Birdsong Learning and Culture: Analogies with Human Spoken Language

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Abstract

Unlike many species, song learning birds and humans have independently evolved the ability to communicate via learned vocalizations. Both birdsong and spoken language are culturally transmitted across generations, within species-specific constraints that leave room for considerable variation. We review the commonalities and differences between vocal learning bird species and humans, across behavioral, developmental, neuroanatomical, physiological, and genetic levels. We propose that cultural transmission of vocal repertoires is a natural consequence of the evolution of vocal learning and that at least some species-specific universals, as well as species differences in cultural transmission, are due to differences in vocal learning phenotypes, which are shaped by genetic constraints. We suggest that it is the balance between these constraints and features of the social environment that allows cultural learning to propagate. We describe new opportunities for exploring meaningful comparisons of birdsong and human vocal culture.

1. INTRODUCTION

Spoken language includes multiple component traits (Hauser et al. 2002, Fitch 2017, Jarvis 2019, Wirthlin et al. 2019). Certain components are nearly ubiquitous among vertebrates, such as auditory learning (including limited speech comprehension by some nonhuman animals) and vocal usage learning, the ability to learn to produce sounds in specific contexts, as when a dog learns to produce a specific bark (innate sound) for food (learned context). However, other components are special to only a few animal lineages, for example, vocal production learning, the capacity to imitate complex vocal sound sequences. This vocal learning component enables culturally mediated transmission of novel sounds, as well as of novel information through sound.

Vocal production learning is absent or very limited in our closest relatives, the nonhuman primates (Janik & Slater 2000, Petkov & Jarvis 2012, Watson et al. 2015, Jarvis 2019). However, it is more advanced and abundant in some more distant relatives, including bats (Knörnschild 2014), dolphins, and whales (Janik 2014), among mammals, and songbirds (Thorpe 1954, 1958; Marler & Tamura 1962; Marler 1970b), parrots (Schachner et al. 2009), and hummingbirds (Baptista & Schuchmann 1990, Jarvis et al. 2000), among birds. Some suboscines, a sister clade to songbirds, possess no vocal plasticity, and other suboscines have rudimentary vocal plasticity (Trainer et al. 2002, Liu et al. 2013). The more advanced vocal learning clades (including humans) are thought to have evolved their vocal learning behavior independently (Petkov & Jarvis 2012, Jarvis et al. 2014, Jarvis 2019). Yet, over the last decade, discoveries about the neuronal and genetic mechanisms of vocal learning have revealed striking mechanistic similarities between spoken language in humans and song in vocal learning birds (Bolhuis et al. 2010, Pfenning et al. 2014, Jarvis 2019).

However, deciphering a set of common "rules" for characterizing vocal learning is not straightforward. Although there is only one primate species with a highly developed vocal learning capacity (humans), there are more than 5,000 songbird species, more than 300 each of parrots and hummingbirds (Jarvis 2004), more than 1,000 bat species (Teeling et al. 2018), and 96 cetacean species (Morin et al. 2020) that are thought to be vocal learners. Among these, there is a great diversity of vocal learning phenotypes. In the twenty-first century, a single species, the zebra finch, has become the dominant vocal learning model organism (Griffith & Buchanan 2010, Nottebohm & Liu 2010, Mello 2014). Just as the laboratory mouse is not representative of all mammals, it would be incorrect to assume that all nonhuman vocal learners or even all songbirds have the zebra finch phenotype. For example, only male zebra finches learn to sing, but in the case of many tropical songbirds both females and males sing (Morton 1996). Similarly, zebra finches have a limited repertoire of vocal elements and very modest syntactic variation in their sequencing, while the repertoires of some other species, such as the chipping sparrow, consist of even simpler, one-syllable songs; still others, especially those belonging to birds that mimic other species, such as the European starling (Eens 1997), include dozens of songs and greater combinatorial syntactic complexity. Although there is striking diversity in both song and social complexity across songbirds (**Figure 1**), very few species have been studied with respect to song learning mechanisms.

Comparisons with human speech development are hampered by shifting views on defining vocal learning (Slater et al. 2000, Petkov & Jarvis 2012, Wirthlin et al. 2019), in addition to our relatively limited understanding of the human vocal learning program (Jarvis 2019). For a time, birdsong learning was widely conceived of as a process of sensorimotor template matching, as in the white-crowned sparrow, an early model songbird (Marler 1970a, 1997). How this process mapped onto spoken language acquisition was unclear. When a different learning program, overproduction and selective attrition, was discovered in swamp sparrows, some researchers interpreted this as evidence of a newfound similarity between songbird and human vocal exploration (Marler & Peters 1982). However, pruning processes in babbling and early language development seem to be less important than was once theorized (Oller 2000).
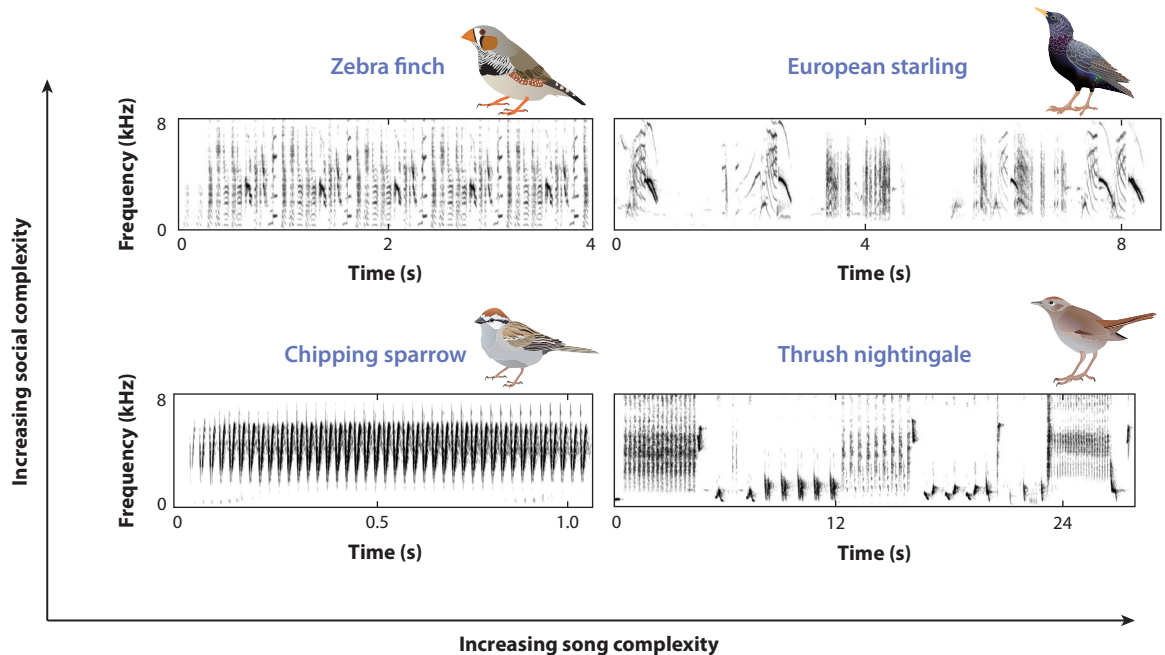
Figure 1

Sonograms depicting the wide diversity in learned song complexity across songbird species. Chipping sparrows produce a one-syllable trill. Zebra finches produce single-motif songs, which vary from one individual to another. Thrush nightingales produce several types of complex songs, with greater diversity. European starlings produce highly complex songs, with both short- and long-range syntactical relationships. Chipping sparrows and thrush nightingales are migratory and territorial, whereas zebra finches and starlings are nomadic/sedentary and group-living. Zebra finch songs were obtained from the Rockefeller University zebra finch song library (forthcoming in Linguistic Data Consortium; see **https://www.ldc.upenn.edu/**). Chipping sparrow, European starling, and thrush nightingale songs were obtained from xeno-canto (see **https://www.xeno-canto.org/574790**, **https://www.xeno-canto.org/543800**, and **https://www.xeno-canto.org/593062**)/CC BY-NC-SA 4.0.

