
Vocal Performance and Sensorimotor Learning in Songbirds

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I. INTRODUCTION

Since the pioneering studies of William Thorpe and Peter Marler, songbirds and their songs have served continuously as an inspirational muse to behavioral biologists (Catchpole and Slater, 2008; Marler and Slabbekoorn, 2004; Marler, 1957; Thorpe, 1958a). This is due not only to songbirds' improbably rich diversity in song form and function, but also to the fascinating intricacy and complexity of the mechanisms that guide vocal production and development. Of particular interest in recent years has been the interplay between evolutionary and proximate realms. Representative questions raised in recent literature reviews well-illustrate this point: How is song diversity and function enriched by varying programs for song learning (Beecher and Brenowitz, 2005; Nelson et al., 1995)? How does variation in mechanisms underlying vocal learning and production contribute to vocal diversity and evolution (Jarvis, 2004; ten Cate, 2004)? How do mechanisms of song learning contribute to the reliability of information encoded in song (Buchanan, 2000; Nowicki et al., 1998)?

This chapter focuses on the interface of vocal performance and song development. Evidence is mounting that birds' vocal performance capacities can limit or bias aspects of the song phenotype (reviewed by Lambrechts, 1996; Podos and Nowicki, 2004; Suthers, 2004; Suthers and Goller, 1997). Less clear is the nature of the relationship between vocal performance and the processes that guide song development. As we review below, songs of many bird species develop through imitative learning, a two-step process in which young birds first memorize the structure of adult models (the "memorization" phase), and then match memorized models by

comparing them to their own developing vocal output (the “sensorimotor” phase). Within the framework of imitative learning, where and how are limits or biases of vocal performance expressed? How might variation in vocal performance influence model imitation? And how might this relationship influence aspects of song function and evolution?

We begin with an overview of recent evidence that pertains to vocal performance and its influence on song production and evolution. Empirical evidence for vocal performance limits in numerous species is accumulating rapidly. We then provide a brief overview of the processes that guide song learning, and argue that a comprehensive understanding of vocal performance requires particular attention to sensorimotor learning. This is because vocal performance biases are most likely expressed as birds attempt to develop and crystallize copies of memorized models. We then consider the implications of the relationship between vocal performance and development for the “developmental stress” hypothesis, which posits that songs produced by adults provide reliable information about singers’ developmental histories. Studies of the developmental stress hypothesis have focused so far on brain development and sensory learning; we suggest expanding the hypothesis to likewise consider vocal performance limitations as expressed and codified during sensorimotor learning. We conclude by describing additional avenues for study suggested by the connections drawn between vocal performance and sensorimotor learning.

II. VOCAL PERFORMANCE

A. ACOUSTIC SIGNAL PRODUCTION AND THE CONCEPT OF PERFORMANCE

As with all types of behavior, acoustic signals are circumscribed in their structure by mechanisms underlying their expression (reviewed by Bradbury and Vehrencamp, 1998). For instance, for vertebrates that produce sound via phonation (pneumatically induced source vibrations), small animals with small source structures tend to vocalize at high frequencies, because of the intrinsically high resonant frequencies of smaller masses (e.g., Gerhardt, 1994; Ryan and Brenowitz, 1985). Similarly, the acoustic frequencies and amplitudes of sounds produced by stridulation (striking of plectrum on file) are dictated largely by the size and arrangement of these structures, and by the neuromuscular mechanisms that control their movement. These and similar examples do not necessarily imply, however, that acoustic output is readily predicted by source anatomy and function. On the contrary, there is substantial room for variation in vocal output within any given mechanistic framework. To return to the example of phonation,

within many animal taxa (e.g., anurans, birds, primates), individuals or species of similar body size vocalize at widely divergent frequencies, in a form of behavioral or evolutionary plasticity that overrides morphological similarities (e.g., Hauser, 1993). This is partly because many individuals or species do not vocalize at frequencies as low as their mechanisms might conceivably allow. Behavioral plasticity is also evident as animals adjust when and where they produce sound, modulating aspects of source–medium coupling and thus vocal output. Orthopterans that stridulate in chambers or burrows, for example, can amplify their calls through resonance matching, to levels beyond that which could be achieved in other acoustic environments (Bennett-Clark, 1987).

A concept with particular utility here is that of “performance,” which addresses the dynamic nature of the relationship between behavioral mechanisms and behavioral output, and the fitness consequences of this relationship (e.g., Arnold, 1983; Irschick, 2003; Wainwright, 1994). Two recurring findings in studies of performance are that animals often perform the same behavior in different contexts with widely varying levels of performance, and that animals typically do not behave at performance maxima during day to day activities, instead reserving maximal performance for key fitness-defining contexts such as predator avoidance. These themes are well illustrated in the literature on locomotion in lizards (Garland and Losos, 1994; Irschick and Garland, 2001). Lizards can be induced to sprint in track tests or on treadmills, from which maximal sprint speeds can be inferred. Observational studies indicate that maximal sprint speeds are approached only rarely in nature, as lizards attempt to evade predators (Irschick, 2003). By contrast, locomotion speeds are much slower in typical contexts, for example, in *Anolis* typically approaching only 10–40% maximum speed (Irschick, 2003). Distinguishing typical versus maximal performance is important because it helps specify the loci on which selection may act. In the case of lizard locomotion, individuals within a given population overlap widely in typical locomotion speeds, but separate reliably in maximal sprint speeds. That is, while all lizards can move at slow speeds, only some can reach the highest speeds. A recent survey of this literature indicates that natural and sexual selection indeed often favor animals that express higher maximal performance capacities (Irschick et al., 2008).

While the concept of performance has been applied with rigor to the study of locomotion and feeding behavior, its utility has been considered only occasionally for behavioral communication displays such as bird songs. Here are five representative questions that can be asked about behavioral communication displays from a performance-based perspective: (1) To what extent do individuals modulate display performance across different contexts, for example, across a breeding season or to different audiences?;

(2) Do signalers sometimes encounter performance limitations as they display, and if so when?; (3) How do individuals vary in maximal display performance?; (4) Are signal receivers particularly attentive to maximal display events, as opposed to typical display events?; and (5) How does variation in maximal display behavior bear upon sexual selection?

These questions seem particularly relevant to the study of avian vocal displays, given the intricate nature of the vocal production mechanism, the complex time-varying structure of many vocalizations, and the corresponding likelihood that performance limits shape aspects of the avian vocal phenotype (Podos and Nowicki, 2004). To elaborate, birds typically generate sounds at the syrinx, a bilateral sound source with partly independent contributions from the left and right sides (Greenewalt, 1968; Nottebohm, 1971; Nowicki and Capranica, 1986; Suthers, 1990). Syringeal tissues vibrate and produce sound when activated by respiratory airflow (Goller and Larsen, 1997), and patterns of breathing are finely coordinated with syringeal activity, such that vocalizations are typically uttered only as birds breathe out (Suthers, 2004). Vocal structure is also influenced by the trachea and associated structures (the “vocal tract”), which selectively filter harmonic overtones and thus enable the production of sounds with high pure-tonal quality (Nowicki, 1987; Nowicki and Marler, 1988). Birds actively modulate vocal tract configurations during song production, in a manner that tracks modulations at the syrinx (Beckers et al., 2003; Hoese et al., 2000; Riede et al., 2006; Westneat et al., 1993). Vocal tract modulations are presumed to enable birds to retain the vocal tract’s resonance function across a range of vocal frequencies. The multiple motor systems of bird song production are coordinated by a complex hierarchical neural control system (Brainard and Doupe, 2002; Jarvis, 2004; Suthers, 2004). Overall, vocal production is a nearly “beak-to-foot effort” (Podos and Nowicki, 2004) that seems to present birds substantial production challenges for its successful execution.

