Early experience shapes vocal neural coding and perception in songbirds

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Abstract

Songbirds, like humans, are highly accomplished vocal learners. The many parallels between speech and birdsong and conserved features of mammalian and avian auditory systems have led to the emergence of the songbird as a model system for studying the perceptual mechanisms of vocal communication. Laboratory research on songbirds allows the careful control of early life experience and high-resolution analysis of brain function during vocal learning, production and perception. Here, I review what songbird studies have revealed about the role of early experience in the development of vocal behavior, auditory perception and the processing of learned vocalizations by auditory neurons. The findings of these studies suggest general principles for how exposure to vocalizations during development and into adulthood influences the perception of learned vocal signals.

Vocal production and perception form our primary means of communication. The role of experience in the neural processing and perception of vocal sounds is an important issue in our pursuit to understand how we acquire and perceive speech and what goes wrong when we can't understand speech. A significant body of work exists on the role of experience in the development of speech processing and perception in typical and language-impaired children (Chandrasekaran, Hornickel, Skoe, Nicol, & Kraus, 2009; Johnson, Nicol, Zecker, & Kraus, 2008; Kuhl, 2000, 2004, 2010; Kuhl, Tsao, & Liu, 2003; Russo, Nicol, Zecker, Hayes, & Kraus, 2005; Russo et al., 2008; Tsao, Liu, & Kuhl, 2004; Warrier, Johnson, Hayes, Nicol, & Kraus, 2004; Werker & Tees, 1992; Wible, Nicol, & Kraus, 2005). Speech perception research is informed and complemented by research on the neural processing and perception of vocalizations in animals whose experiences can be controlled and brains can be studied at the resolution of single neurons. Animals that learn vocalizations are particularly advantageous because they offer the opportunity to manipulate and measure learning that is specific to vocal communication and to correlate learned behavior with neural mechanisms that are influenced by experience.

Though vocal communication is common among animals, vocal learning is rare. Only humans, some cetaceans, and three clades of birds (parrots, hummingbirds and songbirds) are known to learn their vocalizations (Beecher & Brenowitz, 2005). There is some evidence that elephants and bats may be vocal learners as well (Knornschild, Nagy, Metz, Mayer, & von Helversen, 2010; Poole, Tyack, Stoeger-Horwath, & Watwood, 2005). Of these potential animal models, songbirds are by far the most thoroughly studied, and numerous similarities exist between speech and birdsong (Doupe & Kuhl, 1999). Examples include: 1) developmental sensitive periods for vocal learning (Marler, 1997); 2) learning through imitation of adult models (Marler, 1997; Saar, Mitra, Deregnaucourt, & Tchernichovski, 2008); 3) a dependence of vocal behavior on auditory feedback (Konishi, 2004; Woolley,

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2004); 4) individual recognition via unique vocalizations (Catchpole & Slater, 2008; Gentner, 2004); and 5) lateralized vocal processing in sensory and sensorimotor brain regions (George, Cousillas, Richard, & Hausberger, 2005; Hauber, Cassey, Woolley, & Theunissen, 2007; Poirier, Boumans, Verhoye, Balthazart, & Van der Linden, 2009; Williams, Crane, Hale, Esposito, & Nottebohm, 1992). Because of the parallels between speech and birdsong and the evolutionary conservation of vocal processing circuitry (Reiner, Perkel, Mello, & Jarvis, 2008; Reiner, Yamamoto, & Karten, 2005; Wang, Brzozowska-Prechtl, & Karten, 2010), the songbird has emerged as a promising model system for studying the neural basis of learned vocal communication.

Brain mechanisms of vocal perception are a current research focus due, in part, to increased awareness of neurological disorders that include impaired speech perception, such as autism, Asperger Syndrome and auditory processing disorder. Studies published in the last decade indicate that the vocal communication sounds heard early in life provide experience that is needed for the normal development of the auditory system and, consequently, for perceptual processes that underlie vocal communication. Here, I review studies that address how developmental experience shapes auditory perception and the neural coding of sound in songbirds. The role of experience in songbird vocal production and motor coding have been extensively reviewed elsewhere (Brainard, 2004; Doupe, Perkel, Reiner, & Stern, 2005; Fee & Scharff, 2010; Konishi, 2010; Margoliash, 2010; Mooney, 2009), but I will briefly discuss this topic because it is tightly linked to perceptual development.

Songbirds

Songbirds are well studied in the field and laboratory because their vocalizations are diverse and complex, and because they learn to sing. There are over 4000 species of songbirds (Gill & Donsker, 2011) and each has a unique combination of song qualities, including its spectrotemporal acoustics, the developmental timeline for song learning, the number of song types that an individual produces (ranging between one and thousands), sex-based differences in production, the degree to which song development depends on imitation or improvisation, and the seasonality of song (Beecher & Brenowitz, 2005; Brenowitz & Beecher, 2005). In spite of this diversity, the brain regions that subserve song perception and production are conserved. Songbirds share the same basic auditory and vocal motor pathways, and variation in the structure of vocal circuits accurately predicts differences in singing behavior (Moore, Szekely, Buki, & Devoogd, 2011). Species differences in auditory coding and perception have only recently begun to be explored, but the evidence so far indicates that auditory processing also differs among species (Terleph, Mello, & Vicario, 2007; Woolley, Hauber, & Theunissen, 2010).

Most studies that investigate the role of early experience in the neural coding and perception of song are done in the laboratory rather than the field because of the precise experimental control required. For practical reasons, the majority of these studies have focused on the zebra finch (*Taeniopygia gutatta*), Bengalese finch (*Lonchura striata domestica*), and European starling (*Sturnus vulgaris*). Much of this review focuses on findings from these species but the discussions of song behavior and the role of auditory experience in song development include more species.

Song behavior

Male songbirds sing to court females and control aggressive encounters with other males (reviewed in Catchpole & Slater, 2008). In most species, such as the colonial finches (e.g. zebra and Bengalese finches), males learn to sing and females do not. Females do learn to assess male song as a mate choice cue (Catchpole & Slater, 2008; Lauay, Gerlach, Adkins-Regan, & Devoogd, 2004; Zann, 1996). The amount and duration of singing, the song types

that are produced and the acoustic complexity of songs have all been identified as song features that attract females (Hauber, Campbell, & Woolley, 2010; Riebel, 2009), presumably because they indicate reproductive fitness (Nowicki & Searcy, 2004; Riebel, 2009; Zann, 1996). In zebra finches, singing rate and song acoustic complexity are correlated with morphological measures of health, immunocompetence (Holveck, de Castro, Lachlan, ten Cate, & Riebel, 2008; Spencer, Buchanan, Leitner, Goldsmith, & Catchpole, 2005) and other cognitive abilities (Boogert, Giraldeau, & Lefebvre, 2008). Because the acoustic features of song are both species- and individual-specific, song is also used to maintain social relationships with known individuals such as mates and territory neighbors (Clayton, 1988a; Clayton, 1989; Falls, 1982; Miller, 1979a; Riebel, 2000; Riebel, 2003).

Songs and calls are two different categories of vocal signals. Calls are typically short duration (tens-to-hundreds of milliseconds), acoustically simple sounds that are produced by both sexes in many different contexts (Marler, 2004; Vicario, 2004; Zann, 1996). Call production differs from song production in that it does not generally require auditory feedback, although some calls have learned components (Vicario, 2004). Songs, by contrast, are long duration sounds (seconds to minutes) that are acoustically complex, learned by imitation, and depend on auditory feedback. They are highly structured and composed of hierarchically organized acoustic units, like speech. Figures 1A and B show spectrograms (frequency as a function of time, with color indicating intensity) of zebra finch calls and song. Figures 1B–D show spectrograms of song from males of three different species, the zebra finch, the Bengalese finch and the European starling, illustrating the distinct sound patterns that typify the songs of each species. The hierarchically organized acoustic units of song are indicated with colored lines below the spectrograms. The smallest individual acoustic units in songs are "notes." Notes can be grouped together in time into "syllables." A series of syllables that is repeated in a predictable sequence is a song "phrase" or "motif." And a specific combination of phrases that occurs consistently as a unit is a song "type." Some species sing only one motif while others sing many different song types. This standardized nomenclature allows the comparison of song behavior across species and still captures the organization of a wide diversity of species-typical song behavior.

