

## REVIEW

# VARIATIONS ON A THEME: SONGBIRDS, VARIABILITY, AND SENSORIMOTOR ERROR CORRECTION

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**Abstract**—Songbirds provide a powerful animal model for investigating how the brain uses sensory feedback to correct behavioral errors. Here, we review a recent study in which we used online manipulations of auditory feedback to quantify the relationship between sensory error size, motor variability, and vocal plasticity. We found that although inducing small auditory errors evoked relatively large compensatory changes in behavior, as error size increased the magnitude of error correction declined. Furthermore, when we induced large errors such that auditory signals no longer overlapped with the baseline distribution of feedback, the magnitude of error correction approached zero. This pattern suggests a simple and robust strategy for the brain to maintain the accuracy of learned behaviors by evaluating sensory signals relative to the previously experienced distribution of feedback. Drawing from recent studies of auditory neurophysiology and song discrimination, we then speculate as to the mechanistic underpinnings of the results obtained in our behavioral experiments. Finally, we review how our own and other studies exploit the strengths of the songbird system, both in the specific context of vocal systems and more generally as a model of the neural control of complex behavior.

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**Key words:** songbird, vocal control, sensorimotor learning, variability, sensory feedback, animal models.

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## INTRODUCTION

In learned behaviors, the brain uses sensory feedback to detect and correct errors in motor output. To do so, the nervous system must solve a challenging problem: on the one hand, the brain must rely on sensory feedback to correct motor errors; on the other hand, sensory feedback is inherently unreliable, as signals can be contaminated by environmental noise and errors in peripheral or central processing. Studies of multisensory integration and motor planning have shown that the brain can rapidly alter its reliance on different sensory streams based on their statistical properties (Ernst and Banks, 2002; Sober and Sabes, 2005; Faisal et al., 2008). In the context of sensorimotor learning, a common approach to measuring the use of sensory feedback is to perturb signals to a single sensory modality and quantify the resulting change in behavior.

## PROBING SENSORIMOTOR LEARNING IN SONGBIRDS

In a recent study (Sober and Brainard, 2012), we quantified the brain's reliance on sensory information during vocal behavior by using real-time manipulations of auditory feedback in the Bengalese finch, a songbird. Auditory feedback is critical to the initial acquisition of vocal behavior in both songbirds and humans and is used throughout life to correct errors in vocal performance (Houde and Jordan, 1998; Doupe and Kuhl, 1999; Jones and Munhall, 2000; Sober and Brainard, 2009). However, the computations underlying the use of auditory signals in vocal error correction are poorly understood. We

therefore sought to quantify the relationship between two crucial parameters: the magnitude of the sensory feedback error and the magnitude of compensatory motor correction.

### Manipulating auditory feedback in behaving animals

To perform this study, we took advantage of a new technique that uses lightweight headphones to introduce arbitrary errors to a songbird's auditory feedback in real time (Hoffmann et al., 2012). As shown in Fig. 1a, as the bird sang, sound-processing hardware was used to manipulate the acoustic signal, which was then played through speakers inside the headphones with a total processing delay of < 10 ms. We used this technique to alter the bird's experience of its own song's fundamental frequency (which we refer to here as "pitch"). Since the headphones greatly attenuate external sounds, they effectively replace the bird's normal auditory feedback with the pitch-shifted version.

Pitch-shifting auditory feedback evokes a compensatory change in the pitch of vocal output, as shown in Fig. 1b. Here, a 0.5-semitone downward shift in auditory feedback pitch evokes an upward change in sung vocal pitch (Fig. 1b, red). Because pitch shifts were performed relative to the current vocal output, the difference between sung and heard pitches (Fig. 1b, red and black, respectively) was constant despite vocal compensation. Therefore, when the bird changed its song's vocal pitch in the opposite direction of the imposed pitch shift, the bird received auditory feedback more similar to its baseline song. Over 14 days of pitch-shift exposure, we quantified the extent of error correction to the modified auditory feedback (Sober and Brainard, 2012). For example, by the end of the pitch-shift epoch, the example subject shown in Fig. 1b had corrected approximately 80% of the experimentally imposed sensory error. Importantly, this incomplete adaptation does not reflect a biomechanical constraint of vocal production, since multiple studies show behavioral training can produce pitch changes of 1.0 semitone or greater (Tumer and Brainard, 2007; Sober and Brainard, 2009). Furthermore, in manipulations of sensory feedback, incomplete adaptation is a common observation across