To avoid superficial analogies that rest on a single model organism, it is necessary to compare multiple species (Jarvis 2019, Wirthlin et al. 2019). Furthermore, only comparative studies can reveal universal patterns, if they exist (Lattenkamp & Vernes 2018). One fascinating recent study (Love et al. 2019) analyzed song databases of socially isolated and normally reared songbirds from 16 different species and found substantial variability in phonology, syntax, and rhythm, unrelated to phylogenetic relationships. In general, the evidence for a weak phylogenetic signature on bird-song structure suggests that innate constraints on song learning are evolutionarily labile.

The multidimensional skills required for vocal learning (Wirthlin et al. 2019) overlap with many other behaviors, including spatial exploration (Tchernichovski et al. 1998) and social coordination of unlearned vocalizations (Benichov et al. 2016). Sanderlings feeding on the beach, running and searching frantically for isopods in the tidal zone while managing to stay in coordination with the ocean waves and with one another's movements, demonstrate remarkable sensorimotor skills, perhaps as complex as those required for vocal learning. Consistent with these observations, a strong case has been made that vocal learning brain pathways evolved out of motor-learning pathways that control complex, learned nonvocal behaviors (Feenders et al. 2008, Tokarev et al. 2011, Chakraborty & Jarvis 2015, Jarvis 2019). However, vocal learning is special in that it can support a rich and polymorphic culture (Tchernichovski et al. 2017). Local birdsong dialects or parrot learned call dialects, like human spoken languages, may persist over hundreds of

generations (Haugen 1966, MacDougall-Shackleton & MacDougall-Shackleton 2001, Lachlan et al. 2018, Pipek et al. 2018, Wright & Dahlin 2018). Although such dialects can show considerable variation between populations and/or individuals, research on zebra finch song culture suggests that built into the vocal learning mechanism is a stabilizing cultural constraint that resists collapse into uniformity or chaos (O. Tchernichovski, S. Eisenberg-Edidin & E.D. Jarvis, manuscript in review; **https://doi.org/10.21203/rs.3.rs-80497/v1**).

In this review, we examine how vocal learning can generate and perpetuate stable polymorphic cultures, with a focus on comparing bird song culture and human spoken language. We view vocal culture as an extension of vocal development across generations (Fehér et al. 2009). We first describe the biological processes that underlie birdsong and spoken-language learning. We then review how these processes manifest at the macro level of vocal culture. Finally, we explore how dynamic vocal exchanges may accumulate into vocal cultures across generations of learners.

2. BIOLOGICAL PROCESSES THAT UNDERLIE VOCAL LEARNING

To understand vocal learning, and thus how culture is transmitted through vocalizations, we need to consider this trait at multiple biological levels. In the following subsections, we review mechanisms of vocal learning at the behavioral, brain, and genetic levels.

2.1. Behavior

The development of vocal learning after birth proceeds according to similar phases across diverse species (**Figure 2**). In vocal learners, vocal development begins with a sensory acquisition phase, in which auditory memories are formed of sounds heard, for example, the tutor bird's song; analogously, human babies can understand the meaning of speech sounds before they can produce them (Doupe & Kuhl 1999). Then, in a sensorimotor phase, humans and songbirds alike begin to practice and try to produce complex vocal sounds. During this stage, birds produce highly variable vocalizations, which gradually form clusters of discrete vocalization types. The process through which vocalization types (clusters) are formed is entangled with a slow development of combinatorial structure. These processes show similarities across species (Lipkind et al. 2013, 2017, 2019), but their function and outcomes vary, depending on the degree to which combinatorial structure develops (Sainburg et al. 2019). With the transition to adulthood (or seasonally in some birds), learned vocalizations become crystallized, with future learning becoming more difficult or even impossible, depending on the species. As a result, the early juvenile sensory and sensorimotor phases are called the sensitive period for vocal learning (Marler & Peters 1987). In contrast, vocal nonlearners, such as the marmoset among primates (Tchernichovski & Oller 2016, Jones et al. 2018) or the mouse among rodents (Grimsley et al. 2011), go through developmental changes, but these changes do not require external auditory models to copy, even though their development is influenced by social interactions.

With songbirds that can be kept in the lab, an experimentalist can determine when learning starts and how it progresses by controlling the song learning environment, for example, by socially isolating birds or manipulating tutor song exposure. Synthetic songs can be designed to present developing songbirds with specific vocal learning tasks, thereby gaining insights into specific aspects of vocal development such as phonetic or syntactic learning. Experimental research with zebra finches has shown that discrete sound units emerge via differentiation of immature prototype syllables (Tchernichovski et al. 2001), that vocal sequences are constructed in a stepwise manner rather than freely strung together in both zebra finch and early human vocal development (Lipkind et al. 2013), and that phonological matching is prioritized over the correct syntactic context during imitation (Lipkind et al. 2017). This last process could have a shared mechanistic
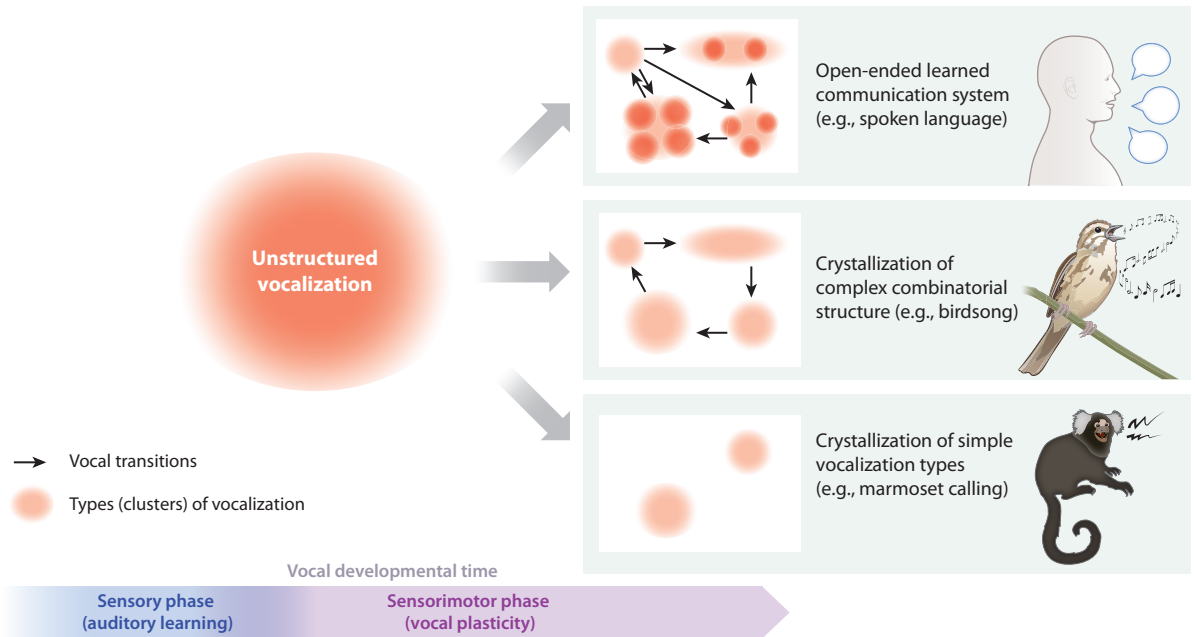
Figure 2

Schematic illustrating the phases and diversity of vocal development phenotypes. We include the marmoset monkey, a vocal nonlearner, as a reference and to illustrate a proposed continuum of vocal learning and plasticity (Petkov & Jarvis 2012, Arriaga & Jarvis 2013). During the early sensory phase of vocal development, animals acquire auditory memories of vocal sounds. The animal's own vocalizations are unstructured and variable. During the sensorimotor phase, vocalizations become more structured and form distinct syllable types, shown as clusters. Gradually, the animal learns to produce combinatorial sequences (*black arrows*) of syllable types. The ranges of clusters produced and their combinatorial structure vary strongly across species.

basis with the chipping sparrow's song learning program, where the juvenile matches one of several song precursors to a tutor's song, morphing whichever precursor is closest to the tutor song in acoustic space (Liu & Nottebohm 2007). There is some evidence that zebra finches and humans alike also use holistic strategies during vocal development, for example, acquiring the temporal framework of a vocal sequence independently of its content (Liu et al. 2004, Hyland Bruno 2017).