Auditory experience and song development

Song learning in many species occurs within a sensitive period, which is a developmentally restricted time period during which juveniles are especially sensitive to experience. Many aspects of the sensitive period vary between species, including its timing, the rigidity of its boundaries, and its dependence on social interactions (Arnold, 1975; Baptista & Petrinovich, 1984, 1986; Bohner, Chaiken, Ball, & Marler, 1990; Eales, 1985; Immelmann, 1969; Marler, 1970; Marler & Peters, 1987; Morrison & Nottebohm, 1993; Slater, Richards, & Mann, 1991; Thorpe, 1958). Sensitive periods for song learning can be extended if a suitable song model is withheld, but they cannot be prolonged indefinitely (Eales, 1985). In most species that have been carefully studied, this period of song learning occurs before sexual maturity in a two-stage process of sensory memorization followed by sensorimotor integration. Each stage is required for the development of normal song behavior in the vast majority of songbirds (Brenowitz & Woolley, 2004; Catchpole & Slater, 2008; Doupe & Kuhl, 1999), and birds that are raised in isolation or deafened as juveniles develop highly abnormal songs (Konishi, 1965; P. Marler, 1970; Price, 1979; Thorpe, 1958, 1961).

The role of auditory experience changes over the course of song learning. During the sensory memorization stage, a juvenile hears and memorizes a "template" of adult song that will guide song development in the later stage of vocal practice (Konishi & Nottebohm, 1969). Figure 2 shows a diagram depicting the developmental timeline of song learning in the male zebra finch. A bird's memory of particular songs is typically assessed by the

vocalizations it eventually produces, and a male of this species will ultimately copy a song he hears between 20 and 60 days of age (Eales, 1985; Immelmann, 1969). The evidence for memory formation during this time comes from studies showing that song exposure before the onset of motor practice is sufficient for juveniles to produce an accurate copy later, in some cases long after the model has been removed (Marler & Peters, 1977, 1982; Searcy, Marler, & Peters, 1981; Thorpe, 1958). Thus, juveniles are receptive to songs before they begin to practice singing and they remember tutor songs at least until the age at which they shape their own songs. The choice of a song model can be influenced by many factors, including the acoustics of the song model and social interactions between the tutor and tutee (Baptista & Morton, 1988; Baptista & Petrinovich, 1984, 1986; Clayton, 1987; Eales, 1985; Price, 1979). Thus, the sensitive period in which early song exposure clearly shapes adult behavior is not just a matter of age, but also depends on the amount and quality of the vocal and social experience.

The vocal motor practice stage of song learning is called sensorimotor integration because, during this time, a vocal motor program is formed to reproduce the previously-formed sensory memory. Initially, young birds produce quiet, highly variable vocalizations called "subsong." This stage of behavioral development is likened to the babbling stage in human speech development (Doupe & Kuhl, 1999). Later, vocalizations become louder and more structured. These "plastic" songs are still less stereotyped than adult songs and often contain notes and syllables that will not be retained in the adult song (Marler & Peters, 1982; Nelson, 2000; Nelson & Marler, 1994). Over time, birds refine their vocalizations into sequences of acoustically well-defined notes, syllables and phrases, forming motifs and song types. Around the time of sexual maturity, song behavior stabilizes and, in many species, song production learning ends. Some improvisation and/or copying errors occur so that no two birds' songs are exactly alike, but under normal conditions the tutee develops a song that is clearly attributable to the available song tutor (Clayton, 1987; Immelmann, 1969).

Sensorimotor integration depends critically on auditory experience because birds use auditory feedback to monitor and shape their own singing. Deafening during sensorimotor integration prevents normal song development, whereas isolation does not (Konishi, 1964, 1965; Marler & Peters, 1977; Price, 1979). The songs of birds that have been deafened during sensorimotor integration show abnormal syllable structure and sequencing. The degree to which the eventual adult song is abnormal depends on when the deafening occurs; birds deafened at later stages in sensorimotor learning produce more normal songs (Konishi & Nottebohm, 1969). The maintenance of normal adult song also depends on auditory feedback (Lombardino & Nottebohm, 2000; Nordeen & Nordeen, 1992; Woolley & Rubel, 1997). In summary, the role of auditory experience in song production is critical at all life stages but transitions from a reliance on hearing other birds sing to an age-dependent reliance on hearing self-generated singing.

Song learning is guided by perceptual biases for conspecific song. Studies using measures of auditory discrimination, such as changes in heart rate, begging calls and perch hops, indicate that juveniles discriminate between conspecific and heterospecific songs and suggest that a young bird's state of arousal increases when it hears its own species' song (Adret, 1993; Dooling & Searcy, 1980; Nelson & Marler, 1993; ten Cate, 1991; Whaling, Solis, Doupe, Soha, & Marler, 1997). For example, juvenile zebra finches preferentially peck keys or pull strings to elicit the presentation of conspecific song over heterospecific song during the sensitive period for song learning (Adret, 1993; Braaten & Reynolds, 1999; ten Cate, 1991). Additionally, juveniles of several species will learn their own species' songs when songs of multiple species are presented in an equivalent manner (Marler, 1970; Marler & Peters, 1977; Thorpe, 1958). This selective learning occurs despite similar auditory spectral sensitivities among species and similar acoustic frequency ranges between conspecific and

heterospecific songs (Dooling & Searcy, 1981; Okanoya & Dooling, 1987). These findings suggest that auditory perceptual biases guide the selection of an appropriate song model and that they are based on spectrotemporal song features rather than simple hearing abilities.

Despite the existence of these perceptual biases, young birds can still learn the songs of other species if they are only presented with those songs (Baptista & Petrinovich, 1984, 1986; Petrinovich & Baptista, 1987; Price, 1979) or if they are raised by adults of another species (Clayton, 1989; Immelmann, 1969; Slater, Eales, & Clayton, 1988; Woolley, et al., 2010; Woolley & Moore, 2011). In cross-fostering/tutoring experiments, birds are transferred *in ovo* or as young nestlings into the nests of birds of another species, and learn the songs of their foster species (Campbell & Hauber, 2009a; Clayton, 1988; Eales, 1987; Immelmann, 1969; Woolley, et al., 2010). This type of experiment has been used to probe the strength of auditory biases as well as gauge the existence and strength of potential motor constraints on song learning.

Early auditory experience and song perception

Song perception is shaped by early auditory experience in both sexes, even in species in which females do not sing. The influence of hearing song on perception and behavior appears to begin shortly after hearing matures. While basic hearing onset in songbirds has not been studied in detail, it is generally accepted that they hear very little until several days after hatching. Zebra finches do not develop adult-like auditory brainstem response thresholds until they approach 20 days of age (Amin, Doupe, & Theunissen, 2007). In agreement with this timing of hearing onset, studies suggest that the impact of auditory experience on song development begins weeks after hatching (Eales, 1985; Immelmann, 1969).

Early experience influences song perception in both highly specific and general ways. The highly specific effects include the memorization of particular songs heard early in life, including but not restricted to the song(s) that serve as the song-copying template (Miller, 1979b; Riebel, Smallgange, Terpstra, & Bolhuis, 2002). Miller (1979b) first used spatial proximity assays to demonstrate that adult zebra finches have perceptual memories of their fathers' songs and are attracted to those songs over other conspecific songs. Those studies were conducted after the birds had reached adulthood, but song discrimination abilities appear to develop quickly in juveniles within the sensitive period for song learning (Braaten, Petzoldt, & Colbath, 2006). While the tutor song memory is obviously important for song development in birds that learn to sing, its significance for non-singing females is less clear. Females may sexually imprint on their fathers' songs to guide their attraction to particular song features or regional dialects during mate choice (Hauber, et al., 2010; Riebel, 2003; Riebel, 2009).