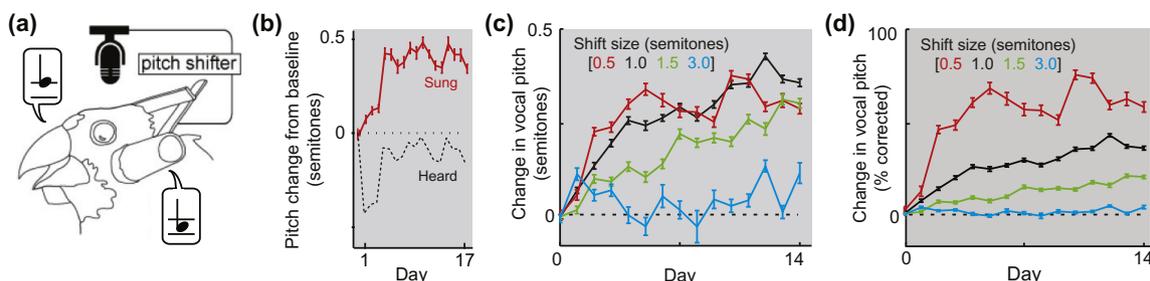
species and systems, perhaps reflecting the influence of conflicting feedback from un-manipulated sensory modalities (Choe and Welch, 1974; Houde and Jordan, 1998).

### Inverse relationship between error size and error correction

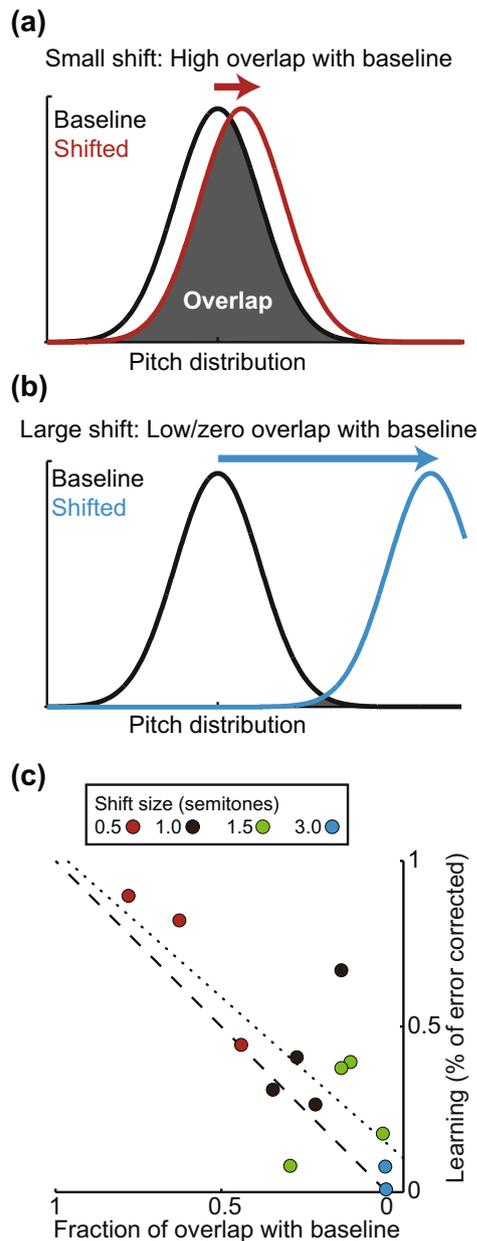
To examine the relationship between sensory error input and motor learning output, we systematically varied the magnitude of the imposed pitch shift. We found an inverse relationship between sensory error size and vocal error correction. Fig. 1c shows group data from the four error sizes examined (0.5, 1.0, 1.5, and 3.0 semitones) and Fig. 1d illustrates that as the size of the sensory error increases, the percentage of the error corrected by changes in vocal output decreases. For example, 0.5-semitone pitch shifts evoked an average adaptive pitch change of approximately 0.3 semitones (Fig. 1c, red) and therefore induced the animal to correct roughly 60% of the imposed sensory error (Fig. 1d, red). In contrast, larger 3.0-semitone shifts led to near-zero changes in vocal output (Fig. 1c, d, blue). This inverse relationship between error size and sensorimotor learning echoes similar findings in studies of arm and eye movements (Robinson et al., 2003; Fine and Thoroughman, 2007; Wei and Kording, 2009; Marko et al., 2012), suggesting that limiting learning in response to large errors is a general principle of sensorimotor control.

