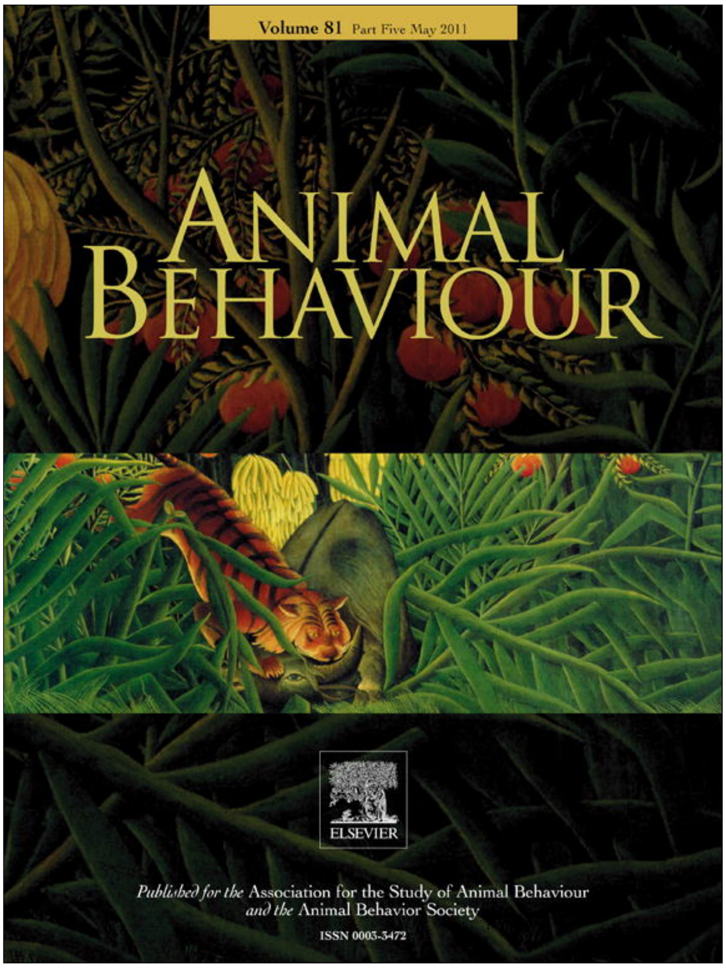

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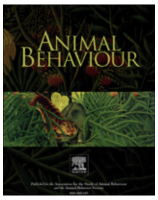

Species and sex effects on auditory processing in brown-headed cowbirds and red-winged blackbirds

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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.

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 ± SD number of hosts used per individual in a single breeding season = 2.34 ± 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.

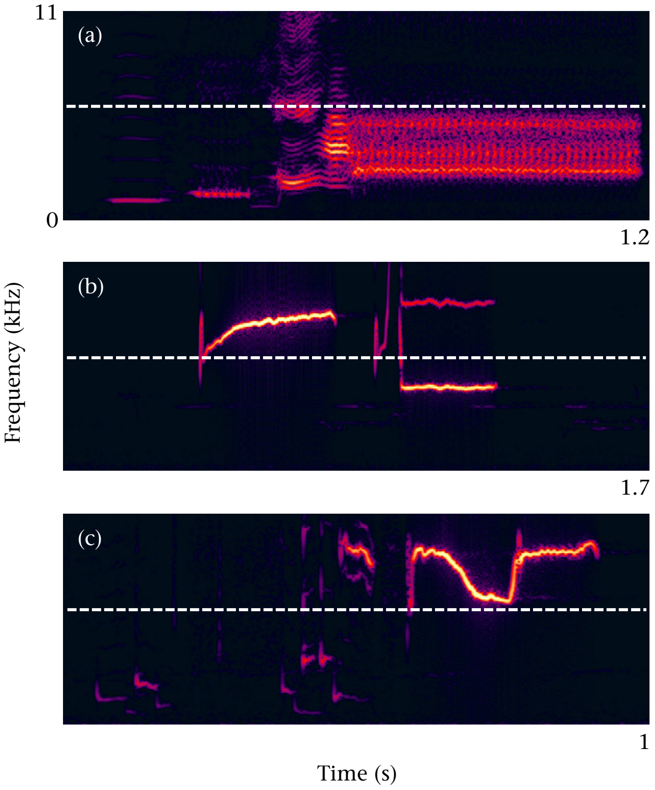

Figure 1. Vocalization exemplars of (a) red-winged blackbird, *Agelaius phoeniceus*, song (b) brown-headed cowbird, *Molothrus ater*, flight whistle and (c) brown-headed cowbird perched song (from Elliot et al. 1997). Spectrograms were created using a 512 point FFT with Blackman–Harris window in Cool 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.

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.

METHODS

Capture and Housing

Brown-headed cowbirds were caught by the U.S. Department of Agriculture Animal and Plant Health Inspection Service (USDA APHIS) using baited walk-in traps during the breeding season (May and early June 2009). Red-winged blackbirds were caught at Purdue University and Lilly Nature Center in West Lafayette, IN, U.S.A. between late March and mid-May 2010. Individuals were weighed and tagged with coloured leg bands. Adult males (mean mass ± SD: cowbird: 46.8 ± 1.5 g; blackbird: 64.5 ± 0.9 g) and females (cowbird: 36.6 ± 2.9 g; blackbird: 39.9 ± 1.3 g) were identified by plumage. Although juveniles were excluded from our analyses, we did not attempt to assess the age of the adult individuals. However, current evidence suggests that the effects of ageing on hearing thresholds is not as great in passerines as it is in mammals (Langemann et al. 1999). Subjects were transported to and subsequently housed at Purdue University in West Lafayette, IN. Each subject was housed with one or two other individuals and provided ad libitum with seed, water and grit, and supplemented with mealworms. After completion of auditory evoked potential experiments, red-winged blackbirds were released and brown-headed cowbirds were transferred to Purdue Animal Care and Use Committee (PACUC) protocol number 08-012.