Songs that feature rapid modulations in vocal frequencies, or rapid repetitions of notes, should be particularly susceptible to performance limitations. For example, consider song production in Northern cardinals (*Cardinalis cardinalis*), which Suthers (2004, p. 281) refers to as an “extraordinary feat of virtuosity.” Cardinal songs typically consist of trilled sequences, with notes repeated numerous times per second, and each often spanning at least two octaves (Suthers, 2004). Measurements of respiratory pressure in the bronchi demonstrate that low frequency note components (below ~3.5 kHz) are produced by the left side of the syrinx, whereas higher frequencies are produced by the right side of the syrinx (Suthers and Goller, 1997). By coordinating the two sides of the syrinx, birds are able to span a range of vocal frequencies with a speed and degree

of precision that presumably could not be achieved if sound production was limited to only a single vocal source. Moreover, note production involves a tight interplay of activation or closure of the two syrinx sides at the appropriate time, of precisely timed respiratory inspirations and expirations, and of precisely modulated vocal tract reconfigurations (Suthers, 2004). Similar patterns have been observed in a diversity of species, confirming the generality of these patterns (Suthers, 2004). Thus the seemingly simple structure of some songbird songs, and of their constituent notes, belies the daunting intricacy and complexity of the vocal performance that enables their production.

B. INFERRING VOCAL PERFORMANCE LIMITS IN SONGBIRDS

How can we know if and when songbirds vocalize at their maximal performance abilities? If birds never push their vocal displays to maximal effort, then the discussion of variation in performance abilities would be largely moot. In general, the most direct way to infer performance limitations in animals is to motivate them with experimental tasks that push their performance envelopes. Motivating animals to perform maximally is fairly straightforward in studies of feeding or locomotion; for the former one merely needs a hungry animal, and for the latter one needs an animal that is under threat from a predator (e.g., in the guise of a scientist wielding a stick) or that is placed in an environment or situation that challenges typical locomotory performance (e.g., Chai and Dudley, 1995; Gillis et al., 2009; Jayne and Ellis, 1998). It is less straightforward to motivate songbirds to sing at high vocal performance. Birds almost never sing for their survival (but see Cresswell, 1994), which means that motivation typically cannot be induced by hunger or fear.

One method that has been used with success to infer vocal performance limitations has been to train young birds with song models that are rigged to challenge birds' vocal abilities. In a study of swamp sparrows (*Melospiza georgiana*), a species that typically produces simple trills, Podos (1996) trained hand-reared males with song models that contained species-typical notes arranged with artificially elevated trill rates. The reasoning behind this approach is that young birds are intrinsically motivated to reproduce model songs with accuracy, yet might encounter performance limitations in reproducing models that challenge their vocal production capacities. The experimental birds in this study proved able to memorize rapid trill models, but unable to reproduce the models at their elevated rates. Instead birds introduced copying inaccuracies in ways suggesting that they had indeed encountered performance constraints during development. Some models were reproduced at slower trill rates, others with notes omitted, and others with "broken" syntax,

in which multisyllable segments were separated by brief pauses (Podos, 1996). The vocal structure of the models used in this study was thus beyond the realm of possibility, at least as specified by the current structure and function of the swamp sparrow vocal apparatus. A parallel demonstration was offered by Zollinger and Suthers (2004) for Northern mockingbirds (*Mimus polyglottis*), which are accomplished vocal mimics of other species. Mockingbirds were reared and exposed to song models from four species, including Wasserslager canaries (*Serinus canaries*), which sing trills that are both rapid and of extended duration. Two mockingbirds that attempted to copy canary trills proved unable to reproduce the “mini-breath” breathing patterns that allow canaries to produce rapid trills of extended duration. Rather, these birds reproduced canary models using “pulsatile” breathing patterns, which required occasional brief pauses between trill segments, thus resulting in broken syntax parallel to that observed in swamp sparrows.

A more common yet less direct approach for inferring vocal performance limits is through descriptive analyses of vocal variation, especially with reference to expectations about vocal performance boundaries. Perhaps the most traditional measure of vocal performance has been song output, that is, the number of vocalizations performed per unit time, or the duration of vocalizations relative to that of silent intervals between songs. Birds with greater levels of vocal proficiency presumably could produce relatively more vocal material per unit time. Indeed there is wide-ranging evidence that birds within given populations vary in their vocal output (e.g., Alatalo et al., 1990; Arvidsson and Neergaard, 1991; Hofstad et al., 2002; Kempenaers et al., 1997; Otter et al., 1997; Pinxten and Eens, 1998; Poesel et al., 2001). It has been difficult, however, to attribute such results with confidence to individual variation in performance abilities, for at least three reasons. First, available evidence indicates that the actual metabolic cost of song production is rather low (Oberweger and Goller, 2001). The absence of a clear energetic cost to song production raises the question of what other costs or constraints could render vocal output an honest signal of vocal performance (Searcy and Nowicki, 2005). Second, individual variation in vocal output might result instead as a correlated effect of food availability, such that birds with ready access to food are able to spend more time singing. This alternative hypothesis is supported by experimental studies in which birds provided with supplementary food sang more, presumably because of reduced time required for foraging (Lucas et al., 1999; Nystrom, 1997; Thomas, 1999). Third, birds which vocalize infrequently may do so not because of a physical inability to produce more, but because of an inability to withstand other kinds of costs associated with increased song output such as increased vulnerability or likelihood of retaliation from territorial neighbors (Vehrencamp, 2001).

Variation in vocal performance abilities may be easier to identify as it occurs with respect to vocal structural parameters, that is, the structure of specific songs, song sequences, or song components (Gil and Gahr, 2002; Podos et al., 2004a). We now review recent advances in the study of two classes of vocal parameters—consistency and trill structure—that link directly to expectations about vocal performance, and for which empirical evidence has been accumulating rapidly. We do not regard these categories as collectively exhaustive, as additional categories of performance constraints can be envisaged.

1. Consistency

Birds' performance abilities might be revealed in their ability to produce repetitive songs or song components with consistency, that is, with little variation across renditions. Variation in the consistency of note structure was illustrated in Lambrechts' (1997) study of great tits (*Parus major*), a species whose songs include trilled sequences of varying tempos. Lambrechts showed that note frequencies within slow trills tend to be highly consistent, but to vary substantially within trills of faster tempo. Birds repeating notes within fast trills presumably face greater difficulties maintaining note frequencies at constant levels. Similarly, Christie et al. (2004) documented, in black-capped chickadees (*Poecile atricapillus*), variation among birds in the consistency of note pitch ratios across song renditions. Some chickadees are able to maintain highly consistent ratios among "fee" and "bee" notes, even as the absolute frequencies of these notes vary, whereas other birds fail to maintain consistent note pitch ratios. In a recent study of chestnut-sided warblers (*Dendroica pensylvanica*), Byers (2007) documented individual variation in song consistency across a number of frequency and temporal song parameters, using coefficients of variation (CV). CVs were found to range from ~3–10% on the stereotyped end of the spectrum to about ~20–35% on the variable end of the spectrum. Other studies of song consistency have focused on the maintenance of consistent timing relationships among songs within bouts (Lambrechts and Dhondt, 1986; Poesel et al., 2001). In all of the above studies, variation in consistency is inferred to be a product of vocal performance, with only the highest quality singers able to perform with the highest levels of consistency.

2. Trill Structure

Many birds' songs include trilled sequences, in which notes or note groups (syllables) are repeated two or more times in sequence (e.g., Podos, 1997; Thorpe and Lade, 1961). Birds' vocal competency might be revealed in their ability to include trilled vocal sequences in their songs and repertoires, given the intricacy of the mechanisms involved in trill production

(see above). In their studies of nightingales (*Luscinia megarhynchos*), Kunc et al. (2006) and Schmidt et al. (2006) found that males challenged with song playback tend to augment the proportion of songs they sing that contain broadband trills. Similarly, Trillo and Vehrencamp (2005) report that banded wrens (*Pheugopedius pleurostictus*) are more likely to produce trilled vocal sequences during intense male–male interactions, border disputes, and also during dawn song as compared to daytime song.