Despite these commonalities, species vary in their development and use of learned vocalizations, from territorial species like the thrush nightingale or song sparrow, where song learning is spread over large spatial scales (Sorjonen 1987, Beecher 2017), to gregarious species like the European starling and zebra finch, which learn and interact in close proximity (Zann 1996, Hausberger 1997). Some songbird species, such as the zebra finch, develop quickly into adults, acquiring their adult song repertoire within 3 months of hatching, and are unable to learn new song repertoires as adults; in addition, only male zebra finches develop learned songs (Immelmann 1969), whereas females have lost the trait (Odom et al. 2014, Choe et al. 2020). Other birds, like African gray parrots, develop slowly over years, living almost as long as humans, and continue learning new vocalizations as adults, with both males and females exhibiting vocal learning (Bradbury & Balsby 2016). Song learning programs can differ across species in other ways, such as in the influence of external models, the influence of the social context, the schedule of sensory and sensorimotor phases of learning, and the number and type of songs acquired (Beecher & Brenowitz 2005, Brenowitz & Beecher 2005). These characteristics are not necessarily independent: A recent comparative study of published data from 67 songbird species (Robinson et al. 2019) demonstrated that song

repertoire size and song learning plasticity (open- versus closed-ended learning) are correlated, suggesting that selection (e.g., sexual) on song characteristics can also determine the window of plasticity for song learning.

2.2. Brain

Spoken language, and therefore speech production learning, is controlled by specialized brain structures. Brain functional connectivity studies in humans together with neural tracing studies in songbirds as well as other nonhuman animals have revealed the brain circuitries necessary for the different components of vocal learning (Jarvis 2019). However, among all of the vocal learning lineages, bird brains are the most accessible and thus have been the best studied; they have also spurred numerous advances in electrophysiological and other measures of neural activity, including in awake and behaving (e.g., singing) birds. Song learning behavior can be measured while recording continuously from sensory and motor neurons in the song control forebrain nuclei (Hahnloser et al. 2002). In vivo electrode recordings, calcium imaging, and functional magnetic resonance imaging (in humans) have recently made it possible to observe the activity of hundreds of those neurons simultaneously during song/speech production and learning (Bouchard & Chang 2014, Liberti et al. 2016, Simonyan et al. 2016, Ibayashi et al. 2020). Optogenetic techniques have been used to isolate the parts of the brain involved in the very early stages of memorizing tutored song (Roberts et al. 2012, Tanaka et al. 2018, Zhao et al. 2019), which is possible because auditory input can be controlled in birds during development.

The use of these and other approaches has enabled comparisons between brain pathways for the different components of spoken language and brain pathways in nonhuman species. Like the behaviors themselves, brain pathways that control more ubiquitous behaviors, like auditory learning, are found in most species (blue area in **Figure 3**), whereas those that control the rare behavior of vocal production learning are found only in the vocal learning species (yellow and red areas in **Figure 3a,b**). In most species, an auditory forebrain circuit consisting of neurons that bring input in from the ears to reach the brainstem and forebrain are involved in the processing and perception of complex sounds, including human speech or birdsong. In vocal learning species there is a phylogenetically convergent forebrain vocal motor learning pathway that consists of a posterior motor pathway involved in the production of learned vocalizations (yellow areas in **Figure 3a,b**), including spoken language, and an anterior vocal learning pathway involved in the acquisition of novel vocalizations (red areas in **Figure 3a,b**), as well as (in humans) complex sequencing of words (Jarvis 2004, 2019). In addition to the presence of this pathway as a specialization of the surrounding motor learning pathway, two specialized connections, common to vocal learning species, have been proposed as critical to the capacity for vocal learning and spoken language: (*i*) a direct and robust connection from the auditory pathway into the anterior vocal learning or spoken-language pathway (blue arrows in **Figure 3b,d**) (Friederici et al. 2017) and (*ii*) a direct projection from the vocal motor cortex to brainstem vocal motor neurons that control the muscles to produce song and speech (green arrows in **Figure 3a,b**) (Fitch et al. 2010, Petkov & Jarvis 2012). Such projections and even the anterior forebrain pathway may be present in a rudimentary manner in some species not considered to be vocal learners (**Figure 3d**), leading to the continuum hypothesis of vocal learning and auditory learning (Petkov & Jarvis 2012, Arriaga & Jarvis 2013), where different species possess these traits to various degrees. Only in humans and the three vocal learning bird lineages have they been found to be present at a robust level. Known differences among vocal learners include extra parallel vocal learning systems in humans and parrots (Chakraborty & Jarvis 2015) and, in humans, more forebrain areas devoted to the processing and production of vocal communication (**Figure 3a** versus **Figure 3b**) (Belyk & Brown 2017).