Auditory experience during ontogeny influences general perceptual preferences as well. Adults of both sexes show preferences for unfamiliar conspecific songs over unfamiliar heterospecific songs that are dependent, at least in part, on early experience. Adult zebra finches that are raised and tutored by zebra finches are more attracted to zebra finch song than to the songs of other species (Braaten & Reynolds, 1999; Campbell & Hauber, 2009a, 2009b; Clayton, 1988b; Clayton, 1989, 1990; Lauay, et al., 2004; Nagle & Kreutzer, 1997; Peters, Searcy, & Marler, 1980). This preference may begin with innate perceptual biases, as described above, because they can still be present in birds raised without tutoring. For example, zebra finches raised in isolation from adult song show spatial proximity preferences for zebra finch song over European starling and canary song (Braaten & Reynolds, 1999). This idea remains somewhat controversial, however, because some studies have failed to find these conspecific preferences in isolation-reared females (Nagle &

Kreutzer, 1997; ten Cate & Mug, 1984). Regardless, early experience unequivocally shapes behavioral song preferences, either by reinforcing innate biases (if they exist), or by counteracting them.

Cross-fostering studies have been used to investigate the role of auditory experience in the formation of song preferences. Because birds of different species produce songs that differ acoustically, cross-fostering provides juvenile subjects with many typical early-life social experiences but alters the acoustics of their experience. Male and female zebra finches that are raised by adults of another species or subspecies fail to show consistent preferences for conspecific songs as adults and show increased attraction to the tutor species' songs (Campbell & Hauber, 2009a; Clayton, 1990). The effects of early experience manipulations on general hearing and perceptual development are only beginning to be examined. In mammals, the few studies that have addressed this indicate that the relationship between juvenile auditory exposure or training and adult perception is complex. For example, rats reared hearing a single tone show an expanded cortical representation of frequencies near that tone but poor perceptual discrimination of those frequencies as adults (Han, Kover, Insanally, Semerdjian, & Bao, 2007). A second example is that gerbils trained as juveniles to detect sounds with amplitude modulations (AM) show better than normal AM detection as adults, but those trained as juveniles to detect frequency modulated (FM) sounds show poorer than normal detection of AM sounds (Sarro & Sanes, 2011). Songbird studies linking vocal experience with the maturation of the auditory system and perceptual skills are needed. So far, two studies have found that birds reared without exposure to adult song have frequency discrimination and song note recognition deficits as adults (Njegovan & Weisman, 1997; Sturdy, Phillmore, Sartor, & Weisman, 2001). In summary, songbirds begin to hear well several weeks after hatching, are sensitive to the early auditory environment in the development of song preferences, form early memories of adult song that guide the development of singing and mate preferences, and may require auditory experience of vocalizations to develop normal auditory perceptual skills.

The effects of learning the songs of another species on general auditory perception have yet to be explored. Studies on this topic may give us a firmer grasp on the relationship between the sounds that birds hear and imitate during development and adult perception. The rich literature on the effects of specific language learning (Kuhl, 2004; Werker & Tees, 1992) on perceptual development in children allows us to make predictions about how cross-tutoring may affect perception in songbirds (with the important caveat that songbirds are learning the communication signals of different species, not of different populations of the same species). One prediction is that birds that learn heterospecific song will exhibit different perceptual boundaries than those that learn conspecific song. This prediction is based on the well-established findings that human perception of phonemic boundaries is profoundly shaped by the specific language that a child hears and learns (Kuhl, 2000). If this perceptual "warping" by auditory exposure to vocalizations also occurs in songbirds, then songbirds could be used to determine the neurophysiological mechanisms of this developmental phenomenon. A second prediction based on the human literature is that birds that learn songs with more pitch information will show better discrimination of pitch contours. This prediction is based on the finding that native users of Mandarin, a language for which differences in pitch carry meaningful information, and native English users differ in their abilities to identify pitch contours (Bent, Bradlow, & Wright, 2006). Because the spectral (pitch) features of songs differ markedly among species, this prediction could easily be tested.

Neural circuits for song perception

Because early experience influences song perception, it must also influence the neural coding of song. This coding can be conceptually divided into two general processing steps. First, sounds are encoded; the auditory periphery and neurons of the ascending auditory system generate neural representations of stimuli in the form of neural impulses that vary with the spectral, temporal and amplitude features of a sound. Second, these neural representations are decoded; the output of encoding networks is interpreted by neurons in higher level brain areas to form meaningful percepts and initiate appropriate behavioral responses. The brain areas underlying these two coding steps in songbirds and mammals are potentially similar given that their auditory systems are organized in much the same way and the areas have comparable connectivity, molecular markers, and functional properties (Karten, 1967, 1968, 1991; Wild, Karten, & Frost, 1993). Figure 3 shows a diagram of the auditory regions and pathways in the songbird brain, their connectivity with the two primary vocal motor nuclei and a list of the comparable brain regions in mammals.

Stimulus encoding occurs primarily between the ear and the first recipient areas of the cortex. Auditory information travels from the cochlea to cochlear nuclei in the hindbrain via the auditory nerve. From there, projections lead either directly to the auditory midbrain (Krutzfeldt, Logerot, Kubke, & Wild, 2010a) or to lateral lemniscal nuclei (Krutzfeldt, Logerot, Kubke, & Wild, 2010b), which then project to the midbrain (Wild, Krutzfeldt, & Kubke, 2010). The avian auditory midbrain is traditionally called the mesecephalicus lateralis dorsalis (MLd) because of its anatomical location, but this nucleus is homologous and functionally similar to the mammalian central nucleus of the inferior colliculus (ICc). Like the ICc, MLd is a nexus for auditory processing because it integrates multiple parallel brainstem pathways and provides the primary input to the ascending thalamo-cortical pathway. It projects to the auditory thalamus (nucleus ovoidalis, Ov), which in turn projects to Fields L2a and L2b in the forebrain, which may be homologous to layer 4 of mammalian primary auditory cortex (Bonke, Bonke, & Scheich, 1979; Butler, Reiner, & Karten, 2011; Fortune & Margoliash, 1992, 1995; Vates, Broome, Mello, & Nottebohm, 1996; Zeng, Zhang, Peng, & Zuo, 2004). The medial portions of MLd and the region that surrounds it receive descending input from the cup of the rostral arcopallium (RA), a vocal motor control nucleus (Mello, Vates, Okuhata, & Nottebohm, 1998). It is possible that this projection carries information about song motor output back to the auditory system, but no studies have addressed this idea.

Areas downstream of L2a and L2b likely function in the decoding of songs. The connections to and among these regions are complex and many are reciprocal (Kelley & Nottebohm, 1979; Mello, et al., 1998; Vates, et al., 1996); see Bolhuis & Gahr, 2006 for review). Subregions L1 and L3 receive input from L2a, and these project to two large auditory regions that surround field L, the caudal medial nidopallium (NCM) and caudal mesopallium (CM) (Mello & Ribeiro, 1998; Vates, et al., 1996). The forebrain regions L3, CM and NCM all have the potential to transmit auditory information that influences song motor production through their projections to the motor nucleus HVC and/or its underlying shelf region (Bauer et al., 2008; Kelley & Nottebohm, 1979). Understanding what aspects of encoded songs are decoded by neurons in these regions may help us to explain how auditory-motor integration occurs during song learning and maintenance (Pinaud et al., 2008).

Two main approaches have been used to probe the respective roles of these brain areas in encoding and decoding processes. The most common method has been electrophysiology, in which the activity of single neurons or small groups of neurons is related to particular features of a stimulus. This experimental approach provides a record of exactly when and

how many times neurons fire in response to sounds, allowing the quantitative analysis of what information in vocalizations is coded and therefore what information is important for perception. For example, single unit studies provide opportunities to measure neurons' response strengths, selectivity and spectrotemporal tuning to different types of songs or a song in different contexts. A second, more recent technique has been to measure neurons' genomic responses to sounds. Neural activity can cause the rapid induction of a particular class of genes, called immediate early genes (IEGs), that is related to functional changes in neurons. The IEG most commonly studied in songbirds is *zenk*, which is an acronym for its mammalian homologues (zif-268, egr-1, ngfi-a, and krox-24) (Mello & Jarvis, 2008). Although *zenk* expression does not directly relate to neuronal firing (London & Clayton, 2008; Stripling, Volman, & Clayton, 1997), it is thought to be important for synaptic structural plasticity and is potentially related to learning processes (Tischmeyer & Grimm, 1999). *Zenk* expression following song exposure can be examined in whole brain regions, allowing the detection of functional changes in many more neurons than is possible in electrophysiological studies. It has been used to identify cortical regions that are involved in song processing, to measure stimulus selectivity and to test the effects experience on auditory function (Mello, Velho, & Pinaud, 2004).