### Constraining learning based on prior feedback

Further analysis suggested that the percentage of vocal error correction is limited based on the distribution of prior sensorimotor experience. Even in adult birds with stable songs, the pitch of a given vocal gesture (or "song syllable") varies across renditions. A bird's baseline pitch variability can therefore be characterized as a probability distribution such as those shown by black curves in Fig. 2a, b. Our feedback perturbation shifts the heard pitch distribution relative to the previously experienced baseline distribution (Fig. 2a; red and black curves, respectively). For small pitch shifts,



**Fig. 1.** Vocal error correction in adult songbirds. (a) Miniature headphones were used to manipulate auditory feedback online. (b) Vocal error correction. In this representative experiment the pitch of auditory feedback was shifted downward by 0.5 semitones for 17 days (gray box indicates time when shift was applied). This manipulation resulted in an adaptive upward change in vocal pitch (red line), which brought the pitch of song heard through the headphones (dashed line) nearly back to its baseline value. (c) Relationship between auditory error size and vocal learning quantified in semitones. (d) Relationship between auditory error size and vocal learning quantified as percentage of the sensory error compensated. As the size of the imposed pitch shift increased from 0.5 to 3.0 semitones, the percentage of vocal error correction decreased. Figure modified from Sober and Brainard (2012). Illustration in (a) by David Nicholson.



**Fig. 2.** The overlap between prior and experienced sensory feedback predicts the extent of vocal error correction. Schematics in (a) and (b) show the baseline probability distributions of vocal pitches (black) and the distributions after smaller (red) and larger (blue) pitch shifts. Smaller shifts result in a relatively high level of overlap between these distributions (gray shaded region); larger shifts result in little overlap. (c) Relationship between sensory overlap (see text) and the percentage of the auditory error corrected during online pitch shifts. Each symbol represents a separate experiment, with colors indicating the pitch shift magnitude in each experiment. The dotted line indicates a significant ( $p < 0.01$ ) regression and the dashed line represents unity. Figure adapted from Sober and Brainard (2012).

the shifted and baseline distributions have a high degree of overlap (Fig. 2a, gray area), but for larger shifts the amount of overlap approaches zero (Fig. 2b). Crucially, when we compared the fraction of overlap between the shifted and baseline distributions to the percentage of vocal error correction, we found that error correction

disappears as overlap approaches zero (Fig. 2c). Our study therefore not only demonstrates an inverse relationship between sensory error size and the extent of error correction but also suggests that an animal's reliance on auditory feedback is constrained by its prior experience of its own behavior.

Limiting error correction based on where sensory feedback falls relative to the distribution of previously experienced feedback represents a simple and robust sensorimotor strategy. Our results suggest that learning is constrained by the probability that a sensory signal could have come from the bird's prior distribution (in the Bayesian sense). Such a model predicts that sensory signals unlikely to have arisen from the prior distribution of feedback, such as those from large pitch shifts, should drive a smaller amount of motor adaptation than the more probable feedback from smaller pitch shifts. This approach has several advantages. First, it uses the statistics of a bird's own sensorimotor experience to compute how much to alter the motor program, rather than requiring the brain to perform an explicit calculation of error relevance or compute an internal model of sensory noise (Fine and Thoroughman, 2007; Wei and Kording, 2009). Second, constraining learning based on prior experience scales error correction with the variability of a behavior. That is, when a behavior is highly variable – as is the case when young songbirds and humans first vocalize – the larger errors fall within the wider baseline distribution and are corrected. Conversely, as the precision of a behavior increases, the baseline distribution narrows, and the propensity to correct large errors decreases. Third, by constraining error correction to the expected distribution of sensory feedback, the brain could optimize its error threshold. If errors are detected in too few renditions, then learning will proceed too slowly. Similarly, coding almost all renditions as errors gives little information about performance. By scaling error detection with expected feedback, the brain could calibrate the threshold for error detection so as to maximize learning.

### Potential neural substrates of error processing

By showing that error correction is limited by the distribution of prior experience, our study suggests a link between the variability of previous sensory feedback and the neural processing of new sensory information. Work from a number of research groups has yielded a detailed picture of the neural responses to auditory stimuli in field L, a forebrain primary auditory area (Nagel and Doupe, 2006; Boumans et al., 2007; Hauber et al., 2007; Grana et al., 2009; Kim and Doupe, 2011). In field L a subset of neurons is highly tuned to acoustic frequency (Nagel and Doupe, 2008). Intriguingly, these auditory neurons are tuned to a range of frequencies that closely approximates the width of the baseline distribution of pitches produced for a given syllable. Therefore, as suggested previously by Nagel et al. (2010), pitch-shifting auditory feedback outside the baseline distribution of motor variability may activate a population of field L neurons largely separate from the population activated by un-shifted feedback. The tuning of neurons in field L suggests two potential models (which are not mutually

exclusive) for how auditory processing might determine the patterns of sensorimotor adaptation shown in Fig. 2. In the first model, large pitch shifts fail to evoke learning because they stimulate a different population of auditory neurons in field L. In the second model, large shifts impair learning by disrupting the integration between auditory inputs and signals related to motor production.