Auditory Evoked Potentials

Auditory evoked potentials were recorded from birds anaesthetized with a combination of ketamine (40–60 mg/kg) and midazolam (6–8 mg/kg) injected into the breast muscle. We tested a total of 18 cowbirds (9 males, 9 females) and 13 red-winged blackbirds (8 males, 5 females). The birds were positioned at the centre of a soundproof test chamber on a microwavable heating pad (Pet Supply Imports, South Holland, IL, U.S.A.) wrapped in towels to maintain body temperature while sedated. We placed a noninverting needle electrode (Nicolet Biomedical, Fitchburg, WI, U.S.A.) under the scalp at the vertex of the head, an inverting electrode under the skin just behind the right auditory meatus, and a ground electrode at the nape of the neck. Auditory stimuli were created in SigGen32 and presented using a computer running TDT BioSig32 software and a TDT II rack-mounted system (Tucker Davis Technologies, Gainesville, FL, U.S.A.). We passed stimuli through a TDT DA1 digital–analogue converter. The sound source was then equalized across frequencies by passing it through a 31-band equalizer (Behringer Ultragraph model FBQ6200). Stimuli were presented through a Crown D75 amplifier and a magnetically shielded speaker suspended 30 cm above the bird's head (RCA model 40-5000; 140–20 000 Hz frequency response). We calibrated the system by playing tones produced by the AP2 sound card with a constant amplitude of 1 V. Sound pressure level (SPL) was monitored with a Bruel & Kjaer precision sound level meter (model 1613, Norcross, GA, U.S.A.) and condenser microphone (model 4131 2.6). Each of the reference stimuli levels was adjusted to 65 ± 1 dB SPL with the Behringer Ultragraph.

Auditory evoked responses, specifically auditory brainstem responses (ABRs), were recorded using the TDT BioSig32 software and a TDT II rack-mounted system after being passed through a DB4 biological amplifier (amplification = 200 000x) and an AD1 analogue–digital converter. Responses were band-pass filtered from 30 Hz to 10 kHz and notch-filtered at 60 Hz.

Focal birds were presented with 8 ms tone bursts with a 1 ms $\cos^2$ onset/offset ramp. Seven frequencies were presented in random order (0.5 kHz, 1 kHz, 2 kHz, 3 kHz, 4 kHz, 6 kHz, 8 kHz and 10 kHz). Each stimulus was presented at intensities ranging from 8 to 72 dB SPL in 8 dB steps. The stimuli were presented in alternating phases (90° and 270°) at a rate of 31.1 stimuli per second. Responses were sampled at 40 kHz for 12 ms beginning 1.2 ms prior to the arrival of the stimulus at the ear. ABRs were averaged across 500 stimulus presentations, and two responses were recorded from each frequency–intensity combination. To ensure that responses were not affected by changes in anaesthesia level, we periodically measured the amplitude and latency of ABR responses to 100 μs broadband clicks. All methods were approved under PACUC protocol number 08-132.

Audiograms

Audiograms were constructed in two ways. The first method we used was the visual detection method, whereby a trained observer determined the lowest-intensity stimulus that evoked a response. The threshold was then estimated as lying halfway between the last detectable response and the next lowest-intensity stimulus. For example, if a response was seen at a stimulus level of 24 dB SPL, but not at 16 dB SPL, then the threshold would be recorded as 20 dB SPL. If a response was not evoked at the highest stimulus level, then no threshold was recorded. The 72 dB responses were expected to occur between 1.5 and 2.5 ms after the onset of the stimulus at the ear. Each subsequent response was expected to occur within 0.4 ms of the response at the previous intensity level. Responses that did not meet these criteria were not included in the analysis. This method has been used to determine thresholds for a number of species, including budgerigars (Brittan-Powell et al. 2002; Brittan-Powell & Dooling 2004) and screech owls (Brittan-Powell et al. 2005).

Second, we used the cross-product technique (Cone-Wesson et al. 1997; Supin et al. 2001). This technique has been used for audiogram threshold determination in house sparrows, *Passer domesticus*, white-breasted nuthatches, *Sitta carolinensis*, tufted titmice, *Baeolophus bicolor*, and Carolina chickadees, *Poecile carolinensis*, as well as threshold determination for auditory filter estimates in white-crowned sparrows, *Zonotrichia leucophrys*, dark-eyed juncos, *Junco hyemalis*, and brown-headed cowbirds (Henry & Lucas 2008, 2009, 2010a, b; Gall & Lucas 2010). The cross-product technique uses the ABR response to the highest-intensity stimulus (72 dB SPL) as a template (Fig. 2a). This template is then cross-correlated with the ABR measured in response to all lower-intensity stimuli (64–8 dB SPL) in PRAAT (v.5.0.33; Boersma & Weenink 2008). A peak occurs in the cross-correlation product at the time of the ABR response peak (Fig. 2b). The cross-correlation estimates the correlation between the template and the focal ABR. The relationship between the correlation coefficient of the cross-correlation product and the intensity of the stimulus is expected to be roughly linear (Cone-Wesson et al. 1997; Henry & Lucas 2008; see also Fig. 1c). The template was also cross-correlated with a concatenation of 100 ABR responses recorded (5–6 from each subject) in the absence of an auditory stimulus (e.g. physiological background noise). These cross-correlation values have a normal distribution with a mean of 0. The mean value + 2 SD provided an upper-bound measure of physiological background noise. Thresholds at each frequency were obtained from the intercept of the cross-correlation intensity function at the upper bound of the physiological background noise (i.e. the dB SPL value at which the stimulus-evoked response cannot be distinguished from background noise). Thresholds were only included in the statistical analysis if the R^2 value for the slope was greater than 0.8 (Henry & Lucas 2008, 2009). Thresholds were difficult to estimate at high frequencies by the cross-correlation method because both red-winged blackbird and brown-headed cowbird responses declined rapidly above 6 kHz. At 10 kHz, therefore, we did not have an adequate number of stimulus levels (i.e. fewer than 3) to use the cross-correlation method to estimate thresholds.

