



## Review article

## Brains for birds and babies: Neural parallels between birdsong and speech acquisition

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## ABSTRACT

Language as a computational cognitive mechanism appears to be unique to the human species. However, there are remarkable behavioral similarities between song learning in songbirds and speech acquisition in human infants that are absent in non-human primates. Here we review important neural parallels between birdsong and speech. In both cases there are separate but continually interacting neural networks that underlie vocal production, sensorimotor learning, and auditory perception and memory. As in the case of human speech, neural activity related to birdsong learning is lateralized, and mirror neurons linking perception and performance may contribute to sensorimotor learning. In songbirds that are learning their songs, there is continual interaction between secondary auditory regions and sensorimotor regions, similar to the interaction between Wernicke's and Broca's areas in human infants acquiring speech and language. Taken together, song learning in birds and speech acquisition in humans may provide useful insights into the evolution and mechanisms of auditory-vocal learning.

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## 1. Introduction: birdsong, speech and language

### 1.1. Acquisition of complex vocalizations in humans and songbirds

Investigation into the evolution of language is severely impaired by a lack of empirical evidence (Berwick et al., 2013; Bolhuis et al., 2014; Chomsky, in this issue). Analysis of historical evidence suggests a relatively recent origin of the language faculty, arising some 80,000–100,000 years ago (Bolhuis et al., 2014; Tattersall, 2012, in this issue; Chomsky, in this issue). Extant evidence suggests that the faculty of language is unique to *Homo sapiens*, and this singularity is a major stumbling block for the comparative analysis of how language evolved (Berwick et al., 2011, 2013; Bolhuis et al., 2014). In principle, a version of the combinatorial computational system that is characteristic of human language (Berwick et al., 2013; Chomsky, in this issue) could have evolved in non-human animals, either through common descent (e.g. in apes) or through convergent evolution (e.g. in songbirds) (Berwick et al., 2013; Bolhuis et al., 2014). However, neither of these possibilities has resulted in a cognitive system in non-human animals that has the essential characteristics of human language (Berwick et al., 2013; Everaert et al., 2015; Berwick and Chomsky, 2016; Chomsky, in this issue). Research has revealed one group of animals as an excellent model of how we rely on sensory input to learn the sounds we use in speech (Marler, 1970). That group of animals is the passerine songbirds, and two lines of evidence support their use as a model to understand how the brain learns to produce the intricate sounds we use in speech.

First, while the vocalizations of apes and monkeys are relatively simple, the songs of songbirds consist of discrete acoustic elements that occur in a certain temporal order. Those elements, commonly called ‘notes’, can be combined as particular sequences into ‘syllables’, syllables into ‘motifs’, and motifs into complete song ‘bouts’ (Fig. 1). In principle, variable song element sequences may be governed by sequential syntactic rules (Okanoya, 2004; Berwick et al., 2011), which Marler (1977) has termed ‘phonological syntax’. However, current evidence shows that birdsong ‘phonological syntax’ does not have the combinatorial complexity that is characteristic of human language syntax (Beckers et al., 2012; in this issue; Berwick et al., 2011, 2013).

Second, just like humans acquire speech during early development, juvenile songbirds learn their songs through a process of vocal imitation (Bolhuis and Everaert, 2013; Bolhuis et al., 2010; Moorman and Bolhuis, 2013). The trait of imitative vocal learning is shared between humans, songbirds, parrots, hummingbirds and some mammals, but not with apes or monkeys (Jarvis, 2006). Human infants are able to acquire speech by imitating the sounds they hear performed by adults and their peers. From the age of about two, humans can learn up to 10 new words per day (Yang, 2006). In zebra finches, as in many other songbird species, only the males sing. Both male and female zebra finches produce calls, which are learned only in the case of males (Simpson and Vicario, 1990). In addition to their calls, zebra finch males also learn their songs. That learning emerges through imitation of an adult conspecific ‘tutor’, and in the natural situation the tutor is usually their father (Moorman and Bolhuis, 2013).

### 1.2. Behavioral parallels between birdsong learning and speech acquisition

Although so far there is no evidence for a human language-like syntactic structure in birdsong (Berwick et al., 2011; Beckers et al., 2012; in this issue), there are some intriguing similarities between songbirds and human infants regarding the process of auditory-vocal imitative learning (Bolhuis et al., 2010; Moorman and Bolhuis, 2013). Auditory-vocal learning in songbirds has some remarkable

parallels with human speech acquisition (Doupe and Kuhl, 1999; Bolhuis et al., 2010; Bolhuis and Everaert, 2013). In many songbird species, song learning proceeds through two phases: a memorization phase, when a long term memory of the tutor song is formed, and a sensorimotor phase, when the bird starts to vocalize, and its own vocal output is ‘matched’ with the information stored in memory (Konishi, 1965a,b; Marler, 1976; Catchpole and Slater, 2008). During the sensorimotor phase the young bird starts to vocalize, and it is thought that its song output is matched with the internal representation of the tutor song that was formed in the memorization phase. Eventually the adult songbird will sing a crystallized song that, in the case of age-limited learners such as the zebra finch (*Taeniopygia guttata*), does not change substantially during adulthood (Catchpole and Slater, 2008).

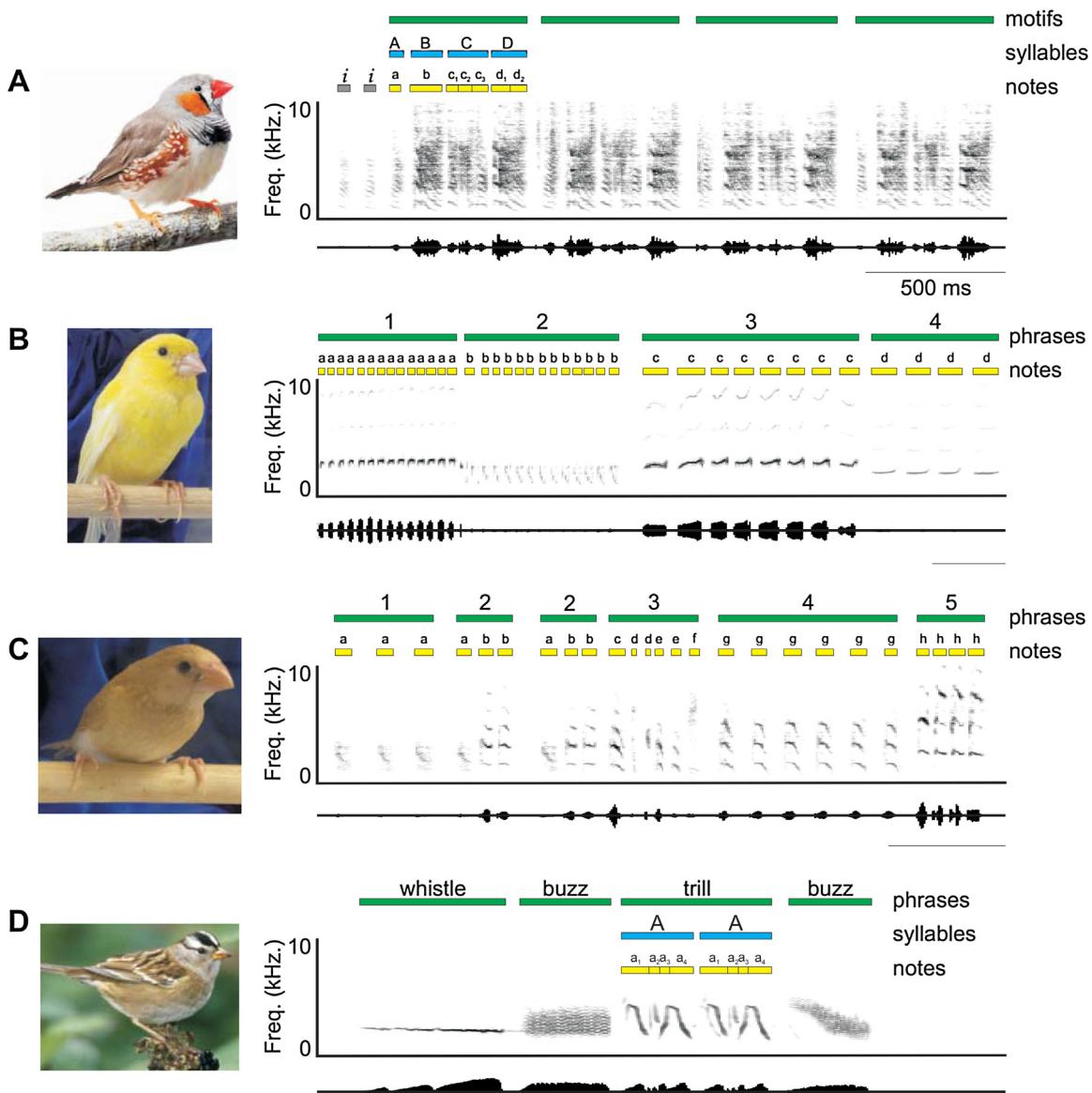
Apart from vocal imitation learning, there are at least two more similarities between song learning in songbirds and speech acquisition in human infants (Bolhuis et al., 2010; Bolhuis and Everaert, 2013; Moorman and Bolhuis, 2013). First, in both humans and songbirds auditory-vocal learning is optimal during a sensitive period early in development. Second, just like human infants go through a ‘babbling’ stage during their sensorimotor acquisition of what will eventually become adult speech, juvenile songbirds go through a transitional phase at the start of vocal production, during which their vocalizations are quite different from those of adult conspecifics. In songbirds, vocalization during the ‘babbling’ phase is known as ‘subsong’. It is followed by ‘plastic song’, when the young individual’s vocalizations gradually come to resemble the adult form, or ‘crystallized’ song (reviewed in Mooney et al., 2008).

