Slater, 2008). Because of the metabolic and predation costs of singing (Catchpole and Slater, 2008; Oberweger and Goller, 2001; Ward and Slater, 2005), the traditional interpretation of this finding is that males that sing more represent higher quality males because they have sufficient energy to allocate to singing and are adept enough to avoid the additional predation cost incurred by singing. However, another interpretation based on the findings reviewed here is that males with higher singing rates enjoy higher reproductive success because they engage in more vocal practice and, as a consequence, perform their songs with greater consistency. This alternative framework predicts that the effect of singing rate on reproductive fitness could be mediated by vocal consistency. This framework also raises the possibility that



singing rate and vocal consistency are additive such that males that produce consistent vocalizations more frequently are more attractive and successful than males that produce less consistent vocalizations less frequently.

In summary, the studies reviewed here suggest a potential contribution of vocal practice to reproductive success. Vocal practice in juvenile birds allows for the development of variable vocalizations into consistent songs, which are important for securing reproductive opportunities, and vocal practice in adult songbirds allows for the refinement and maintenance of consistent song. Vocal practice could contribute to seasonal and age-dependent plasticity in adult vocal consistency as well as individual differences in vocal consistency. Taken together, selection for vocal consistency could act upon mechanisms regulating vocal practice, including the motivation to practice, the ability to learn and improve from vocal practice, and the variability of activity of VMP and AFP neurons. Interestingly, these studies on vocal practice also highlight the importance of vocal variability for vocal plasticity (e.g. to maintain accurate and consistent vocalizations in response to environmental change or peripheral injury). Given the contribution of the AFP to vocal variability and consistency, this suggests that selection has built a circuit that introduces greater levels of variability into the VMP when vocal motor variability is important (e.g. during vocal practice) and less variability when consistency is important (e.g. during courtship interactions).

### Concluding remarks and future directions

Here we review functional, developmental and mechanistic studies dealing with the importance and control of vocal consistency in songbirds. We focus on vocal consistency as a metric for vocal performance because consistent vocal performance depends on the generation of consistent neural commands for song as well as the coordination and resilience of peripheral vocal musculature. Functional (behavioral) studies demonstrate that individual differences in vocal consistency translate into differences in reproductive success. Developmental studies reveal that vocal consistency gradually emerges from variable vocalizations, and mechanistic investigations illustrate that avian forebrain and basal ganglia circuits and sex steroid hormones are involved in the regulation of vocal consistency. In reviewing these studies, we find that examinations at all of these levels of analysis emphasize the importance of vocal practice for vocal consistency. Practice hones the nervous system as well as the vocal periphery so that birds are better able to produce consistent vocalizations. We propose that selection pressure for increased vocal consistency could be acting upon the physiological processes regulating vocal practice in both juvenile and adult songbirds. We hope that this review serves as an example of the power of integrating multiple levels of analysis and encourage similar syntheses in other fields to generate hypotheses about mechanisms underlying behavioral evolution.

Another function of this review is to inspire future lines of inquiry for songbird research and better integration across disciplines. Overall, we encourage more investigations into the relationship between vocal consistency, vocal practice and reproductive success, as well as into mechanisms underlying vocal practice and consistency. The studies published to date are encouraging and motivate similar experiments in other songbird species as well as non-songbird species. It will be important for future studies to elucidate the degree to which vocal consistency influences reproductive success through female preference for consistency (e.g. Woolley and Doupe, 2008) *versus* male–male interactions (e.g. de Kort et al., 2009; Rivera-Gutierrez et al.,

2011). Documenting differences in vocal consistency across song types that serve different functions [e.g. territorial *vs* courtship (e.g. Byers, 1995; Liu and Nottebohm, 2005)] and assessing how experimental manipulations of vocal consistency (e.g. lesions of LMAN) affect a male's attractiveness to females and dominance status could provide insight into the means by which vocal consistency influences reproductive success. It will also be informative to reveal the degree to which developmental experiences that influence song learning and consistency [e.g. nutritional and immunological stress (Holveck et al., 2008; Podos et al., 2009)] do so by affecting vocal practice. Such studies would shed light on the mechanisms of developmental effects. We encourage further studies into the mechanisms underlying seasonal changes in vocal consistency (e.g. Meitzen et al., 2007a; Meitzen et al., 2007b; Meitzen et al., 2009b; Park et al., 2005) that draw parallels with the mechanisms underlying developmental changes in vocal consistency. In particular, given the importance of the AFP to developmental and context-dependent changes in vocal consistency, it will be informative to assess the magnitude of AFP contributions to seasonal changes in vocal consistency (but see Benton et al., 1998). Broadly speaking, it will be important for future studies to disentangle the magnitude of genetic and environmental contributions to individual differences in vocal consistency. Genes, the environment and gene–environment interactions could affect the amount of vocal practice, feedback processing and the organization of central and peripheral pathways, all of which can constrain and influence vocal consistency, and understanding these contributions could provide insight into the biological basis underlying individual differences in reproductive success. Finally, because the importance of vocal consistency has been investigated in only a handful of songbird species, we have not explicitly addressed the influence of evolutionary history on vocal consistency. To gain insight into evolutionary influences, it will be important to reveal how the performance of and preference for consistent songs are affected by phylogenetic history and selection pressure. Relatedly, it has been hypothesized that the VMP and AFP evolved from brain areas that regulate non-vocal motor functions [e.g. flying, walking and foraging; see Feenders et al. (Feenders et al., 2008), Tokarev et al. (Tokarev et al., 2011) and references therein], and it would be useful to understand the degree to which song consistency has specifically been selected for as an indicator of age, experience and song learning ability *versus* indirectly selected for as a by-product of general selection for consistent motor production (reviewed in Byers et al., 2010).

