



Seasonal plasticity in auditory processing of the envelope and temporal fine structure of sounds in three songbirds



Alejandro Vélez ^{a,*}, Megan D. Gall ^{a,b}, Jeffrey R. Lucas ^a

^a Department of Biological Sciences, Purdue University, West Lafayette, IN, U.S.A.

^b Department of Biology, Vassar College, Poughkeepsie, NY, U.S.A.

ARTICLE INFO

Article history:

Received 31 August 2014
 Initial acceptance 20 November 2014
 Final acceptance 22 December 2014
 Published online
 MS. number: A14-00702

Keywords:

acoustic communication
 birdsong
 envelope-following response
 frequency-following response
 hearing
 mixed-species flock
 modulation rate transfer function
 peripheral auditory system
 seasonality
 vocal communication

ABSTRACT

Songs mediate mate attraction and territorial defence in songbirds during the breeding season. Outside of the breeding season, the avian vocal repertoire often includes calls that function in foraging, anti-predator and social behaviours. Songs and calls can differ substantially in their spectral and temporal content. Given seasonal variation in the vocal signals, the sender–receiver matching hypothesis predicts seasonal changes in auditory processing that match the physical properties of songs during the breeding season and calls outside of it. We tested this hypothesis in white-breasted nuthatches, *Sitta carolinensis*, tufted titmice, *Baeolophus bicolor*, and Carolina chickadees, *Poecile carolinensis*. We measured the envelope-following response (EFR), which quantifies phase locking to the amplitude envelope, and the frequency-following response (FFR), which quantifies phase locking to the temporal fine structure of sounds. Because songs and calls of nuthatches are amplitude modulated at different rates, we predicted seasonal changes in EFRs that match the rates of amplitude fluctuation in songs and calls. In chickadees and titmice, we predicted stronger FFRs during the spring and stronger EFRs during the winter because songs are tonal and calls include amplitude-modulated elements. In all three species, we found seasonal changes in EFRs and FFRs. EFRs varied across seasons and matched the amplitude modulations of songs and calls in nuthatches. In addition, female chickadees had stronger EFRs in the winter than in the spring. In all three species, FFRs during the spring tended to be stronger in females than in males. We also found species differences in EFRs and FFRs in both seasons; EFRs and FFRs tended to be higher in nuthatches than in chickadees and titmice. We discuss the potential mechanisms underlying seasonality in EFRs and FFRs and the implications of our results for communication during the breeding season and outside of it, when these three species form mixed-species flocks.

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Reproductive cycles are mediated by changes in hormonal profiles that lead to morphological, physiological and behavioural modifications that in turn function in processes as diverse as mate attraction and production of resources for offspring (Van Tienhoven, 1983). These seasonal changes often include the production of exaggerated traits and displays to attract members of the opposite sex. During the breeding season, for instance, male songbirds produce songs that function in territory establishment and mate attraction (Catchpole & Slater, 2008). Several studies have shown how song production during the breeding season is associated with changes in testosterone levels and anatomical

structures like the size of the syrinx and song nuclei in the forebrain (Brenowitz, 2004; Tramontin & Brenowitz, 2000; Tramontin, Hartman, & Brenowitz, 2000).

Congruent with seasonal changes in song production, growing evidence suggests that central and peripheral auditory processing can also change seasonally in songbirds. Some of these studies suggest that auditory processing is upregulated during the breeding season. At the level of the auditory periphery, for instance, house sparrows, *Passer domesticus*, show enhanced auditory brainstem responses to suprathreshold sounds in the frequency range of vocalizations used during the breeding season (Henry & Lucas, 2009). At higher levels of the auditory pathway, such as the caudomedial nidopallium (NCM) of the auditory forebrain, songs stimulate stronger neural responses during the breeding season in female white-throated sparrows, *Zonotrichia albicollis* (Maney, Cho, & Goode, 2006; Yoder & Vicario, 2012).

* Correspondence: A. Vélez, Department of Biology, Washington University, One Brookings Drive, Campus Box 1137, St Louis, MO 63130, U.S.A.

E-mail address: avelezmelendez@wustl.edu (A. Vélez).

Vocal production in songbirds, however, is not restricted to reproduction. Outside of the breeding season, the vocal repertoire of songbirds includes a variety of calls that function in group cohesion, alerting the presence of predators and announcing the presence of food (Marler, 2004). Furthermore, species that form mixed-species flocks may use heterospecific communication signals to coordinate foraging and antipredator behaviours (Goodale & Kotagama, 2008). Importantly, the physical properties of songs and calls are often very different within species. Differences in the acoustic properties of songs and calls suggest the use of different auditory specializations to process each type of vocalization. Therefore, seasonal changes in auditory processing are expected to match the physical properties of songs in the breeding season and calls outside of the breeding season. This framework of an association between signal properties and receiver processing has been described as the signal–receiver matching hypothesis (Dooling, Lohr, & Dent, 2000; Gall, Brierley, & Lucas, 2012a; Woolley, Gill, Fremouw, & Theunissen, 2009).