## 2. Brains for babies and birds

### 2.1. Neuroanatomical analogies and homologies

Given the similarities in auditory-vocal imitation learning between songbirds and human infants, the question arises as to whether there are also neural parallels. In other words, is evolutionary convergence regarding the learning process (Bolhuis and Wynne, 2009) reflected in the structure and function of the underlying neural mechanisms? At first, this would seem an unlikely prospect. Humans and birds are separated by approximately 600 million years of evolutionary time (Berwick and Chomsky, 2013), and the avian brain is not only much smaller but also organized differently from that of humans (Jarvis et al., 2005). While mammals have a layered cortex, the avian brain consists predominantly of nuclei (Jarvis et al., 2005; Reiner et al., 2004). However, investigations have revealed homologies between some structures in the avian brain and corresponding structures in the mammalian brain (Jarvis et al., 2005). Similarities in connectivity and function are clearly present, such as those between the human neocortex and analogous structures in the avian pallium, including the hyperpallium, mesopallium, nidopallium and arcopallium (Bolhuis and Gahr, 2006; Bolhuis et al., 2010) (Fig. 2). In light of these data, the nomenclature of the avian brain has been revised in order to emphasize the analogies and possible homologies with the brain of mammals (Jarvis et al., 2005; Reiner et al., 2004). In addition, the same genomic transcriptional profiles align across different vocal-learning species such as humans or songbirds, suggesting convergent neurogenetic evolutionary solutions to similar problems (auditory-vocal imitation learning) (Pfenning et al., 2014).

The neural substrate of human speech involves Broca’s area and adjacent motor areas in the inferior frontal cortex. Perception and memory of speech are thought to involve auditory association cortical areas, including Wernicke’s area and surrounding regions in the superior temporal and inferior parietal lobes (Berwick et al., 2013; Bolhuis and Everaert, 2013; Friederici, 2011; Zaccarella and



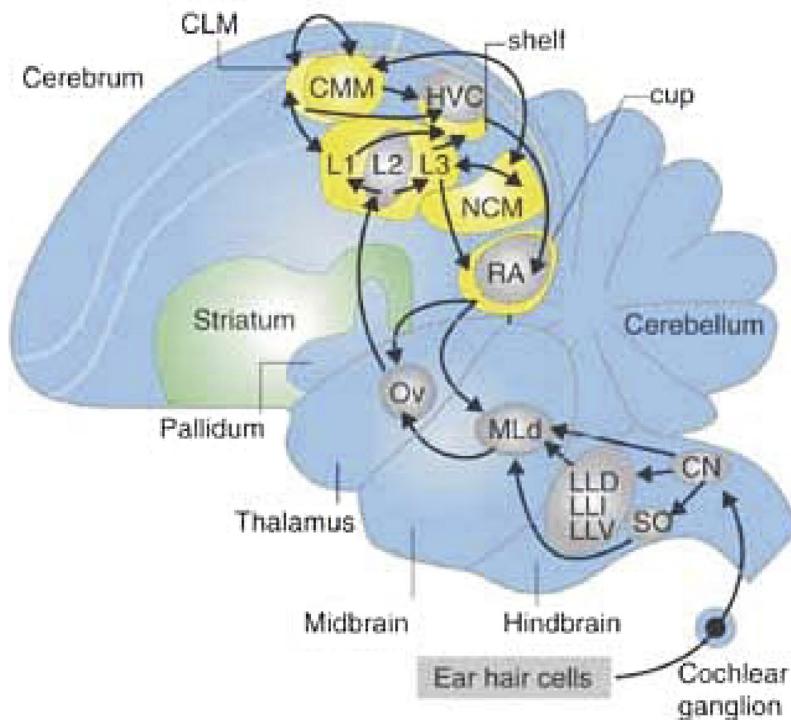
**Fig. 1.** Four species of commonly studied songbirds and their adult songs depicted by a spectrogram (top) and an oscillogram (bottom). Colored boxes above each spectrogram indicate the components of song for each species. In each song, notes are sometimes performed together as syllables, which are then performed in specific sequences known as motifs, phrases or songs. Songs consist of a wide variety of note types and syntaxes. (A) Zebra Finch songs begin with a series of introductory notes (denoted by *i*) followed by a motif that is repeated to form the song. (B) Canary song consists of a series of phrases, and each phrase consists of a single note that is trilled or a multi-note syllable (not shown). (C) Bengalese Finch song also consists of phrases in which the note sequence can vary across songs performed by the same male. (D) White-crowned Sparrow song begins with a whistle followed by other phrases referred to as buzzes or trills. Adapted from Fig. 1 in Mooney et al., 2008. Zebra Finch image courtesy of L. Brian Stauffer (University of Illinois News Bureau). Canary and Bengalese Finch images courtesy of Jonathan Prather. White-crowned sparrow image courtesy of Public Domain Images.

Friederici, in this issue; Hagoort, in this issue). Of course, these networks serve much more complex roles than just production or perception of speech. They are involved in the syntactic and semantic aspects of language, and they interact through a number of connecting pathways (Friederici, 2011; Berwick et al., 2013; Zaccarella and Friederici, in this issue; Hagoort, in this issue).