### Acknowledgements

We thank S. C. Woolley, M. H. Kao, C. A. Botero, S. R. de Kort, T. Warren and M. S. Brainard for their critical readings of the manuscript.

### Funding

J.T.S. was supported by funding from the National Institutes of Health [grant nos F32-MH068055-01, P50-MH-77970] and the Natural Sciences and Engineering Research Council of Canada [grant no. DG 402417-11], and S.L.V. was supported by funding from the National Institutes of Health [grant no. R01-MH60461]. Deposited in PMC for release after 12 months.

### References

- Adkins-Regan, E. (2010). Hormones and the development of communication-related social behavior in birds. In *Oxford Handbook of Developmental Behavioral Neuroscience* (ed. M. S. Blumberg, J. H. Freeman and S. R. Robinson), pp. 639–666. New York: Oxford University Press.

- Andalman, A. S. and Fee, M. S. (2009). A basal ganglia-forebrain circuit in the songbird biases motor output to avoid vocal errors. *Proc. Natl. Acad. Sci. USA* **106**, 12518-12523.
- Arnold, A. P. (1975). The effects of castration on song development in zebra finches (*Poephila guttata*). *J. Exp. Zool.* **191**, 261-278.
- Ashmore, R. C., Wild, J. M. and Schmidt, M. F. (2005). Brainstem and forebrain contributions to the generation of learned motor behaviors for song. *J. Neurosci.* **25**, 8543-8554.
- Ashmore, R. C., Bourjaily, M. and Schmidt, M. F. (2008). Hemispheric coordination is necessary for song production in adult birds: implications for a dual role for forebrain nuclei in vocal motor control. *J. Neurophysiol.* **99**, 373-385.
- Ball, G. F., Castelino, C. B., Maney, D. L., Appeltants, D. and Balthazart, J. (2003). The activation of birdsong by testosterone: multiple sites of action and role of ascending catecholamine projections. *Ann. N. Y. Acad. Sci.* **1007**, 211-231.
- Ballentine, B., Nowicki, S. and Hyman, J. (2004). Vocal performance influences female response to male bird song: an experimental test. *Behav. Ecol.* **15**, 163-168.
- Basham, M. E., Nordeen, E. J. and Nordeen, K. W. (1996). Blockade of NMDA receptors in the anterior forebrain impairs sensory acquisition in the zebra finch (*Poephila guttata*). *Neurobiol. Learn. Mem.* **66**, 295-304.
- Beecher, M. D. and Brenowitz, E. A. (2005). Functional aspects of song learning in songbirds. *Trends Ecol. Evol.* **20**, 143-149.
- Benton, S., Nelson, D. A., Marler, P. and DeVogd, T. J. (1998). Anterior forebrain pathway is needed for stable song expression in adult male white-crowned sparrows (*Zonotrichia leucophrys*). *Behav. Brain. Res.* **96**, 135-150.
- Bhama, P. K., Hillel, A. D., Merati, A. L. and Perkel, D. J. (2011). A novel model for examining recovery of phonation after vocal nerve damage. *J. Voice* **25**, 275-282.