We asked whether seasonal plasticity in peripheral auditory processing matches seasonal changes in signal properties in white-breasted nuthatches, *Sitta carolinensis*, tufted titmice, *Baeolophus bicolor*, and Carolina chickadees, *Poecile carolinensis*, three forest species that form mixed-species flocks in the winter. Nuthatches have the simplest vocal system, followed by titmice and, with the most complex vocal repertoire, chickadees (Lucas, Freeberg, Krishnan, & Long, 2002; Fig. 1). In this manuscript, we categorize bird vocalizations by their function: we define songs as vocalizations used for reproduction purposes and we define calls as vocalizations used in other contexts (Marler & Slabbekoorn, 2004). The songs and calls of nuthatches are structurally similar and can be described as harmonic stacks that differ in duration and

fundamental frequency (Ritchison, 1983). The frequency separation of the harmonics is about 500–600 Hz in nuthatch calls, and about 700–800 Hz in songs (Lucas, Vélez, & Henry, in press; Ritchison, 1983). In contrast, the physical properties of calls and songs vary tremendously in chickadees and titmice. The call repertoire in chickadees, including chick-a-dee and gargle calls, comprises a great variety of note types that include tonal and frequency-modulated elements as well as amplitude-modulated harmonic stacks (Bloomfield, Phillmore, Weisman, & Sturdy, 2005; Lucas & Freeberg, 2007; Smith, 1972). During the breeding season, male chickadees produce songs that contain four to five tonal elements with little or no frequency modulation (Lohr, Nowiki, & Weisman, 1991; Smith, 1972). Titmice songs, predominantly produced by males during the breeding season, are tonal with some slow frequency modulations (Offutt, 1965). During the winter, titmice also produce chick-a-dee calls with elements that can be tonal, frequency-modulated or amplitude-modulated harmonic stacks (Offutt, 1965; Owens & Freeberg, 2007). A property of harmonic sounds, like nuthatch vocalizations and some elements of the calls of chickadees and titmice, is that the separation between frequency elements generates amplitude modulations in the sound envelope at the rate of the frequency separation (Moore, 1993; Viemeister & Plack, 1993). Importantly, the auditory system can process these amplitude fluctuations (Henry, 1997; Lucas et al., in press; Simmons & Buxbaum, 1996), which underscores the importance of different dimensions of acoustic signals for communication (Nelson & Marler, 1990).

We used auditory evoked potentials (AEPs) to evaluate how the auditory system of nuthatches, titmice and chickadees processes tonal and amplitude-modulated sounds during the breeding (spring) and nonbreeding (winter) seasons. AEPs are voltage

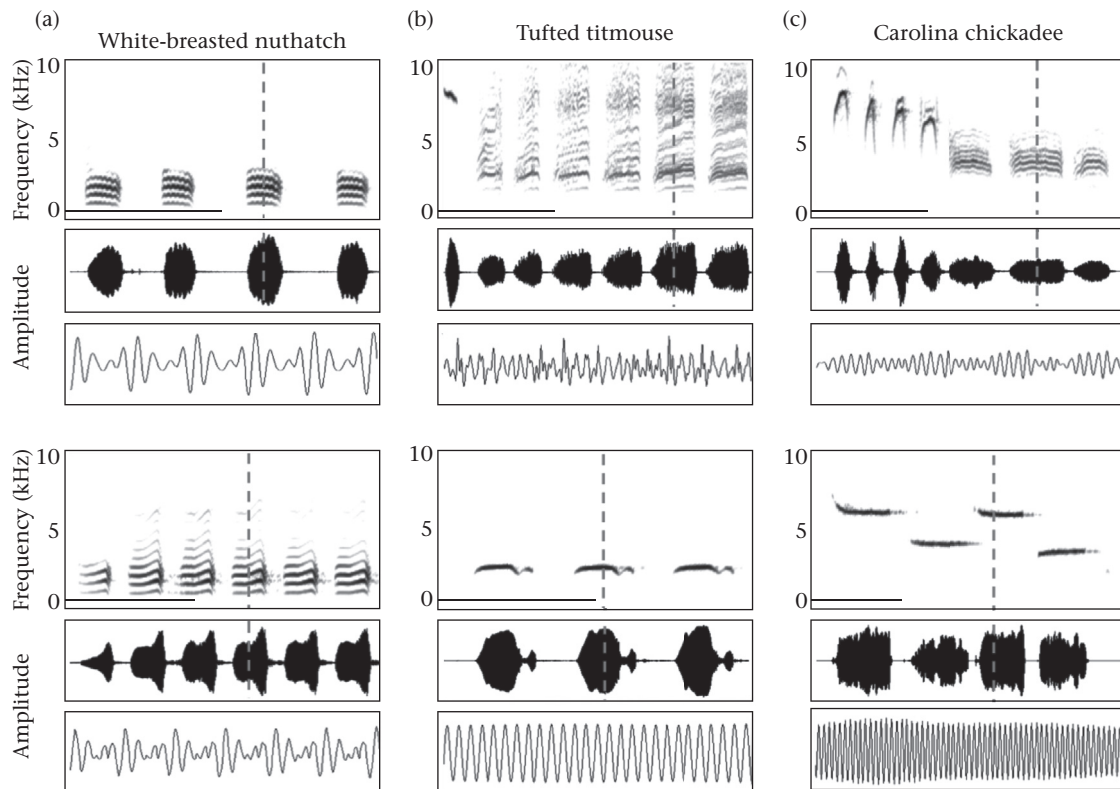


Figure 1. Calls (top row) and songs (bottom row) of (a) white-breasted nuthatches, (b) tufted titmice and (c) Carolina chickadees. The top panel is the spectrogram and the middle panel is the oscillogram of each vocalization. Scale bar in each spectrogram represents 0.5 s. The bottom panel depicts 10 ms of the oscillogram through the dashed vertical grey line in the spectrogram and in the oscillogram of the entire vocalization. Oscillograms are plotted as the normalized amplitude (between +1 and –1) as a function of time.

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