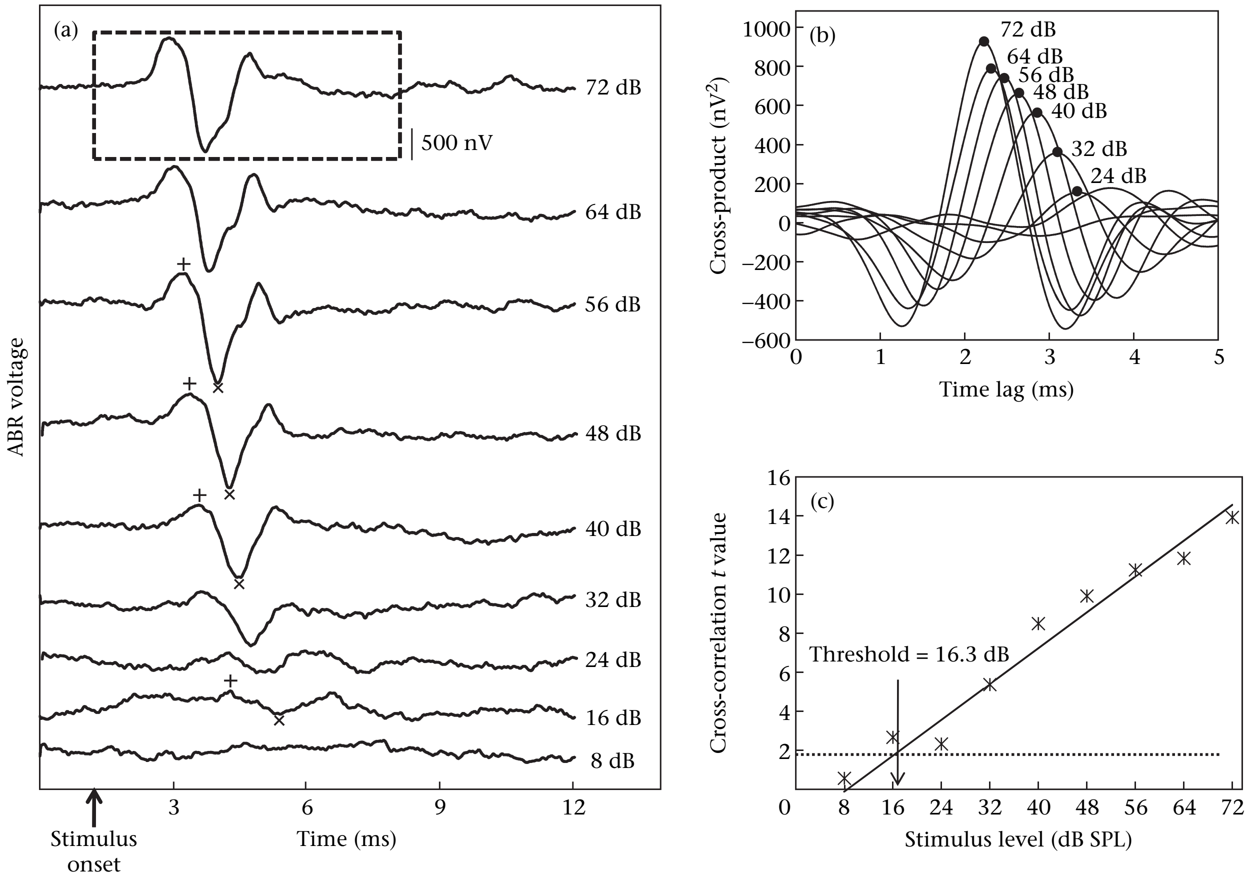

Figure 2. (a) Representative auditory brainstem responses (ABRs) from a single male red-winged blackbird to a 3 kHz stimulus ranging from 8 to 72 dB sound pressure level (SPL). The dashed box indicates the portion of the ABR used to create the template for the cross-correlation analysis. The upper peak (+) and the lower peak (×) were used to determine amplitude. Latency was determined from the upper peak. The thresholds for this individual were 12 dB SPL (visual detection method) and 16.3 dB SPL (cross-correlation method). (b) Cross-products from the cross-correlation analysis as a function of the time lag for each stimulus level. The peak of function represents the strongest correlation between the template and the ABR. Time lags increase with decreasing stimulus level because the latency of the ABR increases. (c) Cross-correlation *t* values as a function of stimulus intensity used to determine thresholds. The dashed line represents the upper bound of the 95% confidence interval for physiological background noise. The threshold was interpolated from the intersection of the *t* value by the intensity function and the upper bound of the physiological background nose.

ABR Amplitude and Latency

Amplitude and latency of the ABR were measured in PRAAT. The amplitude of the ABR was measured from the first positive peak to the first negative peak (Henry & Lucas 2008). Latency was measured from the onset of the stimulus to the first positive peak in the ABR (Fig. 2). High-frequency responses were relatively weak, and peaks were thus more difficult to distinguish than at lower frequencies. Therefore, 8 and 10 kHz responses were excluded from the analysis.

Statistical Design

We ran three repeated measures ANOVAs with Proc MIXED in SAS 9.2 using a within-subject repeated measure design. We used the Kenward–Rogers algorithm to calculate the denominator degrees of freedom. Fractional degrees of freedom were rounded to the nearest integer. Several covariance structures were explored (compound symmetry, first-order autoregressive, unstructured) and the final covariance structure (compound symmetry) was chosen on the basis of Akaike's information criterion (AIC) value. However, there was little qualitative difference between the models. The dependent variables were ABR threshold, ABR peak amplitude (dB re: 1 nV) and ABR peak latency. Cross-correlation thresholds were log transformed, and latency was inverse transformed to meet normality assumptions. Independent variables in the threshold models were species, sex, frequency and their interactions. Independent variables for the ABR amplitude and ABR latency models were species, sex, frequency, intensity and their interactions. Weight was initially included as an independent variable in the models but was not significant and was removed to improve our statistical power. Nonsignificant interaction terms were removed from the model in order of decreasing *P* value. Significant main effects were investigated post hoc with LSMEANS using the DIFF procedure and a Tukey–Kramer adjustment for multiple comparisons. Significant interaction terms were investigated post hoc with the slice option (i.e. simple effects) in LSMEANS. LSMEANS ± SE (backtransformed when appropriate) are reported throughout.

RESULTS

Audiogram: Visual Detection Method

There was a significant main effect of sex ($F_{1,28} = 9.1$, $P = 0.005$) and frequency ($F_{7,208} = 201$, $P < 0.001$) on thresholds estimated by visual detection; however, there was no significant effect of species ($F_{1,28} = 0.56$, $P = 0.46$). Females were, on average, 3.72 ± 1.28 dB more sensitive than males (Fig. 3a). The lack of a species effect suggests that brown-headed cowbirds and red-winged blackbirds have relatively similar lower limits of sensitivity to tones. The best frequency for both species was 3 kHz, although there was no

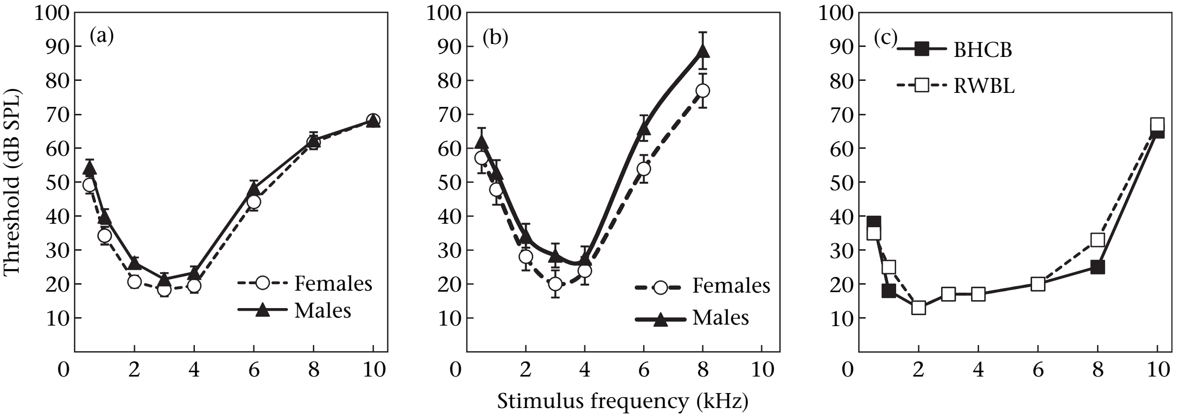

Figure 3. Auditory thresholds (LSMEANS ± SE) as a function of stimulus frequency for males ($N = 17$) and females ($N = 14$) averaged across species. Thresholds were estimated using (a) the visual detection method, (b) the cross-correlation method and (c) a behavioural method (taken from Fig. 7 in Hienz et al. 1977) for brown-headed cowbirds (BHCB) and red-winged blackbirds (RWBL).