- Bolhuis, J. J. and Gahr, M. (2006). Neural mechanisms of birdsong memory. *Nat. Neurosci. Rev.* **7**, 347-357.
- Botero, C. A. and Vehrencamp, S. L. (2007). Response of male tropical mockingbirds to variation in within-song and between-song versatility. *Auk* **124**, 185-196.
- Botero, C. A., Mudge, A. E., Koltz, A. M., Hochachka, W. M. and Vehrencamp, S. L. (2008). How reliable are the methods for estimating repertoire size? *Ethology* **114**, 1227-1238.
- Botero, C. A., Rossman, R. J., Caro, L. M., Stenzler, L. M., Lovette, I. J., de Kort, S. R. and Vehrencamp, S. L. (2009). Syllable type consistency is related to age, social status and reproductive success in the tropical mockingbird. *Anim. Behav.* **77**, 701-706.
- Bottjer, S. W. and Hewer, S. J. (1992). Castration and antisteroid treatment impair vocal learning in male zebra finches. *J. Neurobiol.* **23**, 337-353.
- Bottjer, S. W., Miesner, E. A. and Arnold, A. P. (1984). Forebrain lesions disrupt development but not maintenance of song in passerine birds. *Science* **224**, 901-903.
- Bradbury, J. W. and Vehrencamp, S. L. (2011). *Principles of Animal Communication*, 2nd Edn. Sunderland, MA: Sinauer Associates.
- Brainard, M. S. (2004). Contributions of the anterior forebrain pathway to vocal plasticity. *Ann. N. Y. Acad. Sci.* **1016**, 377-394.
- Brainard, M. S. and Doupe, A. J. (2000). Auditory feedback in learning and maintenance of vocal behaviour. *Nat. Rev. Neurosci.* **1**, 31-40.
- Brainard, M. S. and Doupe, A. J. (2001). Postlearning consolidation of birdsong: stabilizing effects of age and anterior forebrain lesions. *J. Neurosci.* **21**, 2501-2517.
- Brainard, M. S. and Doupe, A. J. (2002). What songbirds teach us about learning. *Nature* **417**, 351-358.
- Brenowitz, E. A. (2004). Plasticity of the adult avian song control system. *Ann. N. Y. Acad. Sci.* **1016**, 560-585.
- Byers, B. E. (1995). Song types, repertoires and song variability in a population of chestnut-sided warblers. *Condor* **97**, 390-401.
- Byers, B. E. (2007). Extrapair paternity in chestnut-sided warblers is correlated with consistent vocal performance. *Behav. Ecol.* **18**, 130-136.
- Byers, B. E. and Kroodsma, D. E. (2009). Female mate choice and songbird song repertoires. *Anim. Behav.* **77**, 13-22.
- Byers, J., Hebets, E. and Podos, J. (2010). Female choice based upon male motor performance. *Anim. Behav.* **79**, 771-778.
- Cardoso, G. C. and Mota, P. G. (2007). Song diversification and complexity in canaries and seedeaters (*Serinus* spp.). *Biol. J. Linn. Soc.* **92**, 183-194.
- Catchpole, C. K. and Slater, P. J. B. (2008). *Bird song: Biological Themes and Variations*. Cambridge, UK: Cambridge University Press.
- Charlesworth, J. D., Turner, E. C., Warren, T. L. and Brainard, M. S. (2011). Learning the microstructure of successful behavior. *Nat. Neurosci.* **14**, 373-380.
- Christie, P. J., Mennill, D. J. and Ratcliffe, L. M. (2004). Pitch shifts and song structure indicate male quality in the dawn chorus of black-capped chickadees. *Behav. Ecol. Sociobiol.* **55**, 341-348.
- Clark, C. W., Marler, P. and Beeman, K. (1987). Quantitative analysis of animal vocal phonology: an application to swamp sparrow song. *Ethology* **76**, 101-115.
- Cramer, E. R. A., Hall, M. L., de Kort, S. R., Lovette, I. J. and Vehrencamp, S. L. (2011). Infrequent extra-pair paternity in banded wrens, synchronously-breeding tropical passerines. *Condor* **113**, 637-645.
- de Kort, S. R. and ten Cate, C. (2004). Repeated decrease in vocal repertoire size in *Stertopelia* doves. *Anim. Behav.* **67**, 549-557.
- de Kort, S. R., Eldermire, E. R., Valderama, S., Botero, C. A. and Vehrencamp, S. L. (2009). Trill consistency is an age-related assessment signal in banded wrens. *Proc. R. Soc. Lond. B* **276**, 2315-2321.
