



INVITED PERSPECTIVES AND REVIEWS

Vocal Learning in Songbirds and Humans: A Retrospective in Honor of Peter Marler

Jill A. Soha & Susan Peters

Biology, Duke University, Durham, NC, USA

CorrespondenceJill A. Soha, Department of Biology, Box
90338, Duke University, Durham, NC 27708,
USA.

E-mail: jill.soha@duke.edu

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Peter Marler made a number of significant contributions to the field of ethology, particularly in the area of animal communication. His research on birdsong learning gave rise to a thriving subfield. An important tenet of this growing subfield is that parallels between birdsong and human speech make songbirds valuable as models in comparative and translational research, particularly in the case of vocal learning and development. Decades ago, Marler pointed out several phenomena common to the processes of vocal development in songbirds and humans—including a dependence on early acoustic experience, sensitive periods, predispositions, auditory feedback, intrinsic reinforcement, and a progression through distinct developmental stages—and he advocated for the value of comparative study in this domain. We review Marler's original comparisons between birdsong and speech ontogeny and summarize subsequent progress in research into these and other parallels. We also revisit Marler's arguments in support of the comparative study of vocal development in the context of its widely recognized value today.

Introduction

Birdsong and human speech are both learned behaviors, and the processes of learning that underlie their ontogenies share many features. Peter Marler described these ontogenetic similarities almost a half century ago (Marler 1970a). Marler was especially well placed to make these early comparisons of vocal development in songbirds and humans for two reasons. First, of course, was his extensive birdsong research experience. At Cambridge University in the 1950s, working in the laboratory of William Thorpe (Thorpe 1954, 1958), Marler was exposed to some of the earliest experiments on song ontogeny. Given Marler's status in the field of ethology today as 'the father of birdsong research,' it is perhaps surprising that he was not a coauthor on those original studies. In a later autobiographical chapter, Marler explained that although his interest in song development and his 'growing conviction that birdsongs must be learned' (Marler 1985, p. 319) led him to work with Thorpe, who gladly took him on as a student, 'paradoxically, my ambitions to work on song learning

were still somewhat frustrated. Although I was involved in many of the experiments on song development, Thorpe made it clear that vocal learning was his domain' (Marler 1985, p. 323).

Despite that intellectual territoriality, those early experiments (in chaffinches, *Fringilla coelebs*) were followed by Marler's own work in juncos (*Junco hyemalis*), song sparrows (*Melospiza melodia*), and—most extensively (before 1970)—white-crowned sparrows (*Zonotrichia leucophrys*). Marler was thus able to observe, first-hand, similarities and differences among species in the process of song development. For example, he noted that both white-crowned sparrows and chaffinches selectively learn conspecific song when tutored with recordings of songs from multiple species and that although their timing may differ, both have sensitive periods during which song acquisition most readily occurs (Thorpe 1958; Marler 1970a). Such comparisons across species revealed generalizations that invited comparison with human speech development.

Second, in addition to his experience with birdsong research, Marler had a wide-ranging intellectual

curiosity. He greatly valued his interactions with colleagues in other fields such as psychology and anthropology; such interactions are a major theme of his autobiographical chapter (Marler 1985). In the early 1960s, as a faculty member in the zoology department at UC Berkeley, Marler co-taught comparative psychology courses and served on the exam committees of several anthropology (primatology) graduate students. In Marler's words, 'hybrid vigor was rampant' (Marler 1985, p. 328) among the zoology, psychology, and anthropology departments. At a conference on primate behavior in Palo Alto in 1962, he and a colleague, Jarvis Bastian, were invited to talk about animal communication and human language, respectively. At Rockefeller University several years later, 'the arrival of George Miller from Harvard [in 1967] was a special blessing for me, opening my eyes to a new universe of research findings on the nature of language, and the development of speech behavior in infancy' (Marler 1985, p. 340). With Miller, he co-organized seminars on the biology of speech. As his own research progressed at Rockefeller, 'the analogies between song learning and speech development [became] increasingly compelling, as my psychological colleagues often point[ed] out' (Marler 1985, p. 340). Thus, a number of professional interactions facilitated Marler's recognition of these analogies and prepared him to write about them in 1970.