*Model 1: Adaptation depends on sensory response patterns.* Our first model proposes that vocal adaptation depends strongly on the subpopulation of field L neurons activated by auditory feedback. For simplicity, we discuss this subpopulation as if it were a static subset of auditory neurons. More realistically, each syllable will activate a different subpopulation, resulting in a dynamic pattern of activity over the course of a song, but the same principles apply.

A previous behavioral study demonstrated that female songbirds' ability to discriminate between the songs of two males fell to chance once the songs were pitch-shifted outside of the baseline range of variation (Nagel et al., 2010). The study's authors proposed that sensory representations of each song might be encoded in the subpopulation of neurons activated by that song. Shifting a song's pitch enough so that it activates a largely separate population of field L neurons, they reason, would cause the bird to treat the shifted song as a different song, and discrimination performance would therefore fall to chance, as observed in their data.

Based on the idea that a song is represented by the population of auditory neurons it activates, we speculate that the subpopulations activated by auditory feedback also play a critical role in determining the extent of vocal adaptation. Small pitch shifts (i.e. those that keep auditory feedback within the baseline pitch distribution) likely stimulate a population of auditory neurons nearly identical to that activated when the bird sings in the absence of a pitch shift. However, although the population of active neurons may be similar to that activated by un-shifted feedback, smaller sensory errors could be encoded by differences in the firing rate or spike timing within this population or subtle differences in the population of neurons activated by shifted feedback. The pattern of activity evoked by small pitch shifts might therefore be similar enough to previously experienced sensory patterns that downstream areas interpret it as arising from the bird's own song (rather than, say, that of another animal) but different enough to evoke adaptive motor changes. In contrast, large shifts that push feedback outside the baseline pitch distribution might activate a largely separate population of field L neurons, creating a pattern of auditory activity that has never occurred due to sensory feedback of the bird's own song. Downstream areas might therefore be unable to interpret this new activity pattern, preventing error detection or vocal adaptation.

*Model 2: Adaptation depends on integration of sensory and motor-related signals.* Our second model proposes that large pitch shifts might fail to evoke adaptation because they disrupt interactions between auditory- and

vocalization-related inputs. The activity of some neurons in field L and a secondary auditory forebrain region, the caudal mesopallium (CM), appears to be modulated by inputs related to vocal motor production (as distinct from sensory feedback). During singing, the firing of many neurons in these areas is time-locked to song (Bauer et al., 2008; Keller and Hahnloser, 2009). In a subset of these neurons, this time-locked activity precedes the first sounds produced during vocalization, and additionally some neurons seem unresponsive to perturbed auditory feedback during vocalization, suggesting that field L and CM receive non-auditory, vocalization-related inputs (Keller and Hahnloser, 2009).

In our second model, adaptation relies on the integration between auditory- and vocalization-related signals in field L and CM. If neurons in these areas receive both auditory and motor-related input signals, then a large pitch shift would evoke auditory activity in a different population of neurons (as described in Model 1 above), while the population receiving vocalization-related signals would presumably stay the same. If error correction relies on the integration of sensory and vocal motor signals, then such a sensory-motor "misalignment" might prevent adaptation by interfering with the brain's ability to separate self-generated feedback from external acoustic noise, improve noisy auditory representations, or perform other computations necessary for learning (Wolpert et al., 1995; Troyer and Doupe, 2000; Keller and Hahnloser, 2009).

In summary, our empirical data indicate that motor learning is constrained by prior sensory feedback (Fig. 2), suggesting a flexible strategy that scales error correction with behavioral variability. Future studies will explore whether using sensory variability to constrain error correction might account for the dramatic changes in learning ability that take place over an animal's lifetime. Additionally, we suggest that such constraints may reflect how auditory (and possibly vocal motor-related) signals are processed in forebrain auditory networks. In the final sections of this review, we will take a broader view of the songbird system, first discussing the similarities between birdsong and human speech and then explaining why songbirds present an excellent model system in which to investigate general neural mechanisms of motor production and plasticity.

## WHY SONGBIRDS?

### Songbirds as an animal model of human vocal control and plasticity

Along with other studies of vocal learning in songbirds, our work exploits the strengths of our chosen model system to reveal how the brain uses auditory information to guide vocal learning. Songbirds provide the best and most widely used animal model for investigating how auditory feedback shapes vocal behavior. Vocal learning appears uncommon across the animal kingdom and has been documented in few mammalian species (Doupe and Kuhl, 1999; Brainard and Doupe, 2013), although many mammals have never been tested for vocal learning. The role of auditory

feedback in regulating vocal behavior is an open question in many non-avian species (Hammerschmidt et al., 2012; Arriaga and Jarvis, 2013; Mahrt et al., 2013), and studies of birdsong have guided the experimental questions and methodologies used in those investigations.