significant difference between 3 and 4 kHz ($t_{60} = 0.8$, $P = 0.42$), nor between 2 and 4 kHz ($t_{57} = 1.2$, $P = 0.23$). Thresholds increased above and below the best frequency. There was no significant difference between 8 and 10 kHz ($t_{2.3} = 2.4$, $P = 0.12$). There were significant differences between all other frequencies ($t_{58} > 2.1$, $P < 0.04$). None of the interaction terms were significant in the visual detection threshold model and were therefore removed. Their removal did not qualitatively change the main effect terms.

Audiogram: Cross-correlation Method

There was a significant main effect of sex ($F_{1,40} = 4.6$, $P = 0.037$) and frequency ($F_{6,123} = 81.1$, $P < 0.001$) but not a significant effect of species ($F_{1,40} = 0.6$, $P = 0.43$) on thresholds. Females were, on average, 7.2 ± 3.74 dB more sensitive than males (Fig. 3b). The lowest threshold for both species was at 3 kHz, with thresholds increasing at frequencies above and below 3 kHz. The 2 kHz threshold did not differ significantly different from the 4 kHz threshold ($t_{119} = 1.9$, $P = 0.05$). However, all contiguous frequencies differed significantly from one another ($t_{108} > 2.6$, $P < 0.009$). None of the interaction terms were significant in the cross-correlation threshold model and were therefore removed. Their removal did not qualitatively change the main effect terms.

Audiogram: Visual Detection versus Cross-correlation

When we included both methods of threshold estimation in our statistical model, we found that thresholds varied significantly between sexes ($F_{1,87} = 17.1$, $P < 0.001$), between frequencies ($F_{6,299} = 99$, $P < 0.001$) and between the two methods ($F_{1,200} = 106$, $P < 0.001$). There was not a significant effect of species ($F_{1,68} = 0.06$, $P = 0.82$) on thresholds, nor were there any significant interaction effects. Females were, on average, 6 ± 1.4 dB more sensitive than males. Thresholds estimated using the visual detection method were, on average, 7.6 ± 0.7 dB lower than thresholds estimated with the cross-correlation method.

ABR Amplitude

There were significant main effects of species ($F_{1,500} = 5.2$, $P = 0.02$; Fig. 4), sex ($F_{1,163} = 36.8$, $P < 0.001$; Fig. 5), frequency ($F_{5,400} = 76.4$, $P < 0.001$) and intensity ($F_{7,804} = 227.3$, $P < 0.001$) on ABR amplitude of the response. Sex differences were larger than species differences. The average ABR amplitude of females was 3.9 ± 0.6 dB higher than that of males, while the average ABR amplitude of brown-headed cowbirds was 1.1 ± 0.5 dB larger than that of red-winged blackbirds. Note that an increase of 6 dB is equivalent to a doubling of amplitude in nV. There were also significant frequency × intensity ($F_{28,796} = 1.8$, $P = 0.007$) and species × frequency × intensity ($F_{40,796} = 1.5$, $P = 0.02$) interactions. The slope of the ABR amplitude by stimulus level function was greatest at 3 kHz. The slope of the ABR amplitude by stimulus level function was shallower above and below 3 kHz, with the slope decreasing as frequencies moved away from the best frequency (3 kHz). This suggests that as stimulus level increases above threshold level (i.e. suprathreshold levels), there is a larger change in neural populations at 3 kHz than at other frequencies. Brown-headed cowbirds had steeper slopes than red-winged blackbirds at 4 kHz (Fig. 4), with higher amplitudes at stimulus intensities of 64 ($t_{818} = .2$, $P = 0.03$) and 72 dB SPL ($t_{843} = 2.4$, $P = 0.01$). Brown-headed cowbirds had shallower slopes than red-winged blackbirds at 0.5 kHz, with higher amplitudes at stimulus intensities of 40 dB SPL ($t_{765} = 2.2$, $P = 0.03$) and 48 dB SPL ($t_{863} = 2.3$, $P = 0.02$). The brown-headed cowbird slope was also shallower at 2 kHz with higher amplitudes at stimulus intensities of 16 dB SPL ($t_{793} = 2.2$, $P = 0.046$) and 24 dB SPL ($t_{881} = 3.4$, $P < 0.001$). The remaining interaction terms were not significant and were removed from the model.

ABR Latency

The latency of the first positive ABR peak differed significantly between species ($F_{1,232} = 17.6$, $P < 0.001$; Fig. 6) and differed marginally between sexes ($F_{1,128} = 4.2$, $P = 0.04$; Fig. 7). Brown-headed cowbirds had shorter latencies than red-winged blackbirds. Females had slightly shorter latencies than males overall. Latency also differed between stimulus frequencies ($F_{5,344} = 27.6$, $P < 0.001$; Figs 6, 7) and intensities ($F_{7,750} = 254.5$, $P < 0.001$; Figs 6, 7). There was also a significant stimulus frequency × intensity interaction ($F_{28,780.1} = 4.2$, $P = 0.03$) whereby the slope of the latency by stimulus level function became steeper above and below 3 kHz. The remaining interaction terms were not significant and were removed from the model.

