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Coevolution in communication senders and receivers: vocal behavior and auditory processing in multiple songbird species

Sarah M. N. Woolley and Jordan M. Moore

Columbia University Department of Psychology 406 Schermerhorn Hall New York, NY 10027

Abstract

Communication is a strong selective pressure on brain evolution because the exchange of information between individuals is crucial for fitness-related behaviors, such as mating. Given the importance of communication, the brains of signal senders and receivers are likely to be functionally coordinated. We study vocal behavior and auditory processing in multiple species of estrildid finches with the goal of understanding how species identity and early experience interact to shape the neural systems that subserve communication. Male finches learn to produce species-specific songs, and both sexes learn to recognize songs. Our studies indicate that closely related species exhibit different auditory coding properties in the midbrain and forebrain and that early life experience of vocalizations contributes to these differences. Moreover, birds that naturally sing tonal songs can learn broadband songs from heterospecific tutors, providing an opportunity to examine the interplay between species identity and early experience in the development of vocal behavior and auditory tuning.

Keywords

estrildid finches; song; experience; learning; sensory coding; perception

Introduction

Communication is a major driving force in evolution because behaviors such as mating, group cohesion and predator avoidance rely on the accurate production and perception of communication signals.^{1–4} Because communication is so closely tied to survival and reproduction, the neural systems that subserve it are likely to be significantly shaped by natural and sexual selection.^{4–5} To ensure the efficient transmission of information, the motor circuits that generate signals must be tightly coordinated with the sensory circuits used to perceive them. How might this occur? To address this question, we study the vocal behavior and functional properties of auditory neurons in multiple species of songbirds. The species we study are closely related and have similar mating systems, yet they produce and perceive songs that differ markedly in their acoustics. Our goal is to understand how species identity and early experience interact to shape the neural systems that underlie vocal communication.

Songbirds are an excellent model system for studying the evolution of vocal communication because the over 4000 diverse species in this group produce songs that vary widely in acoustic features⁶ and they, like humans, are vocal learners.⁷ Species can differ in nearly all aspects of song, including their spectrotemporal acoustics, the number of song types

produced by individuals (ranging from one to thousands), sex differences in singing and the extent to which song behavior changes with season.⁸ The heterogeneity of song acoustics, even between closely-related species, provides especially good opportunities to investigate how the physical properties of a communication signal have evolved in relation to the tuning properties of the sensory system used to perceive that signal. The fact that songbirds learn their songs adds to the richness of this opportunity because the role of developmental influences, in particular that of early social and auditory experience, can be teased apart from the effects of species identity.

Birdsong functions in mate attraction, intrasexual competition and individual recognition⁶. In most species, only males sing. Males produce song to court females and to control aggressive encounters with other males, generally in the context of sexual competition or territory defense.⁶ Females use male song as a mate choice cue. The amount of singing, the number of song types produced and the acoustic complexity of songs have all been identified as traits that are salient to females.^{6, 9} These aspects of singing behavior are presumed to predict potential mate quality.^{10–11} In male zebra finches, measures of song complexity such as number of syllables and singing rate are associated with measures of male health and fitness^{12–13} and foraging-related abilities.¹⁴ Song can be used for species and individual recognition because the acoustic features of song are species-specific and specific to each individual. This allows birds to locate and discriminate between conspecific and heterospecific birds and maintain consistent social interactions with known individuals such as mates and territory neighbors.^{15–19} Male song can also influence female reproductive physiology²⁰ and sexual behavior.^{21–22}

Estrildid Finches

Our studies examine species differences in vocal behavior and auditory processing in three species from the family Estrildidae: the zebra finch (*Taeniopygia guttata*), Bengalese finch (*Lonchura striata domestica*), and blackheart finch (*Poephila acuticauda*). Estrildids are a monophyletic group of approximately 158 species native to Australia, southern Asia and Africa. These birds are highly social vocal learners and exhibit substantial variability in the spectrotemporal acoustics of their species-typical songs. Figure 1 shows the phylogenetic relationships and song spectrograms of five estrildid species. Despite their close relatedness,²³ the songs of these species are distinguished by their divergent spectrotemporal sound patterns. For example, the zebra finch, which is the most thoroughly studied species, sings a spectrally broadband song with harmonic and noisy syllables (Fig. 1, second row). By contrast, the blackheart finch (also called the long-tailed or shafttail finch), which is closely related to²³ and partially sympatric with the zebra finch,^{24–25} sings a tonal song with syllables composed of frequency-modulated sweeps (Fig. 1, third row). This acoustic diversity provides rich opportunities for comparative studies to examine the relationship between vocal behavior and auditory processing in closely-related species.