Here, we review Marler's original comparisons of birdsong learning and human speech learning. We then summarize subsequent advances in research within and beyond the aspects of vocal development addressed in those comparisons. We reflect on Marler's early commentary about the utility of comparative study in this domain and conclude that as research in this area continues, Marler's original work merits continued recognition.

Birdsong and Speech Development: Marler's Original Comparison

Marler first summarized the developmental similarities between birdsong and human speech in a 1970 monograph in the *Journal of Comparative and Physiological Psychology* (Marler 1970a). The central theme of this monograph was not the comparative analysis of vocal development in humans and songbirds, but rather a series of song tutoring experiments with white-crowned sparrows and the resulting elaboration of the auditory template hypothesis postulating that innate auditory specifications guide the selective learning of conspecific song. Placing this study in a comparative context increased its intellectual appeal, of course, and

was particularly relevant given the journal in which the monograph was published.

Marler presented his insights into the parallels between song learning and speech development in a section titled 'Bird Song and Speech Development' on the last page of the Discussion of the 1970 monograph. He began this section by explicitly stating that the outcomes of the two developmental processes are fundamentally different: 'In no sense does song learning generate a language' (Marler 1970a, p. 23). He did not elaborate on this statement, as his focus here was not on the similarities and differences between birdsong and human language as communication systems, but on the ontogeny of these vocal behaviors. He noted that in both humans and white-crowned sparrows:

- 1 Exposure to certain sounds (normally, the vocalizations of adult conspecifics) during development has a crucial impact on the adult repertoire.
- 2 This exposure has the greatest effect during a certain developmental time range, that is, learning proceeds most readily during an early critical period.
- 3 Vocal learning is guided by predispositions to proceed in a certain way. In particular, human babies preferentially attend to speech sounds and young songbirds are predisposed to pay particular attention to the vocalizations of their own species.
- 4 Individuals must hear their own output during vocal development, as auditory feedback guides the matching of this output to what was heard and memorized previously. Auditory feedback is then less important—in Marler's words, it 'becomes redundant' (Marler 1970a, p. 23)—after vocal development is complete.
- 5 At least some vocal learning apparently proceeds without external reinforcement, suggesting that internal reward reinforces the process of matching vocal output to memorized models.
- 6 Vocal motor development proceeds in stages. Young individuals begin by making vocal sounds that do not resemble those of adults, and even deafened individuals produce the earliest versions of these sounds (babbling or early subsong). In normal individuals, the effects of auditory experience then become apparent at the next stage.

On the birdsong side, most of the above points are directly supported by the white-crowned sparrow results presented in the monograph. Marler cited Konishi's deafening studies (Konishi 1964, 1965a,b) earlier in the Discussion section of the monograph, and these support point 4 and part of point 6 above. On the human speech side, in his original presentation, Marler

cited only two references (Fry 1966; Lenneberg 1967) and one personal communication (from T. Bever). Several other references from before and after 1970 also support the songbird and the human sides of these analogies, however, many of which are cited in Doupe & Kuhl (1999).

After presenting these parallels between song and speech development, Marler (1970a) suggested that rather than being mere coincidences, these similarities might reflect features that are necessary to any effective vocal learning system. He argued that the most important of these features is that learning is constrained: 'Vocal learning that was not guided by predispositions to develop more readily in some ways than others might easily drift in functionally inappropriate directions' (Marler 1970a; p. 23). Marler reiterated this idea in an American Scientist article in which he described the similarities between birdsong learning and human speech development for a wider audience: 'Any species whose biology depends in any fundamental way upon a series of complex learning processes can ill afford to leave the directions in which learning will take place to chance' (Marler 1970b; p. 672). Marler & Peters (1981) further clarified the function of constraints on vocal development: Early perceptual constraints act to ensure that vocal production and perception both follow the same 'rules', as is required for any communication system in which all individuals effectively use and understand the same signals.

Subsequent Advances

Since 1970, the phenomena originally raised as points of comparison by Marler have received much attention in both birds and humans. In this section, we summarize this research and also briefly address progress in new areas. We hope to show that over the past 45 years, the combined work of a number of researchers on several aspects of vocal development has validated Marler's idea that songbirds are useful as models in the comparative study of vocal learning.