DISCUSSION

Audiogram Methods

Our results using both ABR methods of audiogram construction and behavioural audiograms (Hienz et al. 1977; see Fig. 3c) suggest that the range of best sensitivity is between 2 and 4 kHz in both

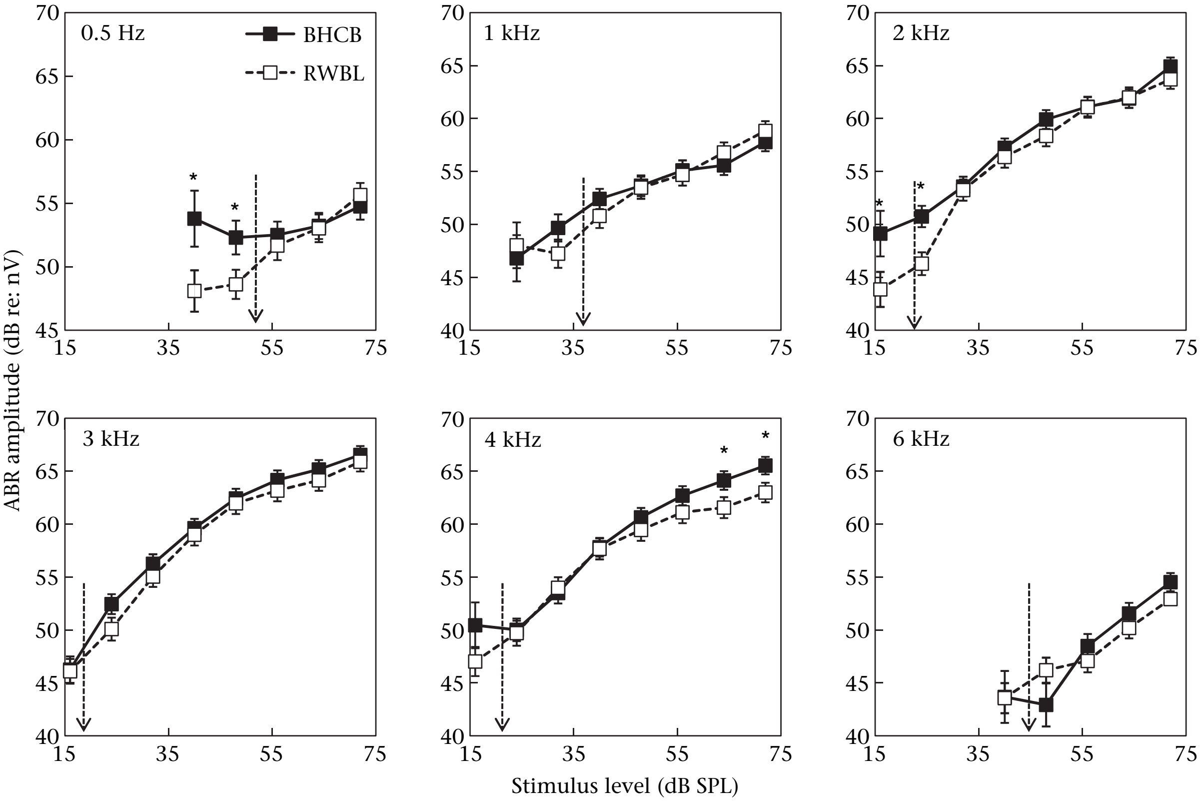

Figure 4. Auditory brainstem response (ABR) amplitudes (LSMEANS ± SE) as a function of stimulus frequency and intensity for brown-headed cowbirds (BHCB, $N = 18$) and red-winged blackbirds (RWBL, $N = 13$) averaged across sexes. Amplitudes are presented in dB re: 1 nV. An increase of 6 dB is equivalent to a doubling of voltage. Dashed arrows indicate thresholds as estimated with the visual detection method.

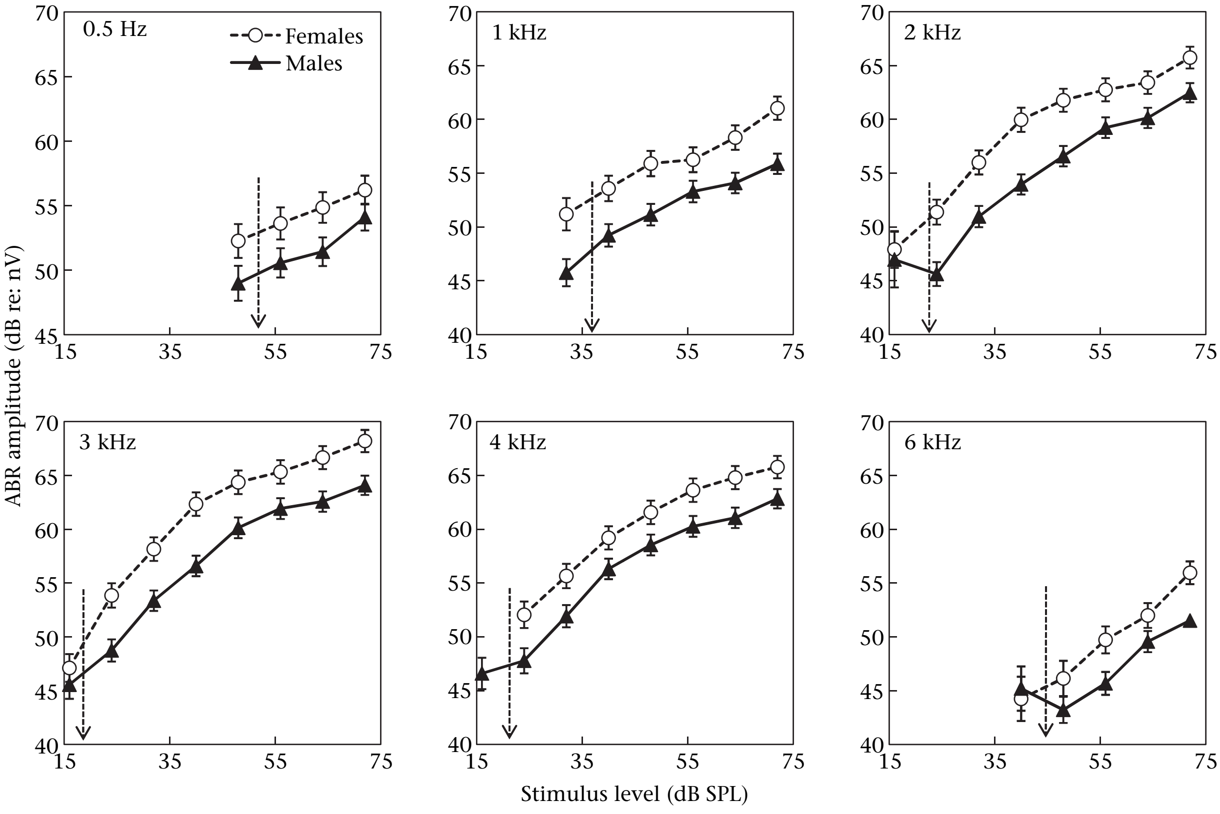

Figure 5. Auditory brainstem response (ABR) amplitudes (LSMEANS ± SE) as a function of stimulus frequency and intensity for male ($N = 17$) and female ($N = 14$) brown-headed cowbirds and red-winged blackbirds, averaged across species. Amplitudes are presented in dB re: 1 nV. An increase of 6 dB is equivalent to a doubling of voltage. Dashed arrows indicate thresholds as estimated with the visual detection method.