- Doupe, A. J. and Kuhl, P. K. (1999). Birdsong and human speech: common themes and mechanisms. *Ann. Rev. Neurosci.* **22**, 567-631.
- Doupe, A. J., Perkel, D. J., Reiner, A. and Stern, E. A. (2005). Birdbrains could teach basal ganglia research a new song. *Trends Neurosci.* **28**, 353-363.
- Doya, K. and Sejnowski, T. J. (1998). A computational model of birdsong learning by auditory experience and auditory feedback. In *Central Auditory Processing and Neural Modeling* (ed. J. F. Poon), pp. 77-88. New York: Plenum.
- Fee, M. S., Kozhevnikov, A. A. and Hahnloser, R. H. (2004). Neural mechanisms of vocal sequence generation in the songbird. *Ann. N. Y. Acad. Sci.* **1016**, 153-170.
- Feenders, G., Liedvogel, M., Rivas, M., Zapka, M., Horita, H., Hara, E., Wada, K., Mouritsen, H. and Jarvis, E. D. (2008). Molecular mapping of movement-associated areas in the avian brain: a motor theory for vocal learning origin. *PLoS ONE* **3**, e1768.
- Gil, D. and Gahr, M. (2002). The honesty of bird song: multiple constraints for multiple traits. *Trends Ecol. Evol.* **17**, 133-141.
- Goldstein, M. H. and Schwade, J. A. (2010). From birds to words: perception of structure in social interactions guides vocal development and language learning. In *Oxford Handbook of Developmental Behavioral Neuroscience* (ed. M. S. Blumberg, J. H. Freeman and S. R. Robinson), pp. 708-729. New York: Oxford University Press.
- Graybiel, A. M. (2005). The basal ganglia: learning new tricks and loving it. *Curr. Opin. Neurobiol.* **15**, 638-644.
- Hahnloser, R. H., Kozhevnikov, A. A. and Fee, M. S. (2002). An ultra-sparse code underlies the generation of neural sequences in a songbird. *Nature* **419**, 65-70.
- Halle, F., Gahr, M. and Kreutzer, M. (2003). Effects of unilateral lesions of HVC on song patterns of male domesticated canaries. *J. Neurobiol.* **56**, 303-314.
- Hampton, C. M., Sakata, J. T. and Brainard, M. S. (2009). An avian basal ganglia-forebrain circuit contributes differentially to syllable versus sequence variability of adult Bengalese finch song. *J. Neurophysiol.* **101**, 3235-3245.
- Hauser, M. D. (1996). *The Evolution of Communication*. Cambridge: MIT Press.
- Hegyi, G., Rosvall, B. and Torok, J. (2006). Paternal age and offspring growth: separating the intrinsic quality of young from rearing effects. *Behav. Ecol. Sociobiol.* **60**, 672-682.
- Hessler, N. A. and Doupe, A. J. (1999). Social context modulates singing-related neural activity in the songbird forebrain. *Nat. Neurosci.* **2**, 209-211.
- Hoeschele, M., Moscicki, M. K., Otter, K. A., van Oort, H., Fort, K. T., Farrell, T. M., Homan, L., Robson, S. W. J. and Sturdy, C. B. (2010). Dominance signalled in an acoustic ornament. *Anim. Behav.* **79**, 657-664.
- Holveck, M.-J., de Castro, A. C. V., Lachlan, R. F., ten Cate, C. and Riebel, K. (2008). Accuracy of song syntax learning and singing consistency signal early condition in zebra finches. *Behav. Ecol.* **19**, 1267-1281.
- Horita, H., Wada, K. and Jarvis, E. D. (2008). Early onset of deafening-induced song deterioration and differential requirements of the pallidum-basal ganglia vocal pathway. *Eur. J. Neurosci.* **28**, 2519-2532.
- Hyman, J., Hughes, M., Searcy, W. A. and Nowicki, S. (2004). Individual variation in the strength of territory defense in male song sparrows: correlates of age, territory tenure, and neighbor aggressiveness. *Behaviour* **141**, 15-27.
- Irwin, R. E. (1990). Directional sexual selection cannot explain variation in song repertoire size in the new-world blackbirds (*Icterinae*). *Ethology* **85**, 212-224.
- Jarvis, E. D., Scharff, C., Grossman, M. R., Ramos, J. A. and Nottebohm, F. (1998). For whom the bird sings: context-dependent gene expression. *Neuron* **21**, 775-788.