Functional activity studies in humans and song learning birds have revealed that the auditory pathway regions are active mainly during processing of sounds, including self-generated vocalizations (Sen et al. 2001, Yi et al. 2019). Processing of species-specific vocalizations is more prominent in higher-order auditory regions (Mello et al. 1992, Romanski & Averbeck 2009, Schneider & Woolley 2013). The activity of these regions is thought to send signals into the vocal learning pathways (Friederici et al. 2017, Jarvis 2019), which utilize that information to modify their own circuitry to learn coordinated control of the respiratory muscles and vocal organ (larynx in humans and syrinx in birds), as well as other orofacial musculature, necessary for producing imitated speech and song. In songbirds, neural activity in the vocal motor pathway is time-locked with the acoustic structure and sequencing of song syllables (Cardin & Schmidt 2003, Leonardo & Fee 2005), whereas neural activity of the anterior vocal learning pathway is associated with
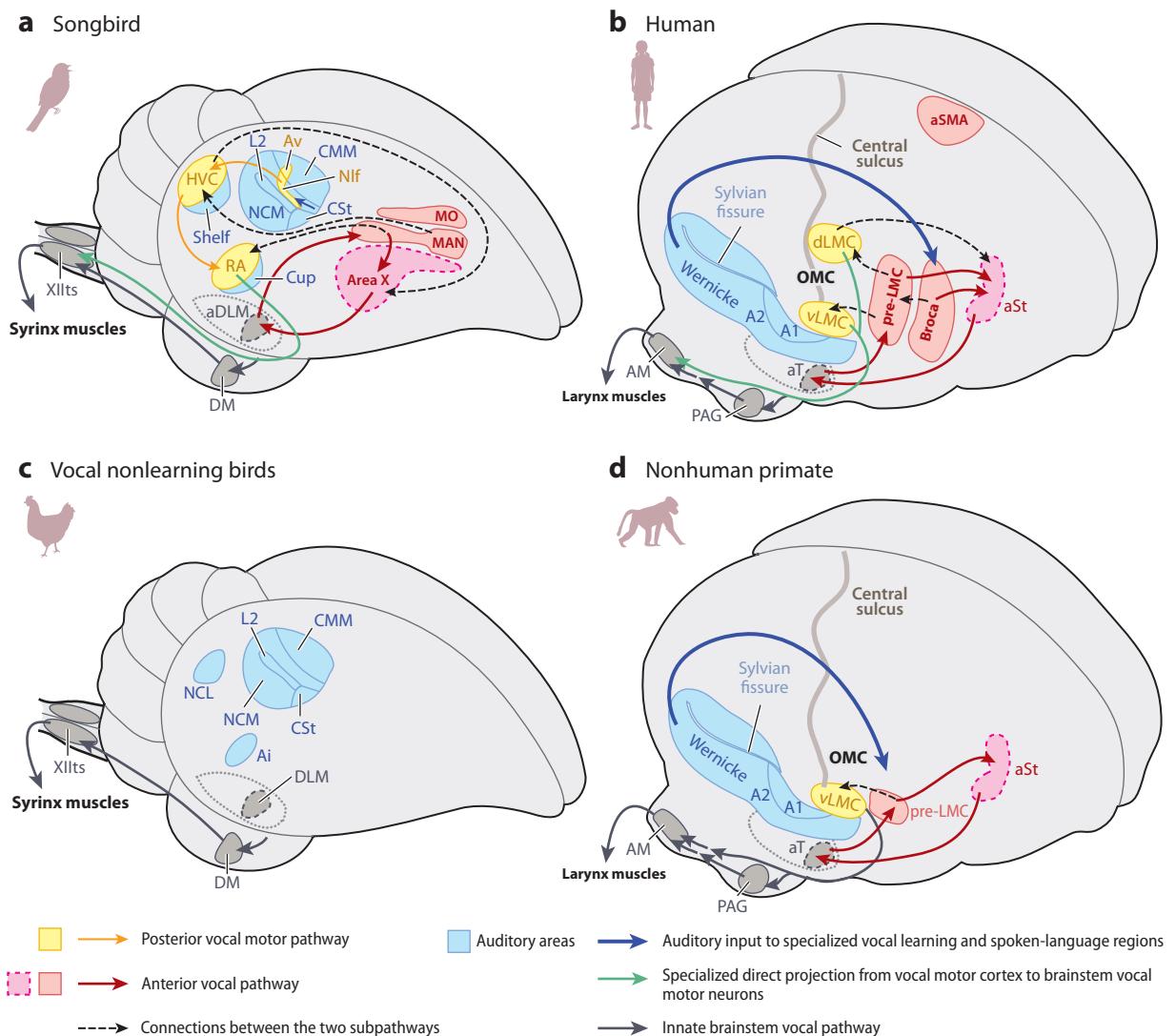
(*Caption appears on following page*)

Brain pathways for auditory learning and for song learning in birds and spoken language in humans. (*a*) Vocal learning pathway of songbirds. (*b*) Vocal learning and spoken-language pathway of humans. (*c*) Innate brainstem vocal pathway in vocal nonlearning birds. (*d*) Vocal pathway in nonhuman primates. Comparable brain regions across species are shown in the same color and projected on smoothed surface brain images. Yellow regions and yellow solid arrows represent the posterior vocal motor pathway; red regions and red arrows, anterior vocal pathway; dashed arrows, connections between the two subpathways; green arrows, specialized direct projection from vocal motor cortex to brainstem vocal motor neurons in vocal learners (*a, b*); dark gray regions, brainstem innate vocal pathway; blue regions, auditory areas; blue arrows, auditory input to specialized vocal learning and spoken-language regions. Subcortical vocal regions are outlined with dotted lines. The yellow and red regions in nonhuman primates (*d*) are less transparent to indicate the continuum hypothesis of a rudimentary forebrain vocal circuit. A subset of connections are shown for simplicity. Abbreviations: A1, primary auditory cortex; A2, secondary auditory cortex; aDLM, anterior dorsolateral medial nucleus of the thalamus; Ai, intermediate arcopallium; Am, nucleus ambiguus; aSMA, anterior supplementary motor area; aSt, anterior striatum speech area; aT, anterior thalamus speech area; Av, avalanche; CMM, caudal medial mesopallium; CSt, caudal striatum; cup, region of cells below RA; dLMC, dorsal laryngeal motor cortex; DM, dorsal medial midbrain nucleus; HVC, a letter-based name; L2, field L2; MAN, magnocellular nucleus of the nidopallium; MO, mesopallium oval nucleus; NCM, nidopallium, caudal medial; NIf, nidopallium interfacial nucleus; NLC, nidopallium, lateral caudal; OMC, oral motor cortex; PAG, periaqueductal gray; pre-LMC, premotor laryngeal motor cortex; RA, robust nucleus of the arcopallium; shelf, shelf of cells below HVC; vLMC, ventral laryngeal motor cortex; XIIts, twelfth vocal motor nucleus, tracheosyringeal part. Figure adapted with permission from Jarvis (2019).

modulating activity of the vocal motor pathway, as well as with premotor activity that instructs the vocal motor pathway's firing (Brainard & Doupe 2002, Fee & Goldberg 2011). It remains difficult to resolve the more detailed neural similarities and differences between humans and vocal learning birds, in part because one cannot perform the same brain manipulation experiments in humans. Nevertheless, the general anatomical principles of vocal learning may yield insights into the neural mechanisms of speech and language acquisition as well as associated disorders.

2.3. Genetics

Unlike neural tracing and neural activity experiments, comparative analyses of gene regulation and genomic sequence can be done on postmortem tissue. Recent studies in birds and mammals have found similarities in the genes regulated in auditory pathways in vocal learning and vocal nonlearning species (Horita et al. 2010, Pfenning et al. 2014), paralleling similarities in their auditory processing. However, although many genes expressed in the vocal learning pathways are similar to those in the surrounding motor learning pathways, a sizable proportion (hundreds to more than 1,000) have specialized up- or downregulation in the human speech and songbird song learning areas relative to the surrounding motor pathways, with the number of genes depending on the brain region and cell type (Pfenning et al. 2014, Lovell et al. 2018). Furthermore, a subset of several hundreds of these genes show convergent specialized regulation in humans and song learning birds (Pfenning et al. 2014). This convergent regulation has allowed researchers to begin to figure out which brain regions and neuron types in song learning birds are similar to or different from those involved in spoken language in humans (Jarvis 2019). The songbird brain areas HVC and RA (robust nucleus of the arcopallium), involved in the production of learned song, are convergent in terms of neuronal composition with the upper and lower cortical layers, respectively, of the human LMC (laryngeal motor cortex), a region of the primary motor cortex involved in the production of learned speech (Pfenning et al. 2014; G. Gedman & E.D. Jarvis, manuscript in preparation). Area X in the avian striatum, a key nucleus of the anterior forebrain pathway necessary for song learning, is most convergent with the ASt (anterior striatum speech area) in the human striatum, also implicated in speech and song learning (Pfenning et al. 2014, Simmonds et al. 2014). To date, no strong molecular convergences have been found for songbird

LMAN (lateral magnocellular nucleus of the nidopallium) and human Broca's area, both of which are involved in higher-level control of song and speech behaviors, including vocal learning.

The specific genes that show convergent specialized regulation inform us as to what is specialized about vocal learning circuits and behavior. They include a battery of genes that control neural connectivity, including in the neurons that make the specialized direct projections to brainstem vocal motor neurons from songbird RA and human LMC (Pfenning et al. 2014, Wang et al. 2015). Other genes are involved in neuroprotection of cells from dying when firing at high rates; songbird vocal learning pathway neurons are known to fire at higher rates than the surrounding motor areas (Adret & Margoliash 2002), and moreover, the syrinx and larynx contain some of the most rapidly firing superfast muscles in avian and mammalian bodies (Riede & Goller 2010, Mead et al. 2017). Still others are genes that control neural plasticity.