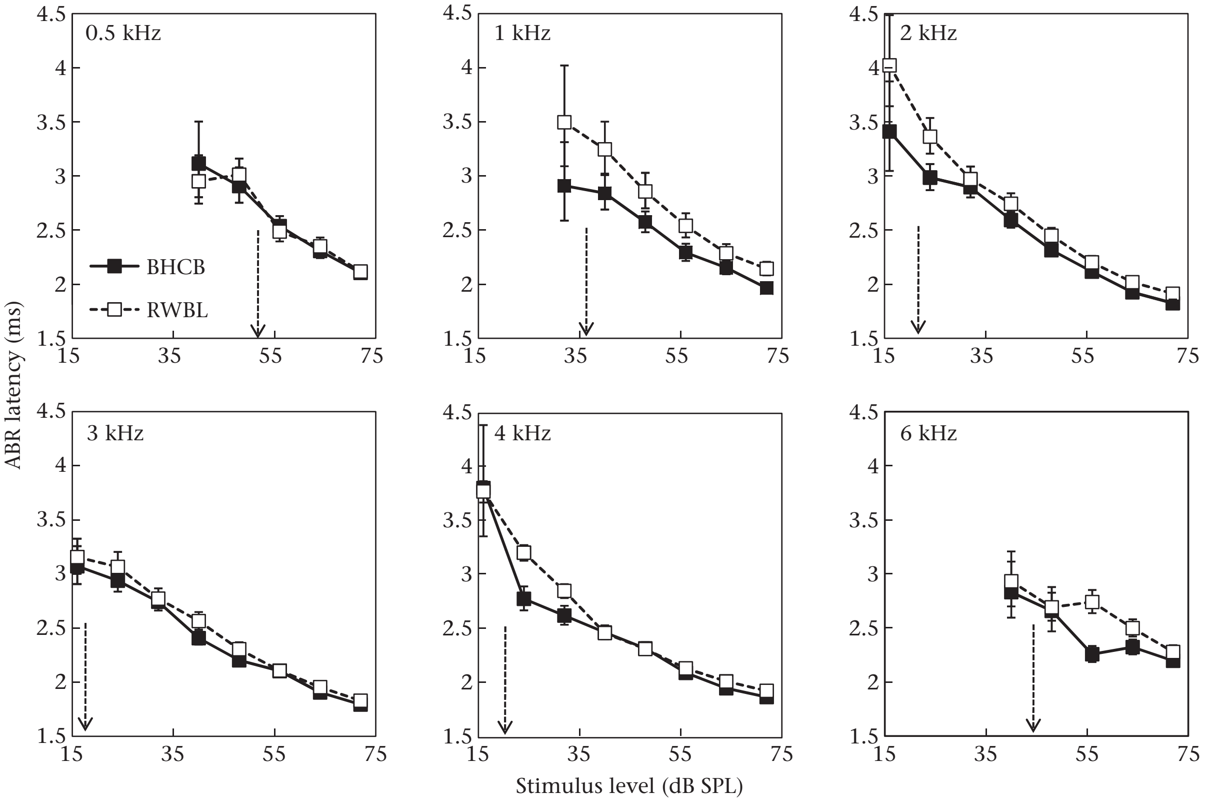

Figure 6. Auditory brainstem response (ABR) latency (LSMEANS ± SE) as a function of stimulus frequency and intensity for brown-headed cowbirds (BHCB, $N = 18$) and red-winged blackbirds (RWBL, $N = 13$). Dashed arrows indicate thresholds as estimated with the visual detection method.

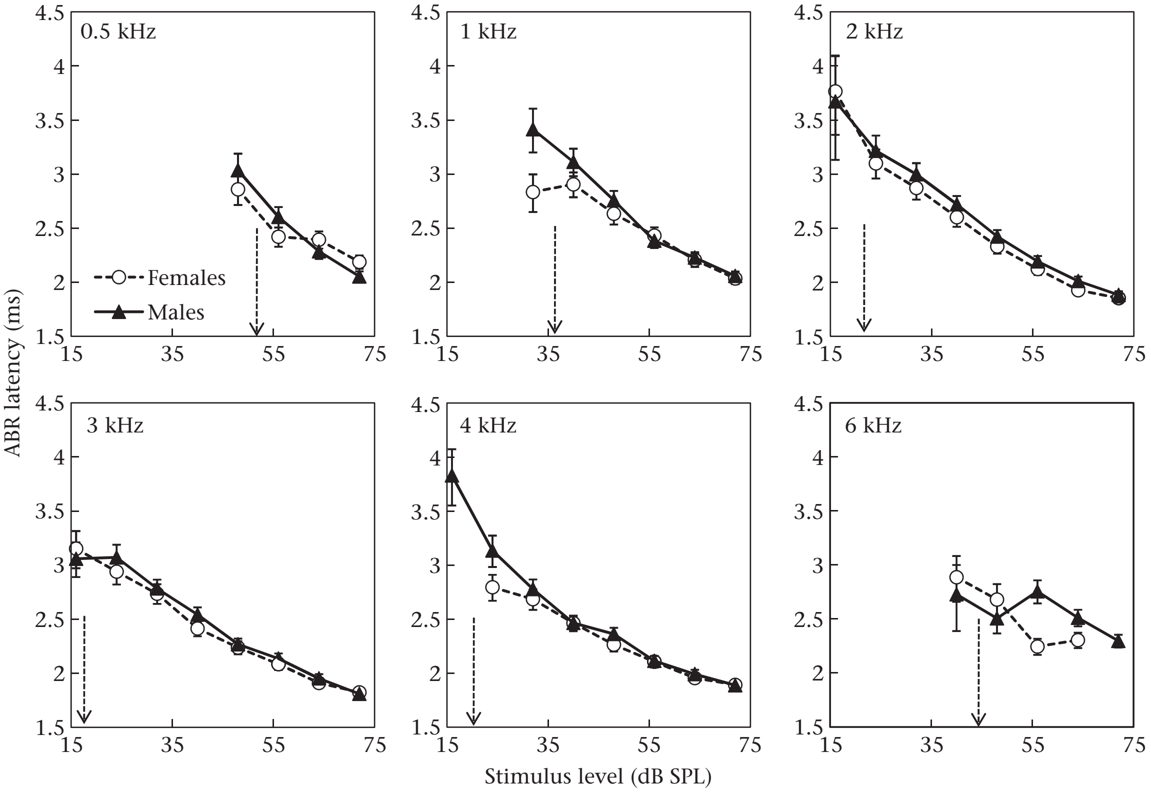

Figure 7. ABR latency (LSMEANS ± SE) as a function of stimulus frequency and intensity for male ($N = 17$) and female ($N = 14$) brown-headed cowbirds and red-winged blackbirds, averaged across species. Dashed arrows indicate thresholds as estimated with the visual detection method.