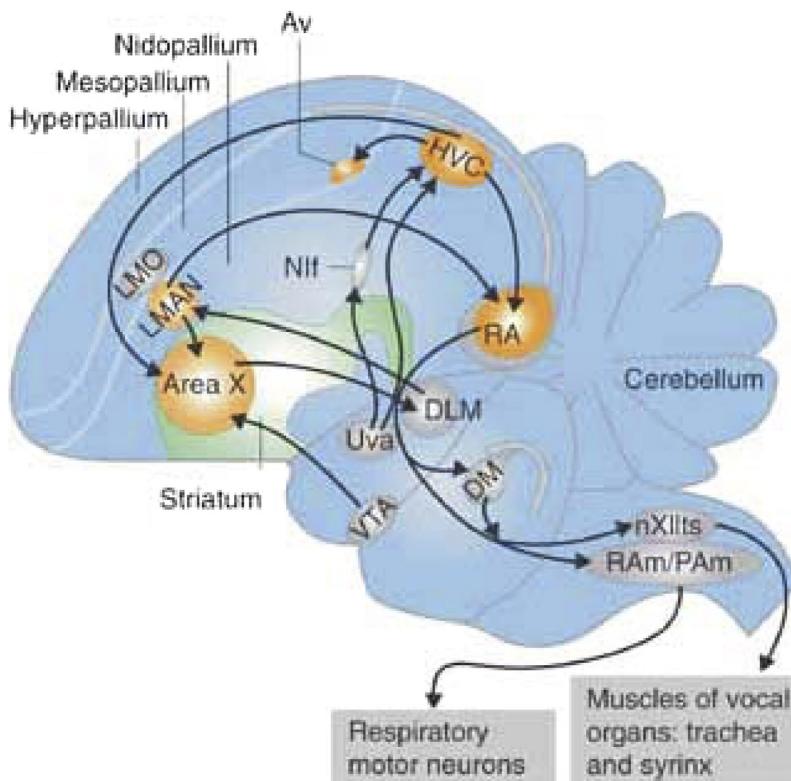
A number of regions involved in song perception, production and learning have been identified in the songbird brain (see Fig. 2). Birdsong is subserved by at least three interconnected neural networks (Bolhuis and Gahr, 2006; Mooney et al., 2008). First, secondary auditory regions, including the caudomedial nidopallium (NCM) and caudomedial mesopallium (CMM, see Fig. 2A), are involved in song perception and are important for the recognition of tutor song (Bolhuis and Gahr, 2006; Bolhuis and Moorman, 2015). Second, the anterior forebrain pathway (AFP) is essential for senso-

rimotor learning and adult song plasticity (Doupe et al., 2005). The AFP is an anterior cortical – basal ganglia – thalamic – cortical loop that originates in HVC (acronym used as a proper name) and passes through Area X (part of the avian basal ganglia, Doupe et al., 2005), the thalamic nucleus dorsolateralis anterior, pars medialis (DLM) and the lateral magnocellular nucleus of the anterior nidopallium (LMAN), and eventually connects with the motor pathway at the robust nucleus of the arcopallium (RA, see Fig. 2B). Third, the song motor pathway (SMP) is involved in song production and certain aspects of song learning (Fig. 2B, reviewed in Mooney et al., 2008). The SMP is a posterior motor pathway connecting the HVC, RA and the tracheosyringeal portion of the nucleus hypoglossus (nXIIts) that contains the neurons that control the muscles of the vocal apparatus. Together, the SMP and AFP pathways are commonly called the ‘song system’.

### A) Auditory pathways



### B) Vocal pathways



**Fig. 2.** Schematic views of the songbird brain. Two parasagittal sections show auditory (A) and vocal motor (B) networks, with interconnected brain regions and nuclei. A: Brain regions depicted in yellow show increased neuronal activation when the bird hears song. The NCM and CMM regions are likely loci for the neural substrate for tutor song memory. B: The orange nuclei show increased neuronal activation when the bird is singing. Depicted are connections between the nuclei of both the song motor pathway (SMP) and the anterior forebrain pathway (AFP). Area X, Area X of the striatum; Av, avalanche; CLM, caudolateral mesopallium; CN, cochlear nucleus; DLM, medial subdivision of the dorsolateral nucleus of the anterior thalamus; DM, dorsomedial subdivision of nucleus intercollicularis of the mesencephalon; HVC, a letter-based name; L1, L2 and L3 are subdivisions of Field L; LLD, lateral lemniscus, dorsal nucleus; LLI, lateral lemniscus, intermediate nucleus; LLV, lateral lemniscus, ventral nucleus; LMAN, lateral

Doupe et al. (2005) have argued that the AFP loop in the song system bears strong similarities in connectivity, neurochemistry and neuron types to the mammalian basal ganglia. In further parallels between songbirds and humans, both LMAN and HVC have been tentatively suggested to correspond functionally to Broca's area (Pfenning et al., 2014). In addition, neural activity related to the animal's perception of song also courses through HVC (Gentner et al., 2000; Okanoya et al., 2001; Prather et al., 2009), suggesting that the functional role of HVC may span features characteristic of both Broca's and Wernicke's areas. Bolhuis and Gahr (2006) suggested that the NCM and the CMM may be analogous with the mammalian auditory association cortex (see Bolhuis et al., 2010 for further discussion).

## 2.2. Interacting neural networks in birdsong and speech

In addition to these neuroanatomical parallels, there is evidence for a similar type of interaction between two neural networks in the brains of songbirds and humans (Bolhuis and Gahr, 2006; Gobes and Bolhuis, 2007; Bolhuis et al., 2010; Bolhuis and Moorman, 2015). As we have argued before, regions in the songbird caudomedial pallium (including the NCM) contain the neural representation of tutor song memory that juveniles acquire prior to attempts at vocal imitation (Bolhuis and Gahr, 2006; Gobes and Bolhuis, 2007; London and Clayton, 2008; Gobes et al., 2010), whereas nuclei in the song system are required for sensorimotor learning and song production. In the case of human speech there is a similar dissociation between Wernicke's area in the superior temporal lobe – primarily involved in auditory perception and memory – and Broca's area in the inferior frontal lobe – particularly involved in vocal production. There is a similar human-avian parallel during speech and song acquisition. Human newborns show increased neural activity in the superior temporal lobe, but not in the inferior frontal cortex, in response to human speech (Imada et al., 2006). An fMRI study in 3-month old infants (which are in the 'cooing' stage of babbling in which syllables are not yet produced) showed activation in the superior temporal cortex (including Wernicke's area) as well as in Broca's area in response to hearing speech (Dehaene-Lambertz et al., 2006). Six- and twelve-month-old infants exhibited elevated activation of both Wernicke's and Broca's areas when exposed to speech sounds (Imada et al., 2006). Taken together, these findings suggest that Wernicke's area is an important part of the neural substrate for speech perception in neonates, and that Broca's area becomes active at a later stage when infants start babbling.

Interestingly, recent evidence supports the idea that the functional distinction between these networks may not be as stark as was previously thought. Both Wernicke's and Broca's areas appear to make at least some contribution to both performance and perception of speech (e.g., Flinker et al., 2015). In parallel to the contributions of those areas to sensory and motor processing of speech sounds, the sensorimotor nucleus HVC has also been implicated in sensory and motor processing of the learned vocal sounds that make up songs (e.g., Prather et al., 2008; Prather et al., 2009; Bolhuis et al., 2010). Together, these data strengthen the parallels between HVC and activity in those regions of the human brain. In addition, it is clear that in human language syntactic and semantic processing there is continual interplay between the two main brain networks (Friederici, 2011; Berwick et al., 2013; Goucha et al., in this issue; Zaccarella and Friederici, in this issue; Hagoort, in this issue). In songbirds, there appears to be a similar dynamic

regarding auditory-vocal learning. In addition to the NCM, HVC might play a role in tutor song memory. Moorman et al. (2015) suggested that the formation of tutor song memory may involve dynamic interaction between the NCM and HVC, perhaps to provide a tutor song template with which to compare the birds' own song (cf. Bolhuis and Gahr, 2006; Gobes and Bolhuis, 2007; Bolhuis et al., 2010; Bolhuis and Moorman, 2015). On the basis of their results, and others, Moorman et al. (2015) suggested that the two brain hemispheres may play different roles in this neural dynamic (see also Section 6.2, below). That is, the left NCM could be involved in tutor song memory processing, while the right NCM may subserve reciprocal interaction between song recognition memory and motor learning systems, including HVC. Although a direct connection between the NCM and HVC is not known, the NCM projects to the CM (caudal mesopallium; Vates et al., 1996), and the CM to HVC (Bauer et al., 2008).

## 3. Rhythmic neural activity in the song system

Rhythmic structure is a central aspect of human spoken language (Langus et al., in this issue; Mol et al., in this issue), and rhythm plays a similarly important role in birdsong. Birdsong consists of individual acoustic elements called notes or syllables (Fig. 1). The spectral properties and duration of each syllable and each intersyllable interval can vary within and across songs, but within a species there is a certain rhythmic pattern by which the song is organized. This behavioral observation has led to the idea that specific properties of the underlying neural mechanism may account for this song rhythm.