Beyond serving as a general model of vocal learning, songbirds provide insight into human vocal production and plasticity because of the similarities between song and speech at the behavioral and neural levels. Classic behavioral studies in songbirds and humans demonstrate that early auditory experience is crucial for the initial acquisition of vocal behavior (Konishi, 1965; Nottebohm, 1968; Ruben and Rapin, 1980), and more recent work has shown that both rely on auditory feedback throughout life to maintain proper production and correct vocal errors (Cowie et al., 1982; Waldstein, 1990; Nordeen and Nordeen, 1992; Okanoya and Yamaguchi, 1997; Woolley and Rubel, 1997). Although early studies of auditory feedback in songbirds focused on the effects of deafening, experimental perturbations have become increasingly sophisticated, allowing quantitative studies of the relationship between auditory information, the statistical structure of motor output, and learning (Andalman and Fee, 2009; Lei and Mooney, 2010; Charlesworth et al., 2011). Human studies of auditory feedback now also use manipulations such as pitch shifts. For example, parallel to our work linking vocal variability to error correction (Fig. 2), two recent human studies show that pitch variability in singing and speaking predicts the ability of human subjects to correct sensory errors induced by pitch shifts (Scheerer and Jones, 2012; Scheerer et al., 2013). These findings suggest that the adult maintenance of song and speech rests on common computational mechanisms, and because therapies that alter auditory feedback may provide treatments for disorders of speech production (Lincoln et al., 2006; Lowit et al., 2010), understanding how feedback drives learning may enhance clinical approaches to vocal rehabilitation.

Birdsong's usefulness as a model for human speech extends beyond its behavioral similarities, as the brain areas and muscles used for song production are analogous to human vocal control mechanisms. In both humans and songbirds, forebrain areas activate brainstem nuclei innervating vocal muscles and respiratory centers. Vocal muscles initiate sound production by moving flexible folds of connective tissue into the path of air flowing through the vocal tract, which causes them to vibrate. Vocal muscles can further regulate acoustic output by varying the tension of the folds (Titze, 1994; Goller and Suthers, 1996; Laje et al., 2002; Trevisan and Mindlin, 2009). Because of the similarities between human and songbird vocal production, chronic recordings and experimental manipulations in songbirds can be used to explore the underlying physiology of motor circuits and vocal muscles and to test hypotheses about central and peripheral control of human vocal production (Fee and Scharff, 2010; Riede and Goller, 2010).

In addition to providing insight into the mechanisms of vocal production, studies of songbirds may illuminate the

neural bases of human vocal learning and error correction. Although the muscular basis of human speech is relatively well understood (Fowler and Saltzman, 1993; Titze, 1993), due to the experimental limitations of studying the human brain the dynamics of neural circuits driving speech production and plasticity remain largely a mystery. In contrast, studies of songbirds using techniques such as brain lesions and neural recordings have yielded a detailed account of how vocal motor activity is organized in the forebrain, refined during development, and modulated by basal ganglia circuits (Leonardo and Fee, 2005; Wohlgenuth et al., 2010; Olveczky et al., 2011; Woolley and Kao, 2015). Additionally, our own studies have quantified how neurons in a motor cortex analog modulate the acoustic structure of individual song syllables (Sober et al., 2008; Tang et al., in press), suggesting a neurophysiological account of how the brain may change a syllable's pitch following manipulations of auditory feedback (Fig. 1). Therefore, although the speech and song systems are not identical, their functional and structural similarities allow us to use findings from songbirds to make predictions about the neural mechanisms that may control the production and plasticity of human speech.

### Songbirds as a general model for complex motor control

The usefulness of songbirds is by no means limited to questions of vocal control. Indeed, songbirds provide one of the best models to study how complex motor behaviors are influenced by sensory feedback. Compared to many behaviors used to investigate motor control, birdsong is produced prolifically and spontaneously, without any need for training by the experimenter. Indeed, the contributions made by songbird studies in part reflect the fact that different laboratories have combined a dizzying array of techniques – sensory perturbations, neural and electromyography (EMG) recordings, targeted lesions, hormone measurements, and genetic and pharmacological manipulations – to study a single behavior (Goller and Cooper, 2004; Remage-Healey et al., 2010; Brainard and Doupe, 2013; Clayton, 2013; Murugan et al., 2013). In contrast, studies of motor control in many other systems employ a variety of non-natural behavioral tasks, requiring extensive training regimens and complicating comparison of results across experiments and laboratories.