Marler's first point, that the adult repertoire is critically influenced by certain sounds heard during development, has been confirmed in a number of additional bird species through tutoring and cross-fostering experiments as well as by raising males without exposure to song, as Thorpe had done with chaffinches and Marler with white-crowned sparrows. Untutored birds develop songs that are highly abnormal in many respects but still display some species-typical characteristics such as duration and repertoire size (e.g. zebra finch *Taeniopygia guttata*: Price 1979;

song sparrow and swamp sparrow *Melospiza georgiana*: Marler & Sherman 1985; grasshopper sparrow *Ammodramus savannarum*: Soha et al. 2009). In humans, it remains common knowledge that an infant adopted from one culture into another will learn the language, and the regional accent, of the adopting culture because this is what he hears while growing up. In the few documented unfortunate cases where children have been raised without linguistic experience, their speech ability is severely impaired. The best recently documented case is 'Genie' who was essentially isolated until the age of 13 and subsequently developed only limited language (Fromkin et al. 1974).

The critical period—now more commonly called the sensitive period or sensitive phase—for song memorization has now been studied in a number of songbird species, revealing considerable variation across species in its timing and duration (Catchpole & Slater 2008). For example, the sensitive phase peaks early in song sparrows and swamp sparrows, at around 50 d of age (Marler & Peters 1987, 1988a), whereas marsh wrens *Cistothorus palustris* can have both an early sensitive period and a second one the following spring (Kroodsma & Pickert 1980). Some birds learn only as young adults (e.g. indigo buntings *Passerina cyanea*: Payne 1981), and finally, some 'open-ended' learners are able to acquire new material much later in life (e.g. village indigobirds *Vidua chalybeata*: Payne 1985; European starlings *Sturnus vulgaris*: Eens et al. 1992). In humans, different aspects of language learning are known to have different sensitive periods, for example, that for phoneme learning is within the first yr of life, whereas syntactic learning peaks between 18 and 36 mo (Ruben 1997; Kuhl 2010). These two windows can be extended, however, as demonstrated by second language learning: The proficiency with which a second language is acquired remains similar to that of native speakers until about 7 yr of age, after which it begins to decline (see Kuhl 2010). In both songbirds and humans, normal maturation, sufficient experience with appropriate stimuli, and social factors all affect the timing of the sensitive periods for vocal learning (Doupe & Kuhl 1999), although details of the physiological mechanisms underlying these effects are still unknown.

The role of perceptual predispositions in vocal development has also been further studied in songbirds and humans. Fledgling sparrows that have not previously heard any songs respond more strongly to conspecific song than to the songs of other species, as indicated by cardiac response (Dooling & Searcy 1980) and vocal response (Nelson & Marler 1993) to playback. The

necessary acoustic features of conspecific song that guide selective learning have been elucidated in a few species. The species-typical structure of individual notes is the most salient cue for young swamp sparrows, whereas song sparrows rely also on song syntax—the presence of multiple phrase types—when selecting material to imitate (Marler & Peters 1981, 1988b). White-crowned sparrows preferentially learn songs that begin with a whistle (Soha & Marler 2000). Predispositions might also guide the preferential learning of some elements over others within a species (zebra finch: Ter Haar et al. 2014). In humans, neonates and prelingual infants have been found to preferentially attend to human speech over non-speech sounds (including complex non-speech sounds with some acoustic properties similar to those of speech; Vouloumanos & Werker 2004, 2007a), although presumably even the 1- to 4-d-old neonates tested in these studies had heard some speech prior to testing. Humans can also hear *in utero*, but this is unlikely to explain the results (Vouloumanos & Werker 2007b). Predispositions for language learning are further reflected in the very early perceptual processing of speech and the changes that occur in this processing during the first yr of life. Very young infants are able to discriminate the phonemes of all languages; subsequently, between 6 and 12 mo of age, exposure to the native tongue rapidly gives rise to a language-specific perceptual map (reviewed in: Eimas et al. 1987; Werker & Polka 1993; Kuhl 1994). The methods of investigation and—given the vastly greater complexity of human language—the nature of the predispositions themselves differ, but studies in humans and songbirds support Marler's claim that in both cases, predispositions play a role in vocal learning.