Some genes with convergent specialized expression in song learning birds and humans (e.g., *SLIT1*) are regulated by a well-studied gene involved in spoken language, *FOXP2*. A heterozygous mutation in this transcription factor causes a speech apraxia in humans; affected individuals have difficulty learning how to sequence complex syllables of sound into complete words and sentences, although they maintain much more normal functioning in auditory learning, comprehension, and many other motor behaviors (Morgan et al. 2017). In mice, initial findings showed that the *FOXP2* mutation reduces intensities of innate calls, perhaps due to developmental delays and somatic weakness (Gaub et al. 2010). More systematic studies of mouse ultrasonic courtship songs revealed that *FOXP2* is necessary for males to switch from producing simple sequences of syllables to more complex ones, which female mice prefer (Chabout et al. 2015, 2016; Castellucci et al. 2016), reminiscent of the vocal sequencing impairments observed in humans. Studies of *FOXP2* function in songbird Area X revealed that, as in humans, the gene is not necessary to produce sounds but is necessary to learn to imitate or modify them appropriately (White et al. 2006, Haesler et al. 2007, Murugan et al. 2013). Altogether, these findings suggest that (*i*) *FOXP2*, presumably in concert with other genes, was first used to modulate innate vocalizations and (*ii*) when vocal learning evolved, the gene and its target molecules involved in neural connectivity were co-opted to develop and control a novel specialized vocal learning circuit with properties similar to but divergent from the surrounding motor learning pathway.

3. SONG/SPEECH LEARNING AND CULTURE

The similarities between biological processes underlying vocal learning in songbirds and humans invite comparison at the macro level of culture. During the mid-twentieth century, Peter Marler and others discovered that patterns of singing behavior in songbirds extend across many territorial individuals in a several-mile radius (Marler & Tamura 1962, Nelson & Marler 1990). These localized singing patterns are sustained across multiple breeding seasons, giving rise to the emergence of local song dialects. Since Marler's initial discovery, much knowledge has accumulated about the social and biological forces that sustain vocal cultures in songbirds, which can now be compared with vocal cultures in humans, including spoken language. We focus the following discussion on providing a biological perspective on species-specific universals in vocal culture.

3.1. Universal Features of Birdsong, Speech, and Music

Both birdsong and human speech are systems whose articulatory basis is a precisely controlled oscillation of the vocal apparatus corresponding to an equally precise acoustic oscillation in perceptually salient features. Birdsong and speech have a similar conceptual organization in terms

of complex sequences of elements drawn from a small, finite set of discrete types of articulatory and acoustic patterns. In both birdsong and human speech, these patterns are culturally learned, with outcomes that vary widely across communities while retaining species-typical characteristics. This similarity led Charles Darwin to hypothesize that human language developed out of singing (Darwin 1871, Fitch 2010), and that birdsong is "the nearest analogy to language," with the referential aspects of human speech gradually overlaid on skills in production and perception originally evolved for song. Whether or not this conjecture is true, the analogies remain striking.

Both spoken language and birdsong are acquired primarily during early life via cultural transmission. However, as opposed to speech, most birdsong is not used for communicating knowledge and is produced mainly in the context of courtship and territorial defense (Catchpole & Slater 2003). In rare cases, birdsong may be referential; in the black-capped chickadee, for example, although the learned song is highly stereotyped, composed of two simple syllables, small acoustic changes to these syllables communicate knowledge of predators and predator size (Templeton et al. 2005). In contrast, a common nightingale sings hundreds of complex song types lacking any apparent semantic referents (Hultsch & Todt 1981). Song complexity may reflect the intensity of sexual selection. It is, to a large extent, a show of performance. Although it is widely believed that birdsong does not convey complex information (Berwick et al. 2013), that does not mean that it is meaningless. For example, there is evidence that in cooperatively breeding species such as the superb starling (*Lamprotornis superbus*), singing behavior can signal identity and even social rank within separate dominance hierarchies. Interestingly, the song motifs of these birds continually accrue complexity over the birds' lifetime (Keen et al. 2016). In some respects, it might be more useful to compare the functionality of birdsong with that of human song rather than speech (Rothenberg et al. 2014, Roeske et al. 2020). Both music and birdsong can exert a strong influence on the behavioral state of listeners. Listening to song has an immediate and specific impact on the reinforcement brain area of the bird (Tokarev et al. 2017), as in humans with chills-inducing music (Salimpoor et al. 2011).

The theory of birdsong universals began with Marler's (1997) observations that song dialects diverge locally but converge globally within a species. That is, although experts may be able to identify the geographical origin of a bird by its song dialect (as with speech dialects), the drift in song dialects across spatial scales appears to be fairly limited. Marler studied the tendency for individuals to converge on a species-typical song structure, and characterized his findings as evidence for universals. The concept of song universals was initially vague, but the idea has been fleshed out in more recent studies, which revealed statistical learning biases that can explain some of the natural convergence to a species-typical song structure, with parallels to both spoken-language development and universals in human music (James & Sakata 2017, Roeske et al. 2020).

Regularities in sequential song structure are among the most salient species-typical characteristics of birdsong. If you hear a bird's song that sounds like two whistles of descending pitch ("fee bee"), you are probably listening to a chickadee. Furthermore, white-crowned sparrows tutored with only pairs of adjacent syllables are capable of reconstructing an entire species-typical song from these pairs (Rose et al. 2004). From a cultural and learning perspective, however, perhaps the more interesting cases are species in which each individual bird sings a unique song sequence. Zebra finches, for example, produce unique but species-typical syllables in a fixed but idiosyncratic order that is not preordained (**Figure 1**). Young birds can be trained to imitate a synthetic song with an arbitrary sequence of syllables, and subsequently even to reverse the syllable order (Lipkind et al. 2013). Nevertheless, it appears that zebra finches still prefer to place certain syllable types in certain positions in their songs. Juvenile zebra finches exposed to song playbacks of random combinations of zebra finch syllable types acquired nonrandom sequences, with high-pitched syllables placed closer to the beginning of their song motif and harmonic sounds in the final

position (James & Sakata 2017). Similarly, in nightingales, when birds were exposed to candidate songs that deviated from the species-typical canonical A–B–C–D pattern, they often made modifications in their imitated versions that recovered the A–B–C–D pattern (Todt & Hultsch 1998). Such statistical biases in the cultural transmission of sequential song structure, which have also been described for canaries (Gardner et al. 2005) and Bengalese finches (James et al. 2020), even if relatively weak, may accumulate across generations to promote convergence toward a species-typical song (Fehér et al. 2009). Overall, these and other findings demonstrate that individual learners actively regularize song diversity to produce species-specific universal "grammars."

Similar regularities can be found in birdsong rhythms. Rhythm is a universal feature of music. Given that there are nearly infinite possible ways of arranging musical notes in time, it is remarkable that musical rhythms across cultures are distributed categorically. Interestingly, a recent study (Roeske et al. 2020) demonstrated that the statistical structure of song rhythms produced by wild thrush nightingales resembles that produced during live performances of music spanning a range of different styles. In particular, isochronous 1:1 rhythms are similarly common in birdsong and human music, while high-ratio birdsong rhythms appear analogous to ornamental musical rhythms. Furthermore, in both species, rhythm categories are stable over an extended range of tempos. These findings raise the possibility that song universals reflect similar constraints on learning motor skills across species. An open question is whether, beyond developmental constraints, such universals might promote the cultural transmission of learned vocalizations.

3.2. Developmental Origins of Song Culture

Why do learning biases exist? Statistical universals in the sequential order of zebra finch songs (James & Sakata 2017) might stem from developmental constraints on song structure. Early in development, birds tend to intersperse unlearned calls toward the end of singing bouts (yellow shading in **Figure 4**), which consist of a single repeated prototype syllable (red shading in **Figure 4**) (Tchernichovski et al. 2001, Aronov et al. 2008). Later in development, some of these innate calls can still be found as stereotyped call-like syllables (brighter yellow shading in **Figure 4**), which naturally appear toward the end of the emerging song motif. We suspect that the reason these innate calls often appear toward the end of the motif is because the call-like syllables tend to be added to the core motif late in development.