Evidence for the differentiation between encoding in lower auditory regions and decoding in higher auditory regions comes from studies that relate neural responses to the physical properties of stimuli. Specifically, these experiments determine how well a neural impulse can be characterized and predicted by the linear spectral and temporal song properties or whether other aspects of the song, such as behavioral salience or previous experience, must be included in the characterization. Generally speaking, lower auditory regions such as MLd contain neurons whose song responses can be explained by their spectral and temporal tuning properties (Ramirez et al., 2011; Schneider & Woolley, 2010, 2011; Woolley & Casseday, 2004, 2005; Woolley, Fremouw, Hsu, & Theunissen, 2005; Woolley, Gill, Fremouw, & Theunissen, 2009; Woolley, Gill, & Theunissen, 2006). The tuning properties of neurons in these areas are robust to stimulus salience and behavioral state (Schumacher, Schneider, & Woolley, 2011). In contrast, song responses in higher regions such as NCM and CM are more mysterious, showing sparse responses that are highly selective and that habituate to stimulus repetitions (Chew, Mello, Nottebohm, Jarvis, & Vicario, 1995; Gentner, 2004; Terleph, Mello, & Vicario, 2006). The responses of these neurons cannot be explained simply by measuring stimulus acoustics and neuronal spectrotemporal tuning. Our progress in understanding the neural mechanisms of perception will rely on accurate explanations of both encoding and decoding processes and the role of experience in their development.

Early experience and the auditory coding of vocalizations

The importance of auditory experience for the development of auditory coding properties has been demonstrated in both songbirds (see below) and mammals (Chang, Bao, Imaizumi, Schreiner, & Merzenich, 2005; Chang & Merzenich, 2003; de Villers-Sidani, Chang, Bao, & Merzenich, 2007; Sanes & Constantine-Paton, 1985; Yu, Sanes, Aristizabal, Wadghiri, & Turnbull, 2007; Zhang, Bao, & Merzenich, 2001). Studies in mammals have used auditory deprivation and sound exposure manipulations such as rearing in noise (Chang & Merzenich, 2003) or in tones (Han, et al., 2007; Yu, et al., 2007), but they have not studied the effects of these manipulations on the neural coding of vocalizations. Studies with songbirds, by contrast, have specifically addressed how manipulations of the vocal environment influence auditory responses to vocalizations and have found that early-life experiences significantly impact vocal neural coding in the midbrain and cortex.

Midbrain

The songbird auditory midbrain is a focus for understanding how songs are encoded by single neurons and neuronal populations. Unlike neurons in downstream processing regions, midbrain neurons respond robustly to a wide variety of sounds including tones (Schneider & Woolley, 2011; Schumacher, et al., 2011; Woolley & Casseday, 2004), noise (Woolley & Casseday, 2005; Schneider & Woolley, 2011) both conspecific and heterospecific song (Schneider & Woolley, 2010; Woolley, et al., 2009; Woolley, et al., 2006; Woolley, et al., 2010). The responses of single midbrain neurons are reliable, meaning that they produce highly similar responses to the same stimulus presented multiple times (Figure 4A; Schneider & Woolley, 2010; Woolley & Casseday, 2004, 2005). This is in contrast to the context-sensitive and habituating (decreasing over time) responses of neurons in some forebrain regions (see below). The robust and reliable responses of midbrain neurons to different types of sounds allow the direct comparison of neural responses to song and to other sounds in the same single neurons. This has led to several insights about how the spectral and temporal properties of songs are encoded by "low level" neurons and how these areas contribute to perceptual functions such as the discrimination of individual songs.

Each single midbrain neuron has a unique complement of spectral, temporal and intensity tuning properties which determines the sounds to which it responds (Woolley & Casseday, 2004, 2005) and the features of songs that it encodes (Figure 4; Schneider & Woolley, 2010, 2011; Schumacher, et al., 2011; Woolley, et al., 2005; Woolley, et al., 2009; Woolley, et al., 2006). Figure 4A shows the responses of eight midbrain neurons to the same song and illustrates how different neurons respond to different acoustic features of a song. The temporal patterns of each neuron's responses provide a basis for measuring their tuning properties; differences in the response patterns to different songs are due to each neuron's spectrotemporal tuning and the unique acoustics of each song. Accordingly, the responses of most midbrain neurons are well characterized by linear-nonlinear models of tuning such as spectrotemporal receptive fields (Calabrese, Schumacher, Schneider, Paninski, & Woolley, 2011; Schneider & Woolley, 2011; Schumacher, et al., 2011), indicating that these neurons faithfully encode specific spectral and temporal features of vocalizations. When a large number of midbrain neurons, are considered together, their responses can be used to reconstruct the songs that evoked the responses (Ramirez, et al., 2011). Neurons with reliable responses that differ between songs could provide a basis for the discrimination between songs sung by different males and potentially contribute to individual recognition during social interactions. For example, the spike trains evoked by presentation of a set of songs can be used to accurately discriminate among the individual songs in the set of songs in midbrain (Schneider & Woolley, 2010) and field L neurons (Narayan, Ergun, & Sen, 2005; Narayan, Grana, & Sen, 2006; Wang, Narayan, Grana, Shamir, & Sen, 2007).

Comparing the spectrotemporal tuning of single neurons and the acoustic properties of natural sounds has shown that zebra finch auditory midbrain neurons are tuned for the spectrotemporal modulations that are found in vocalizations (Woolley, et al., 2005). The spectrotemporal tuning properties of individual neurons also cluster into functional groups that encode specific acoustic features of songs that may relate to perceptual sound features such as pitch, rhythm and timbre (Woolley, et al., 2009). In the mammalian auditory brainstem, different classes of physiological responses correspond to distinct anatomical cell types, but the functional classes of songbird auditory neurons have not been linked to defined cell types. Additionally, many zebra finch auditory midbrain neurons have extra-classical receptive fields many auditory midbrain neurons have extra-classical receptive fields (RFs), consisting of sideband excitation and sideband inhibition (Schneider and Woolley, 2011). The modulation of responses by frequency information that falls outside of the classical RF (a classical RF is determined by recording responses to single tones that vary in frequency and intensity) makes these neurons sensitive to the structure of spectrally

correlated sounds such as the noisy bursts of sound energy and harmonic stacks that characterize both zebra finch song and speech. In summary, the responses of auditory midbrain neurons to songs and other sounds show that, while many more sounds than just songs are coded in this region, tuning mechanisms exist at this early level in the auditory processing stream to encode the acoustic properties of songs, forming high fidelity neural representations which can be used by downstream neurons to decode information such as song quality, species identity and individual identity.

Early auditory experience influences the development of information coding capacity and firing rate in auditory midbrain neurons. The term "information" refers to a response's capacity to encode information about a stimulus (Strong, de Ruyter van Steveninck, Bialek, & Koberle, 1998) and is a function of firing rate, the change in firing rate over the time course of a response, the rate of change in firing rate, and response reliability (Hsu, Woolley, Fremouw, & Theunissen, 2004). Woolley et al. (2010) cross-fostered juvenile male zebra finches into the nests of Bengalese finches and recorded midbrain auditory responses to zebra finch and Bengalese finch songs in the cross-fostered zebra finches, normally-reared zebra finches, and normally-reared Bengalese finches. Neurons in the cross-fostered zebra finches showed significantly lower information coding capacity and firing rates in response to both zebra finch and Bengalese finch songs than did neurons from normally-raised zebra finches (Figure 4B, upper plots). Information and firing rates were also lower in Bengalese finch neurons. These results suggest that early experience of Bengalese finch song rather than zebra finch song led to the development of low responsivity and coding capacity in both zebra and Bengalese finches. It is important to note, however, that cross-fostering as used in Woolley et al. alters the acoustic environment in general, the song learning process and the acoustics of songs that are eventually produced. Any or all of these factors may impact development of midbrain auditory responses. For example, Bengalese finches sing less often and more quietly than do zebra finches (Immelmann, 1969; Woolley personal observation), potentially leading to differences in the levels of acoustic exposure between birds raised by zebra finches and those raised by Bengalese finches. Experiments in which juveniles are tutored by conspecific and heterospecific adults in the same acoustic environment will help to distinguish among these potential sources of experience-based differences in auditory coding.