The crucial role of auditory feedback in birdsong development was firmly established by Konishi's finding that deafening after song memorization but before song production disrupts the development of normal song. Konishi documented this in five songbird species: dark-eyed junco and yellow-eyed junco *Junco phaeonotus* (Konishi 1964), American robin *Turdus migratorius* and black-headed grosbeak *Pheucticus melanocephalus* (Konishi 1965a), and white-crowned sparrow (Konishi 1965b). Subsequent studies in six additional species confirmed that although some song features (i.e. duration and gross segmentation) are relatively unaffected, early deafening generally results in the development of abnormal note structure, reduced note stereotypy, and smaller note repertoires (northern cardinal *Cardinalis cardinalis*: Dittus & Lemon 1970; red-winged blackbird *Agelaius phoeniceus*: Marler et al. 1972; canary *Serinus canarius*:

Marler & Waser 1977; zebra finch: Price 1979; song sparrow and swamp sparrow: Marler & Sherman 1983). In humans, evidence that auditory feedback is required for speech development is less direct, as early deafness prevents young children not only from hearing themselves but also from continuing to receive necessary auditory input from others. However, speech still deteriorates considerably with deafness in late childhood (Plant & Hammarberg 1983), after language production is well developed, suggesting that auditory feedback remains necessary at least until puberty (Doupe & Kuhl 1999). Adult-onset deafness causes deterioration of speech but to a lesser extent than deafness in childhood (Waldstein 1990). Modified (delayed) auditory feedback also disrupts speech more in children than in adults (MacKay 1968). In songbirds, deafening in adulthood results in song deterioration depending on species and age at deafening (Lombardino & Nottebohm 2000; Konishi 2004) and modification of feedback results in rapid degradation of adult song (zebra finch: Leonardo & Konishi 1999). Thus, in addition to the role of auditory feedback in vocal development that was noted by Marler, but contrary to his statement that this feedback 'becomes redundant' in adulthood, it has been found that songbirds and humans share a reliance on auditory feedback to maintain adult vocalizations.

Marler's next point of comparison concerns the role of external reinforcement in vocal development. Marler (1970a) stated that 'In both birds and man some vocal learning seems to occur independently of extrinsic reinforcement, indicating that the act of matching vocalization with sounds heard may have intrinsic reinforcing properties'. Indeed, laboratory tape-tutoring experiments by Marler and others had demonstrated that some songbirds can learn apparently normal song in the absence of any social influence (chaffinch: Thorpe 1958; song sparrow: Mulligan 1966; white-crowned sparrow: Marler 1970a), and in humans, it is common knowledge that children babble even when nobody is listening and that a child's progress in speech development occurs largely, if not entirely, without explicit praise. Marler's statement holds true, but social influences in song and speech learning have attracted greater interest, and several studies have documented potent effects of social interaction in both systems. For example, both observation of adult (tutor–tutor) interactions and engagement in direct (tutor–student) interactions have been shown to influence song development in song sparrows (Beecher & Burt 2004; Burt et al. 2007). Tutoring by live adult males of another species can override the innate

predisposition to learn conspecific song (zebra finches: Immelmann 1969; white-crowned sparrows: Baptista & Petrinovich 1986), and through contingent social reinforcement, interaction with conspecific individuals at later stages of vocal development can affect song production or retention (cowbirds: West & King 1988; white-crowned sparrows: Nelson & Marler 1994; song sparrows: Nordby et al. 2007). In humans, contingent social reinforcement has been found to influence the phonological features of babbling at 8 mo of age (Goldstein et al. 2003). In addition, exposure to live adults speaking a foreign language results in greater phoneme discrimination by infants than does exposure only to video or audio recordings, and infants that are more engaged with the live speaker exhibit greater learning (Kuhl 2010). Phonetic learning of a second language even in adulthood might also be facilitated by social interaction and its effect on attention (Guion & Pederson 2007).