Internal trill characteristics might also be dictated by singers' vocal performance abilities. Trill rate, that is, the number of syllables delivered within a trill per unit time, should be limited in part by birds' abilities to perform rapid modulations of the syrinx, respiratory, and vocal tract motor systems, as described above. For trills of slow to moderate tempo, birds normally take "mini-breaths" between every note and syllable. Use of mini-breaths maintains birds' respiratory tidal volume at fairly constant levels, thus enabling the production of trills of extended duration (Hartley and Suthers, 1989). To produce faster trills, however, birds typically shift to "pulsatile" respiration, in which respiratory tidal volume is depleted rapidly, thus limiting trill duration (Hartley and Suthers, 1989). Increasing trill rates may thus reduce maximal trill durations (Suthers, 2004).

Another widespread structural tradeoff that appears to define many trills is between trill rate and frequency bandwidth, that is, the range of frequencies a trill spans. This tradeoff was first described for 34 species of emberizid songbirds and has been attributed to a performance constraint on trill production (Podos, 1997; see also Podos and Nowicki, 2004). A brief explanation for this tradeoff is as follows: Increases in either trill rate or frequency bandwidth are expected to push a bird's performance envelope, because of required increases in the rapidity or scope of required syrinx, respiratory, and vocal tract reconfigurations. If a bird maximizes its trill rate, it necessarily limits the time span during which frequency modulations can be performed within given syllables, and thus necessarily sets limits on frequency bandwidth. Likewise, producing syllables that span broad frequency bandwidths requires corresponding long periods of time, thus limiting trill rate. In actuality, the tradeoff between the two parameters is not linear but triangular, because birds can produce trills that are both slow and narrowband, well below the hypothesized performance limit. An upper boundary regression of the triangular distribution defining the trill rate \times frequency tradeoff has thus been used to infer maximal performance limits (Podos, 1997; see also Ballentine, 2006; Podos, 2001; Podos and Nowicki, 2004). Tradeoffs between trill rate and frequency bandwidth have since been described in greater detail for two of those emberizid species, swamp sparrows (Ballentine et al., 2004; Liu et al., 2008) and dark-eyed juncos (*Junco hyemalis*; Cardoso et al., 2007), as well as for a number of additional

species or groups including yellow warblers (*Dendroica petechia*; Beebee, 2004, with trills described as “phrases”), oropendolas and caciques (Icteridae; Price and Lanyon, 2004), banded wrens (Illes et al., 2006), red-winged blackbirds (*Agelaius phoeniceus*; Cramer and Price, 2007), and brown skuas (*Catharacta antarctica*; Janicke et al., 2008). The observed tradeoff in brown skuas may arise through a mechanism distinct from that in passerines, given that vocalizations in this species are not pure tonal, and that frequency bandwidth is adjusted not by modulation of fundamental frequencies but rather via enhancement or suppression of harmonic overtones (Cardoso, 2008; Janicke and Hahn, 2008).

Other structural relationships identified within trills illuminate additional possible loci of variation in vocal performance. Forstmeier et al. (2002) showed that in dusky warblers (*Phylloscopus fuscatus*), trills (or strophes) with rapid frequency modulations contain less signal energy, measured as relative amplitude, as compared to trills with more limited frequency modulations. Signaling advantages gained by enhanced frequency modulation might thus be offset by reductions in amplitude and thus overall signal efficacy. Brumm and Slater (2006) report that chaffinches (*Fringilla coelebs*) switch song types more frequently when singing songs with fast trills, perhaps as a result of motor fatigue (see also Lambrechts and Dhondt, 1988). Birds that can produce many consecutive iterations of a song type with fast trills may thus be able to distinguish themselves from other singers in a population.

Performance limitations likely shape trill structure in additional ways that have not yet been explored. To illustrate, consider two hypothetical trills, A and B (Fig. 1). Both trills contain syllables comprised of two notes, each a simple frequency sweep with identical frequency ranges. Moreover, syllables are produced with identical durations and tempos. In trill A, the two notes alternate in direction of frequency modulation, with the first note sweeping upward and the second note sweeping downward. By contrast, the two notes in trill B syllables are modulated in the same direction, both sweeping upward. A simple analysis of trill rate, frequency bandwidth, or the relation between these two parameters would suggest identical performance levels for these trills. However, we would actually expect trill A to be easier to produce than trill B. In trill A, during the silent intervals between notes, the vocal apparatus (particularly the syrinx and vocal tract) would already be in an appropriate configuration for the production of the next note, because of the frequency match between the end of the prior note and the start of the next note. By contrast, trill B would require considerable syrinx and vocal tract reconfiguration during silent intervals, to account for the difference between the ending and starting frequency of sequential notes. Many similar scenarios can be envisioned, not only with respect to trills but also to other types of vocal parameters.

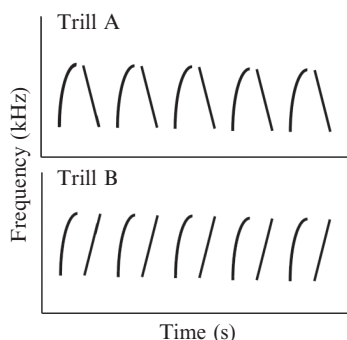


FIG. 1. Two hypothetical trills, equivalent in trill rate and frequency bandwidth, but which would still be expected to differ in performance requirements. See text for further explanation.

C. DOES PERFORMANCE MATTER?

Inferring limits on vocal performance is a worthwhile task in its own right, because it allows us to document the ranges of song variants that may be expressed within a species or population (Podos, 1997; Podos et al., 2004a). Of perhaps greater interest is the possibility that signal receivers attend to performance variation among singers, and use this information to differentiate singers in terms of their quality. The question of whether vocal performance provides a reliable indicator of singer quality represents an area of significant recent activity (e.g., Gil and Gahr, 2002; Searcy and Nowicki, 2005).

With respect to variation in vocal output, high song rates have been linked to a range of factors associated with fitness such as territory quality, food availability, metabolic condition, and immunocompetence (reviewed by Podos et al., 2004a). However, while song rate variation is likely shaped in part by performance abilities, alternative hypotheses for observed variations in vocal output have been difficult to exclude (see above). More definitive conclusions have been emerging from studies focusing on song consistency and trill structure.

Available evidence indicates that birds that sing with high consistency fare better in attributes related to reproductive success (reviewed by Byers, 2007). Lambrechts and Dhondt's (1986) study of great tits revealed that males that deliver songs with more consistent timing, as measured by variation in internote intervals, tend to be socially dominant. Social dominance in black-capped chickadees is also revealed by consistency, not in the timing of delivery but in internote frequency ratios (Christie et al., 2004). In their study of blue tits (*Cyanistes caeruleus*), Poesel et al. (2001) found that

males with consistent inter-song intervals tend to sire larger clutches. Similarly, Byers (2007) found that female chestnut-sided warblers tend to choose extra-pair mates who sing with high consistency in frequency and timing parameters. In this latter study, a comparison of singing by extra-pair mates and cuckolded social fathers revealed superior consistency among the extra-pair mates. Dusky warblers who sing with consistently high relative amplitudes across trill syllables ("peak performance") appear to enjoy enhanced longevity and greater success in achieving extra-pair paternity (Forstmeier et al., 2002). Finally, male brown skuas that produce vocalizations with higher peak performance, and also with relatively high trill rates and frequency bandwidths ("vocal deviation"), obtain disproportionately high reproductive success (Janicke et al., 2008). Descriptive studies such as these, which report correlations among song performance and measures of reproductive success, are invaluable yet face one major limitation: It is not known whether signal receivers respond directly to variation in vocal performance *per se* or to other indicators of male quality with which vocal performance might correlate. More comprehensive conclusions about the functional consequences of vocal performance variation thus require experimental studies, in which song performance variants are presented via playback in the absence of singing males (see Searcy and Andersson, 1986, p. 508, for a parallel argument). A number of recent studies have taken this approach:

Schmidt et al. (2008) tested whether the presence versus absence of trills may have functional consequences. Territorial male nightingales were presented simulated rivals from two playback speakers, the first speaker broadcasting songs that featured some rapid broadband trills, and the second speaker broadcasting nontrilled songs exclusively. Birds were found to respond much more strongly to the playback speaker broadcasting trills, thus suggesting that trills are regarded by rivals as particularly aggressive signals. However, these results contrast with those reported for blue tits by Doutrelant et al. (1999) and Poesel and Dabelsteen (2006), who found no response differences to playback of trilled versus nontrilled songs. It is not yet clear if and how the ability to deliver broadband trills varies among singers of differing quality.