Another developmental origin of species-typical vocal sequences is the process of in situ differentiation of vocal sounds (Tchernichovski et al. 2001). For example, zebra finches typically begin bouts of song with repeated short syllables termed introductory notes (light blue shading in **Figure 4**) (Price 1979). During development, some of these introductory notes differentiate into song syllables. As with the unlearned calls, syllables that are derived from introductory notes tend to appear at the edge of the song motif, but in this case they appear at the proximal edge, namely at the beginning of the motif. Lipkind et al. (2013) showed that still-developing zebra finches have the capacity to change the combinatorial order of syllables already learned. However, this process is laborious, and this may be a general feature of the emergence of a vocal combinatorial capacity during development. A comparative analysis of vocal babbling in human infants showed that once the infant learns to produce a new syllable type, it takes several months for the infant to combine it with other syllable types (Lipkind et al. 2013). The laborious nature of combinatorial learning might account for the persistence of song patterns across generations within a population, perhaps giving rise to some of the local birdsong dialects that Marler discovered.

More generally, during song development, highly variable sounds are "compressed" into stereotyped song elements (red shading in **Figure 4**), which morph from highly modulated broadband sounds into complex articulated acoustic structures. In some species, this process reduces
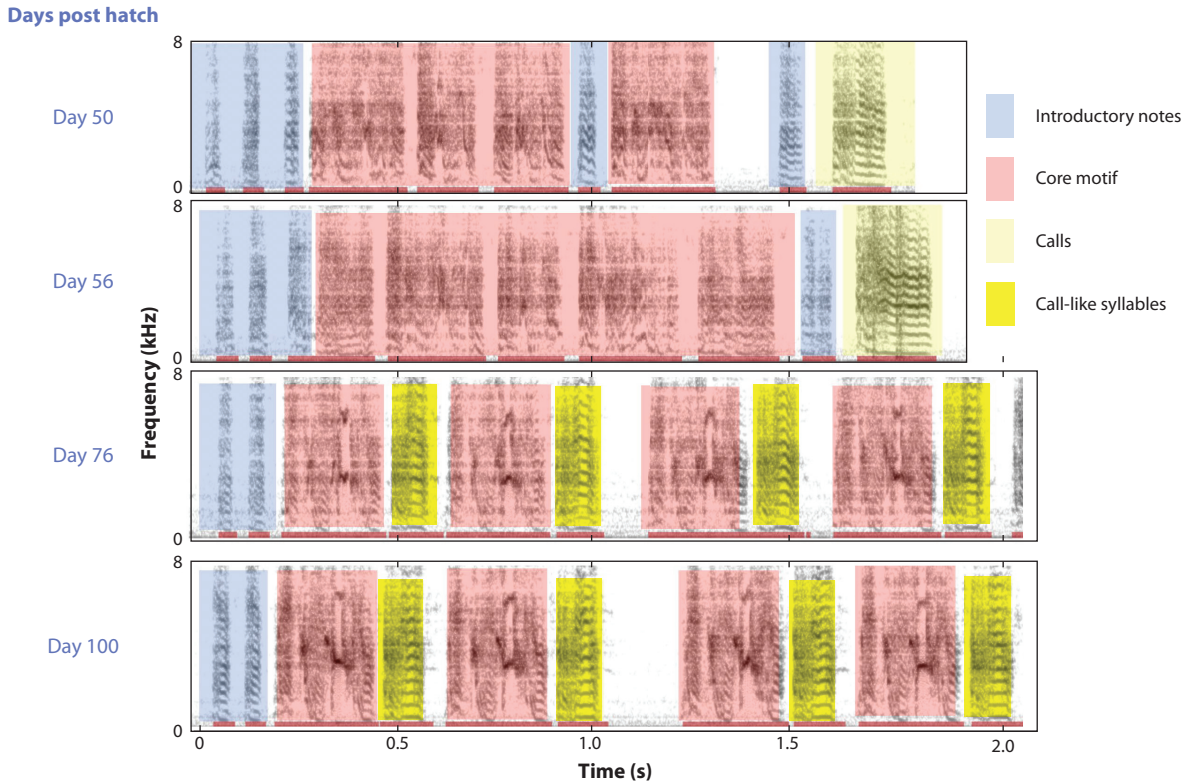
Figure 4

Song development in an example zebra finch showing the ontogeny of the mature song sequence. (*Top to bottom*) Representative sonograms illustrate stages of juvenile song learning between days 50 and 100 post hatch. Light blue represents introductory notes; red, core motifs; yellow, calls (early) and call-like syllables (later).

complexity to one or two syllable types. In other species, tens or even hundreds of syllable types emerge (**Figure 2**). As illustrated in **Figure 4**, the compression process has a combinatorial dimension that imposes constraints on the relative positions of syllable types in the adult song. Additional constraints on learning depend on the duration of the sensitive period in a species, how the spatial network of territories is structured, and how often potential tutors can interact with juveniles. Among the greatest challenges of future studies will be to figure out exactly how species variability in developmental constraints on song learning adds up to different song cultures. In the next section, we elaborate on the possible role of dynamic social interactions in shaping birdsong culture.

4. TOWARD A PRAGMATICS OF BIRDSONG: CULTURE AT THE LEVEL OF VOCAL COORDINATION

Across human cultures, conversation exhibits anticipatory turn-taking, in which turns are timed faster than language is processed (Stivers et al. 2009); turn-taking also appears early in development prior to speech, in prelinguistic infant communication (Bruner 1975). Recent years have seen growing interest in extending the sociolinguistic concept of turn-taking (Schegloff et al. 1974,

Levinson 2016) to animal communication systems (Logue & Stivers 2012, Takahashi et al. 2016, Demartsev et al. 2018, Pika et al. 2018, Okobi et al. 2019). This work has remained largely distinct from vocal learning research (an exception focusing on the ontogeny of turn-taking in starlings is Henry et al. 2015), despite recent efforts by Levinson (2016) and others to link turn-taking to the origins of human language. Intriguingly, in songbirds the same brain centers that enable song learning also enable coordinated vocalization (Benichov et al. 2016). Vocal turn-taking is not limited to vocal learners (consider, e.g., frog antiphonal calling), but the intersection of vocal learning (the capacity to imitate complex vocalizations) and the development of "communicative competence" in songbirds (King & West 2002) is ripe for investigation (Hyland Bruno & Tchernichovski 2019, Searcy & Nowicki 2019). A better understanding of the pragmatics of birdsong—how learned vocalizations are used socially (Gros-Louis et al. 2010)—would help clarify potential parallels between avian and human vocal culture. In this section, we provide a rationale for viewing song learning as a fully social process, highlight some issues pertaining to the cultural transmission of interaction patterns, and present examples of song–call interactions between male and female adult zebra finches that illustrate plasticity in a so-called stereotyped learned behavior (the male song) and mutual engagement involving the innate vocalizations of nonsinging females.