Based on examining the structure of individual birds' songs as they progress through development, Saar and Mitra (2008) proposed that there is a developmental trajectory of the rhythm and patterning of zebra finch songs. They showed that the relatively quick rhythm (3.7 notes per sec) in the song of a 45 day old zebra finch changed into a slower rhythm (1.7 Hz) by the time that same bird was 65 days old. Another study used a similar technique but quantified the development of rhythmic patterning using the inter-onset interval of song syllables in Bengalese finch (*Lonchura striata var. domestica*) songs (Sasahara et al., 2015). By examining the developmental trajectory of inter-onset intervals of song syllables, they were able to show that these were initially brief (approximately 80–100 ms) in Bengalese finch songs. As the song developed, however, those intervals slowed and gradually differentiated into several narrowband peaks (approximately 85–140 ms), reflecting differentiation of song syllables. These data revealed that rhythmic pattern of the Bengalese finch song become more stereotyped as the song phonology develops.

In parallel with these behavioral observations, efforts have been made to determine the neural mechanisms of rhythm generation in birdsong. One of the central questions here is whether the song rhythm is constructed based on the processing speed of the underlying neurons. By cooling or warming cells within nucleus HVC, Long and Fee (2008) showed that song units expanded by 30% when cells were cooled by as much as 8 °C and shrunk by 10% when cells were warmed by as much as 5 °C. The same treatment applied at the level of RA did not change the song length, suggesting that HVC may contain a clock mechanism for directing the rhythmic production of birdsong. In further support of parallelism in the mechanisms that underlie birdsong and speech, Long et al. (2016) found that, in humans, cooling Broca's region or the speech motor cortex in the

magnocellular nucleus of the anterior nidopallium; LMO, lateral oval nucleus of the mesopallium; MLd, dorsal part of the lateral nucleus of the mesencephalon; NIf, interfacial nucleus of the nidopallium; nXIIts, tracheosyringeal portion of the nucleus hypoglossus (nucleus XII); Ov, nucleus ovoidalis; PAm, nucleus paraambiguus medullaris; RA, robust nucleus of the arcopallium; RAm, nucleus retroambiguus medullaris; SO, superior olive; Uva, nucleus uvaformis; VTA, ventral tegmental area. Reproduced, with permission, from Moorman et al., 2011. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

left hemisphere affected the timing or articulation of speech. These data suggest that there are distinct neural mechanisms underlying timing and other aspects of vocal communication.

The next questions are how the song rhythm may be represented in HVC and whether the rhythm is organized within HVC or through additional extrinsic circuits. A recent study recorded local field potentials from identified neurons in HVC of singing zebra finches (Markowitz et al., 2015). Results showed that projection neurons were activated synchronously at an average of 30 Hz. Interestingly, this synchronous activity was not time-locked with syllable onset or offset. Moreover, interneurons fired in antiphase with the projection neurons, suggesting that at least part of the mechanism underlying rhythm resides within HVC. This is because the alternating activity of projection neurons and interneurons provides stable rhythmic activity. It is thought that the sparse activity of many cells may converge onto one recipient cell and be summed to yield the 30 Hz synchronized activity evident in local field potentials. Those results also match with an earlier study of the synfire chain-like sparse activity expressed by HVC neurons (Hahnloser et al., 2002). Another study investigated the shortest interval between note onset times in zebra finch songs, and those authors found that songs comprise chunks of sound and internote intervals that occurred at a rate of around 30 Hz (Norton and Scharff 2016), consistent with the idea that rhythmic neural activity at that rate may play an important role in shaping the rhythm of song performance.

Questions remain as to how such organized rhythmic patterns appear during development and whether that synchronous firing is an inherent characteristic of HVC or is programmed by the architecture of inhibitory and excitatory neurons. One aspect of these questions was answered by Okubo et al. (2015) through very detailed developmental electrophysiological studies. By chronically recording multiple projection neurons in HVC, they found that when two syllables emerged from a prototype syllable, a population of neurons that fired together for the prototype syllable split to form two populations of neurons that fire for each of the two syllables. Those authors suggested that this process continues until the final crystallized adult song emerges.

Further research is needed to understand how the 30 Hz rhythm found in the local field potentials of HVC neurons may be related to the syllable-associated sparse code of the same populations of neurons. One possibility is that the 30 Hz rhythm is more or less innately determined by the architecture of the microcircuit within HVC, and the exact timing of firing for each projection neuron is shaped by auditory feedback during the sensorimotor stage of song learning. One way to test this would be to examine whether deafened or isolate-reared birds show the 30 Hz rhythm in the absence of proper auditory input.

Up to now we have been discussing rhythm in solo song, however rhythm is important not only in organizing structured songs but also in coordinating social behavior. Dancing is also highly associated with singing in birds (Laland et al., 2016). In zebra finches, body movements occur mostly at the beginning and ending of song motifs (Ullrich et al., 2016). By studying rhythms in a behavior that is not directly related to song control, we may be able to identify some undiscovered aspect of song control. Along those lines, zebra finches exchange short calls among socially affiliated individuals, especially between members of a mated pair. Behavioral observations revealed that these short calls "crystallize" in pitch and duration so that calls became more distinctive within a few days (Benichov et al., 2016). Latencies in responding in both birds were initially variable but eventually became stable, with a mean latency at around 200 milliseconds. This behavior obviously requires mechanisms to establish precise timing. Moreover, this behavior was observed in both males and females, suggesting that it may be independent of HVC, since female zebra finches possess only a small, rudimentary HVC. In further support of a role for learn-

ing in this behavior, when a vocal robot that played a broadband noise at around 200 ms was introduced to the dyad interaction, birds quickly learned to avoid the noise by shifting the temporal window to a longer latency. This "jamming avoidance" response occurred in both males and females. When RA was lesioned, both males and females lost the ability to perform the "jamming avoidance" response. Results of this lesioning study suggest that HVC is not the only site necessary for rhythm production. Regions including RA may also be necessary to coordinate social rhythm in zebra finches. Since the region around RA also contains auditory areas, the study does not conclude whether it is auditory information, motor information, or information involving both systems that is required for social rhythmic coordination in zebra finches.

In addition to the synchronization of social behavior in finches, synchronization to external stimuli has also been studied in parrots. Using a public video database, Schachner et al. (2009) examined thousands of video and audio recordings to examine the degree to which animals synchronize their motor behavior to the rhythm of music. They found that only elephants and a few parrot species showed significant entrainment to music. Based on this result, Patel et al. (2009) proposed a "vocal learning hypothesis" of rhythmic synchronization. According to this hypothesis, brain structures necessary for vocal learning also establish the basis for rhythmic synchronization. This could include sensory-motor mirroring in the HVC (Prather et al., 2008; Fujimoto et al., 2011). If vocal-to-auditory, or auditory-to-vocal translations are represented in such a system, rhythmic synchronization could be a byproduct of that.

In an operant setting, budgerigars, a species of vocal learning parrots, were trained to peck keys in synchrony with a rhythmic sound and flashing light, and those birds showed clear evidence of synchronization to a wide range of stimuli (Hasegawa et al., 2011), supporting the vocal learning hypothesis. However, the social synchronization in the female zebra finches described above (Benichov et al., 2016) and evidence of synchronization in other species in which the degree of vocal learning remains unclear (e.g., sea lions; Cook et al., 2013) are counter examples to this hypothesis. Recent evidence, however, suggests that sea lions and other pinnipeds may have the ability to intentionally control their vocal output, which is thought to be a precursor to vocal learning (Reichmuth and Casey, 2014).