The stages of vocal ontogeny have been described more thoroughly since 1970 in both songbirds and human infants, enabling a more informative comparison across species. In songbirds, song production begins when the bird is less than a year old but nearing sexual maturity. The initial song output, called *subsong*, is quiet and highly variable, containing a wide range of frequencies and durations, with virtually no repeated elements and no sounds that resemble models memorized during the critical period (Marler & Peters 1982a,b). During the subsequent *plastic* stage, song output becomes louder and more structured, and song patterns can be identified as resembling those of adults although they are sung with variability. This variability diminishes from early to late in the plastic stage. Progress toward adult song occurs on multiple levels: The morphology of the elements that comprise the song becomes more consistent, song length decreases toward the duration of normal adult song, and the pattern in which elements are delivered becomes more regular and species-typical (Marler & Peters 1982a,b). Finally, the patterns that compose the *crystallized song* of adults are extremely stereotyped. Across species, the timing of the onset of each stage differs and the length of each stage varies from several weeks to months (Hultsch & Todt 2004; Catchpole & Slater 2008).

In humans, the stages of speech development leading up to first word production have been described in detail (Oller 1980; Stark 1980; Oller et al. 1999). In their first 2 mo of life, during the *phonation stage*, infants produce what are known as 'quasivowels', vowel-like sounds with limited resonance. Over the next month or so, during the *articulation* (or *gooing*)

stage, infants produce more normal phonation as well as their first consonant-like elements. During mo 4–6, in the *expansion* (or vocal play) *stage*, infants exhibit exploratory vocal behavior including bilabial trills (raspberries) and manipulation of pitch (squealing and growling) and amplitude (yelling). During this stage, infants also produce *marginal babbling*, or primitive protophones that are articulated from a consonant sound to a full vowel sound but without the timing that is crucial for syllable perception. In *canonical babbling* (6–10 mo of age), the timing relationship between consonants and vowels begins to conform to the rules of the ambient language and thus can be identified, for example, as/ba/or/da/(Oller 1980). Phonemes are often reduplicated in a rhythmic structure (e.g./bababa/) in canonical babbling, and parents typically recognize these sounds as the first attempts at speech (Oller 1980). As infants approach 12 mo, they begin to change vowels and/or consonants in successive syllables (e.g./babi/or/bada/) during *variegated babbling*. At this time, they also produce contrasts of syllabic stress, a category referred to as *gibberish*. Infants may produce phonetically consistent forms (protowords) used in relation to an object or an action as early as 10 mo (Oller 1980).

In the songbird literature, it has been common to describe subsong as analogous to human babbling. However, given the timeline described above, it is more accurate to compare subsong to the stages of speech development prior to canonical babbling—the phonation, articulation, and expansion stages. It is early plastic song, in which adultlike song notes can first be identified, that is analogous to canonical babbling, in which syllabic units are also first identified. Recent work also indicates that during plastic song and during the transition from reduplicated to variegated babbling, respectively, both songbirds and humans add novel combinations of sounds to their repertoires in a stepwise manner rather than simultaneously (Lipkind et al. 2013). In terms of motor development, an intriguing similarity in the earliest stages of vocal ontogeny is that during subsong, song sparrows vocalize with their beaks closed (Podos et al. 1995) and likewise, during their first mo of life (in the phonation stage), infants typically produce quasivowels with their mouths closed (Oller 1980). During subsequent stages, both songbirds and humans must learn to coordinate vocal tract movements with the output of the vocal organ (Podos et al. 1995; Polka et al. 2007). An important contrast, however, is that most songbirds are probably working with a fully mature vocal tract from early in song development, given that passerine growth tapers off shortly after

fledging (O'Connor 1984), whereas the vocal tract of infants is dynamically changing during their first yr of life (Kuhl & Meltzoff 1996; Polka et al. 2007), so during early speech development, humans must learn to coordinate vocal tract movements with a changing apparatus.