Besides being produced frequently and spontaneously, birdsong has statistical properties that make it ideal for investigating the control and modification of complex behavior. The rich acoustic structure of song allows us to study how neurons and muscles control and coordinate a range of behavioral parameters (such as pitch and sound amplitude) during the developmental acquisition of motor patterns and during adult learning (Deregnacourt et al., 2004; Tchernichovski et al., 2004; Tumer and Brainard, 2007; Hoffmann and Sober, 2014). Bengalese finch song also varies in syllable sequence, allowing the study of how the brain orders component gestures into complex

patterns (Fujimoto et al., 2011; Warren et al., 2012; Lipkind et al., 2013). In these respects, birdsong occupies a “sweet spot” for the study of neural and behavioral variability: song contains enough variation to allow the study of motor variability and probabilistically sequenced behavior yet is sufficiently stereotyped that a single motor pattern will be produced many times within a single experimental session.

Along these lines, the songbird’s greatest strength may be that it offers an experimentally accessible neural circuit in which to study the interplay between motor variability, sensory processing, and learning. Theories of reinforcement learning posit motor variability as a critical component in the learning process, suggesting that motor variation is used to explore and evaluate the space of possible motor commands (Barto et al., 1983; Doya and Sejnowski, 1998). In songbirds, the brain areas governing vocal learning and performance are anatomically segregated and highly specialized for song, and the same structures that actively introduce acoustic variability into birdsong are also required for vocal learning (Brainard and Doupe, 2000; Kao et al., 2005; Olveczky et al., 2005; Warren et al., 2011). Songbirds therefore provide a well-defined neural circuit in which to explore the role of centrally programmed motor variability, and studies combining computational, behavioral, and neurophysiological approaches will continue to yield insights into the neural basis of sensorimotor learning.

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## REFERENCES

- Andalman AS, Fee MS (2009) A basal ganglia-forebrain circuit in the songbird biases motor output to avoid vocal errors. *Proc Natl Acad Sci USA* 106:12518–12523.
- Arriaga G, Jarvis ED (2013) Mouse vocal communication system: are ultrasounds learned or innate? *Brain Lang* 124:96–116.
- Barto AG, Sutton RS, Anderson CW (1983) Neuronlike adaptive elements that can solve difficult learning control-problems. *IEEE Trans Syst Man Cybern* 13:834–846.
- Bauer EE, Coleman MJ, Roberts TF, Roy A, Prather JF, Mooney R (2008) A synaptic basis for auditory-vocal integration in the songbird. *J Neurosci* 28:1509–1522.
- Boumans T, Theunissen FE, Poirier C, Van Der Linden A (2007) Neural representation of spectral and temporal features of song in the auditory forebrain of zebra finches as revealed by functional MRI. *Eur J Neurosci* 26:2613–2626.
- Brainard MS, Doupe AJ (2000) Interruption of a basal ganglia-forebrain circuit prevents plasticity of learned vocalizations. *Nature* 404:762–766.
- Brainard MS, Doupe AJ (2013) Translating birdsong: songbirds as a model for basic and applied medical research. *Annu Rev Neurosci* 36:489–517.
- Charlesworth JD, Tumer EC, Warren TL, Brainard MS (2011) Learning the microstructure of successful behavior. *Nat Neurosci* 14:373–380.
- Choe CS, Welch RB (1974) Variables affecting intermanual transfer and decay of prism adaptation. *J Exp Psychol* 102:1076–1084.