Nevertheless, birds remain important and useful models in which to study rhythmic synchronization between the brain and behavior. They will facilitate future studies of fundamental questions such as: What is the neural mechanism for the 30 Hz oscillation in HVC and how is this related to real-time vocal production? How does that 30 Hz oscillation develop during ontogeny from the juvenile to the adult state? It is known that spontaneous firing rates during sleep decrease as zebra finches mature (Nick and Konishi 2004), suggesting that the 30 Hz rhythm might follow a similar pattern. What is the relationship between rhythms in song and rhythms in social behavior? Answering these questions in birds should provide clues to help us also understand the neural mechanisms that underlie rhythmicity in human speech and music.

#### 4. Processing of auditory feedback

Ascending auditory pathways in songbirds follow the general plan of the vertebrate auditory system (Wheatcroft and Qvarnstrom, 2015). Auditory input is coded by the basilar papilla of the cochlea, and neural activity is relayed to the cochlear nucleus. From there, the auditory pathway continues to the midbrain auditory region MLD, the thalamic relay nucleus Ov, and the primary cortical area Field L. Auditory information then diverges from Field L to various brain regions, including higher auditory areas such as NCM, and auditory-motor integration sites such as HVC and

NIf. These pathways clearly carry auditory information, but an understanding of how auditory information interacts with motor information in the song system has remained elusive.

Like human speech (Fairbanks, 1955), songbirds also require auditory feedback regarding their own song performance not only to acquire the song as juveniles, but also to maintain the song as adults. This has been shown by deafening (Konishi, 1965a,b; Nordeen and Nordeen, 1992; Okanoya and Yamaguchi, 1997), by distorting auditory feedback (Fukushima and Margoliash, 2015; Leonardo, 2004; Leonardo and Konishi, 1999), or by changing the pitch using a helium atmosphere (Nowicki, 1987; Yamada and Okanoya, 2003). Relatively early in the process of exploring the role of auditory feedback, a prominent idea was that errors were processed through a pathway involving the basal ganglia (Brainard and Doupe, 2000). In this model, auditory feedback is compared with a hypothetical internal template, and any error between the feedback and template is computed in that basal ganglia pathway (Area X and output from LMAN to the song motor system). More recent studies, however, are suggesting updates to this simple model.

As explained in the following section (mirror neurons), some projection neurons emerging from HVC have a mirror neuron-like property (Prather et al., 2008; Fujimoto et al., 2011). These are neurons that fire when listening to a specific part of the song (often an isolated syllable) or singing the same part of the song. Because these neurons continue to fire during singing even when auditory feedback is distorted (Kozhevnikov and Fee, 2007; Prather, 2013; Prather et al., 2008), the activity of these neurons is thought to be related to the motor performance of song.

This finding raised the question of where a possible auditory-motor interaction may occur in the songbird brain. Hamaguchi et al. (2014) investigated this using intracellular recording from the HVC projection neurons in singing zebra finches. They used delayed auditory feedback to dissociate motor activity and auditory feedback, and they found that singing-related activity in the projection neurons was not affected by this procedure. Their results indicated that auditory input to the HVC is gated off while the bird is singing. Additional results also suggested that the site of auditory-motor interaction should be found elsewhere. By using an altered feedback technique, Ali et al. (2013) found that the basal ganglia pathway is necessary for changing spectral features of the song but not the temporal features of the song (see also Hampton et al., 2009), suggesting that auditory feedback may be processed in two different pathways including the basal ganglia pathway.

Another pathway for auditory feedback may involve a novel region that is not considered to be a part of the song system. By utilizing anatomical and electrophysiological techniques, Mandelblat-Cerf et al. (2014) found that a region of the arcopallium just below the RA, AIV, received input from higher auditory regions including the CM, NC, and the HVC-shelf. Furthermore, neurons in AIV responded to degraded auditory feedback and lesioning this area when the bird is young disrupts vocal learning. Furthermore, AIV projects to the midbrain dopamine area VTA, suggesting an involvement of auditory evaluation of ongoing songs.

Auditory feedback is usually thought to be used to detect errors in motor production and to correct ongoing motor behavior. However, auditory feedback could be used in other ways. Many species of birds use repeated syllables. The number of repetitions is usually stochastically distributed rather than exactly determined. Bengalese finches often sing such songs. Wittenbach et al. (2015) hypothesized that the number of repetitions might be determined by weakening auditory feedback as the syllable was repeated. As predicted, deafened Bengalese finches reduced number of syllable repetitions, suggesting that feedback may affect not only the spectral composition but also the sequencing of individual notes.

In sum, although the exact mechanisms by which auditory feedback works to maintain songs remains incompletely understood,

we now have a lot of evidence suggesting there may be multiple pathways and multiple sites of interaction between auditory and motor signals. Songbirds should provide useful models to understand the sensory-motor interactions in speech production.

## 5. Mirror neurons in birdsong learning and speech acquisition

Since the time of their discovery, mirror neurons have been considered attractive candidates to underlie how humans learn and maintain the sounds we use in speech (Iacoboni, 2009). First discovered in recordings of individual cortical neurons in primates, an individual mirror neuron is active both when the monkey performs an action and when the monkey observes that (di Pellegrino et al., 1992). That correspondence between sensory perception and motor action suggested that activity of those cells may provide a link through which animals could engage in imitative learning. Additional experiments revealed that sensory-evoked activity of mirror neurons also extends to auditory inputs (Kohler et al., 2002). The sounds that were capable of activating those neurons were not sounds used in communication, but they did reveal the possibility of an audiomotor correspondence in the activity of individual cells. Over more than two decades of study, investigators have described many types of mirror neurons in the monkey cortex (Rizzolatti and Craighero, 2004; Rizzolatti and Fogassi, 2014). The functional roles of those cells remain largely speculative, but careful study of the sensorimotor correspondence evident in mirror neurons may provide insight into how auditory information is integrated with motor performance to enable organisms to learn the sounds used in vocal communication.

Speculation regarding the neural mechanisms underlying speech and language predates the discovery of mirror neurons; however the properties exhibited by mirror neurons make them well suited to play important roles in vocal learning and communication. For example, Rizzolatti and Arbib (1998) have emphasized that "mirror neurons appear to represent a system that matches observed events to similar, internally generated actions, and in this way forms a link between the observer and the actor." They also draw parallels between their findings in the ideas of linguists such as Alvin Liberman (1993) who noted that "in all communication, sender and receiver must be bound by common understanding about what counts ... the processes of production and perception must somehow be linked; their representation must, at some point, be the same." This idea is sometimes described as the Motor Theory of speech perception. Such comments generated interest in whether mirror neurons exist in humans and whether they might play a role in speech and language. Interestingly, studies using imaging and transcranial stimulation revealed the presence of a "mirror system" in humans (Fadiga et al., 1995; reviewed in Rizzolatti, 2005). Groups of cells were found to be active in association with performance and perception of the same task, and regions that expressed that sensorimotor correspondence included regions implicated in speech, such as Broca's area in the frontal lobe (Rizzolatti, 2005). That finding revealed that specific brain sites were active in both states and therefore constituted a "mirror system", but it left open the question of whether individual neurons were active in both states. Mukamel et al. (2010) addressed that question directly. In data collected during surgical intervention to treat epilepsy, they found that individual neurons in the human cortex were active in association with both performance and perception. Those data reveal the presence of mirror neurons in the human brain, but they also highlight the difficulty in obtaining those data and the challenges inherent in studying neurons with sufficient resolution to assess whether individual cells act as mirror neurons. Researchers continue to turn to primates as an animal

model that enables collection of those high resolution data, however those animals do not express the richly detailed vocal learning that characterizes acquisition and maintenance of the sounds used in speech and language. To investigate the possible role of mirror neurons in vocal learning, researchers have turned to songbirds because an abundance of behavioral and neurophysiological data have revealed that songbirds rely on vocal learning to acquire and maintain their songs just as we rely on it to learn the sounds used in speech.

