



## Species and sex effects on auditory processing in brown-headed cowbirds and red-winged blackbirds

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Brown-headed cowbirds, *Molothrus ater*, and red-winged blackbirds, *Agelaius phoeniceus*, are frequently used as model systems for communication and vocal learning; however, relatively little is known about their auditory processing. Although auditory space and acoustic signal space are assumed to coevolve, it is less clear when, or even if, sex differences are expected in auditory processing. Here we explored frequency-specific auditory responses using auditory brainstem responses (ABRs). We generated sex-specific audiograms using two methods: visual detection and cross-correlation. We also measured the amplitude and latency of ABRs to stimuli over a range of frequencies (0.5–6 kHz) and intensities (8–72 dB sound pressure level). Thresholds generated by both methods were good predictors of behavioural thresholds in the best frequency range (2–4 kHz). The visual detection method resulted in a slightly better correspondence with behavioural thresholds than the cross-correlation method above and below best frequencies. We found no significant differences between red-winged blackbird and brown-headed cowbird ABR thresholds; however, overall, females had lower thresholds than males. Sex differences were larger than species differences for ABR amplitude, while latency differences were greater between species than between sexes. Taken together our results suggest that despite high-frequency vocal elements, brown-headed cowbirds do not have enhanced high-frequency auditory sensitivity when measured with auditory evoked potentials. Moreover, we show that females have greater auditory sensitivity than males, which is generally not seen in other passerine species.

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Vocalizations, particularly of avian species, have been well studied, and design rules have emerged that link the structural features of vocalizations to their function (Catchpole & Slater 2008). The design of acoustic signals, even those with the same function, can vary substantially based on a number of factors such as habitat, communication range, or intended receiver (Bradbury & Vehrencamp 1998). When species identity is not important to the receiver, as is the case with avian mobbing calls, vocal signals tend to be convergent in structure (Ficken & Popp 1996). However, when species identity is important to the receiver, vocal signals, particularly those involved in mate attraction and courtship, tend to have species-specific spectral and temporal features.

The design rules that govern the auditory system of receivers have received relatively less attention (reviewed in Dooling et al. 2000). However, a general expectation has emerged that the spectral and temporal features of species-specific vocalizations

would be reflected in the auditory system (Konishi 1970; Dooling et al. 2000). Indeed, recent evidence from a number of species suggests that the species-specific spectral properties of acoustics signals are closely linked to auditory processing (Konishi 1970; Lucas et al. 2007; Henry & Lucas 2009, 2010b). For example, a wide variety of songbirds are maximally sensitive to the frequencies of their own song, and some songbirds show up-regulation of sensitivity at those frequencies during the breeding season (Lucas et al. 2007; Henry & Lucas 2009, 2010b). In addition, the upper limits of frequency sensitivity are correlated with maximum frequencies found in vocalizations (Konishi 1970). It has also been hypothesized that sex differences in auditory processing may occur if there are different pressures on males and females to detect acoustic stimuli (Gall & Lucas 2010), although general trends of sex-specific auditory processing have yet to be described.

Here we explore species- and sex-specific auditory processing in two closely related icterids: the red-winged blackbird, *Agelaius phoeniceus*, and the brown-headed cowbird, *Molothrus ater*. Both red-winged blackbird vocalizations (males: oak-a-lee; females: teer, chit) and brown-headed cowbird vocalizations (males: perched song, flight whistle; females: chatter or rattle) have spectral energy in the 1–6 kHz frequency range (Armstrong 1992; Lowther 1993; Yasukawa

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& Searcy 1995), which is generally considered the frequency range for communication in passerines (Fig. 1; Dooling et al. 2000). However, brown-headed cowbird perched songs also have spectral energy that regularly exceeds this frequency range ( $>6$  kHz; Fig. 1). Based on the hypothesis that signal space and auditory space coevolve, we would predict that brown-headed cowbirds should have greater sensitivity to high frequencies than red-winged blackbirds, which do not have vocalizations in these higher-frequency ranges. Moreover, brown-headed cowbirds would be expected to have neural populations tuned to a wide range of frequencies for processing components of conspecific vocalizations that cover a broad range of frequencies, while red-winged blackbirds should have neural populations tuned to a narrower range of frequencies.