red-winged blackbirds and brown-headed cowbirds. There was a significant difference in threshold estimates based on the method used, with visual detection thresholds, on average, 7.6 ± 0.7 dB lower than those of cross-correlation thresholds. However, there was no method × frequency interaction. This indicates that the magnitude and direction of differences between the methods was similar across all frequencies. Although the means at high frequencies appeared to be more different than the means at lower frequencies, there was also greater variance in threshold estimates at high frequencies for both methods, which may have contributed to this trend. The difference in thresholds is probably due to the number of points needed to estimate thresholds and the criterion for the threshold level. The visual detection method allows thresholds to be estimated with only a single detectable response, while the cross-correlation method requires at least three intensity levels to produce a recordable response (i.e. 56–72 dB SPL) to estimate the threshold. Therefore, at higher frequencies, we were better able to estimate thresholds with the visual detection method than with the cross-correlation method because we had measureable evoked responses at few stimulus intensities. Furthermore, cross-correlation thresholds probably produced higher thresholds because background noise levels were explicitly invoked in the criterion for threshold estimation with the cross-correlation method, but were not used in the visual detection method.

In most avian species, ABR thresholds tend to be 25–30 dB above behavioural thresholds (Dmitrieva & Gottlieb 1994; Woolley & Rubel 1999; Brittan-Powell et al. 2002), partly because transient responses by definition exclude temporal integration. We observed a similar trend here, although the visual detection method yielded a closer correspondence with behavioural thresholds than the cross-correlation method. In addition, the differences between behavioural (Fig. 3c; taken from Hienz et al. 1977) and ABR thresholds were smallest in the range of best hearing for both models. Differences in thresholds were fairly pronounced above 6 kHz, particularly between the cross-correlation and behavioural thresholds, which is not uncommon in comparisons of audiograms of behaviour versus those based on auditory evoked potentials. Auditory evoked potential thresholds generally show greater differences from behavioural thresholds at frequencies with smaller neural populations because behavioural thresholds can be the result of a very small or nonsynchronous population of neurons firing (Konishi 1970), while evoked potentials require larger and synchronous neural discharge to be recorded (Hall 2007). The number of single units tuned to each frequency correlates well with the shape of the audiogram; however, behavioural thresholds are more closely associated with the thresholds of the single units (Konishi 1970). It is possible, therefore, that blackbirds or cowbirds may have small populations of neurons with low thresholds that are tuned to high frequencies.

Amplitude and Latency

We found small differences in amplitude between species and substantial differences in amplitude of responses between sexes. These sex differences may be caused by size dimorphism between the sexes, but it is surprising, then, that we observed no difference in threshold levels and small differences in amplitude between species, as red-winged blackbirds are substantially larger than brown-headed cowbirds. Moreover, in our initial model we included weight as an independent factor, but found that it was not a significant predictor of any of the response variables, suggesting that size differences, at best, contribute marginally to the differences we observed.

The increase in the amplitude of responses was a linear function of stimulus intensity at stimulus intensities near threshold. At high intensities, response amplitude showed compressive growth with stimulus intensity. Our results are consistent with a cochlear amplifier or active process operating in cowbirds and blackbirds. The basilar membrane is a nonlinear tonotopic system (Rhode 1971; Ruggero et al. 1997; Geisler 1998). This means that each place on the basilar membrane is maximally excited by a single frequency (the best or characteristic frequency, CF). At CF, the response of the basilar membrane to stimulation is nonlinear, with greater gain at low intensities of stimulation (approximately linear growth) than at high intensities of stimulation. Compressive growth contributes to the frequency selectivity of the auditory system and also is thought to protect the ear from damage at high stimulus intensities (Ruggero et al. 1997; Geisler 1998).

The amplitude of the frequency-specific auditory evoked response reflects the number or synchrony of single neural units responding to the stimulus frequency (Hall 2007). Synchronous firing and a large population of neurons improves temporal resolution through integration and more accurate time-locked responses to stimulus structure (Gleich & Manley 2000; Hall 2007). Greater temporal resolution and neural synchrony can also play an important role in the utilization of interaural time difference for sound source localization, while increased spectral sensitivity can enhance sensitivity to interaural intensity differences (Klump 2000).

There generally was very little difference in latency between males and females, although females had slightly shorter latencies than males. This trend is in line with results seen in mammals (Hall 2007). There was also a significant, but small, difference in latency between the species, with brown-headed cowbirds having slightly shorter latencies than red-winged blackbirds. The latency of the first peak was between 1.5 and 2.5 ms for all frequencies at 72 dB SPL and generally increased by ~0.2 ms per 8 dB decrease in stimulus intensity. Latency was shortest at the best frequencies and increased above and below the best frequency. Our results match well with previous findings in other passerine species (Brittan-Powell et al. 2002; Henry & Lucas 2008).

In mammals, latency can reflect both synaptic integration time and the travelling time of sound waves on the cochlea (Hall 2007). This leads to a systematic increase in latency with a decrease in stimulus frequency. However, in birds, latency is shortest at the best frequencies and increases as stimulus frequency increases or decreases (Brittan-Powell et al. 2002; Lucas et al. 2007; Henry & Lucas 2008). This suggests that synaptic integration time, due to either small neural populations or nonsynchronous responses (Hall 2007), is largely responsible for shifts in latency in songbirds.

High-frequency Hypothesis and Comparison with Other Passerines

We predicted that brown-head cowbirds would have greater auditory sensitivity at high frequencies than red-winged blackbirds based on the hypothesis that auditory sensitivity and vocal signals are expected to coevolve (Konishi 1970). Previous behavioural work found no significant difference between the audiograms of these two species and no significant difference between the sexes (Fig. 3c; Hienz et al. 1977). However, the statistical power to detect such differences in Hienz et al.'s (1977) study was lacking because of small sample sizes. Moreover, Hienz et al. (1977) reported only on detection ability and not on discrimination.