Human subcortical auditory structures including the midbrain have also been a recent focus for asking how hearing and producing vocalizations or spectrotemporally patterned sounds such as music may shape auditory processing and perception. Auditory brainstem responses to speech sounds develop during the time in which children are developing speech skills (Johnson, et al., 2008). This suggests that maturation of subcortical auditory processing interacts with early language experience. Support for this hypothesis includes the finding that native speakers of Mandarin, a tonal language, show stronger and more accurate subcortical encoding of pitch changes over time than do native speakers of English (Krishnan, Xu, Gandour, & Cariani, 2005). Considering the tuning properties of songbird midbrain neurons and the effects of cross-tutoring on song coding in the midbrain, we might predict that early tonal language experience modulates the development of frequency tuning specificity and firing rates to speech sounds in human auditory midbrain neurons. Childhood language impairments have also been correlated with deficits in subcortical pitch coding and temporal structure (Lorenzi, Gilbert, Carn, Garnier, & Moore, 2006; Russo, et al., 2008). It is possible, therefore, that developmental studies in songbirds will identify potential neural mechanisms for language-specific auditory perception in humans.

The involvement of subcortical structures in speech perception deficits indicates that understanding how "low level" auditory regions encode vocalizations will be important for future prevention and remediation of communication disorders. Recalling that songbird

midbrain neurons fall into functional groups based on their spectrotemporal tuning, and that each group encodes acoustic features that are important for different percepts such as pitch or rhythm, we could predict that auditory midbrain neurons in humans with impaired speech perception show weak functional grouping or missing groups (Woolley, et al., 2009). In theory, different stimulus classes that are each designed to drive responses in one of the functional groups (e.g. either pitch or rhythm) could be used to test for the presence and strength of functional tuning groups in the midbrains of humans with and without language impairment.

Primary auditory cortex

Neurons in field L respond, on average, slightly less robustly and reliably to songs and other sounds than do midbrain neurons. Nevertheless, they show spectrotemporal tuning properties that are similar to those in the midbrain. As in the midbrain, field L neurons can be classified into functional groups based on their spectrotemporal tuning properties and the major groups are shared with the midbrain (Woolley, et al., 2009). Despite these general similarities with the midbrain, field L neurons show a wider range of tuning properties and response selectivity, as measured by average firing rate, for conspecific song over other sounds such as noise and tone complexes (Grace, Amin, Singh, & Theunissen, 2003; Hauber, et al., 2007). This selectivity for song over synthetic sounds is weakly present in juveniles that are just beginning to produce subsong (Amin, et al., 2007) and is present in non-singing females (Hauber, et al., 2007) suggesting that the emergence of song selectivity does not require vocal motor learning. However, the strength of song selectivity and general responsivity in field L are lower in juveniles than in adults, indicating that forebrain auditory processing matures while developing birds are hearing and learning adult song (Amin, et al., 2007). There is some debate over how song responses such as selectivity differ between the primary thalamo-recipient regions (L2a and L2b) and the secondary subregions L1 and L3, but several studies examining responses to song syllables or synthetic sounds agree that L1 and L3 neurons tend to show more complex tuning than do L2a neurons (Bonke, et al., 1979; Capsius & Leppelsack, 1999; Cousillas et al., 2004; Leppelsack & Vogt, 1976; Lim & Kim, 1997; Nagel & Doupe, 2008; Sen, Theunissen, & Doupe, 2001). Thus, similar to other sensory systems, the auditory coding of song information becomes progressively more complex and nonlinear from midbrain to higher cortex.

Developmental exposure to vocalizations affects general responsivity and neural selectivity for songs and song features in field L. (Maul et al., 2010) tested the effects of isolation from early song experience on global activity in the auditory cortices of adult zebra finches using functional magnetic resonance imaging (fMRI) in which blood oxygenation level difference (BOLD) signals are used to identify brain regions that are "activated" during stimulus processing or behavior. They found that isolation-reared males had highly abnormal BOLD responses to sound presentation, with regions of activation that were significantly larger than in males raised normally. The cortical responses in isolation-reared males were also highly variable and lacked the selectivity for conspecific song over other sounds such as tones that characterized responses in colony-raised males. Just 30 seconds of song exposure a day reduced the abnormal forebrain responses, but the responsive areas remained broadly distributed. By contrast, isolation-reared females showed brain activation patterns that were similar to those of colony-raised males. These results suggest that early song exposure affects the male auditory system differently than the female auditory system, possibly because males learn to sing and females do not. These results are consistent with multi-unit electrophysiological recordings in field L of starlings, a species in which both males and females sing (Cousillas, et al., 2004). Cousillas et al. (2004) found that raising birds without song exposure resulted in abnormally low response selectivity of field L neurons; many more recording sites responded to a variety of song features in isolation-reared birds than in

wild caught birds that presumably developed hearing adult song (Figure 5A). A similar study found that the degree to which responses lacked normal song-selectivity varied according to how long the young birds were isolated from adult song (Figure 5B; George et al., 2004). In wild-caught birds, neural responses to song whistles were temporally phasic and anatomically mapped according to the whistle frequency, but neither of these characteristics was observed in the neural responses recorded from isolation-reared birds. These results suggest that normal spectrotemporal tuning of field L neurons and the consequent response selectivity for songs or specific song features depend on early auditory experience. It also suggests that the effects of song experience on auditory processing extend into adulthood. Hauber et al. (2007b), however, failed to find a correlation between early song experience and field L response selectivity at the level of single neurons in non-singing female zebra finches (Hauber, Woolley, & Theunissen, 2007). It is possible that developmental vocal experience only shapes field L response selectivity in vocal learners.

Because song is a social behavior, the importance of developmental experiences other than sound has begun to be explored. Isolation-rearing studies often conflate three developmental factors that may influence song coding and perception. First, birds are raised without hearing adult songs, resulting in deficient experience of vocalizations specifically. Second, birds are raised in environments that are acoustically impoverished compared with colony-raised or wild caught birds, resulting in abnormal auditory experience in general. Third, birds are raised with limited social experience compared to birds raised in families, usually in colonies that include several families and both sexes. These factors may all be important for perceptual development and are difficult to isolate experimentally. The idea that social experience specifically influences auditory development is intriguing, and it is plausible in the case of song processing because normal song development relies on social interactions. Similarly, the importance of social interactions for language learning in children and the normal development of cortical responses to speech sounds is well established (Kuhl, 2010).

The hypothesis that early social (rather than auditory) experience influences vocal processing in the songbird auditory cortex was tested by Cousillas et al. (2006). Starlings were raised in three different social settings with varying exposure to other juveniles and adults but with the same auditory experience. The electrophysiological response selectivity of field L neurons to song stimuli was then compared among birds raised under the different social conditions. The neurons from socially-deprived birds showed less response selectivity than did those from birds raised in a social setting, suggesting that early social experience does influence vocalization coding. A later study in which singing female starlings were raised only by adult males that do not normally serve as tutors for females (females typically learn from other females; Hausberger, Richard-Yris, Henry, Lepage, & Schmidt, 1995; Poirier et al., 2004) showed similar deficits in field L response selectivity (Cousillas, George, Henry, Richard, & Hausberger, 2008). These studies have led to the conclusion that both auditory and social experiences influence the development of auditory coding in songbirds that naturally live in social groups.

As in the midbrain, field L neurons in zebra finches that have been cross-fostered by Bengalese finches show decreased information coding capacity and firing rates compared to neurons in zebra finches raised normally (Figure 4B, lower plots; Woolley, et al., 2010). The responses of neurons from cross-fostered zebra finches are also highly similar to the responses of neurons from Bengalese finches. These results suggest that general auditory forebrain responsivity, in addition to selectivity, is significantly affected by early experience and that the acoustics of vocalizations that are heard may be important for auditory development.