Estrildid finches are practical for laboratory studies because they readily mate, raise young, learn to sing and produce song in captivity. Aspects of behavioral and neural development from egg to adult can be studied and experimentally manipulated. For example, the behavioral trajectories and changes in brain circuitry that occur during song learning have been intensively studied in zebra finches,^{26–33} and mechanisms controlling song production have been studied in adult zebra and Bengalese finches (also called society finches).^{32, 34–35} More recently, zebra finches have been studied to examine the relationship between vocal acoustics and the tuning properties of auditory neurons,^{36–41} and both zebra and Bengalese finches have been used to investigate the effects of early life experience on the development of song preferences.^{42–45} But, until recently, no studies have taken advantage of the

extensive acoustic variation in the songs of estrildid finches to ask how vocal motor and auditory systems may have coevolved.

Song Learning in Estrildid Finches

Songs are long duration vocalizations (seconds to minutes) that are acoustically complex, composed of hierarchically organized and structured units, and are stereotyped to varying degrees among species. The most basic acoustic unit in song is called an “element” or “note,” which is a continuous sound. Notes can be grouped together to form “syllables,” which are commonly defined as stereotyped note sequences separated by silent gaps that are shorter than 25 milliseconds. A series of syllables that is repeated in a predictable sequence is referred to as a “motif,” and motifs that occur regularly constitute a song “type.” A succession of multiple motifs is called a song “bout.”

Estrildid finch song learning occurs before sexual maturity and requires the memorization of a tutor song followed by vocal practice in which birds use auditory feedback to shape their songs over time. Birds that are raised in isolation or deafened as juveniles develop abnormal songs that lack the structure and many acoustic features of normal adult song, but they still show some species-typical features.^{46–47} A juvenile male zebra finch copies the song that it is repeatedly exposed to between 20 and 60 days of age, but not before or after that time.^{48–49} Song learning in Bengalese finches follows a similar timeline,⁵⁰ but it appears to take slightly longer in blackheart finches (Woolley and Moore, unpublished observations). As a demonstration of the highly social nature of these birds, interactions between tutor and tutee, including visual and physical contact, facilitate song imitation.^{47, 49, 51–52} At sexual maturity, song behavior becomes stereotyped and, in the species that have been studied thus far, adults do not normally modify or learn new songs.

As one might expect, song learning is biased toward the imitation of conspecific over heterospecific song. These biases may involve both vocal motor and auditory circuits, but auditory perception appears to be particularly important. Studies measuring behaviors such as changes in heart rate, begging calls and perch hops indicate that songbirds, including naïve juveniles, are more responsive to conspecific than heterospecific song.^{53–56} Juvenile zebra and Bengalese finches that are exposed to both types of song are much more likely to copy conspecific song elements.^{18, 52} Such preferences are apparently not due to differences in hearing thresholds for the predominant sound frequencies in these songs because both species sing broadband songs and they have similar audiograms.⁵⁷ Together, these studies suggest that early auditory biases guide the identification and learning of conspecific songs, and such biases are potentially due to the spectrotemporal tuning properties of auditory neurons rather than basic hearing abilities.

Though conspecific songs are preferentially learned, many studies have shown that zebra finches will learn Bengalese finch songs if they are not given an opportunity to interact with adult zebra finch males.^{58,48, 59–61} This ability to learn heterospecific song demonstrates that motor circuitry and the physiology of the vocal apparatus do not prevent birds from copying the songs of other species, and it supports the idea that auditory mechanisms subserve conspecific song learning biases. There are some important caveats to this conclusion, however. First, the songs of cross-tutored birds usually retain the tempo of conspecific song, even when the birds have never been exposed to it.^{59, 61} This suggests that birds have a predisposition to produce species-typical sounds in addition to a perceptual bias. Second, social interactions experienced early in life are likely important for tutor selection and could serve to gate the encoding of auditory information. Third, the extent of estrildid song copying capacities remains unknown because zebra and Bengalese finch songs are acoustically quite similar. Cross-tutoring birds that naturally sing slow, tonal songs with the

songs of species that sing fast, broadband songs will be more informative about the vocal imitation abilities of estrildid finches (see below). Such cross-tutoring experiments also create the opportunity to test how early auditory and social experiences influence the tuning properties of auditory neurons.

Auditory Coding in Estrildids

Species differences in song have been studied for decades, but the relationships between these differences and those in auditory coding have only recently been examined. Initially, the spectral and temporal tuning properties of zebra finch auditory midbrain and forebrain neurons (usually in anesthetized, adult males) were characterized to investigate the relationship between auditory coding and the acoustics of natural sounds.^{36–41, 62–68} This work has led to the general conclusion that the firing patterns of midbrain and primary forebrain neurons to songs are reliable (i.e. similar over multiple trials) and can be largely explained by their spectrotemporal tuning properties.