- Kao, M. H. and Brainard, M. S. (2006). Lesions of an avian basal ganglia circuit prevent context-dependent changes to song variability. *J. Neurophysiol.* **96**, 1441-1455.
- Kao, M. H., Doupe, A. J. and Brainard, M. S. (2005). Contributions of an avian basal ganglia-forebrain circuit to real-time modulation of song. *Nature* **433**, 638-643.
- Kao, M. H., Wright, B. D. and Doupe, A. J. (2008). Neurons in a forebrain nucleus required for vocal plasticity rapidly switch between precise firing and variable bursting depending on social context. *J. Neurosci.* **28**, 13232-13247.
- King, A. P., West, M. J. and Goldstein, M. H. (2005). Non-vocal shaping of avian song development: parallels to human speech development. *Ethology* **111**, 101-117.
- Kobayashi, K. I. and Okanoya, K. (2003). Context-dependent song amplitude control in Bengalese finches. *Neuroreport* **14**, 521-524.
- Konishi, M. (1965). The role of auditory feedback in the control of vocalization in the white-crowned sparrow. *Z. Tierpsychol.* **22**, 770-783.
- Konishi, M. (2004). The role of auditory feedback in birdsong. *Ann. N. Y. Acad. Sci.* **1016**, 463-475.
- Korsia, S. and Bottjer, S. W. (1991). Chronic testosterone treatment impairs vocal learning in male zebra finches during a restricted period of development. *J. Neurosci.* **11**, 2362-2371.
- Kroodsma, D. E., Liu, W. C., Goodwin, E. and Bedell, P. A. (1999). The ecology of song improvisation as illustrated by North American sedge wrens. *Auk* **116**, 373-386.
- Lambrechts, M. and Dhondt, A. A. (1986). Male quality, reproduction, and survival in the great tit (*Parus major*). *Behav. Ecol. Sociobiol.* **19**, 57-63.
- Lambrechts, M. and Dhondt, A. A. (1988). The anti-exhaustion hypothesis: a new hypothesis to explain song performance and song switching in the great tit. *Anim. Behav.* **36**, 327-334.
- Leblois, A., Wendel, B. J. and Perkel, D. J. (2010). Striatal dopamine modulates basal ganglia output and regulates social context-dependent behavioral variability through D1 receptors. *J. Neurosci.* **30**, 5730-5743.
- Leonardo, A. and Fee, M. S. (2005). Ensemble coding of vocal control in birdsong. *J. Neurosci.* **25**, 652-661.
- Leonardo, A. and Konishi, M. (1999). Decrystallization of adult birdsong by perturbation of auditory feedback. *Nature* **399**, 466-470.
- Liu, W. C. and Nottebohm, F. (2005). Variable rate of singing and variable song duration are associated with high immediate early gene expression in two anterior forebrain song nuclei. *Proc. Natl. Acad. Sci. USA* **102**, 10724-10729.
- Liu, W. C. and Nottebohm, F. (2007). A learning program that ensures prompt and versatile vocal imitation. *Proc. Natl. Acad. Sci. USA* **104**, 20398-20403.
- Livingston, F. S. and Mooney, R. (2001). Androgens and isolation from adult tutors differentially affect the development of songbird neurons critical to vocal plasticity. *J. Neurophysiol.* **85**, 34-42.
- Long, M. A., Jin, D. Z. and Fee, M. S. (2010). Support for a synaptic chain model of neuronal sequence generation. *Nature* **468**, 394-399.
- MacDougall-Shackleton, S. A. (2011). The levels of analysis revisited. *Philos. Trans. R. Soc. Lond. B* **366**, 2076-2085.
- Margoliash, D., Staicer, C. A. and Inoue, S. A. (1991). Stereotyped and plastic song in adult indigo buntings, *Passerina cyanea*. *Anim. Behav.* **42**, 367-388.



- Marler, P. (1997). Three models of song learning: evidence from behavior. *J. Neurobiol.* **33**, 501-516.
- Marler, P. and Peters, S. (1982). Structural changes in song ontogeny in the swamp sparrow, *Melospiza georgiana*. *Auk* **99**, 446-458.
- Marler, P., Peters, S., Ball, G. F., Dufty, A. M., Jr and Wingfield, J. C. (1988). The role of sex steroids in the acquisition and production of birdsong. *Nature* **336**, 770-772.
- McCasland, J. S. (1987). Neuronal control of bird song production. *J. Neurosci.* **7**, 23-39.