Higher Auditory Cortex

Two auditory processing regions, NCM and CM, receive input from field L but show a variety of complex response properties that are not found in field L. The responses of many neurons in these areas are not accurately predicted by linear-nonlinear models such as spectrotemporal receptive fields. The responses of NCM and CM show species-specific selectivity (Mello & Clayton, 1994; Stripling, Kruse, & Clayton, 2001) that is likely related to complex spectrotemporal (Terleph, et al., 2007) but that also depends on recent stimulus history (Chew, et al., 1995; Gill, Woolley, Fremouw, & Theunissen, 2008; Mello, Nottebohm, & Clayton, 1995; Mello & Clayton, 1994), the sound environment (Terleph, Lu, & Vicario, 2008) and the behavioral salience of the song stimuli (Gentner, 2004; Gentner & Margoliash, 2003; Thompson & Gentner, 2010). For example, NCM expression of *zenk* habituates to repeated presentation of the same song (Mello, et al., 1995) and electrophysiological responses to song repetitions systematically decrease (Chew, et al., 1995). Additionally, training adult birds to recognize songs alters the responses of NCM and CM to those songs; CM neurons respond more to song motifs that are present in perceptually learned songs than to those in unlearned songs (Gentner & Margoliash, 2003) and similar learning processes lead to weaker responses in NCM neurons (Thompson & Gentner, 2010). Thus, auditory experience continues to influence vocal processing in adulthood. Species-specific response selectivity, song-specific adaptation, and adult learning effects in NCM and CM responses to vocalizations make these auditory regions particularly interesting for asking how developmental experience shapes song processing and perception.

Significant effects of early experience on vocalization coding in NCM have been demonstrated using both *zenk* expression and electrophysiology (Figures 5 and 6). Similar to field L, neurons in the NCM of starlings that have been deprived of adult song experience are less selective for song features than are NCM neurons in wild-caught starlings (Figure 5C; George et al., 2010). This finding contributes to the general conclusion that exposure to adult song during development is necessary for the normal maturation of the songbird auditory cortex. The addition of behavioral measures that test the role of early song exposure in perceptual development will be necessary to determine the behavioral relevance of the neural coding effects described here.

Because NCM neurons show conspecific song selectivity, stimulus-specific adaptation, and effects of adult recognition learning, it has become a focus for understanding the neural basis of the tutor song memories. Because females that do not sing also memorize their fathers' songs (Miller, 1979b), it seems likely that the tutor song memory could be stored in auditory processing circuits in addition to vocal motor circuits. In zebra finches, forebrain *zenk* expression becomes sensitive to song playback at the age that birds begin to memorize tutor songs but not before (Jin & Clayton, 1997; Stripling, et al., 2001). NCM *zenk* expression following song presentation is lower in juvenile males and females that have not experienced adult song than in juveniles that have heard song, suggesting that *zenk* expression in general is influenced by early auditory experience (Jin & Clayton, 1997; Tomaszycki & Adkins-Regan, 2005). *Zenk* expression following presentation of the tutor song and other songs does not differ in the adult NCM (Terpstra, Bolhuis, & den Boer-Visser, 2004) but it is higher in response to tutor song playback in the female CM (Figure 6A; Terpstra, Bolhuis, Riebel, van der Burg, & den Boer-Visser, 2006) and in the CM and NCM of juvenile males that are in the process of learning to produce song (Figure 6B; Gobes, Zandbergen, & Bolhuis, 2010). *Zenk* expression levels in NCM are correlated with the accuracy of song learning (Bolhuis, Hetebrij, Den Boer-Visser, De Groot, & Zijlstra, 2001; Bolhuis, Zijlstra, den Boer-Visser, & Van Der Zee, 2000), and song learning is impaired by disruptions of *zenk* expression. London and Clayton (2008) tested the effects of pairing song tutoring sessions and blockade of the signal-regulating kinase that controls *zenk* induction in the auditory cortex on song production learning in zebra finches. Birds

that had *zenk* expression blocked during tutoring produced poor copies of the model song, while birds that did not receive the kinase inhibitor during tutoring accurately copied the song (Figure 6C). These results and a study in which lesions of NCM disrupted behavioral responses to tutors' songs but not auditory discrimination learning (Gobes & Bolhuis, 2007), provide strong evidence for the idea that NCM is involved in the storage of information about the tutor's song. Electrophysiological data examining the habituation rates of NCM responses to tutor songs also suggest that NCM neurons store information about tutor songs (Phan, Pytte, & Vicario, 2006). In summary, neural processing in the songbird auditory cortex develops under the influence of early auditory experience, is important for the tutor song memorization that precedes song development and remains sensitive to song experience in adults.

Conclusions

The songbird is proving to be a highly informative animal model for studying the neural coding and perception of learned communication vocalizations. A rich history of behavioral and neurobiological studies on song production learning has paved the way for using songbirds to ask how experience shapes the development of auditory function and perception in the context of vocal communication. The studies that were reviewed here have identified some fundamental effects of auditory experience on song processing and perception, but there is still a great deal to be learned. There are at least four major questions that need to be addressed. How does early-life song exposure influence the development of tuning properties in auditory neurons? Is the development of perceptual skills such as the ability to recognize and/or discriminate among individual songs dependent on early song experience? How does experience facilitate the emergence of neural selectivity that is likely to be important for song decoding in the auditory cortex? How are auditory memories of individual birds' songs represented in neural circuits? Approaches that include careful experience manipulations, perceptual tests and measures of auditory coding at multiple levels of analysis are needed to answer these questions. In particular, the combination of measures at the single neuron, neuronal population and global neural response (e.g. fMRI) levels will be helpful for understanding how auditory processing leads to the perception of meaningful social messages. Lastly, understanding the mechanisms of vocal perception in songbirds may lead to insights into how early speech exposure shapes auditory processing and speech perception in humans.