4.1. Pragmatics in Birdsong Learning

As mentioned above (Section 2.1), song learning can be studied with experimental control by substituting a live tutor with playbacks of the tutor song. Still, in zebra finches, imitation is more accurate in the presence of a real adult bird (Derégnaucourt et al. 2013). Interestingly, the natural family group context does not yield universal perfect imitation, an effect that may be explained by social inhibition among siblings developing at different rates, perhaps receiving unequal attention from a tutor (Tchernichovski & Nottebohm 1998), as well as balanced imitation toward a specific typical level of syllable diversity (O. Tchernichovski, S. Eisenberg-Edidin & E.D. Jarvis, manuscript in review). Although birdsong learning research has tended to focus on song imitation, evidence exists that the song signal itself is not the only thing that songbirds acquire during sensitive periods for song development. The performed repertoires of nightingales, for example, reflect the context (i.e., training session) in which different song models were heard during development (Hultsch & Todt 1989). Importantly, learning about the local vocal culture does not require vocal production learning: In species where females do not sing, they may nevertheless be enculturated by the songs in their environment (O'Loghlen & Rothstein 1995). Stable regional song dialects are maintained by assortative mating wherein nonsinging females develop culturally transmitted preferences for local songs, and thereby perpetuate their natal vocal traditions (Nottebohm 1972, Freeberg et al. 1999). In some species, as demonstrated in the brown-headed cowbird and the zebra finch, females can also shape male song learning by providing contingent feedback on juvenile performance using vocal or visual cues (West & King 1988, Carouso-Peck & Goldstein 2019). Although an avian analog of infant-directed speech ("motherese") has only been speculated, social interactions with a tutor or other members of the social group may also play a role in guiding birdsong development, akin to the influences of social reinforcement on babbling and early linguistic development (Goldstein et al. 2003, Carouso-Peck et al. 2020). For songbird species in which this is the case, song learning may be intertwined with learning patterns of social interaction that continue later in life.

Even so, social interactions are also salient for song acquisition in solitary, territorial migratory songbirds, in terms of both song signal and function. For example, song sparrows (*Melospiza melodia*) develop repertoires that match the songs of the adult males in the region where they attempt

to stake out a territory (Beecher 2017). They do so by interacting with or eavesdropping on the adults, who use their largely overlapping repertoires to mediate territorial conflicts in countersinging interactions with neighbors, where song matching from shared repertoires serves as an honest aggressive signal (Akçay et al. 2013). Comparative studies show that territoriality is associated with regional clustering of song types (Baker & Cunningham 1985), and regional dialects are found in most territorial, migratory species studied (Podos & Warren 2007). On the other hand, studies of group-living birds show that song sharing can be affiliative (Brown & Farabaugh 1997). That the same terminology is used for both competitive and cooperative systems is confusing, especially if we wish to draw comparisons with linguistic dialects. While it is evident that great diversity exists in the ways in which song learning may be influenced by the social environment (Soma 2011, Ljubičić et al. 2016), further studies of birdsong learning in different social contexts are needed in order to elucidate the role of vocal learning in the ontogeny of social behavior. To make progress in this direction, the social functions of song should be investigated rather than assumed, for instance, to serve solely for mate attraction and territorial defense. Longitudinal studies will be important for understanding how the time course of the ontogeny of communicative competence tracks with that of other aspects of vocal development (Geberzahn & Hultsch 2004). Complementary neurobiological studies would be useful, for example, to test the roles of oxytocin and other socially relevant molecules in the brain in vocal learning during social interactions (Baran et al. 2017, Theofanopoulou et al. 2017).

4.2. Duetting: Birdsong Culture Based on Interaction

Despite an overrepresentation of temperate species in the birdsong literature, cooperative vocal exchanges such as choruses and duets are more common than previously thought, and in these communication systems females are fully active participants, not just choosy arbiters. Nonagonistic, coordinated singing interactions are associated with year-round territoriality (absence of migration) and long-term social bonds (Logue & Hall 2014, Tobias et al. 2016). Synchronized duetting is most common in male–female partnerships in tropical species (Hall 2004). Ecological predictors of duetting therefore also predict the existence of female song, both duet and solo, although females of some species in temperate areas also produce solo songs (Langmore 1998, Riebel 2003, Riebel et al. 2019). Recent phylogenetic reconstruction has revealed that female song is ancestral in songbirds; thus, species where the female does not sing means that one sex lost the trait (Odom et al. 2014) and the associated functioning brain pathway (Choe et al. 2020). Complete absence of female song can therefore be regarded as a special case of a general pattern of derived sexual dimorphism; in duetting birds and other species where both males and females sing, species-specific sex differences can still be observed in brain and behavior (Brenowitz et al. 1985, Gahr et al. 2008, Fortune et al. 2011, Hoffmann et al. 2019), plumage ornamentation (Soma & Garamszegi 2015, Webb et al. 2016), and ontogeny (Hall 2009, Geberzahn & Gahr 2013, Riebel 2016, Riebel et al. 2019).

Duets typically have clearly defined sex roles, and so duetting species represent the curious scenario in which separate male and female dialects exist simultaneously while contributing to a single interactive vocal culture. How does a tightly coordinated duetting ritual develop? It is not obvious how the standard phases of birdsong learning (see Section 2) can explain the coordination of learned song parts. While needed longitudinal studies of the ontogeny of duetting have yet to be carried out (Logue & Krupp 2016, Rivera-Cáceres & Templeton 2019), evidence exists that so-called duet codes (also known as interaction rules) may be acquired during both juvenile learning (Rivera-Cáceres et al. 2018), in interactions with the same-sex parent, and adult learning (Rivera-Cáceres et al. 2016), in extended interactions with a partner. Missing from the classic picture of

song learning is a phase for acquiring a representation of the partner's song (Fortune et al. 2011, Hoffmann et al. 2019). One can imagine a use for such a mechanism even in the absence of full duetting, for instance, in social species where birdsong serves broad communicative functions. Beyond the dyad, plain-tailed wrens exhibit four-part synchronized singing (Mann et al. 2006), as just one example of the many forms of chorusing that exist in nature (Ravignani et al. 2019). The use of learned representations of nonself in communal signaling may extend even to learning other species' songs and, therefore, learning to participate in an interspecific chorus (Malavasi & Farina 2013).

4.3. Interactive Singing and Implications for Cultural Transmission

In zebra finches, mated pairs coordinate parental care by exchanging unlearned calls (Elie et al. 2010), and females use their very rudimentary neural song system to control the timing of their calls (Benichov et al. 2016). In addition, male zebra finch song shows structural plasticity above the level of the crystallized core song motif (Hyland Bruno & Tchernichovski 2019). These findings challenge a prevailing caricature of zebra finch vocal culture in which male learned song is highly stereotyped and females are incapable of vocal learning. No studies to date have systematically investigated the intersection of male and female vocal flexibility in zebra finch communication. However, one can see occasional female calls, unmentioned, in published sonograms of male song (e.g., figure 1b of Kozhevnikov & Fee 2007). This is because female birds are commonly used in neuroethological studies to induce male singing, presumably by their visual presence (Fee et al. 2004). But female calls may not be merely innate vocal responses to the male song. Indeed, one documented example (Williams 2004) suggests that the placement of female calls can bias male song delivery by influencing the frequency of rare song elements.

Figure 5 presents evidence that both male and female zebra finches can adjust their vocalization patterns to a partner (J. Hyland Bruno & O. Tchernichovski, unpublished data). Two males and two females were allowed to interact freely in pairs, and the timings of their vocalizations were separately analyzed (**Figure 5a**). Both males produced both more and longer song bouts with one of the two females (purple shading in **Figure 5a**). In addition, a greater proportion of both males' song syllables were covered by this female's calls (the temporal overlap was 13% and 12% with the green and blue males, respectively, compared with 5% and 2% for the orange female). Note that neither of the females' calls were issued at fixed intervals. Interestingly, the timing of both females' calls (red bars and traces in **Figure 5a**) corresponds to some of the structural regularities of both males' songs, even though the more voluble male's song (green shading in **Figure 5a**) is only quasi-periodic (**Figure 5a,b**), suggesting that the coordination of covocalizations in male–female song–call duets is unique to a pair and the product of mutual adaptation as well as individual vocal styles.