- Meitzen, J., Moore, I. T., Lent, K., Brenowitz, E. A. and Perkel, D. J. (2007a). Steroid hormones act transsynaptically within the forebrain to regulate neuronal phenotype and song stereotypy. *J. Neurosci.* **27**, 12045-12057.
- Meitzen, J., Perkel, D. J. and Brenowitz, E. A. (2007b). Seasonal changes in intrinsic electrophysiological activity of song control neurons in wild song sparrows. *J. Comp. Physiol. A* **193**, 677-683.
- Meitzen, J., Thompson, C. K., Choi, H., Perkel, D. J. and Brenowitz, E. A. (2009a). Time course of changes in Gambel's white-crowned sparrow song behavior following transitions in breeding condition. *Horm. Behav.* **55**, 217-227.
- Meitzen, J., Weaver, A. L., Brenowitz, E. A. and Perkel, D. J. (2009b). Plastic and stable electrophysiological properties of adult avian forebrain song-control neurons across changing breeding conditions. *J. Neurosci.* **29**, 6558-6567.
- Mooney, R. (2009). Neurobiology of song learning. *Curr. Opin. Neurobiol.* **19**, 654-660.
- Nordeen, K. W. and Nordeen, E. J. (1992). Auditory feedback is necessary for the maintenance of stereotyped song in adult zebra finches. *Behav. Neural Biol.* **57**, 58-66.
- Nottebohm, F. and Liu, W. C. (2010). The origins of vocal learning: new sounds, new circuits, new cells. *Brain Lang.* **115**, 3-17.
- Nottebohm, F., Stokes, T. M. and Leonard, C. M. (1976). Central control of song in the canary, *Serinus canarius*. *J. Comp. Neurol.* **165**, 457-486.
- Nottebohm, F., Nottebohm, M. E. and Crane, L. (1986). Developmental and seasonal changes in canary song and their relation to changes in the anatomy of song-control nuclei. *Behav. Neural Biol.* **46**, 445-471.
- Nowicki, S. and Searcy, W. A. (2004). Song function and the evolution of female preferences: why birds sing, why brains matter. *Ann. N. Y. Acad. Sci.* **1016**, 704-723.
- Oberweger, K. and Goller, F. (2001). The metabolic cost of birdsong production. *J. Exp. Biol.* **204**, 3379-3388.
- Okanoya, K. and Yamaguchi, A. (1997). Adult Bengalese finches (*Lonchura striata* var. *domestica*) require real-time auditory feedback to produce normal song syntax. *J. Neurobiol.* **33**, 343-356.
- Ölveczky, B. P., Andalman, A. S. and Fee, M. S. (2005). Vocal experimentation in the juvenile songbird requires a basal ganglia circuit. *PLoS Biol.* **3**, e153.
- Ölveczky, B. P., Otchy, T. M., Goldberg, J. H., Aronov, D. and Fee, M. S. (2011). Changes in the neural control of a complex motor sequence during learning. *J. Neurophysiol.* **106**, 386-397.
- Park, K. H., Meitzen, J., Moore, I. T., Brenowitz, E. A. and Perkel, D. J. (2005). Seasonal-like plasticity of spontaneous firing rate in a songbird pre-motor nucleus. *J. Neurobiol.* **64**, 181-191.
- Podos, J. (1997). A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution* **51**, 537-551.
- Podos, J., Sherer, J. K., Peters, S. and Nowicki, S. (1995). Ontogeny of vocal tract movements during song production in song sparrows. *Anim. Behav.* **50**, 1287-1296.
- Podos, J., Lahti, D. C. and Moseley, D. L. (2009). Vocal performance and sensorimotor learning in songbirds. *Adv. Study Behav.* **40**, 159-195.
- Prather, J. F., Peters, S., Nowicki, S. and Mooney, R. (2008). Precise auditory-vocal mirroring in neurons for learned vocal communication. *Nature* **451**, 305-310.
- Price, J. J. and Lanyon, S. M. (2004). Patterns of song evolution and sexual selection in the oropendolas and cacias. *Behav. Ecol.* **15**, 485-497.
- Price, J. J., Friedman, N. R. and Omland, K. E. (2007). Song and plumage evolution in the new world orioles (*Icterus*) show similar lability and convergence in patterns. *Evolution* **61**, 850-863.
- Pytte, C. L., Gerson, M., Miller, J. and Kirn, J. R. (2007). Increasing stereotypy in adult zebra finch song correlates with a declining rate of adult neurogenesis. *Dev. Neurobiol.* **67**, 1699-1720.