The songbird auditory system shares a basic organization with the mammalian auditory system. Figure 2 shows a diagram of the primary auditory pathways in the songbird brain. The avian auditory midbrain nucleus is called the mesecephalicus lateralis dorsalis (MLd) and, like the mammalian inferior colliculus, is a nexus for auditory processing because it integrates multiple parallel brainstem pathways and provides the predominant input to the thalamocortical ascending pathway.^{69–71} In males, MLd also receives descending input from the cup of rostral arcopallium (RA_{cup}).⁷² MLd projects to the auditory thalamus, nucleus ovoidalis (Ov), which then sends projections to the primary forebrain region field L.^{73–74} Field L has several, highly interconnected subdivisions and projects to secondary auditory forebrain regions, the caudal medial nidopallium (NCM) and caudal mesopallium (CM),^{72, 75–76} see⁷⁷ for review).

The songbird auditory midbrain is a focus for examining how the spectrotemporal tuning properties of neurons relate to song encoding. Unlike auditory areas in the forebrain, midbrain neurons respond strongly to a wide variety of sounds including tones,^{36, 78–79} noise,^{37–38, 41, 62, 64} synthetic sounds that mimic aspects of song³⁷ and both conspecific and heterospecific song.^{40–41, 61–64} The robust and reliable responses of midbrain neurons to different sounds allow the direct comparison of individual neurons' responses to song and other sounds. Comparisons of responses to song and to noise led to the discoveries that zebra finch auditory neurons are tuned to the spectrotemporal modulations that characterize vocalizations.³⁸ Similar findings have been made in mammals; midbrain neurons in bats are preferentially tuned to frequency sweeps commonly found in communication vocalizations⁸⁰ and neurons in rats are tuned to durations that characterize many conspecific vocalizations.⁸¹

The spectrotemporal tuning properties of auditory midbrain neurons determine the simple sounds to which neurons respond and the features of complex sounds that they encode.^{36–38, 40–41, 63, 78–79} Each neuron is tuned to a different range of frequencies, intensities and temporal patterns that determine its firing patterns in response to songs. Additionally, some neurons respond only to sound onsets while others respond continuously throughout sound presentation.^{36–37} In awake birds, most midbrain neurons show substantial spontaneous firing and reliably respond to specific spectrotemporal features of the songs' syllables. Figure 3 shows the spiking responses of single MLd neurons in an awake zebra finch and blackheart finch to the songs of three different estrildid species (Bengalese, blackheart and zebra finches). These neurons are also well suited to investigate relationships between song and auditory coding because the neurons are “linear,” meaning that their response properties to song can be accurately characterized by linear models, such as

spectrotemporal receptive fields (STRFs). Because these neurons also respond well to simple sounds such as noise and tones, their frequency, intensity and temporal tuning can be assessed using multiple types of stimuli and can be directly compared with their tuning properties measured from responses to songs. Such comparisons have revealed stimulus-dependent tuning in single neurons whereby the spectral and temporal sound patterns to which neurons respond differ during song processing and the processing of other complex sounds.⁴¹ The tuning patterns observed in responses to songs could provide a basis for the neural discrimination of songs produced by different males, potentially contributing to individual recognition during social interactions.^{63, 82–84}

Forebrain neurons in field L of anesthetized males respond, on average, less robustly and reliably to stimuli than do midbrain neurons, but they show spectrotemporal tuning properties to song that are similar to those in the midbrain.^{38, 40} Also like the midbrain, neurons in the primary forebrain can be classified into functional groups based on their spectrotemporal tuning properties, and the major groups are shared between the midbrain and forebrain.⁴⁰ Zebra finch field L neurons in both sexes show response selectivity, in terms of average firing rate, for conspecific song over synthetic sounds such as noise and tone complexes^{85–86} but not for conspecific song over Bengalese finch song.⁶¹