Several laboratories have detected neurons in the songbird brain whose properties suggest that those cells may function as auditory vocal mirror neurons. In the earliest studies of those cells, researchers found a region of the songbird forebrain (the nucleus HVC) in which cells were active both when the bird sang and when it heard song played to it through a speaker (Katz and Gurney, 1981; McCasland and Konishi, 1981). Just as in the case of humans, these data revealed the possibility of a “mirror system”, but they left open the question of whether some cells were active during hearing but others were active during vocalization, or whether one and the same neuron may be active in both states. In subsequent studies, researchers have sought to characterize the properties of individual neurons. The first study to reveal the presence of auditory-vocal mirror neurons in the songbird brain took advantage of natural behaviors expressed by swamp sparrows (Prather et al., 2008). Specifically, male swamp sparrows use song to defend their territory, and they will often “countersing” in response to hearing songs, even in response to hearing playback of their own songs. Thus, swamp sparrows can be induced to sing the same song type that was played to them as an auditory stimulus just seconds earlier, providing a natural and efficient means of examining the neural representation of one and the same vocalization in both the auditory and the motor domains. Recordings of auditory activity in individual corticostriatal (HVCX) neurons revealed that those cells were selectively active in association with one vocalization but not others (Prather et al., 2008). For example, an individual HVCX neuron was typically active in association with only one element of the bird's vocal repertoire. Those recordings also revealed that HVCX neurons represented that vocalization using very sparse bursts of action potentials. Additional experiments revealed that the auditory activity of those cells was not simply related to low-level auditory processing. Instead, auditory activity of those cells was related to the animal's perception of the song stimulus (Prather et al., 2009). Thus, HVCX neurons express at least one half of the sensorimotor correspondence that we would expect of auditory-vocal mirror neurons: each cell expresses a selective and temporally precise representation of a specific vocal behavior.

The next step was to investigate the activity of those same HVCX neurons when the bird sang. Just as those neurons expressed selective and temporally sparse representations in the auditory domain, they also expressed nearly identical representations in the vocal motor domain (Prather et al., 2008). Specifically, individual HVCX neurons were active in association with performance of one song but not others in the bird's vocal repertoire. Invariably, the song for which a cell was active in the auditory domain was also the song for which it was active in the vocal motor domain, and those vocal motor action potentials were sparse and temporally precise, just as they were in the auditory domain (Fig. 3A). Individual cells expressed bursts of action potentials in association with a specific vocalization regardless of whether it was heard or sung, and the timing of those bursts was precise and identical in both the sensory and motor domains (Fujimoto et al., 2011; Prather et al., 2008). Thus, individual HVCX neurons express a sensorimotor correspondence that is precise in both selective representation of one vocal behavior and precisely aligned timing of action potentials in each domain.

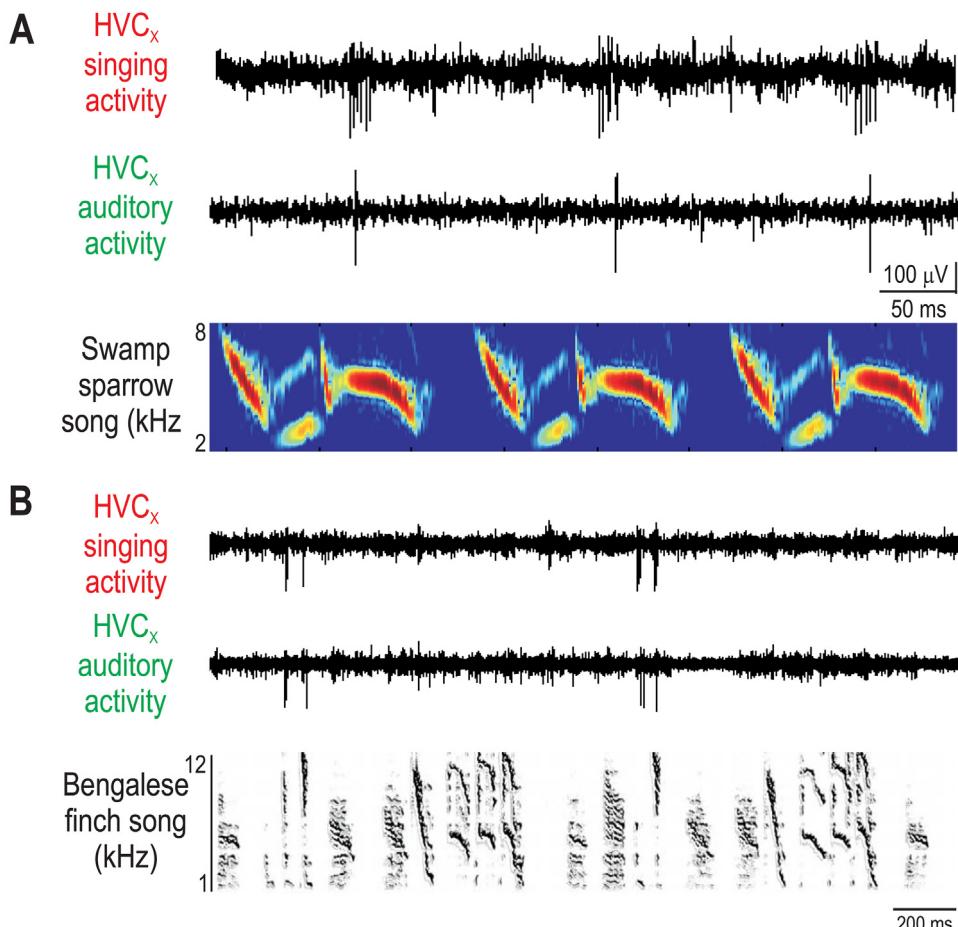
Subsequent studies extended those observations beyond swamp sparrows into multiple species, including Bengalese finches and canaries (Fig. 3B) (reviewed in Prather, 2013). An advantage of that extended approach is that the song syntax of those species is more complex than it is in swamp sparrows, enabling researchers to discern the scale of vocal features encoded by individual neurons. Fujimoto and colleagues (2011) demonstrated that HVCX neurons in Bengalese finches encode an array of structural and syntactical features, including individual notes and specific note transitions. Across the population of HVCX cells, it is thought that their activity collectively represents the entire vocal repertoire. In studies of zebra finches, Keller and Hahnloser (2009) found evidence suggesting that cells expressing a precise sensorimotor correspondence may exist not only within premotor cortical areas (HVC) but also in primary auditory cortex. Their data suggest that this pattern of activity may arise in multiple brain regions and may be used to compare performance versus a sensory report of the associated behavioral outcome. These comparative observations suggest that a precise sensorimotor correspondence in cortical cells is not simply a trait of one songbird species or another. Instead, is a broadly conserved trait of vocal learning species. An important future goal will be to explore the processes through which a precise sensorimotor correspondence arises in such cells during development and what role that correspondence may play in the acquisition and maintenance of learned vocalizations.

The nature of the sensorimotor correspondence expressed by HVCX neurons is reminiscent of the properties expressed by mirror neurons in primates. Many mirror neurons characterized in primates have been described as “broadly congruent”, meaning that those cells were active in association with more than one action, and the actions represented by an individual neuron were similar but not identical in the sensory and motor domains (Gallese et al., 1996). Additional recordings revealed a subset of mirror neurons that were described as “strictly congruent”, meaning that those cells are active in association with only one action, and the patterns of activity are identical in the sensory and motor domains (Gallese et al., 1996). Data from songbirds suggest that HVCX neurons may act as strictly congruent auditory-vocal mirror neurons, forging an anatomical link between auditory perception and vocal production. The variety of songbird species and the associated variety of vocal syntax make songbirds ideal subjects in which to continue our investigation into how the brain enables songbirds and humans alike to learn their vocalizations.