Two details in Marler's comparisons of the stages of vocal development were incorrect, based on subsequent findings on human speech development. First, Marler wrote that 'The song of a white-crowned sparrow deafened early in life resembles an early stage of normal subsong, and a child deafened early will babble normally (Lenneberg 1967)' (Marler 1970a; p. 23). It was believed in the 1970s that babbling was the same in normal and deaf infants, but we now know that although they might produce similar sounds (e.g. raspberries, squeals, etc.) during the vocal play stage, hearing-impaired infants display a later onset and a reduced amount of canonical babbling as well as delayed and possibly incomplete development of the full range of consonant sounds (Stoel-Gammon & Otoma 1986; Oller & Eilers 1988; Oller 2000; Moeller et al. 2007). Second, Marler wrote that "The shaping of vocalizations as a result of prior auditory experience is first manifest in the young bird as subsong and in the child as the transition from 'babbling to adult intonation without articulation'" (Marler 1970a; p. 23). Marler would have substituted 'plastic song' for 'subsong' in this analogy following Marler & Peters (1982a,b), as plastic song is when imitations of tutor material become evident. On the human side, although it is not clear which stages of the detailed speech development timeline above correspond to those mentioned here, we now know that acoustic experience affects speech development even before the canonical babbling stage. Kuhl & Meltzoff (1996) found that vowel production by 20-wk-old infants changed upon exposure to vowels in a laboratory setting: Vowel categories became more clustered, and infants listening to a particular vowel produced vocalizations that resembled that vowel more. Other research has shown differences in both vowels and consonants in the canonical babbling of infants raised in different languages (de Boysson-Bardies et al. 1989; Rvachew et al. 2006; Lee et al. 2010).

Recent insights from both avian and human vocal learning research suggest parallels beyond those covered in Marler's original summary and provide promising directions for future research. For example, statistical learning—the ability to perceive and learn from the statistical regularities that exist in the environment—might be a shared mechanism underlying

the perceptual side of vocal development in both humans and songbirds. Statistical learning was first identified in human infant word perception in the 1990s (Saffran et al. 1996). It was applied to the phenomenon of categorical perception when Maye et al. (2002) demonstrated that the distribution of sounds along a phonetic continuum can influence the later discrimination of a pair of speech sounds (/ta/and/da/) by 8-mo-old infants. Whether statistical learning occurs during song ontogeny in birds remains to be investigated, but categorical perception of song elements in adult birds suggests that it might. Both the production of phonemelike categories of notes (Marler & Pickert 1984) and categorical perception of note types (Nelson & Marler 1989) have been demonstrated in adult swamp sparrows. In addition, category boundaries differ between populations within this species (Prather et al. 2009) just as phoneme categories differ across human languages (e.g. Lisker & Abramson 1970; Miyawaki et al. 1975), and the categorical perception of swamp sparrow notes can depend on context, that is, their position within the song syllable (Lachlan & Nowicki 2015) just as position within a word influences phonemic perception in human speech (Samuel 2011). Finally, just as humans perceive some phoneme exemplars as being more representative or 'better' than others (Samuel 1982; Volaitis & Miller 1992), adult swamp sparrows can discriminate between typical and atypical exemplars of a syllable type (Lachlan et al. 2014), and statistical learning could explain this ability as well.

Another phenomenon that song and speech development might share is a dependence on off-line processing during sleep. Sleep has been linked to the enhanced learning of some tasks by possibly allowing off-line consolidation of recently acquired memories in the form of patterns of neural activity (Shank & Margoliash 2009; Margoliash & Schmidt 2010). As vocal learning requires the creation of memories, the function of sleep in vocal learning may also be important, and this has been explored in zebra finches. Shank & Margoliash (2009) demonstrated that playback of tutor song to juvenile males did not influence singing on the day of exposure but that striking tutor-song-specific neuronal activity in a song nucleus (RA) was recorded the following night, which in turn induced tutor-song-specific changes in singing the next day. Circadian variation in song production quality has also been demonstrated in zebra finches (Derégnaucourt et al. 2005). In humans, the role of sleep consolidation has been investigated in a novel speech learning task (generalization of synthetically produced phonological categories across different

acoustic patterns) in adults; researchers demonstrated that sleep facilitated performance on this task, most likely by refining and stabilizing the representations (Fenn et al. 2003). The role of sleep in speech development remains to be studied, however. A fruitful line of research would be to investigate infant circadian rhythms during canonical babbling, before and after napping.