- Reiner, A., Perkel, D. J., Mello, C. V. and Jarvis, E. D. (2004). Songbirds and the revised avian brain nomenclature. *Ann. N. Y. Acad. Sci.* **1016**, 77-108.
- Rivera-Gutierrez, H. F., Pinxten, R. and Eens, M. (2010). Multiple signals for multiple messages: great tit, *Parus major*, song signals age and survival. *Anim. Behav.* **80**, 451-459.
- Rivera-Gutierrez, H. F., Pinxten, R. and Eens, M. (2011). Songs differing in consistency elicit differential aggressive response in territorial birds. *Biol. Lett.* **7**, 339-342.
- Sakata, J. T. and Brainard, M. S. (2006). Real-time contributions of auditory feedback to avian vocal motor control. *J. Neurosci.* **26**, 9619-9628.
- Sakata, J. T. and Brainard, M. S. (2008). Online contributions of auditory feedback to neural activity in avian song control circuitry. *J. Neurosci.* **28**, 11378-11390.
- Sakata, J. T. and Brainard, M. S. (2009). Social context rapidly modulates the influence of auditory feedback on avian vocal motor control. *J. Neurophysiol.* **102**, 2485-2497.
- Sakata, J. T., Hampton, C. M. and Brainard, M. S. (2008). Social modulation of sequence and syllable variability in adult birdsong. *J. Neurophysiol.* **99**, 1700-1711.
- Scharff, C. and Nottebohm, F. (1991). A comparative study of the behavioral deficits following lesions of various parts of the zebra finch song system: implications for vocal learning. *J. Neurosci.* **11**, 2896-2913.
- Schmidt, M. F. (2003). Pattern of interhemispheric synchronization in HVC during singing correlates with key transitions in the song pattern. *J. Neurophysiol.* **90**, 3931-3949.
- Searcy, W. A. and Yasukawa, K. (1996). Song and female choice. In *Ecology and Evolution of Acoustic Communication in Birds* (ed. D. E. Kroodsma and E. H. Miller), pp. 454-473. Ithaca, New York: Cornell University Press.
- Slabbekoorn, H. and Ripmeester, E. A. (2008). Birdsong and anthropogenic noise: implications and applications for conservation. *Mol. Ecol.* **17**, 72-83.
- Smith, G. T., Brenowitz, E. A., Wingfield, J. C. and Baptista, L. F. (1995). Seasonal changes in song nuclei and song behavior in Gambel's white-crowned sparrows. *J. Neurobiol.* **28**, 114-125.
- Smith, G. T., Brenowitz, E. A., Beecher, M. D. and Wingfield, J. C. (1997). Seasonal plasticity in testosterone, neural attributes of song control nuclei, and song structure in wild songbirds. *J. Neurosci.* **17**, 6001-6010.
- Sober, S. J. and Brainard, M. S. (2009). Adult birdsong is actively maintained by error correction. *Nat. Neurosci.* **12**, 927-931.
- Sober, S. J., Wohlgemuth, M. J. and Brainard, M. S. (2008). Central contributions to acoustic variation in birdsong. *J. Neurosci.* **28**, 10370-10390.
- Sohrabji, F., Nordeen, E. J. and Nordeen, K. W. (1990). Selective impairment of song learning following lesions of a forebrain nucleus in the juvenile zebra finch. *Behav. Neural Biol.* **53**, 51-63.
- Stepanek, L. and Doupe, A. J. (2010). Activity in a cortical-basal ganglia circuit for song is required for social context-dependent vocal variability. *J. Neurophysiol.* **104**, 2474-2486.
- Suthers, R. A. and Zollinger, S. A. (2008). From brain to song: the vocal organ and vocal tract. In *Neuroscience of Birdsong* (ed. H. P. Zeigler and P. Marler), pp. 78-98. Cambridge: Cambridge University Press.
- Suthers, R. A., Vallet, E., Tanvez, A. and Kreutzer, M. (2004). Bilateral song production in domestic canaries. *J. Neurobiol.* **60**, 381-393.
- Sutton, R. S. and Barto, A. G. (1998). *Reinforcement Learning: an Introduction*. Cambridge, MA: MIT Press.
- Tchernichovski, O., Mitra, P. P., Lints, T. and Nottebohm, F. (2001). Dynamics of the vocal imitation process: how a zebra finch learns its song. *Science* **291**, 2564-2569.