## 6. Brain lateralization in speech and birdsong

### 6.1. Lateralization of vocal control

There is brain lateralization in speech and language in human babies, infants and adults (Friederici, 2011; Moorman et al., 2015; Moorman and Nicol, 2015). Roughly, the left hemisphere is involved in syntax and semantics while the right hemisphere is activated during processing of prosodic structure (Friederici, 2011). More generally, lateralization of neural structure and function are prominent features in humans and a broad range of other species, and lateralization of motor control is clearly evident in human behavior (reviewed in Corballis, 2012). Because cognitive behaviors are less dependent on the spatial and mechanical properties of the environment than physical movements, it is perhaps surprising that many cognitive functions are also associated with at least some degree of lateralized control. For example, emotional processing, spatial attention, and the recognition of human faces are all more strongly associated with activity in the right hemisphere than in corresponding structures in the left hemisphere (reviewed in Chance, 2014; also reviewed in Corballis, 2014). The preva-



**Fig. 3.** HVCX neurons exhibit a precise sensorimotor correspondence. (A) That is evident in the activity of cells recorded in adult swamp sparrows singing-related and auditory activity (top) in association with several syllables of the primary song type (shown as a spectrogram, bottom). Adapted from Fig. 3 in Prather et al., 2008. (B) A similar correspondence between singing-related and auditory activity is also evident in individual HVCX neurons of Bengalese finches, suggesting that a precise sensorimotor correspondence is a general property of HVCX neurons (singing-related activity (red, top) in HVC<sub>x</sub> cells of adult male Bengalese finches was phasic, occurring during a select portion of the polysyllabic song (bottom)). The same cell also responded phasically at the same part of the song when it was presented as an auditory stimulus (green, middle)). Adapted from Supplementary Fig. 3 in Prather et al., 2008. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

lence of lateralized control of behavior suggests that lateralization likely confers important advantages. Such benefits could include specialization and the avoidance of redundancy. Grouping of functionally related structures into lateralized structures may also yield more efficient circuits, reducing the need for callosal or other commissural connections and increasing the speed of communication between portions of the relevant circuit. Together with the prevalence of lateralized control, these possible benefits have generated intense interest in possible mechanisms through which lateralization emerges in ontogeny and is preserved throughout life.

One of the most thoroughly characterized examples of lateralized control of behavior is evident in the arrangement of brain sites related to speech and language (reviewed in Ocklenburg et al., 2014). Language is associated with a network of specialized areas spanning frontal, temporal and parietal areas, and there is a stark asymmetry in the contributions of the left and right hemispheres. For example, areas in the left hemisphere are associated with focal syntax, temporal properties of speech, and the brief transitions that are present in the sounds that compose speech (Friederici, 2011). In contrast, corresponding areas in the right hemisphere are more closely associated with prosody, spectral properties of speech, and emotional valence of the sounds used in vocal communication (reviewed in Chance, 2014; Friederici, 2011). Variation in the characteristics of different languages has also provided insight into

how speech and language are processed in the brain. For example, prosody is processed primarily by the left hemisphere in languages in which pitch plays an important role in communicating the meaning of individual sounds (reviewed in Friederici, 2011). Those data support the idea that language processing regions are associated with specific cognitive aspects of language (e.g., word meaning) as opposed to physical properties of the acoustic signal (e.g., spectral properties).

In noting the prevalence of handedness in chimpanzees (e.g., Biro et al., 2006; Humle and Matsuzawa, 2009), some authors have speculated that dominance of the right hand and the associated left cortical areas may provide insight into possible origins of human speech. Specifically, anatomical asymmetry and the presence of mirror neurons in the brains of humans and nonhuman primates have led to speculation that those systems may be precursors for the neural circuits that underlie human spoken language (Corballis, 2012). In early studies of the mirror system in primates, neural activity was most closely associated with manual grasping, and those cells were found in areas of the prefrontal cortex that include sites that are considered the homolog of Broca's area in the human brain (di Pellegrino et al., 1992; Rizzolatti and Arbib, 1998). With additional study, it was found that mirroring also extends to orofacial movements (Gallese et al., 1996). Interestingly, in a study where humans were asked to open their mouths while grasping an object,

the size of the subject's gape increased with the size of the object that they grasped. Similarly, when subjects were asked to open their hands while grasping objects with their mouths, the degree of hand opening was also related to the size of the object being grasped by the mouth (Gentilucci et al., 2001). This has been taken as support for the idea that neural control of precise orofacial movements may have emerged from a system that was dedicated to precise manual movements. In additional studies of mirror neurons, it was found that some of those cells are even responsive to auditory stimuli (Keysers et al., 2003; Kohler et al., 2002). Curiously, responses of those auditory-responsive cells in nonhuman primates do not extend to conspecific vocalizations, leading some researchers to criticize the idea that speech may have emerged from a neural system specialized for orofacial gestures. Proponents of that idea, however, have interpreted unresponsiveness to conspecific vocalizations in nonhuman primates as evidence that incorporation of vocalizations into the mirror system must have been a later evolutionary development (Gentilucci and Corballis, 2006). Researchers have proposed that vocal components were gradually incorporated with manual and facial gestures, and that over time, vocal gestures gradually assumed dominance, perhaps because they are less physically demanding while still capable of broad behavioral diversity.

The legacy of such a putative transition from manual to vocal gestures may also be evident in the lateralization of control in signed languages that are externalized through manual gesture. Brain areas associated with spoken language are also activated in association with performance of linguistic gestures in signed languages (Horwitz et al., 2003). Some researchers have asserted that the legacy of the manual origin of spoken language may even be evident in our use of manual gestures to emphasize spoken points and our reliance on hand gestures when attempting to communicate with people who speak a different language (Corballis, 2012).

Lateralization of vocal behavior is also clearly evident in how songbirds control the function of their vocal structure. In contrast to the human vocal structure (larynx) that contains one set of sound generating vocal folds, the songbird vocal structure (syrrinx) contains two sets of vocal folds (Suthers and Zollinger, 2004). In their song performances, songbirds can control each of these sound generating sources independently (Suthers, 1997). In addition, the properties of those two sources are slightly different, such that one is slightly larger (typically the left side) and therefore more resonant in production of low frequencies, and the other is slightly smaller and more resonant in production of higher frequencies (Suthers and Zollinger, 2004). An especially clear example of how syringeal asymmetry is exploited is evident in the songs of Northern Cardinals. Individual notes in cardinal songs span wide frequency bandwidths, typically consisting of a down-sweep from high to low frequencies. The early portion of the note contains high frequencies that are performed by only the right side of the syrrinx (Zollinger and Suthers, 2004). Midway through the production of the note, the bird ceases airflow on the right side and initiates vocalization using the left side, and the transition is so seamless that it is nearly impossible to detect by ear (Zollinger and Suthers, 2004). The result is a wide-bandwidth frequency down-sweep that exploits the physical properties of the vocal apparatus to achieve performances that would otherwise be much more challenging or perhaps even impossible.

Lateralization of vocal behavior is also evident in the neural control of song production. The neural pathways that innervate the muscles that control the syringeal vocal folds are ipsilateral, such that each hemisphere of the forebrain is responsible for control of one set of vocal folds in one half of the syrrinx (Suthers, 1997). Because of that arrangement, the transition between vocalization on the left and the right sides of the syrrinx also represents a transition of neural control between circuits in the left and right hemispheres. Both sides contribute to song production, indicating

that song is not exclusively lateralized to either hemisphere, but as in the case of human speech there appears to be hemispheric dominance in the control of song production. Nottebohm et al. (1976) found that lesioning integral components of the song control system in the left hemisphere of canaries eliminated production of the majority of notes of each bird's vocal repertoire. That pattern was consistent across birds that they studied, leading them to conclude that vocal production was left-lateralized in canaries just as it is in humans. In subsequent work, Okanoya and colleagues did a similar analysis of the lateralization of both song production and song perception in another distantly related species (Bengalese finches, Okanoya et al., 2001; Okanoya and Watanabe, 1994). Despite the phylogenetic distance between Bengalese finches and canaries, both species are left-dominant, suggesting that lateralized brain control, and more specifically left-dominant control, is a broadly conserved feature of song production. In an elegant study using zebra finches, Hahnloser and his colleagues found that both hemispheres are essential for song production, and dominance of song production switches rapidly between each hemisphere throughout the duration of the song (Wang et al., 2008). Together, these studies highlight the diversity of vocal characteristics and different forms of hemispheric dominance among songbird species. Comparative studies of these and other species afford a rich opportunity to explore the mechanisms through which such patterns emerge and exert their influence on learning and performance of vocalizations (Brenowitz, 1997; Brenowitz and Zakon, 2015).