In both songbirds and humans, behavioral and neural evidence indicates that vocal learning can include the formation of long-term memories even for sounds that are not subsequently used (or heard) in adulthood. Adult white-crowned sparrows typically sing only one song type, which does not change from year to year, but early in the spring they may temporarily 're-express' additional songs that they heard and rehearsed early in life (Hough et al. 2000). Playback experiments have shown that adult nightingales *Luscinia megarhynchos* too can recall songs that they heard during their sensitive phase but did not include in their own repertoires (Gerberzahn et al. 2002). In swamp sparrows, HVC neurons respond to tutor models even when imitations of those models were sung only transiently or possibly not at all (Prather et al. 2010). In humans, early childhood experience with the Korean language results in faster re-learning in adulthood—specifically, early experience correlates with better identification and production of Korean phonemes relative to novice learners of that language—even if subsequent exposure to Korean has been limited or absent (Oh et al. 2003, 2010). In addition, international adoptees from China who are separated from their birth language at about 13 mo of age and tested on average 12.6 yr later still display brain activation to lexically relevant tonal aspects of Chinese that is identical to that of native speakers, even though the adoptees have had no subsequent exposure to or conscious recollection of that language (Pierce et al. 2014). The function of persistent memory in vocal learning in both humans and songbirds is a potentially interesting topic for further study.

Finally, our understanding of the neural and genetic mechanisms of vocal development has grown rapidly, and some similarities between songbirds and humans have been found even at these levels. Although Marler did not address these in his 1970 monograph, he did include the lateralization of neural control as an additional parallel between birdsong and speech development in the *American Scientist* article (Marler 1970b) citing newly published work by Nottebohm (1970). The system of brain nuclei underlying birdsong was first discovered later that decade (Nottebohm et al. 1976), and much has since been learned about its

function in song learning (e.g. memorization: Nordeen & Nordeen 2008; control of vocal plasticity: Brainard 2008; for a general review, see Mooney 2009). Developmental changes in activity in brain areas involved in vocal learning have been documented in songbirds (e.g. Volman 1993; Doupe 1997) and are now being studied in humans using neuroimaging techniques in infants and young children (Kuhl 2010). At a general level, speech and song development both depend on hierarchically organized networks of specialized brain areas that receive input from the auditory system and control the vocal organs. More specifically, our understanding of the homologies between avian and mammalian brains has improved (Reiner et al. 2004; Ferries & Perkel 2008), and we now know that the anterior forebrain pathway (AFP) underlying song learning in birds is anatomically and functionally part of the cortical–basal ganglia (CBG) circuitry that also subserves motor learning in mammals (see Doupe et al. 2005). Analogues in the human brain have not been identified for all known song system nuclei, but similarities at the cellular, neurophysiological, and molecular levels have been documented between some song nuclei and certain speech-related regions of the human brain. Most recently, following complete sequencing of the human (Venter et al. 2001) and zebra finch genomes (Warren et al. 2010), transcriptome analysis has shown that songbird Area X (an AFP nucleus) and human putamen exhibit convergent expression profiles of 78 genes relative to neighboring striatum (Pfenning et al. 2014). The functions in vocal learning of genes with such convergent localization can now be investigated comparatively. Genes known to influence the development of speech in humans might also function in song development; the transcription factor FOXP2 is currently the best-studied example (White 2010; Wohlgemuth et al. 2014). FOXP2, in combination with its target genes, is thought to act in neural differentiation during development and synaptic plasticity in adulthood. In general, methodological advances continue to facilitate comparative study of the neural and genetic mechanisms of song and speech development.

The Value of Comparative Study of Vocal Learning

Peter Marler initially promoted the validity and the utility of comparing birdsong learning and human speech development over 40 years ago. He did this both in the *Journal of Comparative and Physiological Psychology* monograph (Marler 1970a) and in the *American Scientist* paper (Marler 1970b) referred to earlier. Written for different audiences, these papers

emphasized different points in support of the value of birdsong as a model for speech learning. In the monograph, written for comparative psychologists, Marler summarized several earlier investigations in which psychologists had used conditioning to modify animal vocalizations and then contrasted these with 'zoological research' on natural birdsong learning, which had revealed 'several analogies between human and avian vocal learning which have not hitherto been acknowledged in the psychological literature' (Marler 1970a; p. 2). In the *American Scientist* article, written for a more general audience, Marler began by asserting that animal studies are relevant to understanding humankind and that contrary to common perception, this is equally true 'in the psychological realm as in physiology' (Marler 1970b, p. 669).