These data show snapshots of four "first dates," but zebra finches form lifelong pair bonds, as well as other long-lasting relationships, including with same-sex members of the social group, and the strength of these ties can be observed in their moment-to-moment behavioral coordination (Prior et al. 2020). It is not unreasonable to speculate that dyadic song–call coordination may grow with familiarity, leading to the development of idiosyncratic joint vocal performances. Perhaps there may even be group-level interaction patterns that emerge over time. If so, vocal interaction cultures, like dialects, may be inherited during development and transmitted across generations. Since zebra finch song is in fact interactive and rarely exists as an isolated signal, the developing juvenile would have to possess mechanisms that filter out all the interactive vicissitudes of the tutor's singing, in order not to acquire a pragmatics of song. But even if such filters exist, would it not be more adaptive to make use of that information, rather than relearn it by trial and error?
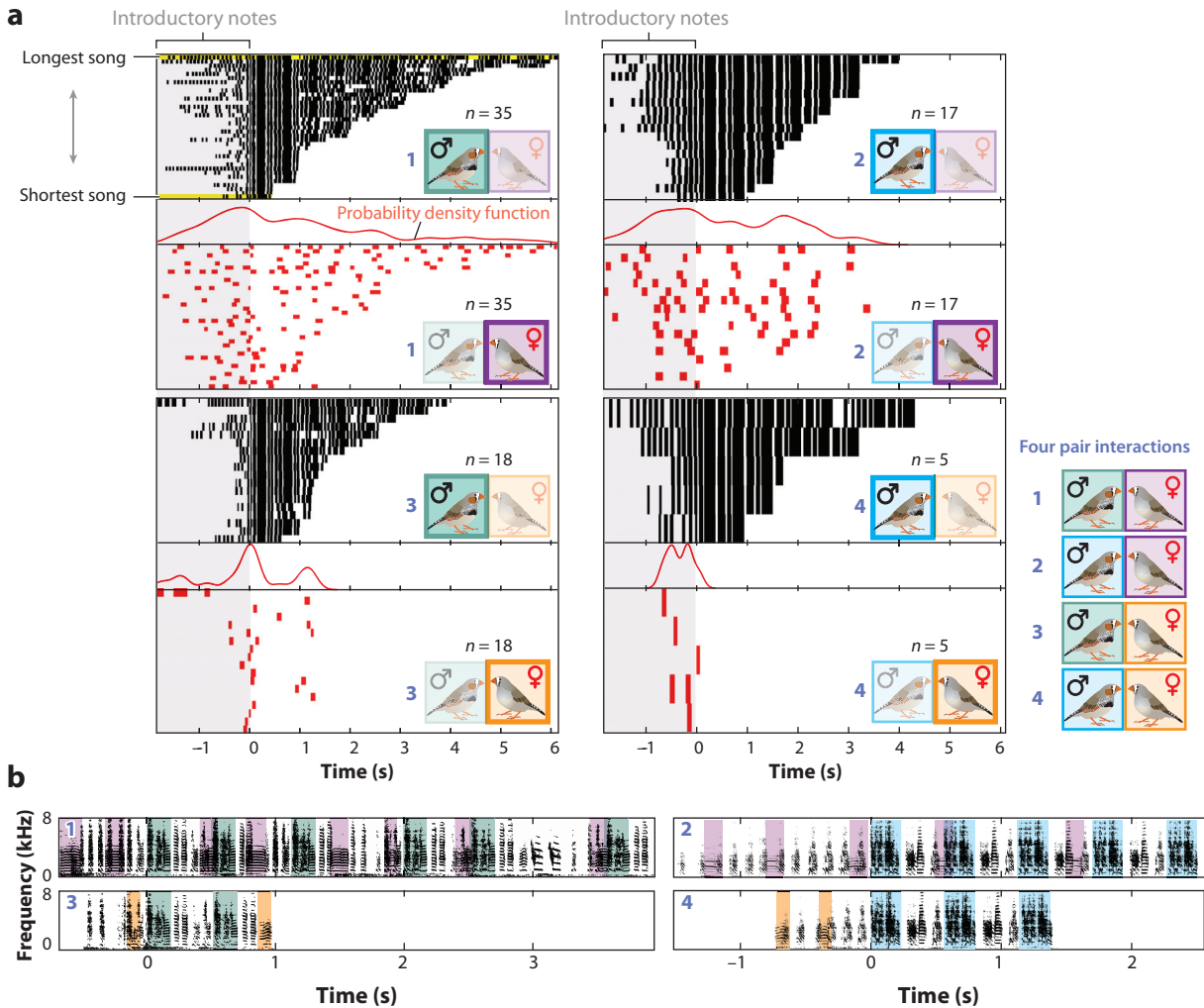
Figure 5

Zebra finch song–call duets exhibit mutual adaptation. (*a*) The male (*black*) and female (*red*) parts of song–call duets performed by two male (*green and blue shading*) and two female (*purple and orange shading*) zebra finches during four pair interactions (*quadrants 1–4*) lasting one hour each. Data are presented as sorted rasters of the source-separated binary amplitude signal (sounds notated by *black and red bars*, with the width of each bar showing the duration of a given sound). Each row represents the male or female part of one song–call duet, with time on the *x* axis and rows sorted vertically from longest to shortest (e.g., highlighted in *yellow* in the upper left panel) and aligned to the onset of the first motif in each male song bout (introductory note epochs are shown in the *gray shaded areas*). Within each quadrant, rows from male and female rasters correspond to the same duet, and the probability density function of the female calls is included in between the male and female rasters (*red traces*). The number of renditions per pair (*n*) is shown by the number of rows in each raster: 35 (*upper left quadrant*), 18 (*lower left*), 17 (*upper right*), and 5 (*lower right*). (*b*) Sonograms of representative duets from each of the four pairings. Female calls in the sonograms are indicated by purple or orange shading; all other vocalizations are male, with the first syllable of each song motif shaded green or blue to highlight the differences in the two males' song patterns. Note the blue bird's relatively greater stereotypy (*right*) as compared with the quasi-periodic song of the green bird (*left*).

5. CONCLUSIONS

In this review we have summarized findings demonstrating that, despite the evolutionary distance between songbirds and humans, there is a remarkable mechanistic similarity between birdsong learning and language learning, including shared genes that regulate birdsong learning and human speech, similar brain mechanisms that regulate song and speech production, and similar developmental constraints on vocal learning. We emphasize that the mechanistic similarities in the processes of vocal learning can lead to diverse structural and functional outcomes.

Studying song learning in birds permits experimentation in the emergence of vocal cultures, which is rarely ethical or feasible in humans. Such studies have shown, for example, that birdsong culture can emerge de novo via built-in biases in the imitation process (Fehér et al. 2017). Biases that shape vocal culture within a species can be explained, at least in part, by constraints on song learning. Studying birdsong development has revealed that the combinatorial structure of song syllables develops in a stepwise manner (Lipkind et al. 2013). Similar constraints can be shown in human infant babbling, and yet the outcomes are obviously different. We suggest that such different outcomes may be largely the result of quantitative variation in the intensities of different features of song learning, for example, in the level of compression of syllable types and in the duration of combinatorial learning across species. Understanding the mechanisms of this variation, for example, at the genomic level, could be useful in elucidating prelingual speech development.

Finally, we suggest that studying dynamic vocal interactions in songbirds can shed light on the interactive features of speech and language. On one hand, although zebra finch song is highly stereotyped, vocal exchanges are highly plastic, and zebra finch calls are precisely and flexibly coordinated. On the other hand, canaries, which produce much more complex and plastic songs (Cohen et al. 2020), are much less social: They do coordinate their vocalization to some extent, but in a much slower, and probably simpler, manner in comparison to zebra finches. Studying the variability in the pragmatics of vocal communication across different songbird species could reveal certain continuities and converging mechanisms with pragmatics of spoken language. As our capacity to integrate across genomic, brain, behavioral, and cultural levels improves, it should become possible to detect different layers of shared mechanisms across animal vocal cultures, inclusive of human speech and language.

DISCLOSURE STATEMENT

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