## 6.2. Lateralization during auditory-vocal learning

In an additional parallel to human speech, neural processing of song appears to be lateralized in not only sites related to song production but also sites related to song perception. In another landmark study by Nottebohm and his students, Cynx et al. (1992) found that birds that received lesions in auditory-processing areas in either the left or the right hemisphere expressed different forms of perceptual impairment. Birds that had their right sides preserved fared better on discrimination of spectral properties of song, whereas birds that had their left sides preserved performed better in discriminating different songs performed by different individuals. Thus, the two halves of the songbird brain process conspecific vocalizations differently, just as is the case for human processing of the sounds used in speech and language. Hemispheric asymmetry in areas related to perception has also been found by others, and the functional contribution of that asymmetry appears to emerge in an experience-dependent process (Minagawa-Kawai et al., 2011; Olson et al., 2016). These findings add to the ever-increasing number of parallels between birdsong and human speech. The experimental tractability and the precision with which behavioral and neurophysiological data can be sampled in songbirds make them ideal subjects for continuing research into the neural basis of learned vocalizations in birds and humans.

Moorman et al. (2012) found that in awake juvenile zebra finches, neuronal activation in the NCM and HVC was left-lateralized. The left NCM of awake juveniles was dominant when the bird was exposed to tutor song, while HVC of awake, non-singing zebra finches was left dominant irrespective of the stimulus (tutor song, novel song or silence) to which they were exposed. More recently, Moorman et al. (2015) demonstrated differential lateralization of neuronal activation in the NCM and HVC in juvenile male zebra finches during sleep. The strength of song learning was correlated with the lateralization ratio in the NCM during sleep, with greater song similarity related to stronger neuronal activation in the left hemisphere. When the experimental subjects were divided into "poor learners" and "good learners", the authors found that for the NCM, the right hemisphere was predominantly activated during sleep in poor learners, while the left hemisphere was

dominant in good learners. HVC activation of sleeping juveniles was right-dominant independent of the strength of song learning. Taken together, the findings of Moorman and colleagues suggest differential lateralization of neuronal activation depending on the behavioral state of the animal (sleeping or awake).

[Moorman et al. \(2015\)](#) noted that poor learners exhibiting neuronal activation predominantly in the right NCM, while neuronal activation in good learners was left-lateralized, is reminiscent of language-related lateralization in humans that are acquiring a new language. In fact, language-related neuronal activation is already left-dominant in babies and infants (e.g., [Holowka and Petitto, 2002](#); [Peña et al., 2003](#); [Dehaene-Lambertz et al., 2002, 2010](#); [Mahmoudzadeh et al., 2013](#)). In children and adults who are acquiring language or learning a second language, brain regions activated during speech perception were initially right-dominant or bilateral and encompassing relatively large areas. With increased language proficiency, neural activity shifted to the left side of the brain or was reduced in extent, with left-dominance at higher ages and more developed language abilities (see [Mahmoudzadeh et al., 2013](#); [Moorman and Nicol, 2015](#); for reviews).

[Moorman et al. \(2015\)](#) speculated on the possible functional significance of this kind of brain lateralization in both humans and songbirds (cf. [Moorman and Nicol, 2015](#)). For example, for humans it has been suggested that the left-sided auditory cortex is more efficient than the right in processing speech-like temporal patterns. Similarly, for songbirds it has been suggested that there is a functional division of the two brain hemispheres. In starlings, song processing in the left hemisphere might be more focussed on individual recognition of birds far away, while the right hemisphere may be specialized for analysing long and complex song sequences performed by birds in close proximity ([Zatorre et al., 2002](#)). Another hypothesis is that lateralization improves performance when two tasks are executed simultaneously ([Lust et al., 2011](#); [Moorman and Nicol, 2015](#)). Language lateralization seems to be beneficial for performance; there are clinical examples of lateralization abnormalities associated with language impairments such as dyslexia ([Johnson et al., 2013](#)). Aberrant lateralization might also affect language performance in autism ([Pierce, 2011](#)) and schizophrenia ([Sommer et al., 2001](#)).

Hemispheric specialisation with a unilateral temporal memory representation was found in filial imprinting in domestic chicks, where the left IMM (intermediate and medial mesopallium) has been shown to be a permanent memory store, while the right IMM is implicated in the formation of a temporal memory store elsewhere in the brain (the hypothetical S'; [Horn, 2004](#)). In juvenile zebra finches, the right NCM could have a similar role to the right IMM of chicks, being involved in the formation of a representation of bird's own song in the song system. In that case, the more the birds already learned from their tutor's song, the less neural interaction is needed and the less activation we would find in the right NCM. Given the parallels that exist between birdsong and human speech, [Moorman et al. \(2015\)](#) suggested that lateralized neuronal activation during sleep may also be important for speech and language acquisition in human infants, and lateralization might be a fundamental process for auditory-vocal learning.

## 7. Conclusions and future directions

The faculty of language as a computational mechanism appears to be unique to the human species. There are remarkable similarities across humans and songbirds in their ability to learn their vocalizations, but those abilities seem to be absent in non-human primates. These similarities afford an opportunity to harness the experimental advantages of songbirds to learn about the neural circuits and mechanisms underlying auditory-vocal learning.

Among the similarities between birdsong and human speech, we have highlighted recent findings about rhythmicity and the role of auditory feedback in each, and we have described what is known about the sensory and motor representations of vocal behavior and the hemispheric lateralization of analogous (and in some cases homologous) neural structures that underlie speech and birdsong. Consideration of all of these findings has revealed several questions that should serve as important goals in future studies. Those questions include:

- 1) Where is the neural substrate of memory of auditory models located in the brain, and how is that recalled and used to shape development of vocal proficiency?
- 2) How is activity in multiple circuits integrated to enable comparison of motor performance and sensory feedback in service of acquisition and maintenance of vocal behaviors?
- 3) How are rhythm and sequencing of vocal performance encoded in the activity of vocal motor circuits, and how does that precise, clock-like stereotypy emerge from the highly variable vocalizations that emerge during early development?
- 4) What is the functional significance of the precise, phasic representation of specific sounds in the activity of auditory-vocal mirror neurons, and through what pattern of sensorimotor interplay does that representation emerge during development?
- 5) What is the functional significance of lateralization of auditory-vocal learning and the control of vocal performance?

In each of these questions, an important ancillary theme is: how do answers that are gleaned from songbirds provide insight into the neural basis of human speech? There is an expanding body of research that reveals the close parallels between birdsong and human speech ([Bolhuis and Everaert, 2013](#)). Those links are evident both behaviorally and in the structure and function of the underlying neural circuits. The variety of songbird species and the associated diversity of vocal behaviors such as different types of phonological syntax, different sizes of vocal repertoires and different abilities to acquire new sounds throughout adulthood make them ideal subjects in which to continue our investigation into how the brain enables songbirds and humans alike to learn their vocalizations.

Finally, comparing birdsong and human speech can inform us about the evolution of speech and language. The data that we have reviewed here supports the conclusion by [Berwick et al. \(2013\)](#) that three factors are important in the evolution of speech and language. First, there is homology as to the underlying neural and genetic mechanisms. That is, similar genes and brain regions are involved in auditory learning and vocal production in humans, apes, mice, songbirds and other animals. Second, there is evolutionary convergence as to the mechanisms of auditory-vocal imitation learning, which occurs in humans and songbirds, but not in apes, monkeys or mice. Third, it would seem that the computational cognitive system that we call language is unique to the human species. As [Berwick et al. \(2013\)](#) suggested, the first two factors may have contributed to the emergence of spoken language in the human lineage.

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