With regard to variations in trill structure, female canaries and swamp sparrows were found to solicit copulations more frequently and more vigorously in response to playback of trills with comparatively or artificially high trill rates and frequency bandwidth (Ballentine et al., 2004; Draganoiu et al., 2002; Vallet and Kreutzer, 1995; Vallet et al., 1998). Territorial male red-winged blackbirds were also found to discriminate songs of high versus low trill rates and frequency bandwidth, although responses were stronger

to low rather than high-performance songs (Cramer and Price, 2007). One possible explanation for the direction of this response is that territorial males found high-performance songs relatively intimidating (Collins, 2004; Cramer and Price, 2007; Searcy and Nowicki, 2000).

Other recent playback studies have focused on variation in either trill rate or frequency bandwidth alone. Illes et al. (2006) used a two-speaker design to assess whether male banded wrens discriminate playback trills that vary by trill rate, pairing slow trills against fast trills. Birds were found to approach faster trills first, suggesting that fast trills are perceived by territory owners as a more immediate threat. More telling were subsequent reactions; after initial approach, test subjects were generally repelled by the faster trills, and to a degree that corresponded to the overall performance levels of these songs relative to the song population. This finding was expanded upon in Schmidt et al.'s (2008) study of night-ingales, a species in which approximately half of all males remain unmated throughout a given breeding season. Males that remained unmated responded to song playback in a manner parallel to that described by Illes et al. (2006) for banded wrens; birds avoided playback trills to degrees corresponding to trill rates. However, males that eventually paired later in the season showed the opposite trend, responding more aggressively to playback trills with higher trill rates. Male responses to songs of varying performance levels may thus vary with signaling context and with attributes of signal receivers. de Kort et al. (2009) presented territorial banded wrens with playback songs from three categories; control, with experimentally increased frequency bandwidths, or with experimentally decreased frequency bandwidths. The strongest territorial responses were directed toward unmanipulated songs. Detailed analysis of response patterns suggests that low-bandwidth songs were perceived as comparatively nonthreatening, whereas high-bandwidth songs were perceived as unusually intimidating.

Emerging descriptive and experimental evidence thus indicates that vocal performance varies among individuals, and suggests that singers who maximize vocal performance gain advantages in song function and ultimately in reproductive success. For these reasons, the specific processes by which varying vocal performance shapes the vocal phenotype merit special attention. As we argue below, the impact of vocal performance on song structure in songbirds is likely realized most significantly during vocal development and especially during sensorimotor learning. Before addressing the specifics of this argument, we provide a general overview of the process of vocal imitation, with emphasis on sensorimotor learning.

III. SONG LEARNING IN SONGBIRDS

Along with a handful of other vertebrate groups, songbirds develop vocalizations through imitative learning (“production learning,” Janik and Slater, 2000). Songbirds are especially renowned for the accuracy and precision with which song models can be memorized and reproduced. In this section, we offer a brief review of the processes that underlie imitative learning, first with regard to factors that govern the acquisition and memorization of song models, and second with regard to sensorimotor learning, in which song memories are transformed into vocal output (Marler, 1970). This review is based largely on research on sparrows and zebra finches (*Taeniopygia guttata*), for which the majority of data are available; additional research on song learning in other bird groups will undoubtedly reveal additional kinds of song learning and development programs.

A. SONG ACQUISITION

Song acquisition occurs as young birds listen to song models and commit them to memory. A major theme to emerge from over half a century of empirical studies is that song acquisition is often circumscribed by innate predispositions, such that only a subset of potentially available models are memorized. A first example of this concerns species that show innate predispositions in recognizing and memorizing song models of conspecifics versus heterospecifics (Braaten and Reynolds, 1999; Nelson, 2000a; Slater et al., 1988; Soha and Marler, 2001; Thorpe, 1958b). Remarkably, this preference can be based on the acoustic structure of models alone, in the absence of social tutors, as has been shown in song learning studies in which birds are presented song models over loudspeakers (Dooling and Searcy, 1980; Marler and Peters, 1977; Soha and Marler, 2000). Innate predispositions for learning conspecific songs have been mapped to particular regions of the avian forebrain, within which neurons respond more strongly to conspecific than to heterospecific song (e.g., Chew et al., 1995; Doupe, 1997; Janata and Margoliash, 1999). A second bias in song acquisition is that birds are often predisposed to learn songs mainly during a “sensitive period” of song acquisition, during the first months of their lives (Kroodsma and Pickert, 1980; Marler and Peters, 1987). Certain neural structures, including song nuclei that are only found in birds that learn their songs, develop in parallel with this sensitive period and are thought to enable and then restrict vocal model input (Bottjer, 2004; Konishi and Akutagawa, 1985; Nottebohm et al., 1976).

Model acquisition can also be shaped significantly by birds’ social interactions (Beecher and Burt, 2004; Beecher et al., 2007; Nelson, 1997; Nordby et al., 2007; West and King, 1988). Zebra finches, for instance, prefer to learn

songs from their own fathers or other similarly plumaged males (Clayton, 1988; Mann and Slater, 1995), whereas birds such as the song sparrow (*Melospiza melodia*) and chipping sparrow (*Spizella passerina*) tend to learn their songs from males that are nearby (Beecher et al., 1994; Liu and Kroodsma, 2006). In some species, males copy a single tutor among several available singers (e.g., zebra finches, Mann and Slater, 1995), whereas in other species males integrate elements of several tutors into their final songs (e.g., savannah sparrows, *Passerculus sandwichensis*, Wheelwright et al., 2008; nightingales, Hultsch and Todt, 1989). Birds reared by heterospecific tutors may copy the songs of their foster parents (Baptista and Petrinovitch, 1984).

These and parallel lines of evidence suggest that birds possess innate neural representations or “templates” that target specific tutor songs for acquisition, and which can be shaped by social influences (Adret, 2004; Marler, 1976, 1997). The neural template is presumably crystallized in the first few months of a bird’s life, at least in “age-limited” or “closed-ended” learners (Marler and Peters, 1987). By contrast, some species, for example, European starlings (*Sturnus vulgaris*) and Northern mockingbirds, retain the ability to memorize new songs throughout their lives. Some species that were traditionally classified as close-ended learners now appear, according to recent evidence, to be able to learn new song material as adults, at least under specific social contexts (Brenowitz and Beecher, 2005). We revisit this topic in the final section.