Acknowledgments

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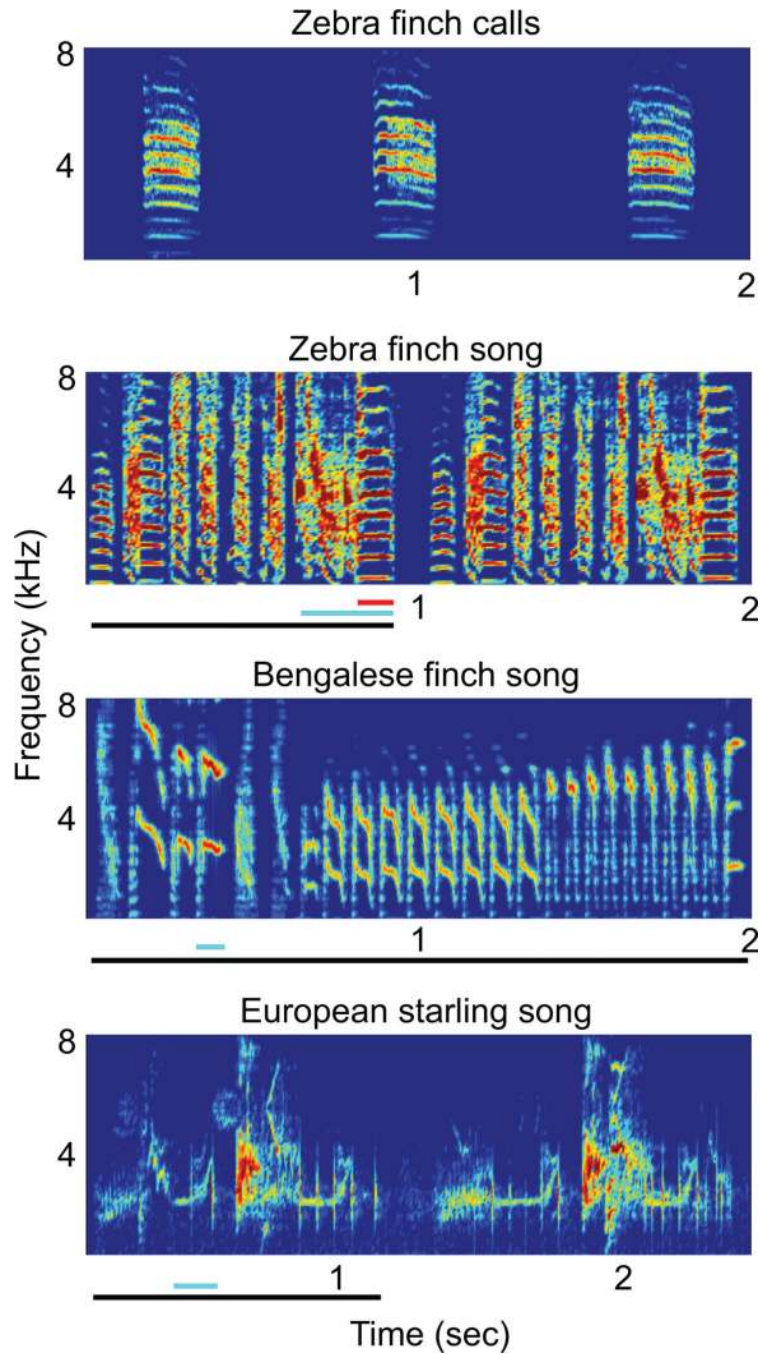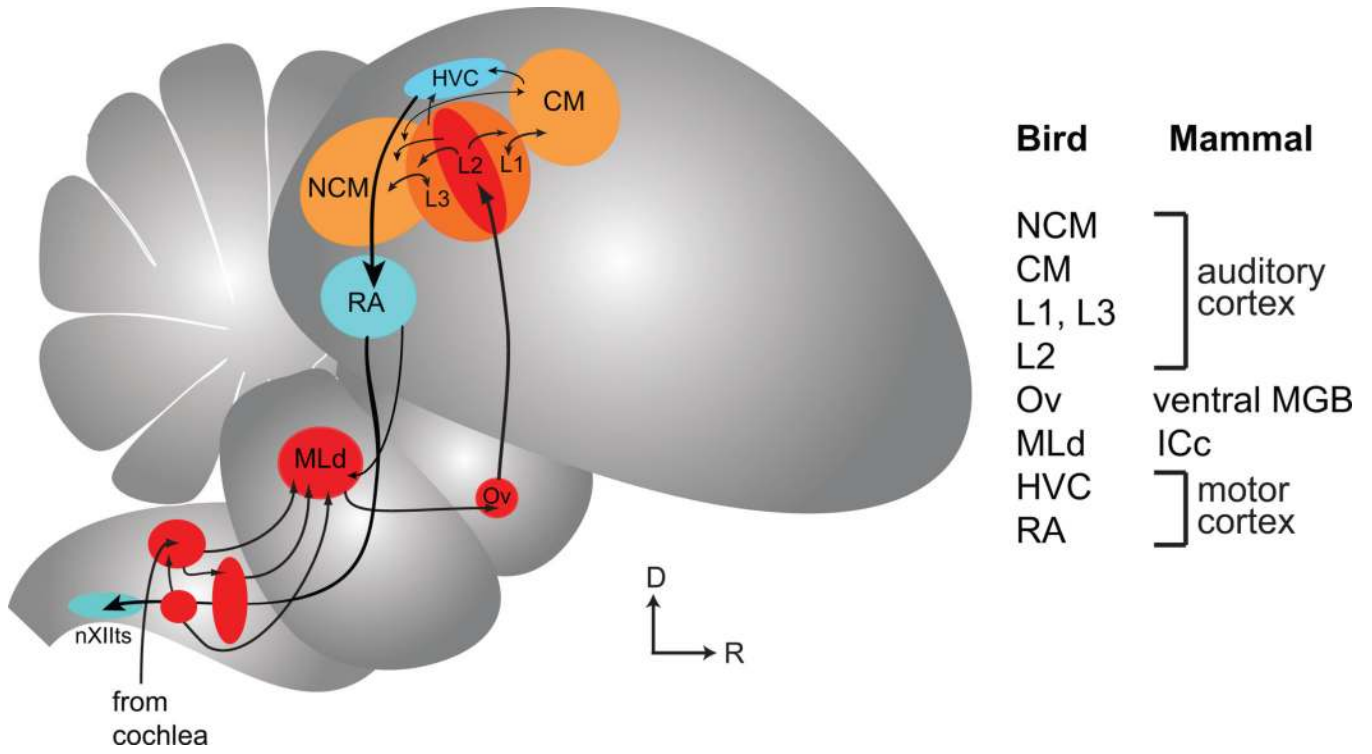
Figure 1.
Spectrograms (frequency over time plots) show the acoustic differences between calls and songs, and among the songs of different species. Color indicates intensity. Blue is low and red is high. Below the song spectrograms, a red line is placed under a song note, blue lines are under syllables and black lines are under motifs.
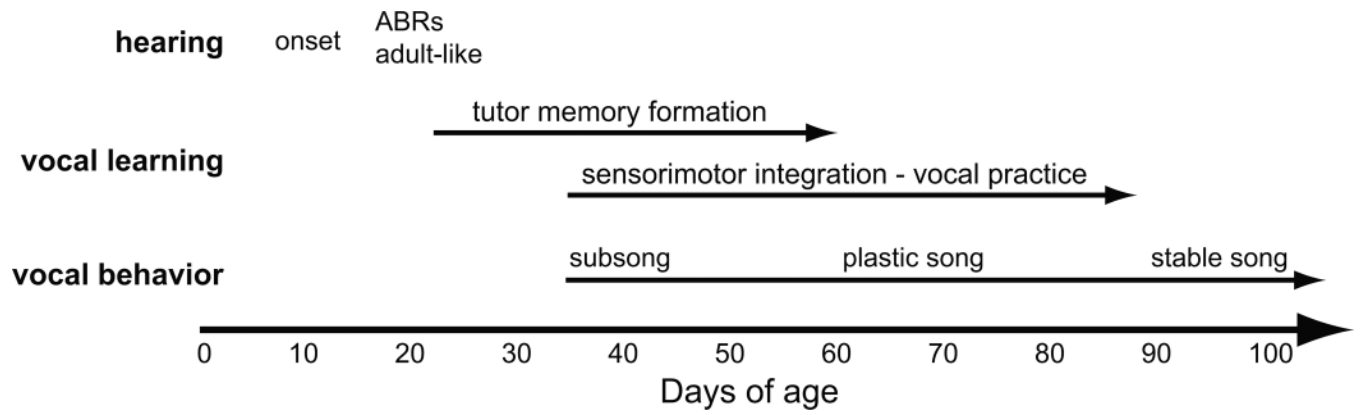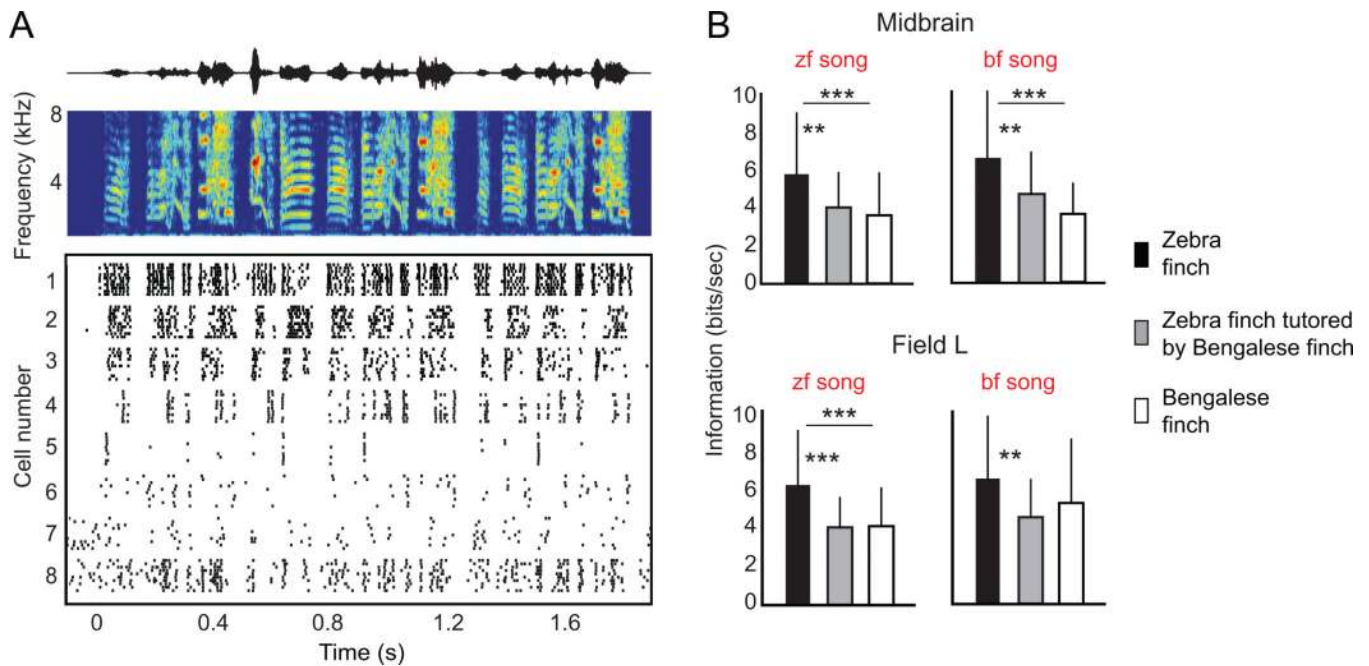
Figure 2.
Time line diagram shows song development as it related to age and hearing development. ABRs is the abbreviation for "auditory brainstem responses", which are measured during presentation of tones or clicks to determine basic subcortical auditory function.
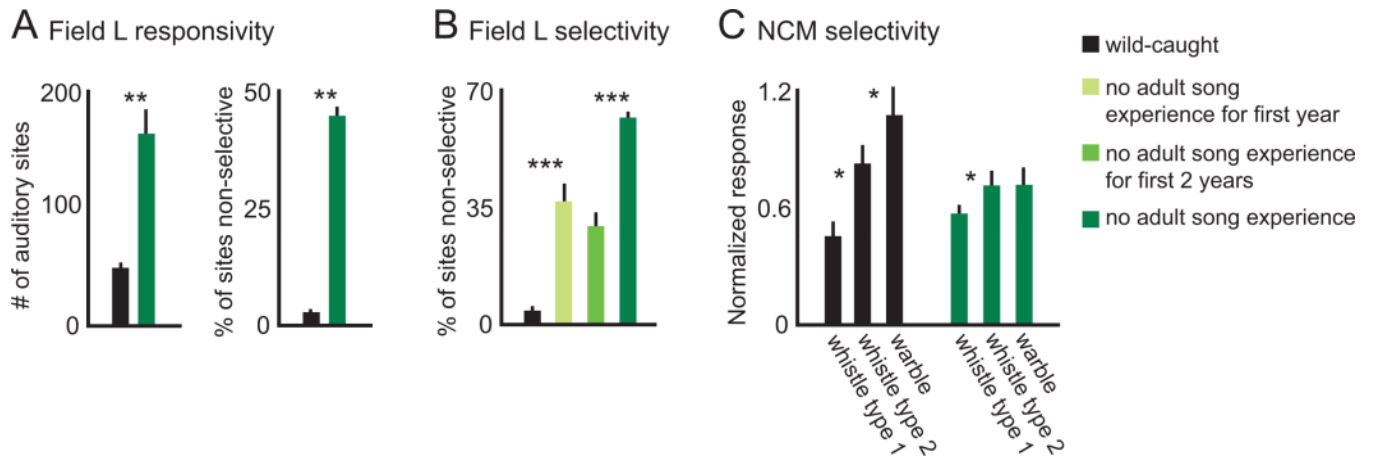
Figure 3.
Schematic diagram shows the primary songbird auditory processing regions and circuitry (red) and relationship with the primary vocal motor circuit controlling song production (blue). vMGB is ventral medial geniculate body and ICc is central nucleus of the inferior colliculus.
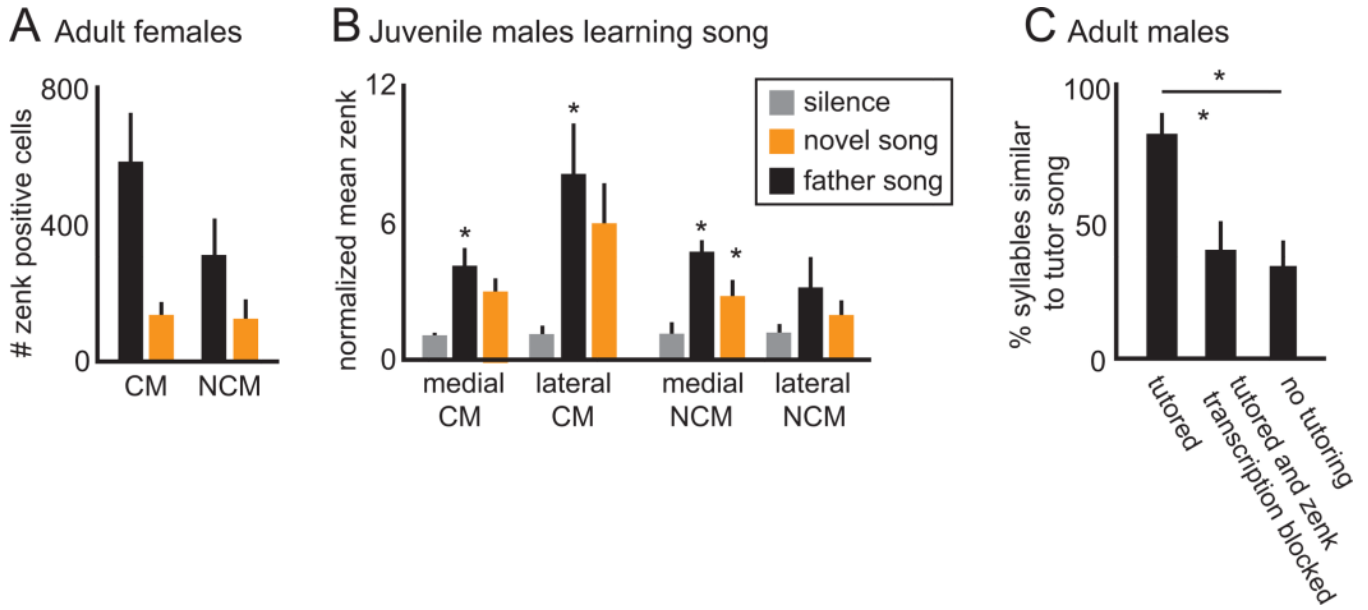
Figure 4.
Single neuron responses to song and effects of early song experience on information coding in single midbrain and primary forebrain neurons. A. Amplitude waveform and spectrogram of a song presented to birds while recording midbrain responses are above spike rasters. Rasters show the spike times of 8 single neurons responding to the song. Responses to ten presentations of the song are shown for each neuron. Neurons' responses to the same song differ in firing rate and pattern; each neuron reliably responds to different acoustic features of the song. Adapted from (Schneider & Woolley, 2010). B. Information in responses of single midbrain (upper) and primary forebrain (lower) neurons recorded from zebra finches, zebra finches tutored by Bengalese finches and Bengalese finches. Neurons from zebra finches tutored by Bengalese finches had lower information coding capacity than did neurons from zebra finches tutored by zebra finches. Adapted from (Woolley, et al., 2010). Error bars are 1 SD. ** p < 0.01, *** p < 0.001.