Species differences in auditory coding

Species differences in midbrain responses to song have been found in zebra and Bengalese finches.⁶¹ We compared the information coding capacity, average firing rate and spike train dynamics of midbrain and primary forebrain (field L) neurons in anesthetized adult male zebra and Bengalese finches. Information coding capacity refers to the ability of a neuron's responses to encode information about a stimulus such that the stimulus can be identified in a set of stimuli.⁸⁷ The information coding capacity of a neural response to a stimulus is measured in terms of mutual information, which quantifies the dependence of a response on a stimulus. Spike train dynamics include the reliability of neural responses over multiple trials, and the dynamic ranges and distributions of time-varying firing rates observed in responses. Information coding was examined by measuring the mutual information between songs and the responses of individual neurons to those songs.⁸⁸ Both midbrain and primary forebrain neurons in the zebra finch showed higher information coding capacity than those in the Bengalese finch, respectively, and this effect was largely due to higher average firing rates in zebra finch neurons than in Bengalese finch neurons. The greater information coding capacity of zebra finch neurons was observed in the responses to both zebra finch and Bengalese finch songs, indicating that conspecific and heterospecific songs are encoded with comparable information. Among the twelve analysis measures of responses to conspecific and heterospecific songs in zebra and Bengalese finch neurons, only one difference between the coding of conspecific and heterospecific song was found; Bengalese finch forebrain neurons responded with slightly higher information coding to conspecific song than to heterospecific song. This difference was not found in zebra finch neurons or Bengalese finch midbrain neurons. In summary, this study showed that species differences in the neural coding of song exist in both the midbrain and primary forebrain, but that most individual neurons produce responses to conspecific and heterospecific songs that have the same mutual information. While illuminating, the comparison of auditory processing in zebra and Bengalese finches is not ideal for asking whether the spectrotemporal tuning properties of auditory neurons differ between species. This is because zebra and Bengalese finch songs are quite similar; both are spectrally broadband and temporally fast (Fig. 1).^{18, 48, 61} It therefore remains unknown if estrildid species that exhibit larger differences in song acoustics exhibit parallel differences in auditory tuning.

In order to compare auditory coding properties in species with very different song acoustics, our current studies include the blackheart finch. This species' song is characterized by tonal, long duration syllables in which most energy spans a narrow frequency range with pronounced frequency-modulated sweeps (Figs. 1, 3 and 4). The spectrotemporal features of blackheart finch song differ greatly from those of the zebra and Bengalese finch song, allowing us to investigate whether auditory tuning relates to the acoustic properties of conspecific vocalizations. For example, we are testing the hypothesis that, on average, blackheart finch auditory neurons show narrower frequency tuning and more sustained temporal responses than do zebra finch auditory neurons. Differences in both spectral and temporal response properties have been found in NCM of zebra finches and canaries (*Serinus canaria*)⁶⁶, which sing tonal songs with many rapid, frequency-modulated sweeps. This finding suggests that midbrain and primary forebrain neurons may also differ among estrildid species that produce very different songs.

Effects of vocal learning on auditory coding

Differences in information coding between zebra and Bengalese finch auditory neurons appear to result from differences in early auditory experience of vocalizations and/or vocal learning.⁶¹ We examined the role of vocal experience in the development of midbrain and primary forebrain song coding properties by cross-fostering zebra finch nestlings into the nests of Bengalese finches. This manipulation altered the auditory and social environment and the motor learning of the developing zebra finches; they heard exclusively Bengalese finch song and then learned to produce reasonably accurate copies of their Bengalese finch tutors' songs. The cross-fostering resulted in significant effects on the information coding capacity of both midbrain and forebrain neurons when recorded in anesthetized adult males. Neurons in zebra finches raised by Bengalese finches showed the same information coding capacity and average firing rates as Bengalese finch neurons, and significantly lower information coding capacity and firing rates than neurons in normally-raised zebra finches. Thus, early life experiences can shape the coding properties of midbrain and forebrain auditory neurons.

This study led to three new questions about the effects of early life experience on species differences in auditory coding. First, how drastically can early auditory exposure shape auditory processing? Second, are species differences in auditory processing observed when birds are raised in the same vocal-acoustic environment? Third, how are differences in auditory response properties, such as information coding capacity and firing rate, paralleled by differences in spectrotemporal tuning? To address these questions, we are cross-fostering juvenile blackheart finches (tonal singers) and juvenile zebra finches (broadband singers) into the nests of other conspecifics (blackheart and zebra finches, respectively) or into the nests of Bengalese finches (broadband singers). With this design, birds of three different species develop in the same general vocal-acoustic environment – a multi-species colony – but some are tutored with conspecific song and others are tutored with heterospecific song. In the case of the zebra and blackheart finch juveniles that are cross-tutored by Bengalese adults, birds that naturally produce very different sounds are raised and tutored by the same heterospecific tutors. In this way, we control for the potential influences of the general vocal-acoustic environment and focus on the role of vocal learning (including both sensory and motor components) in the development of auditory processing.