B. SENSORIMOTOR LEARNING

Often after a winter of silence, during which time memorized songs are neither heard nor practiced, birds gradually translate memorized model songs into vocal output (Marler and Peters, 1982a,b). At first, birds produce sounds that are relatively indistinct and not clearly related to any model song. This has been called “subsong” and is analogous to human infant babbling. Subsequently, birds produce structurally deficient yet recognizable versions of memorized song, called “plastic song,” which over time increasingly resemble memorized model songs. This process involves auditory feedback, such that birds hear their own vocal output, compare this output to stored representations of song models, and refine their vocalizations accordingly (Brumm and Hultsch, 2001; Margoliash, 2002; Marler, 1997; Slater, 1989). After a month or two of practice, songs “crystallize” into a stereotypic form, which then changes very little if at all across the remainder of a bird’s life (Marler and Peters, 1982a).

A key role for auditory feedback in sensorimotor learning was first demonstrated in studies in which young birds were deafened after the memorization phase. Birds that cannot hear themselves practice are

found to produce very different songs than do unimpaired birds—their vocal output is comparatively variable, lispy, and lacks the clear tonality of normal songs (Konishi, 1965a,b). These sounds do retain some structural features of normal song, to an extent that some species-specific aspects of song can be recognized (Marler and Sherman, 1983; Nottebohm, 1972). By contrast, if birds are deafened after songs have crystallized, they continue to sing virtually normal songs (Nottebohm, 1968). This indicates that the role of auditory feedback is much less pronounced after songs achieve their final form. These experiments together demonstrate that birds' own vocal output, and the perception of that output, is central to the process by which model songs are converted into accurate imitations during sensorimotor learning (Brainard and Doupe, 2000). There is also evidence that sensorimotor learning involves specialized neural circuitry in the forebrain, which is to some extent integrated with circuitry that mediates song perception and adult vocal motor control (Aronov et al., 2008; Brainard and Doupe, 2002).

Sensorimotor learning also appears to provide birds with opportunities for distilling larger repertoires of memorized models into smaller subsets of copies to be crystallized (Beecher and Brenowitz, 2005; Nelson, 1992). Birds sometimes practice more song types earlier in development than they will eventually crystallize, and appear to retain those song types that will be most useful in social interactions. In field sparrows (*Spizella pusilla*), for instance, males settling on a territory initially sing multiple song types (Nelson, 1992). Following a series of interactions with neighboring males, however, individuals typically delete all song types but one from their repertoires. The song type that remains usually matches the song of a neighbor, and is sung by the individual for the rest of his life (Nelson, 1992). Song sparrows undergo a similar process, in which song types that poorly match neighbors are deleted during the selective attrition process (Nordby et al., 2007).

Overall, sensorimotor learning contributes significantly to the plasticity of birds' songs and song repertoires. Sometimes birds introduce "innovations," that is, structural variations or modifications of model songs, and other times introduce "inventions," that is, novel elements that bear no relationship to individual model songs (Hughes et al., 2002; Janik and Slater, 2000). Innovations and inventions are presumably shaped during sensorimotor ontogeny, and are crystallized as permanent features of song. One putative function for innovation has been identified in song sparrows. As mentioned above, song sparrows selectively delete songs from their repertoires that poorly match neighboring males, reflecting the importance of song matching in this species (Nordby et al., 2007). However, before crystallization, some songs have been observed to be modified to be less

similar to the neighbor songs they match. The interpretation here is that song matching is important, but that individual recognition may be important as well, with birds rendering their songs increasingly distinctive (yet still recognizable to song type) gaining advantages in individual recognition (Nordby et al., 2007).

IV. VOCAL PERFORMANCE AND SENSORIMOTOR LEARNING

A. THE DEVELOPMENT OF MOTOR PROFICIENCY

As outlined above, sensorimotor learning encompasses a number of related processes that underlie the translation of memorized songs into vocal output, and the crystallization of vocal structure from variable to stereotyped form. The challenges inherent in these processes are often framed in neural terms, and rightly so. Vocal models are initially imprinted into a neural template (Marler, 1976; Slater, 1989; see above), and neural mechanisms presumably enable access to this template, guiding the development and refinement of additional neural circuits that come to control vocal output. Much remains to be learned about the interplay of neural circuits that guide song perception, memorization, production, and motor refinement (e.g., Aronov et al., 2008; Brainard and Doupe, 2002; Jarvis, 2004; Zeigler and Marler, 2008).

We hypothesize that young birds face additional challenges during sensorimotor development that relate specifically to vocal performance. Young birds presumably need to learn how to correctly operate the multiple motor systems involved in singing, and to coordinate them in a manner that enables successful vocal output. The challenges in doing this can be daunting even for simple songs, and it seems unlikely that birds possess requisite vocal abilities upon hatching. Rather, vocal motor competency likely develops gradually, in tandem with the development of neural competency. The need to develop motor competency is one potential adaptive explanation for the protracted nature of sensorimotor learning.

Empirical data on the development of vocal motor competency, which could be used to evaluate the above hypothesis, are relatively few and far between. Descriptive studies that focus solely on developmental changes in song structure (e.g., Marler and Peters, 1982a,b) do not necessarily provide insight into performance constraints or biases *per se*, because specific developmental milestones might be achieved principally through the refinement of relevant neural mechanisms, as is generally assumed in discussions of template theory. For instance, the increasingly precise coordination of vocal motor systems is achieved in part via maturation of the neural circuits

that link these systems (Wild, 1997). More informative are studies that observe and measure motor correlates of vocal ontogeny. A study of cardinals showed that young birds at the subsong stage of vocal development lack the ability to precisely coordinate expiratory breathing with syringeal activation, as determined through simultaneous recording and measures of respiratory airflow (Suthers, 2004). This lack of coordination potentially explains abrupt onsets and offsets of notes that characterize subsong. Similarly, young song sparrows were shown to introduce vocal tract modulations only during late stages of song ontogeny, after note structure had developed near-crystallized form (Podos et al., 1995). Increasing application of vocal tract modulations resulted in songs with increasing tonal purity and may have been delayed in development so as allow birds to match learned patterns of syringeal output.

A complementary approach for assessing the development of motor competency is experimental, involving the presentation of probe training models to young birds and then tracking subsequent patterns of learning. Probe training models typically possess some conspecific song features, to ensure their viability as models, yet vary in other parameters that allow tests of the learning capacity of interest. Here we describe two sets of such studies. The first focused on the development of pure-tonal vocal structure in song sparrows (Nowicki et al., 1992; Peters and Nowicki, 1996). Songbirds of this and other species typically produce songs that are highly pure-tonal, meaning that little energy is expressed in harmonic overtones (Nowicki and Marler, 1988). In the two focal studies, young birds were presented with training models in which notes expressed typical phonological structure yet contained artificially high levels of energy in harmonic overtones (achieved by recording birds as they sang in a helium-enriched environment, see Nowicki, 1987). Presentation of "harmonic" models enabled a test of the hypothesis that pure-tonal structure is learned, as might be expected given the key role of learning in the development of many other vocal parameters. However, birds were found to reproduce harmonic models mostly without harmonic content, thus arguing against the imitative learning hypothesis. These data instead suggest that song sparrows possess an innate propensity to develop songs with pure-tonal structure, which in turn might be shaped by an innate bias to produce songs using vocal tract postures that enhance tonal purity (Peters and Nowicki, 1996). This motor bias likely emerges gradually during the sensorimotor phase (Podos et al., 1995), supporting the hypothesis that sensorimotor learning functions in part to enable motor as well as neural refinement of the vocal mechanism.

The second set of experimental studies speaks more directly to the development of vocal proficiency in the face of performance challenges. These studies, described earlier, involved presentation of unusually rapid

trills to young swamp sparrows and mockingbirds (Podos, 1996; Zollinger and Suthers, 2004). Young birds of both species proved unable to accurately reproduce rapid models, in directions that suggested that birds encountered performance limits during development. An important limitation of both of these sets of studies, however, is that they revealed only the end-product of vocal motor development. By contrast they did not document the time courses or developmental trajectories over which motor biases were expressed.