- Clayton DF (2013) The genomics of memory and learning in songbirds. *Annu Rev Genomics Hum Genet* 14:45–65.
- Cowie R, Douglas-Cowie E, Kerr AG (1982) A study of speech deterioration in post-lingually deafened adults. *J Laryngol Otol* 96:101–112.
- Deregnacourt S, Mitra PP, Feher O, Maul KK, Lints TJ, Tchernichovski O (2004) Song development: in search of the error-signal. *Ann N Y Acad Sci* 1016:364–376.
- Doupe AJ, Kuhl PK (1999) Birdsong and human speech: common themes and mechanisms. *Annu Rev Neurosci* 22:567–631.
- Doya K, Sejnowski T (1998) A computational model of birdsong learning by auditory experience and auditory feedback. In: Poon P, Brugge J, editors. *Central auditory processing and neural modeling*. New York: Plenum. p. 77–88.
- Ernst MO, Banks MS (2002) Humans integrate visual and haptic information in a statistically optimal fashion. *Nature* 415:429–433.
- Faisal AA, Selen LP, Wolpert DM (2008) Noise in the nervous system. *Nat Rev Neurosci* 9:292–303.
- Fee MS, Scharff C (2010) The songbird as a model for the generation and learning of complex sequential behaviors. *ILAR J* 51:362–377.
- Fine MS, Thoroughman KA (2007) Trial-by-trial transformation of error into sensorimotor adaptation changes with environmental dynamics. *J Neurophysiol* 98:1392–1404.
- Fowler CA, Saltzman E (1993) Coordination and coarticulation in speech production. *Lang Speech* 36(Pt 2–3):171–195.
- Fujimoto H, Hasegawa T, Watanabe D (2011) Neural coding of syntactic structure in learned vocalizations in the songbird. *J Neurosci* 31:10023–10033.
- Goller F, Cooper BG (2004) Peripheral motor dynamics of song production in the zebra finch. *Ann N Y Acad Sci* 1016:130–152.
- Goller F, Suthers RA (1996) Role of syringeal muscles in controlling the phonology of bird song. *J Neurophysiol* 76:287–300.
- Grana GD, Billimoria CP, Sen K (2009) Analyzing variability in neural responses to complex natural sounds in the awake songbird. *J Neurophysiol* 101:3147–3157.
- Hammerschmidt K, Reisinger E, Westekemper K, Ehrenreich L, Strenzke N, Fischer J (2012) Mice do not require auditory input for the normal development of their ultrasonic vocalizations. *BMC Neurosci* 13:40.
- Hauber ME, Cassey P, Woolley SM, Theunissen FE (2007) Neurophysiological response selectivity for conspecific songs over synthetic sounds in the auditory forebrain of non-singing female songbirds. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 193:765–774.
- Hoffmann LA, Kelly CW, Nicholson DA, Sober SJ (2012) A lightweight, headphones-based system for manipulating auditory feedback in songbirds. *J Vis Exp*:e50027.
- Hoffmann LA, Sober SJ (2014) Vocal generalization depends on gesture identity and sequence. *J Neurosci* 34:5564–5574.
- Houde JF, Jordan MI (1998) Sensorimotor adaptation in speech production. *Science* 279:1213–1216.
- Jones JA, Munhall KG (2000) Perceptual calibration of F0 production: evidence from feedback perturbation. *J Acoust Soc Am* 108:1246–1251.
- Kao MH, Doupe AJ, Brainard MS (2005) Contributions of an avian basal ganglia-forebrain circuit to real-time modulation of song. *Nature* 433:638–643.
- Keller GB, Hahnloser RHR (2009) Neural processing of auditory feedback during vocal practice in a songbird. *Nature* 457:187–190.
- Kim G, Doupe A (2011) Organized representation of spectrotemporal features in songbird auditory forebrain. *J Neurosci* 31:16977–16990.
- Konishi M (1965) The role of auditory feedback in the control of vocalization in the white-crowned sparrow. *Z Tierpsychol* 22:770–783.
- Laje R, Gardner TJ, Mindlin GB (2002) Neuromuscular control of vocalizations in birdsong: a model. *Phys Rev E Stat Nonlin Soft Matter Phys* 65:051921.