Because songbirds were at the time the only animals known to learn their natural vocalizations, Marler (1970a,b) next described the superiority of birdsong learning over certain other possible models of human speech development. He wrote that although it would be logical to look to vocal ontogeny in apes and monkeys, studies of non-human primates are of limited use to understanding normal speech development because although a few apes had (with much effort) been trained to produce human speech sounds, vocal imitation does not naturally occur in these animals. He further argued that the imitation of human speech sounds by captive parrots or mynahs is not an informative model because such imitation of other species is not characteristic of normal vocal development in these species. He asserted that natural birdsong development, in which learning normally plays a key role, promised to be most informative from a comparative standpoint.

Indeed, songbirds have since become the best-studied animal model of vocal learning. Based on the many established similarities between song learning and speech development, phenomena discovered in one system can now lead to corresponding discoveries in the other. The role of FOXP2 in vocal learning (first documented in speech; see White 2010) and the effect of contingent social reinforcement on developing vocal phonology (first documented in bird song; Goldstein et al. 2003) are two cases in which this has occurred. This mutual scientific exchange has further increased the number of known parallels between the two systems. As a result, experimental study of the neural and molecular bases of vocal learning in songbirds is increasingly likely to yield information relevant to understanding the mechanisms of human speech development. Examples of specific topics for which songbirds might serve as an informative model

include the action of audition in speech learning and maintenance (Mooney 2009), the brain systems linking social learning with sensorimotor learning (Kuhl 2010), the role of neurogenesis in sensory and sensorimotor learning (Brainard & Doupe 2013), and mechanisms of non-imitative ('adaptive') vocal learning (Tchernichovski & Marcus 2014).

As songbirds continue to provide important insights particularly into the neural mechanisms underlying vocal development, comparative study across a broader range of taxa is an increasingly promising area for future research. In recent decades, vocal learning has been documented to varying degrees in parrots (Todt 1975), hummingbirds (Baptista & Schuchmann 1990; Gaunt et al. 1994), bats (Jones & Ransome 1993; Boughman 1998), seals (Ralls et al. 1985; Van Parijs et al. 2003), cetaceans (Payne & Payne 1985; Tyack 1997), and elephants (Poole et al. 2005). Not all of these are as easy to study as songbirds, so it is unlikely that we will ever learn as much about vocal ontogeny in all of these groups as we know in songbirds. But broader comparative study is crucial. As evolutionary biologists are well aware, and as Brainard & Fitch (2014) reiterate in the context of research on vocal learning, comparisons involving only two clades have minimal statistical and explanatory power. Increasing the diversity of organisms in which vocal development is studied increases the likelihood of success with respect to Peter Marler's suggestion (Marler 1970b, p. 669) that 'If we can only achieve a more thorough understanding of the rules that govern the behavior of animals, we may then be in a better position to develop more revealing hypotheses about ourselves'.

Conclusion

New insights into the similarities and differences between human speech development and vocal learning in animals continue to attract wide interest. In this domain, as in all areas of science, research builds on prior work, and both foundational studies and subsequent advances should be cited. The former is particularly important because early studies often represent a novel approach or shift in perspective that has had a lasting effect in the field. In the case of birdsong ontogeny as a model for human speech development, Peter Marler worked to change the perception that the comparative study of animals and humans in the behavioral realm was any less valid or less informative than that in the physiological realm. He asserted that studies of animal behavior are just as relevant for understanding humans as are studies of

animal physiology, and wrote that 'if this is not yet obvious to most people, I believe it is because our understanding of animals is still so incomplete' (Marler 1970b, p. 669). Research by Marler and colleagues in animal communication has helped to increase this understanding, and the studies that build on that research continue to do so today.

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