B. UNFOLDING OF MOTOR BIASES

Perhaps the most direct method for documenting the influence of performance biases on song development would combine the above approaches, meeting three criteria: (1) documenting motor correlates of vocal ontogeny, for example, through direct studies of syringeal, respiratory, or vocal tract motor pattern development (e.g., Suthers, 2004); (2) training birds with song models modified to exhibit nontypical performance levels, in order to initiate modifications to song models to match birds' individual levels of vocal proficiency (e.g., Podos, 1996); and (3) tracking patterns of song ontogeny, in order to determine the sequence and timing of changes imposed on song models (e.g., Marler and Peters, 1982a). We know of no study that has met all three criteria, although one study, which we now discuss, has met the latter two criteria (Podos et al., 2004b). In this study, young swamp sparrows were presented three classes of song models: normal songs (as controls), songs with rapid trill rates, and songs with normal trill rates yet constructed with broken syntax, that is, with pauses interspersed between multisyllable segments (as described in Podos et al., 1999). Rapid trill models were expected to be difficult or impossible to reproduce in their original forms, because of performance limitations, whereas broken syntax models were anticipated to be unusually easy to reproduce, because of the presence of pauses between multisyllable segments. Of greater interest for our purposes was how and when birds would introduce modifications to memorized song models. Two contrasting scenarios for the expression of motor biases were envisioned. On the one hand, birds might have recognized early on, while acquiring and memorizing experimental models, that these experimental models did not match their own vocal capabilities, being either unusually difficult to produce or unusually easy to produce. According to this scenario, birds might have modified their song templates during the memorization process, well before they had any significant vocal experience. Modifications would thus have been purely neural in nature. On the other hand, birds memorizing models might be unable to anticipate future difficulties (or unusual ease of production) they

would encounter later in model reproduction. According to this scenario, birds would only introduce modifications to memorized songs during sensorimotor ontogeny, as they discovered mismatches between their own vocal abilities and those required for accurate model reproduction. Tracking of song copies during ontogeny provided strong support for the latter scenario (Podos et al., 2004b). Birds were observed to employ a number of tentative motor solutions before settling on solutions that defined the crystallized copies, for example, broken syntax for copies of rapid trill models or removal of pauses from within copies of broken syntax models (Podos et al., 2004b).

It thus appears that swamp sparrows possess the ability to calibrate the final structure of memorized models to better suit their own levels of vocal proficiency, and that this calibration begins and then ends during sensorimotor learning (Podos et al., 2004b). Conclusions about the broader relevance of this “calibration hypothesis” await parallel studies in additional species. Nevertheless it seems timely to speculate on the significance of this proposed link between performance biases and sensorimotor learning. One area of particular relevance, to which our attention now turns, concerns the “developmental stress” hypothesis.

V. VOCAL PERFORMANCE AND DEVELOPMENTAL STRESS

A. THE DEVELOPMENTAL STRESS HYPOTHESIS: OVERVIEW

In most songbird species, songs are produced by males and are used primarily for two functions: to repel territorial male rivals, and to attract potential mates. Towards these ends, songs of many species have evolved certain characteristics including high levels of complexity (Kroodsma and Byers, 1991; Searcy and Andersson, 1986; Searcy and Yasukawa, 1996), song patterns typical of local versus distant populations (e.g., Baker and Cunningham, 1985; Podos and Warren, 2007; Searcy et al., 2002), and high levels of performance (reviewed here). Why should receivers respond deferentially (males) or preferentially (females) to singers that produce songs with these characteristics—or, in more expansive terms, to singers that are able to successfully learn and reproduce songs with these characteristics?

The developmental stress hypothesis provides one possible answer to this question. In songbirds, aspects of song that reliably indicate singer quality are presumably of interest to both sexes. For females, choosing a high-quality mate might ensure direct benefits such as territory quality, or indirect benefits in the form of good genes for her offspring. For males, evaluation of singer quality might provide useful information about

whether to escalate or withdraw from impending territorial conflicts. In support of these expectations, a number of studies have identified correlations between male quality and song features (Searcy and Yasukawa, 1996). For example, one measure of song complexity, repertoire size, has been shown to correlate with reproductive success in several bird species including song sparrows (Hiebert et al., 1989), great reed warblers (*Acrocephalus arundinaceus*; Hasselquist, 1998; Hasselquist et al., 1996), and great tits (Lambrechts and Dhondt, 1986; McGregor et al., 1981). Similarly, birds sometimes gain higher reproductive success by singing songs with features typical of local versus distant dialects (e.g., MacDougall-Shackleton et al., 2002; Stewart and MacDougall-Shackleton, 2008). High-performance songs might also contribute to enhanced reproductive success (reviewed above). These kinds of observations do not, however, necessarily pinpoint mechanisms by which song features could become reliable (Maynard Smith and Harper, 2003; Searcy and Nowicki, 2005). From a proximate perspective, what would keep lower quality males from producing songs with more effective features? What costs or developmental constraints would curtail this kind of deception?

Nowicki et al. (1998, 2002a) proposed that learned song features attain reliability because song learning occurs during a restricted time window, when birds are young and confront severe stresses associated with nutritional needs. Altricial juvenile songbirds are completely dependent on their parents for food, and large percentages of young birds indeed die because of an inability of parents to provide sufficient food (O'Connor, 1984; Ricklefs and Peters, 1981). Although body growth in young songbirds is typically rapid, the development of brain regions integral to the acquisition and production of song unfolds over a protracted time period, coinciding with when birds are likely to experience nutritional stress. Because of the dependence of nutrition on successful brain development, adult song structure may thus provide receivers with reliable information about singers' early nutritional history (Nowicki et al., 1998, 2002a). Song structure may also reveal variation among singers in the quality of genes underlying phenotypic outcomes such as brain development or body condition. Moreover, to the extent that parental care is heritable, song structure may inform females about the quality of paternal care prospective mates could provide, because males raised by well-provisioning fathers are more likely to become good caregivers themselves.

As an aside, it is useful to note that young birds face additional stresses beyond poor nutrition—for example, in fighting parasitic infection—which has led to adoption of the more general term for the developmental stress hypothesis (e.g., Buchanan et al., 2003). It is also useful to view developmental stresses within the broader context of life history theory

(e.g., Gustafsson and Sutherland, 1988). In a general sense, stresses might introduce constraints on signal development without tapping into highly specified developmental pathways, or might impose incidental consequences of the complex relationships between developmental timing, ecological resource availability, and life history stages (e.g., Krause et al., 2009). However, the elaborate neural circuitry that mediates song learning and development does provide a specific mechanism on which developmental stresses can act, and thus through which individual variation in singer quality might manifest (Nowicki et al., 1998).

B. THE DEVELOPMENTAL STRESS HYPOTHESIS: EVIDENCE

Experimental tests of the developmental stress hypothesis for bird song learning have generally proceeded by manipulating a source of stress—food availability (by limited feeding or by brood size manipulation), parasite load, stress hormone levels, or social context—and then measuring the resulting effect on song features and song-system brain nuclei, particularly HVC and RA, which appear to develop only through about day 50, at least in zebra finches (reviewed by Nowicki et al., 1998). The volume of these song nuclei is known to correlate with repertoire size (Brenowitz and Kroodsma, 1996; Kroodsma and Canady, 1985), and likely mediates the expression of other song features as well (Vu et al., 1994; Yu and Margoliash, 1996). Zebra finches raised under developmental stress conditions show reductions in HVC size (Buchanan et al., 2004; but see Gil et al., 2006). In song sparrows, song nuclei growth is affected by developmental stress even before the onset of song learning; three song nuclei were measured at day 23–26 posthatch, and HVC in both sexes was found to be significantly smaller in nutritionally stressed birds than in control birds (MacDonald et al., 2006).