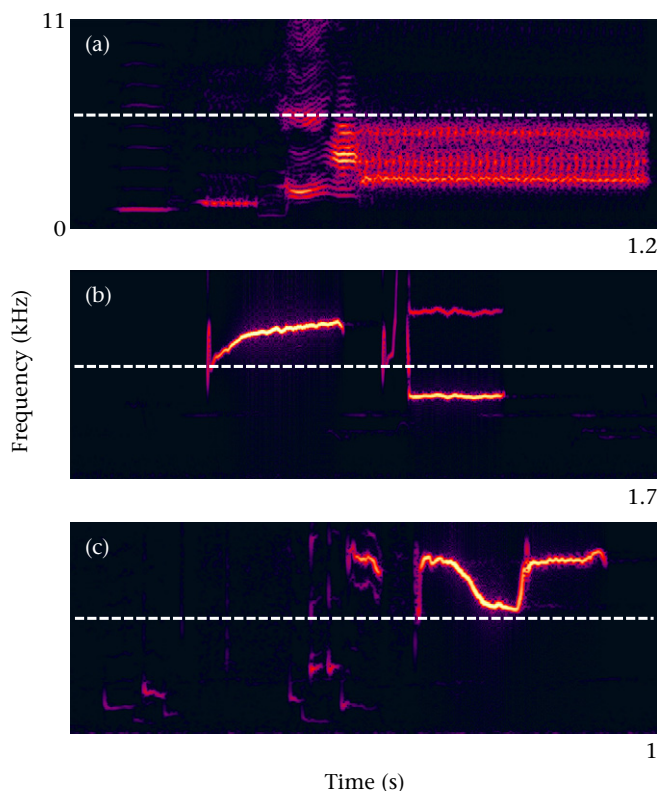
Furthermore, the strong sexual dimorphism and breeding biology of both species could result in sex differences in auditory processing. In red-winged blackbirds, males arrive first on the breeding grounds and establish territories (Yasukawa & Searcy 1995). Female red-winged blackbirds later engage in mate choice and use male vocalizations as a criterion in mate selection (Yasukawa et al. 1980; Yasukawa 1981). Therefore, during the breeding season the acquisition and processing of acoustic information, particularly mate attraction and copulation signals, may be of greater value to females than males. Although there is no a priori reason to expect differences in the frequency range of females and males based on mate location or choice, we would expect females to be more sensitive than males for locating mates and for fine-scale discrimination of potential mates' vocalizations.

Brown-headed cowbirds are brood parasites and are host generalists at both the species level ( $>150$  species parasitized; Friedmann

& Kiff 1985) and the individual level (average  $\pm$  SD number of hosts used per individual in a single breeding season =  $2.34 \pm 0.95$ ; Strausberger & Ashley 2005). It has been hypothesized that female cowbirds attend to the vocalizations of heterospecifics in order to localize or select potential hosts (e.g. eavesdropping; Clotfelter 1998; Parejo & Avilés 2007). Females, therefore, may have enhanced sensitivity, particularly in the frequency range of host vocalizations to detect hosts over long distances. However, there is no reason to assume males would have enhanced sensitivity to host vocalizations, as they do not assist in nest searching and are not expected to attend to heterospecific vocalizations. Furthermore, although males do not establish territories (Dufty 1982a, b), females do engage in mate choice and evaluate potential mates based on their vocalizations (Yokel & Rothstein 1991). This further suggests that females should have greater suprathreshold sensitivity than males, to allow females to assess mate quality.

The auditory space of both red-winged blackbirds and brown-headed cowbirds has previously been described with behavioural methods (Hienz et al. 1977). Brown-headed cowbirds and red-winged blackbirds were found to have relatively similar auditory thresholds; however, the sample size limitations of the behavioural methods prevented statistical comparisons of species and sex effects. Here we use auditory evoked potentials to examine frequency-specific responses of male and female red-winged blackbirds and brown-headed cowbirds. Auditory evoked potentials are gross electrical potentials generated by the synchronous response of neurons in the auditory nerve and brainstem to auditory stimuli and are measured with electrodes placed on or below the skin of the head (Hall 2007). We used a specific class of auditory evoked potentials called auditory brainstem responses (ABR), which are responses to stimulus onset. ABRs are electrical potentials that are generated within 5–10 ms after the onset of the acoustic stimulus. Early ABR peaks are relatively unaffected by anaesthetic or sedative drugs (Hall 2007); therefore, ABRs allow for relatively rapid testing of peripheral hearing responses in passerines (Woolley & Rubel 1999; Brittan-Powell et al. 2002; Lucas et al. 2002; Henry & Lucas 2008, 2009, 2010a, b), providing explicit tests for species and sex effects.

We examined three aspects of the ABR: thresholds, response amplitude and latency. ABR thresholds were determined using two methods: visual detection and cross-correlation. The shape of audiograms obtained with behavioural and ABR methods are well correlated, although ABR thresholds are generally 30–35 dB above behavioural estimates, partly due to a lack of temporal integration (Brittan-Powell et al. 2002). ABR amplitudes reflect the strength of the neural response to a stimulus and tend to be correlated with the size of the neural population that is tuned to that frequency (Hall 2007). Finally, ABR latency is a measure of lag time associated with peripheral processing. In mammals, ABR latency tends mainly to reflect the time it takes for the travelling wave to move down the cochlea (Hall 2007). However, birds have much shorter cochleae than mammals (Gleich et al. 1994) and consequently ABR latency is thought to reflect the synaptic integration time associated with specific frequencies of stimuli (Henry & Lucas 2008). We predicted that if the auditory properties of species reflect their vocal repertoire, brown-headed cowbirds would have lower thresholds, higher amplitude ABRs and shorter ABR latencies than red-winged blackbirds, particularly at high frequencies (i.e. above 6 kHz). This should facilitate better detection and finer-scale resolution of high-frequency elements of the brown-headed cowbird song. We also predicted that females of both species would have lower thresholds, higher ABR amplitudes and shorter latencies than males to facilitate mate location and choice, as well as host detection in brown-headed cowbirds.



**Figure 1.** Vocalization exemplars of (a) red-winged blackbird, *Agelaius phoeniceus*, song (b) brown-headed cowbird, *Molothrus ater*, flight whistle and (c) brown-headed cowbird perched song (from Elliot et al. 1997). Spectrograms were created using a 512 point FFT with Blackman–Harris window in Cool Edit Pro (v.2). All spectrograms are shown with a frequency range of 0–11 kHz. The dashed white line indicates the presumed upper limit of communication in passerines, 6 kHz.

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