Figure 5.
Effects of juvenile exposure to adult song on responsivity and selectivity of neuronal recording sites in the starling auditory cortex. A. The number of electrophysiologically mapped forebrain sites that respond to auditory stimuli is higher in acoustically deprived birds. Adapted from (Cousillas, et al., 2004). B. The selectivity of primary forebrain sites to different song features is lowest for birds reared with no adult song experience, intermediate for birds exposed to adult song as young adults and highest for wild-caught birds. Adapted from (George, et al., 2004). C. The selectivity of higher forebrain neural responses for song features is lower in birds reared without adult song exposure than in wild-caught birds. Adapted from (George, et al., 2010). Error bars are 1 SE. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Figure 6.
Immediate early gene responses to tutor song versus other songs in auditory cortex. A. Father song presentation results in more *zenk* expression in the female zebra finch CM and NCM than does novel song presentation. Adapted from (Terpstra, et al., 2006). B. A similar effect in juvenile male zebra finches in the vocal practice stage of song development. Adapted from (Gobes, et al., 2010). C. Comparison of the percentage of syllables that were similar to tutors' syllables when birds received tutoring and no brain manipulation, tutoring with forebrain *zenk* transcription blocked and no tutoring. The *zenk* blockade resulted in impaired song learning. Adapted from (London & Clayton, 2008). Error bars are 1 SE. * p < 0.05.