Developmental stresses may compromise a broad array of adult song features. Initial experimental work focused on the potential effect of developmental stress on song learning accuracy. Nowicki and colleagues (2002a) raised swamp sparrows collected between days 4 and 7 posthatch. From the time of collection to 28 days of age, birds in a control group were fed until satiation, whereas birds in an experimental group were fed only 70% of the average control group food intake. Despite remaining healthy, experimental birds proved to be significantly poorer learners, copying song models with reduced accuracy. Experimental groups also differed in the onset of sensorimotor development, such that experimental birds began practicing earlier. As expected, nutritional stress profoundly affected brain structure; both HVC and RA were significantly smaller in the nutritionally stressed birds. Results of similar studies on zebra finches have yielded mixed results. Gil et al. (2006) raised zebra finches in either large or small broods, thereby

manipulating food availability, and found no effect on song features or on the size of song nuclei. Zann and Cash (2008) similarly found no effect of nutritional stress on song learning accuracy. A study by Holveck et al. (2008) controlled for the potentially confounding effects of sibling learning and tutor song quality. While the number of copied song elements did not vary between groups, element transitions were copied with significantly less accuracy by birds raised in large broods.

Another song feature that has drawn interest in the developmental stress literature is repertoire size. An observational study of great tit populations inhabiting areas of varying heavy metal pollution reported striking variations in repertoire size, with males at the highly polluted site having significantly smaller repertoires, as compared to males at two other sites (Gorissen et al., 2005). Another observational study, in song sparrows, compared repertoire size to HVC volume and levels of stress (Pfaff et al., 2007). These researchers found that song sparrows with large repertoires were in relatively good condition, exhibited less physiological stress (measured by heterophil to lymphocyte ratios), and had more robust immune systems (measured by lymphocytes per red blood cell). In an experimental study of canaries, Spencer et al. (2005a) found that birds infected with malaria showed reduced HVC volume, smaller repertoires, and lower levels of song complexity. Soma et al. (2006) found that brood size manipulations had a pronounced effect on body size and song complexity, measured by both numbers of notes and syntactical complexity. To date, most experimental tests of developmental stress have focused on bird species with relatively limited note or song repertoire sizes—zebra finches, canaries, and Bengalese finches (*Lonchura striata*), and swamp sparrows. More definitive inferences about the relationship between developmental stress and repertoire size await experimental studies in species with larger repertoires.

Song learning accuracy and repertoire size are not the only song features that appear to be influenced by developmental stress. In the Zann and Cash (2008) study mentioned above, developmental stress led to reductions in syllable rate and maximum syllable frequency. And in the Holveck et al. (2008) study above, nutritionally stressed finches sang song bouts with less temporal consistency, as measured by inter-motif duration. Buchanan et al. (2003) raised European starlings with either unpredictable food supplies or with *ad libitum* food availability, and found that birds in the former condition later sang less in terms of bout numbers, time spent singing, and song duration. Adult barn swallows (*Hirundo rustica*) infected with Newcastle-disease virus produced one song feature, the rattle, with shortened duration, but were able to maintain other song features at control levels (Dreiss et al., 2008). Finally, in the Gorissen et al. (2005) study mentioned above, birds from a polluted site, which presumably experienced greater levels of developmental stress, sang at lower rates.

A number of studies suggest that song features influenced by developmental stress are attended to in social interactions. Nowicki et al. (2002b) played songs of developmentally stressed and nonstressed males to wild-caught female song sparrows from the same population. These songs differed in the accuracy with which they had been learned. Females were found to give significantly more copulation solicitation displays in response to accurately learned songs than to poorly learned songs. In another study of female choice, Spencer et al. (2005b) presented female zebra finches with songs from males raised with limited food, or with corticosterone injections, or under nonstress control conditions. When given a choice, females perched more often and for longer periods of time near playback of control songs than near playback of experimental songs, thus indicating preferences for songs of unstressed males. By contrast, Naguib et al. (2008a) found only minor effects of brood size manipulation on male songs, and no female preference for unstressed males. In starlings, song duration is a trait that is both negatively affected by nutritional stress (Buchanan et al., 2003) and discriminated against by females (Eens et al., 1991; Mountjoy and Lemon, 1996).

C. ADULT SONG AS AN INDICATOR OF SENSORIMOTOR-PHASE STRESSES?

The studies reviewed above indicate that developmental stress can impede the expression of a diverse array of vocal parameters. Some of these parameters, especially repertoire size and song learning accuracy, seem particularly likely to be influenced by early brain development and sensory learning, in accordance with original predictions of the developmental stress hypothesis. Other impacted parameters, however, such as song output and element duration, seem more likely to be shaped by birds' vocal performance capacities. Of key relevance here is emerging evidence that stressed birds appear to develop songs with lower levels of performance, for example, lower song output, reduced note or song duration, or lower consistency (Buchanan et al., 2003; Dreiss et al., 2008; Gorissen et al., 2005; Holveck et al., 2008; Zann and Cash, 2008). What would lead stressed birds to develop songs with lower levels of performance?

One possible answer to this question concerns singer condition. Perhaps birds that suffer stress as juveniles retain poor condition into adulthood and are thus unable to reproduce song models with baseline performance levels. Empirical evidence to date, however, suggests that birds stressed as juveniles typically recover baseline body size and condition as adults (e.g., Nowicki et al., 2002a). A more plausible answer to the question posed focuses on the learning process, and more specifically on the proposed relationship between vocal performance and sensorimotor learning.

Consider young birds that face stresses during their first weeks of life. As predicted by the developmental stress hypothesis, birds might fail to develop functional brain nuclei with sufficient robustness, and thus be unable to develop large repertoires or to reproduce model songs with accuracy. However, if the effects of stress extend into the sensorimotor period, additional negative impacts on song ontogeny might manifest in the realm of vocal performance. For instance, birds recovering from early stress might lack baseline abilities to reproduce challenging vocal features such as rapid trills or notes of extended duration, and thus crystallize songs with low performance levels. In the final accounting, songs would thus indicate not only bird's neural capacities as they existed during sensory learning, but also their performance capacities as they existed during sensorimotor learning.

This proposed extension of the developmental stress hypothesis is mostly speculative at the present time. It is virtually unknown as to whether the performance variables highlighted earlier in this chapter—duration, consistency, and trill structure—are indeed influenced by variation in developmental stress. For example, do stressed birds develop song repertoires with relatively poor consistency (Byers, 2007) or with fewer broadband trills (e.g., Kunc et al., 2006; Schmidt et al., 2006)? Do stressed birds develop trills with poorer consistency in note frequencies (Lambrechts, 1997), with narrowed frequency bandwidths (e.g., Podos, 1997) or with lower relative amplitudes (Forstmeier et al., 2002)? In addressing these types of questions it would seem especially useful to combine experimental manipulations of developmental stress with profiles of sensorimotor ontogeny, in order to attempt to document any resultant calibration of performance (Podos et al., 2004b).

VI. FUTURE DIRECTIONS

The connections, we have drawn in this chapter between vocal performance and sensorimotor learning suggest at least three avenues for further exploration. First, much remains to be learned about how individuals vary in their vocal performance abilities, and about how this variation might contribute to vocal signal evolution. Empirical studies of performance, as reviewed above, will continue to be invaluable in this regard. However, advances of a conceptual nature are also needed, particularly in terms of documenting how vocal performance contributes to overall patterns of signal evolution (Podos et al., 2004a). One challenge is in defining “performance,” which in its broadest sense can refer to actions that animals employ using available mechanisms. We recommend adopting a more

restricted definition of vocal performance, in line with its standard usage in the fields of ecological morphology and biomechanics. This definition would meet three criteria: (i) vocal performance is receiver-independent, that is, based solely on physiological, metabolic, biomechanical, cognitive, motor, or other proximate properties of the signal producer; (ii) performance maxima in vocal expression are reached when animals encounter upper limits in the attributes listed above; and (iii) resulting variations in vocal parameters enhance signal reliability, insofar as these vocal parameters are uncheatable (Maynard Smith and Harper, 2003).