Although it is well known that zebra finches can learn Bengalese finch song,^{48, 61, 89} it is unknown whether species that naturally sing tonal songs with long duration syllables can do the same (see Fig. 1). Recent cross-tutoring experiments demonstrated that blackheart finches can indeed learn to sing broadband, temporally rapid songs (Fig. 4). Figure 4A shows a spectrogram of a Bengalese finch tutor's song, the song of a blackheart finch tutee,

the song of that tutee's biological father, the song of a zebra finch tutee (raised separately from the blackheart finch tutee) and that tutee's biological father. Accurately copied syllables are labeled on the tutor and tutee spectrograms and expanded in Figure 4B. Interestingly, the blackheart finch tutee also produces tonal syllables that are of long duration, unlike any of the syllables in his tutor's song but similar to typical blackheart finch song syllables (Fig. 4A, second row). This production of species-typical song syllables in the absence of conspecific tutoring is reminiscent of "isolate" songs produced by zebra finches raised without access to adult males,⁴⁷ and it suggests that songs can include species-typical aspects without tutoring.

Our cross-species song learning experiments show that estrildid finches can learn songs that differ significantly from their natural songs. The surprisingly versatile song copying and production abilities of these birds suggest that the propensity to copy conspecific over heterospecific song in estrildid finches is due to auditory perceptual biases and/or the effects of social interactions rather than vocal motor limitations, as has been described in other songbird taxa⁹⁰. Because blackheart finch song differs so dramatically from Bengalese finch song, blackheart finches tutored by conspecifics will learn songs with very different acoustics from those raised by Bengalese finches. We are currently studying whether the acoustics of vocalizations heard and learned during development influence the spectral and temporal tuning properties of auditory midbrain and forebrain neurons. These studies will allow us to begin to understand how the vocal motor behavior of senders and the auditory systems of receivers may match in vocal communicators.

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Figure 1.

Cladogram and spectrograms of the songs of five estrildid finch species show the the phylogenetic relationships and spectrotemporal diversity of song among species. The species are owl finch (*Taeniopygia bichenovii*), zebra finch, blackheart finch, Bengalese finch, and strawberry finch (*Amandava amandava*).

Figure 2. Sagittal view of the primary auditory (black) and vocal motor (gray) pathways in the male songbird brain. NM, nucleus magnocellularis; NL, nucleus laminaris; SON, superior olivary nucleus; LL, lateral lemniscus; MLd, mesencephalic lateral dorsal nucleus; Ov, nucleus ovoidalis; L, field L; CM, caudal mesopallium; NCM, caudomedial nidopallium; HVC is a proper name; RA, robust nucleus of the arcopallium.

Figure 3.

The spiking responses of one single zebra finch (ZF) auditory midbrain neuron (upper) and one single blackheart finch (BhF) auditory midbrain neuron (lower) to Bengalese (BgF) (top), blackheart (middle) and zebra (bottom) finch songs. Recordings were made from awake males. Spectrograms of the songs that were presented to birds are shown above raster plots showing the responses of each neuron during the song presentation (row) and across multiple presentations of the same song (columns). Neurons from each species produce robust and reliable responses to the songs of all three species, but each neuron responds to different spectrotemporal features of the songs.

Figure 4.

The songs of a Bengalese finch (BgF) tutor, blackheart finch (BhF) and zebra finch (ZF) tutees and the biological fathers of the tutees show that juvenile estrildids will copy heterospecific songs even when the spectrotemporal acoustics of their natural songs differ dramatically from heterospecific tutors' songs. A. First, a song motif recorded from a Bengalese finch tutor, with syllables that were copied by tutees labeled by black boxes and numbers. Second, a song motif recorded from an adult blackheart finch that was tutored by the Bengalese finch, with the syllables that it copied from the tutor labeled by boxes and numbers. Third, a motif recorded from the blackheart finch tutee's father. Fourth, a song motif recorded from an adult zebra finch that was tutored by the Bengalese finch, with the syllables that it copied from the tutor labeled by boxes and numbers. Fifth, a song bout consisting of several motifs recorded from the zebra finch tutee's father. B. Bengalese finch tutor, blackheart finch tutee and zebra finch tutee syllables that are highly similar show that both blackheart and zebra finch tutees copied song from the Bengalese finch tutor. The syllables shown are the same as those labeled by boxes and numbers in A. The blackheart finch tutee copied two syllables and the zebra finch tutee copied three syllables from the Bengalese finch tutor. Similarity scores between syllables in tutors' songs and copied syllables in tutees' songs measured using Sound Analysis Pro⁹¹ were 58.8 ± 5.9 (mean $\pm$ SD, unitless measure). Similarity scores between tutee syllables and syllables from the songs of their genetic fathers were 11.7 ± 1.8 .