- Teramitsu, I. and White, S. A. (2006). FoxP2 regulation during undirected singing in adult songbirds. *J. Neurosci.* **26**, 7390-7394.
- Tinbergen, N. (1951). *The Study of Instinct*. Oxford: Clarendon Press.
- Tokarev, K., Tiunova, A., Scharff, C. and Anokhin, D. (2011). Food for song: expression of C-fox and ZENK in the zebra finch song nuclei during food aversion learning. *PLoS ONE* **6**, e21157.
- Troyer, T. W. and Doupe, A. J. (2000). An associational model of birdsong sensorimotor learning I. Efference copy and the learning of song syllables. *J. Neurophysiol.* **84**, 1204-1223.
- Tumer, E. C. and Brainard, M. S. (2007). Performance variability enables adaptive plasticity of 'crystallized' adult birdsong. *Nature* **450**, 1240-1245.
- Vallet, E. and Kreutzer, M. (1995). Female canaries are sexually responsive to special song phrases. *Anim. Behav.* **49**, 1603-1610.
- Vehrencamp, S. L., Hall, M. L., Bohman, E. R., Depeine, C. D. and Dalziel, A. H. (2007). Song matching, overlapping, and switching in the banded wren: the sender's perspective. *Behav. Ecol.* **18**, 849-859.
- Vu, E. T., Mazurek, M. E. and Kuo, Y. C. (1994). Identification of a forebrain motor programming network for the learned song of zebra finches. *J. Neurosci.* **14**, 6924-6934.
- Vu, E. T., Schmidt, M. F. and Mazurek, M. E. (1998). Interhemispheric coordination of premotor neural activity during singing in adult zebra finches. *J. Neurosci.* **18**, 9088-9098.
- Wang, C. Z., Herbst, J. A., Keller, G. B. and Hahnloser, R. H. (2008). Rapid interhemispheric switching during vocal production in a songbird. *PLoS Biol.* **6**, e250.
- Ward, S. and Slater, P. J. (2005). Heat transfer and the energetic cost of singing by canaries *Serinus canaria*. *J. Comp. Physiol. A* **191**, 953-964.
- Warren, T. L., Tumer, E. C., Charlesworth, J. D. and Brainard, M. S. (2011). Mechanisms and time course of vocal learning and consolidation in the adult songbird. *J. Neurophysiol.* **106**, 1806-1821.
- Wegrzyn, E., Leniowski, K. and Osiejuk, T. S. (2010). Whistle duration and consistency reflect philopatry and harem size in great reed warblers. *Anim. Behav.* **79**, 1363-1392.
- West, M. J. and King, A. P. (1988). Female visual displays affect the development of male song in the cowbird. *Nature* **334**, 244-246.
- White, S. A., Livingston, F. S. and Mooney, R. (1999). Androgens modulate NMDA receptor-mediated EPSCs in the zebra finch song system. *J. Neurophysiol.* **82**, 2221-2234.
- Wild, J. M. (2008). Birdsong: anatomical foundations and central mechanisms of sensorimotor integration. In *Neuroscience of Birdsong* (ed. H. P. Zeigler and P. Marler), pp. 136-151. Cambridge: Cambridge University Press.
- Wiley, R. H. (2000). A new sense of the complexities of bird song. *Auk* **117**, 861-868.
- Williams, H., Crane, L. A., Hale, T. K., Esposito, M. M. and Nottebohm, F. (1992). Right-side dominance for song control in the zebra finch. *J. Neurobiol.* **23**, 1006-1020.
- Wohlgemuth, M. J., Sober, S. J. and Brainard, M. S. (2010). Linked control of syllable sequence and phonology in birdsong. *J. Neurosci.* **30**, 12936-12949.
- Woolley, S. C. and Doupe, A. J. (2008). Social context-induced song variation affects female behavior and gene expression. *PLoS Biol.* **6**, e62.
- Woolley, S. M. and Rubel, E. W. (1997). Bengalese finches *Lonchura striata domestica* depend upon auditory feedback for the maintenance of adult song. *J. Neurosci.* **17**, 6380-6390.
- Yu, A. C. and Margoliash, D. (1996). Temporal hierarchical control of singing in birds. *Science* **273**, 1871-1875.
- Zollinger, S. A., Riede, T. and Suthers, R. A. (2008). Two-voice complexity from a single side of the syrinx in northern mockingbird *Mimus polyglottos* vocalizations. *J. Exp. Biol.* **211**, 1978-1991.