Both detection and discrimination are important aspects of communication, but are not synonymous and provide different information about auditory processing. For instance, the amount of threshold recovery is a common measure of hearing damage following noise exposure. If thresholds recover to normal levels, sensory cells in the cochlea (i.e. inner and outer hair cells) are assumed to be relatively undamaged and hearing loss is generally presumed to be minimal. However, Kujawa & Liberman (2009) have recently shown that although noise exposure of short duration may not permanently alter sensory cells or auditory thresholds, noise exposure can shear afferent neural connections at the hair cell synapse and result in delayed loss of cochlear ganglion cells. The loss of these connections results in smaller ABR and compound action potential amplitudes, but no change in threshold. The loss of afferent synapses could have profound affects for the processing of sounds in noise and the ability to discriminate fine-scale features of acoustic stimuli (Kujawa & Liberman 2009). Therefore, small ABR amplitudes do not provide robust information about behavioural auditory thresholds, but do suggest that discrimination ability would be poor.

In birds, ABR responses are relatively robust across a range of frequencies that encompasses the behavioural frequency range of hearing. Previous work suggests that auditory sensitivity and vocal production are correlated. For instance, passerine species with high-frequency vocal components have relatively low thresholds as determined with the ABR cross-correlation method (e.g. tufted titmouse: 33 dB SPL at 6.4 kHz; Henry & Lucas 2008; Carolina chickadee: 38 dB SPL at 6 kHz, 55 dB SPL at 8 kHz; Henry & Lucas 2010b). In dark-eyed juncos, we can record responses at 10 kHz down to 32 dB SPL (M. D. Gall & J. R. Lucas, unpublished data). Species with lower-frequency vocalizations tend to have higher thresholds at high frequencies (white-breasted nuthatch and house sparrow ~47 dB SPL at 6.4 kHz; Henry & Lucas 2008). Based on findings in other species, we predicted that brown-headed cowbirds would have lower thresholds than red-winged blackbirds in order to process their high-frequency vocal elements. However, surprisingly, we found no significant difference between the species and very high thresholds as determined by cross-correlation in brown-headed cowbirds (~ 60 dB SPL at 6 kHz). Moreover, thresholds at high frequencies were substantially higher than previously investigated species evaluated using the same cross-correlation technique.

We also expected that we would find greater amplitude ABR responses in brown-headed cowbirds at high frequencies, to permit fine-scale processing of high-frequency vocal elements. ABR amplitudes are strongly correlated with the size of the neural population responding to a particular frequency; therefore, larger ABR amplitudes should permit finer processing of acoustic stimuli (Hall 2007). Previous work suggests that species with higher-frequency vocalizations have greater ABR amplitudes at high frequencies. For instance, at 64 dB SPL, Carolina chickadees have an ABR amplitude of about 64 dB nV at 6 kHz, and tufted titmice have an ABR amplitude of about 57 dB nV at 6.4 kHz. At 64 dB SPL, white-breasted nuthatches and house sparrows both have an ABR amplitude of about 53 dB nV at 6.4 kHz (Henry & Lucas 2008). Brown-headed cowbirds and red-winged blackbirds have ABR amplitudes of 53 dB nV and 51 dB nV, respectively, at 6 kHz and 64 dB SPL, which are closer to the amplitudes of house sparrows and white-breasted nuthatches than they are to the amplitudes of chickadees or titmice. Again, this is surprising for the brown-headed cowbird given the vocalizations of this species.

Biological Significance of Sex Differences

Overall, our results suggest that the auditory system of females is more sensitive than that of males in brown-headed cowbirds and red-winged blackbirds. In contrast, most studies of auditory evoked potentials have either not considered sex (Brittan-Powell et al. 2002; Lucas et al. 2002; Brittan-Powell & Dooling 2004; Brittan-Powell et al. 2005), or found limited evidence of sex effects. Although we found a significant difference in thresholds between males and females, these differences were relatively small (3.7–7.2 dB) compared to threshold shifts that we associate with hearing damage in humans (e.g. >20 dB; Hall 2007). However, thresholds differing by 3–7 dB may still have relatively substantial effects on the communication ranges of the sexes. For instance, using a model that included avian masked thresholds, Nemeth & Brumm (2010) found that a 5 dB increase in the vocalizations of blackbirds and great tits could lead to a 130–160% increase in the linear distance of communication and a concomitant increase of 140–250% in the active space (m^2) of a signal. Therefore, even relatively small differences in threshold between the sexes could offer a substantial increase in the active listening space of females compared to males.

The active listening space may be particularly important for females discriminating among male songs, as previous work has shown that thresholds for discrimination between songs are about 3.29 dB greater than thresholds for detection of songs in budgerigars and zebra finches. This translates to a 145% increase in linear communication distance for detection compared to the linear communication distance for discrimination (Lohr et al. 2003). Concomitantly, this leads to the active space for detection being more than twice the size of the active space for discrimination. Therefore, a change in threshold of only 3.7 dB could more than double the active space for discrimination of songs in females compared to males. These results are also in line with our previous findings that brown-headed cowbird females have narrow auditory filters and a greater ability to process stimuli in noise (Gall & Lucas 2010). These auditory filter differences are expected to even further enhance the ability of females to discriminate among songs compared to males.

Sex differences in auditory processing could be due to different hormonal profiles of males and females during the breeding season (Cristol & Johnsen 1994; Johnsen 1998). Work in midshipman fish suggests that hormones and their receptors regulate sex and seasonal differences in auditory processing (Sisneros 2009). The recent discovery of aromatase and oestrogen receptors in the inner ear of zebra finches (Noirot et al. 2009) suggests that this may also be true in birds. Currently, only one study has explicitly linked the level of circulating sex hormones to the peripheral processing of auditory stimuli in birds (Caras et al. 2010), wherein the authors found that implanting nonbreeding season birds with either oestradiol (females) or testosterone (males) resulted in a shift in auditory thresholds. However, the authors found no significant differences between males and females.

Although the vocal production and auditory processing of species are thought to coevolve (Henry & Lucas 2008), it is less clear when, or even if, sex-specific auditory processing is expected to occur. This is particularly surprising, since sex-specific vocal production has been extensively explored (Catchpole & Slater 2008). Here we propose a general framework for when sex differences are expected to occur. (1) Sex differences in auditory processing should be greatest when females have little prior experience with individual males and use male vocalizations as a major criterion for locating mates or for mate choice. (2) The sexes should differ in auditory processing if there are differences in the vocal signals being directed at each sex. (3) Auditory processing may differ between the sexes if the range of communication differs between the sexes. (4) Auditory processing is known to be seasonally plastic (Lucas et al. 2002, 2007; Henry & Lucas 2009); thus, we expect sex differences in auditory processing to be greatest during the breeding season, or during times of pair formation, when it occurs outside of the breeding season. This general framework could be used to predict if and when patterns of sex-specific auditory processing are likely to occur based on the ecology and behaviour of the species.

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