In some species, performance variations may be found to bear only minimally on patterns of vocal evolution, particularly for species or populations that sing below maximum performance capacities. A possible example of this is Slabbekoorn and Smith's (2000) study of African black-bellied seed-crackers (*Pyrenestes ostrinus*), for which marked beak size variation appears to have no influence on patterns of vocal evolution. More commonly, vocal performance variation will likely impose a detectable yet only partial impact on vocal evolution. The evolution of trilled vocal parameters, for instance, has been shown to be shaped not only by vocal performance (receiver-independent limitations) but also by how these signals are learned, perceived, and influenced by the acoustic transmission properties the environment (e.g. Hansen, 1979; Nelson and Poesel, 2007; Podos, 1997; Wiley, 1991). This point is nicely reinforced in Naguib et al.'s (2008b) study of signal transmission in nightingales. These authors demonstrated that broadband trills, the presence of which reliably reflects male pairing success (Schmidt et al., 2006, 2008), experience substantial reductions of frequency bandwidth over relatively short distances, because of frequency-dependent signal attenuation.

A second avenue for further exploration concerns the potential role of vocal morphology in shaping song production. Vocal signals are known to be circumscribed by morphological parameters, and some vocal phenotypes made possible by specific morphological adaptations. An elegant example of this is provided in Fitch's (1999) study of tracheal elongation, a phenomenon in which tracheae are longer than they would appear to need be, sometimes coiled repeatedly in birds' sterna. Tracheal elongation has evolved repeatedly in diverse avian taxa and has now been linked to a specific acoustic phenomenon called formant frequency dispersion. In brief, birds with longer effective tracheae are able to produce calls in which acoustic energy achieves greater separation among vocal harmonics (Fitch, 1999, 2004). This appears to exaggerate birds' size, and thus may have evolved as an adaptive ploy for circumventing signal reliability with respect to information transmitted about body size (Fitch and Hauser, 2003). For this and parallel examples that do not involve imitative learning

(e.g., *Thamnophilidae*; Seddon, 2005), mapping of vocal output to vocal morphology presumably occurs with little or no auditory feedback, and vocal output presumably emerges mostly as a consequence of birds' vocal apparati. However, how does this mapping unfold in birds that learn their songs, and who thus have the opportunity to calibrate song structure during sensorimotor ontogeny? Might the timing and trajectory of this mapping provide reliable information about male developmental histories?

Consider the songs of Darwin's finches of the Galápagos Islands. Darwin's finches are typical close-ended learners, insofar as they copy songs from adults during their early lives and then retain song structure intact for the remainder of their lives (Bowman, 1983; Grant and Grant, 1996, 1997). Variation in beak morphology has been recently identified as a possible factor in shaping vocal evolution, particularly within the ground finches (*Geospiza* spp.). More specifically, birds with large beaks, adapted for applying strong crushing forces to food items, appear to face limits in the velocity of vocal tract modulations they can employ, thus possibly explaining the lower-performance songs these birds produce (Herrel et al., 2009; Huber and Podos, 2006; Podos, 2001). Might sensorimotor learning influence the expression of morphology-dependent performance limits in this system? Consider, to illustrate, a young finch that learns to sing by copying an adult with comparatively inferior vocal performance capacities, perhaps with the adult tutor possessing a beak larger than that of the learner. In this situation, two contrasting developmental scenarios can be envisioned. First, the young finch might copy the adult song accurately in all parameters. Accuracy in the reproduction and delivery of individual song types might be favored in species with small repertoires, such as the Darwin's finches, for which a vast majority of birds sing only a single song type. In this scenario, the bird would sing below his vocal potential, thus obscuring the relationship between vocal morphology and realized performance. At the other extreme, the developing bird might adjust his vocal output to capitalize on his superior vocal potential, for example, by augmenting trill rate or frequency bandwidth. Such calibration would enhance the relationship between vocal morphology and realized performance. At least two lines of evidence support the latter scenario. First, comparisons of songs from tutors and tutees indicate low levels of imitative accuracy (e.g., Grant and Grant, 1996, their Figs. 7 and 8). Plasticity in song transmission might arise in part from birds' abilities to calibrate their output to individual vocal performance capacities. Second, within one species with wide-ranging beak variation, correlations between beak morphology and vocal performance are quite strong (Huber and Podos, 2006; Podos, 2001). To the extent that the

second scenario is valid, adult songs would thus reflect the singer's vocal performance capacities, as well as his success in developing vocal morphology, at the time of sensorimotor learning—consistent with our proposed expansion of the developmental stress hypothesis.

A third avenue for further exploration concerns the diversity of learning programs birds express in nature. In strictly close-ended or “age-limited” learners, the crystallization process might act to preserve, for the life of an individual, information about his condition or performance abilities as they were manifest during sensorimotor learning. However, an array of songbird species acquire new songs well into adulthood, and thus undergo life long learning. In such “open-ended” learners, opportunities abound for recalibration to current performance limitations. For example, Botero et al. (2009) recently demonstrated that tropical mockingbirds (*Mimus gilvus*) sing learned syllable types with greater structural consistency as they age, perhaps because they achieve greater vocal proficiency with experience. Opportunities for postlearning recalibration may occur in species that do not have obviously open-ended learning programs. Some species that appear to be close-ended have recently been shown to retain the ability to learn some new songs later in life (e.g., Todt and Geberzahn, 2003), or to be able to adjust the structure of crystallized songs to a minor degree (e.g., Ballentine, 2009; Dalziell and Cockburn, 2008; de Kort et al., 2008; DuBois et al., 2009; Sakata et al., 2008;). Each year, males of many species sing plastic song before the breeding season, coinciding in time with the regrowth of song nuclei (Brenowitz et al., 1991; Meitzen et al., 2009; Nelson, 2000b; Nottebohm et al., 1986). Perhaps, in some species, this annual process allows birds to recalibrate their songs to current performance levels. Insights into how different species align with the different possibilities raised here will await further empirical study.

VII. SUMMARY

This chapter addresses the interplay of vocal performance, sensorimotor learning, and vocal evolution in songbirds. Vocal performance is increasingly recognized as an influential factor in song evolution, particularly with respect to vocal output, song consistency, and trill structure. We argue here that a comprehensive understanding of vocal performance requires attention to sensorimotor learning, a developmental phase during which birds attempt to reproduce song models memorized earlier in life. New research indicates that birds calibrate song structure during sensorimotor ontogeny in order to best match their own vocal performance capacities. Because of this relationship, performance-related features may provide reliable

indicators of male quality as manifest during sensorimotor learning. We review evidence in support of the “developmental stress” hypothesis, and propose that this hypothesis be expanded to also consider vocal features crystallized during sensorimotor learning. We suggest avenues for future research that document relationships between vocal performance, morphology, and song learning programs.

Acknowledgments

We thank Vincent Janik, Nicola Clayton, Klaus Zuberbühler, and Marc Naguib for inviting this contribution. A subsong-level version of this chapter was presented by JP at the 2008 International Conference on Vocal Communication in Birds, at St Andrews University, Scotland, held in honor of Peter Slater on his retirement. Hats off to Peter! We thank Marc Naguib, Bruce Byers, and an anonymous reviewer for feedback on a plastic song-level version of the manuscript. Any failure to achieve high intellectual performance or to articulate a crystallized argument is purely our own. The authors were supported by NSF grant 0347291 (to J.P.), and by the Biology department and the graduate program in Organismic and Evolutionary Biology (OEB) at the University of Massachusetts Amherst.

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