- Lei H, Mooney R (2010) Manipulation of a central auditory representation shapes learned vocal output. *Neuron* 65:122–134.
- Leonardo A, Fee MS (2005) Ensemble coding of vocal control in birdsong. *J Neurosci* 25:652–661.
- Lincoln M, Packman A, Onslow M (2006) Altered auditory feedback and the treatment of stuttering: a review. *J Fluency Disord* 31:71–89.
- Lipkind D, Marcus GF, Bemis DK, Sasahara K, Jacoby N, Takahasi M, Suzuki K, Feher O, Ravbar P, Okanoya K, Tchernichovski O (2013) Stepwise acquisition of vocal combinatorial capacity in songbirds and human infants. *Nature* 498:104–108.
- Lowit A, Dobinson C, Timmins C, Howell P, Kroger B (2010) The effectiveness of traditional methods and altered auditory feedback in improving speech rate and intelligibility in speakers with Parkinson's disease. *Int J Speech Lang Pathol* 12:426–436.
- Mahrt EJ, Perkel DJ, Tong L, Rubel EW, Portfors CV (2013) Engineered deafness reveals that mouse courtship vocalizations do not require auditory experience. *J Neurosci* 33:5573–5583.
- Marko MK, Haith AM, Harran MD, Shadmehr R (2012) Sensitivity to prediction error in reach adaptation. *J Neurophysiol* 108:1752–1763.
- Murugan M, Harward S, Scharff C, Mooney R (2013) Diminished FoxP2 levels affect dopaminergic modulation of corticostriatal signaling important to song variability. *Neuron* 80:1464–1476.
- Nagel KI, Doupe AJ (2006) Temporal processing and adaptation in the songbird auditory forebrain. *Neuron* 51:845–859.
- Nagel KI, Doupe AJ (2008) Organizing principles of spectro-temporal encoding in the avian primary auditory area field L. *Neuron* 58:938–955.
- Nagel KI, McLendon HM, Doupe AJ (2010) Differential influence of frequency, timing, and intensity cues in a complex acoustic categorization task. *J Neurophysiol* 104:1426–1437.
- Nordeen KW, Nordeen EJ (1992) Auditory feedback is necessary for the maintenance of stereotyped song in adult zebra finches. *Behav Neural Biol* 57:58–66.
- Nottebohm F (1968) Auditory experience and song development in chaffinch *Fringilla coelebs*. *Ibis* 110:549.
- Okanoya K, 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.
- Olveczky BP, Andalman AS, Fee MS (2005) Vocal experimentation in the juvenile songbird requires a basal ganglia circuit. *PLoS Biol* 3:e153.
- Olveczky BP, Otchy TM, Goldberg JH, Aronov D, Fee MS (2011) Changes in the neural control of a complex motor sequence during learning. *J Neurophysiol* 106:386–397.
- Remage-Healey L, London SE, Schlinger BA (2010) Birdsong and the neural production of steroids. *J Chem Neuroanat* 39:72–81.
- Riede T, Goller F (2010) Peripheral mechanisms for vocal production in birds – differences and similarities to human speech and singing. *Brain Lang* 115:69–80.
- Robinson FR, Noto CT, Bevans SE (2003) Effect of visual error size on saccade adaptation in monkey. *J Neurophysiol* 90:1235–1244.
- Ruben RJ, Rapin I (1980) Plasticity of the developing auditory system. *Ann Otol Rhinol Laryngol* 89:303–311.
- Scheerer NE, Jones JA (2012) The relationship between vocal accuracy and variability to the level of compensation to altered auditory feedback. *Neurosci Lett* 529:128–132.
- Scheerer NE, Liu H, Jones JA (2013) The developmental trajectory of vocal and event-related potential responses to frequency-altered auditory feedback. *Eur J Neurosci* 38:3189–3200.
- Sober SJ, Brainard MS (2009) Adult birdsong is actively maintained by error correction. *Nat Neurosci* 12:927–931.
- Sober SJ, Brainard MS (2012) Vocal learning is constrained by the statistics of sensorimotor experience. *Proc Natl Acad Sci USA* 109:21099–21103.
- Sober SJ, Sabes PN (2005) Flexible strategies for sensory integration during motor planning. *Nat Neurosci* 8:490–497.
- Sober SJ, Wohlgemuth MJ, Brainard MS (2008) Central contributions to acoustic variation in birdsong. *J Neurosci* 28:10370–10379.
- Tang C, Srivastava K, Chehayeb D, Nemenman I, Sober SJ (in press) Millisecond-scale motor encoding in a cortical vocal area. *PLoS Bio*.
- Tchernichovski O, Lints TJ, Deregnaucourt S, Cimenser A, Mitra PP (2004) Studying the song development process: rationale and methods. *Ann N Y Acad Sci* 1016:348–363.
- Titze IR (1993) Current topics in voice production mechanisms. *Acta Otolaryngol* 113:421–427.
- Titze IR (1994) Principles of Voice Production. Prentice Hall.
- Trevisan MA, Mindlin GB (2009) New perspectives on the physics of birdsong. *Philos Transact A Math Phys Eng Sci* 367:3239–3254.
- Troyer TW, Doupe AJ (2000) An associational model of birdsong sensorimotor learning I. Efference copy and the learning of song syllables. *J Neurophysiol* 84:1204–1223.
- Tumer EC, Brainard MS (2007) Performance variability enables adaptive plasticity of 'crystallized' adult birdsong. *Nature* 450:1240–1244.
- Walstein RS (1990) Effects of postlingual deafness on speech production: implications for the role of auditory feedback. *J Acoust Soc Am* 88:2099–2114.
- Warren TL, Charlesworth JD, Tumer EC, Brainard MS (2012) Variable sequencing is actively maintained in a well learned motor skill. *J Neurosci* 32:15414–15425.
- Warren TL, Tumer EC, Charlesworth JD, Brainard MS (2011) Mechanisms and time course of vocal learning and consolidation in the adult songbird. *J Neurophysiol* 106:1806–1821.
- Wei K, Kording K (2009) Relevance of error: what drives motor adaptation? *J Neurophysiol* 101:655–664.
- Wohlgemuth MJ, Sober SJ, Brainard MS (2010) Linked control of syllable sequence and phonology in birdsong. *J Neurosci* 30:12936–12949.
- Wolpert DM, Ghahramani Z, Jordan MI (1995) An internal model for sensorimotor integration. *Science* 269:1880–1882.
- Woolley SC, Kao MH (2015) Variability in action: contributions of a songbird cortical-basal ganglia circuit to vocal motor learning and control. *Neuroscience*. 296:39–47.
- Woolley SM, Rubel EW (1997) Bengalese finches *Lonchura striata* domestica depend upon auditory feedback for the maintenance of adult song. *J Neurosci* 17:6380–6390.