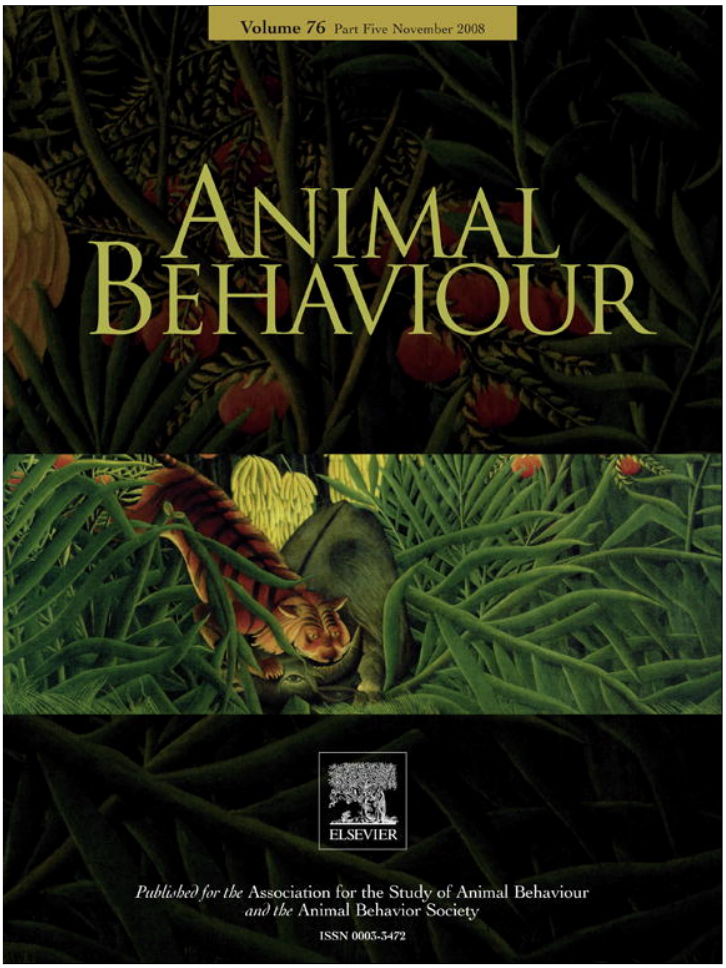

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Coevolution of auditory sensitivity and temporal resolution with acoustic signal space in three songbirds

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Coevolution between senders and receivers is expected to produce a close match between signal design and sensory biology. We evaluated this hypothesis in songbirds by comparing aspects of acoustic signal space with the frequency range of auditory sensitivity and temporal resolution in tufted titmice, *Baeolophus bicolor*; house sparrows, *Passer domesticus*; and white-breasted nuthatches, *Sitta carolinensis*. Auditory measurements were made electrophysiologically from the scalp using two classes of auditory-evoked potentials: the auditory brain-stem response (ABR) and the envelope-following response (EFR). ABRs to tone-burst stimuli indicated maximum sensitivity from 2.2 to 3.2 kHz in all species, but 12–14 dB greater sensitivity in titmice than in sparrows and nuthatches at 6.4 kHz (the highest frequency tested). Modulation rate transfer functions based on EFRs to amplitude-modulated tones suggested greater temporal resolution in titmice and sparrows than in nuthatches. Conservation of the frequency range of maximum sensitivity across species resulted in a mismatch with the dominant frequency of song in sparrows. The mismatch may reflect auditory constraints coupled with selection for high-frequency song and relaxed selection for a close match between sender and receiver due to small territory size. Consistent with coevolution between senders and receivers, high-frequency sensitivity varied with the maximum frequency of species-specific vocalizations, whereas temporal resolution varied with the maximum rate of envelope periodicity. Enhanced high-frequency sensitivity of the titmouse may reflect a specialization for processing high-frequency communication signals such as alarm calls.

Keywords: acoustic signal space; audiogram; auditory brain-stem response; *Baeolophus bicolor*; envelope-following response; house sparrow; modulation rate transfer function; *Passer domesticus*; *Sitta carolinensis*; temporal resolution; tufted titmouse; white-breasted nuthatch

The songbirds, or oscine passerines, rely on vocal signals for a variety of functions including mate attraction, territory advertisement, cohesion of social groups and predator alarms (reviewed in Kroodsma & Miller 1996; Hauser & Konishi 1999; Marler & Slabbekoorn 2004). Studies of communication in a wide variety of songbirds reveal extensive diversity in the acoustic space of signals (Nelson & Marler 1990). That is, species-specific vocalizations differ across multiple acoustic dimensions including dominant frequency, maximum frequency, duration, and patterns of frequency modulation and amplitude modulation. In light of the importance of communication in songbirds, coevolution between senders and receivers is expected to produce a close match between signal space and auditory capabilities (Endler 1992). Compared to vocalizations, however, species differences in auditory capabilities remain relatively less explored. We focus here on the frequency range of auditory sensitivity and temporal resolution.

The frequency range of auditory sensitivity has been measured in approximately 20 of 5000 extant songbird species. In most species, sensitivity is greatest from 2 to 3 kHz and decreases rapidly above 5–6 kHz. Little variation has been observed across songbird species, and much of this variation can be explained by body size. In general, smaller species are more sensitive to high frequencies and larger species are more sensitive to low frequencies (reviewed in Dooling et al. 2000; Gleich et al. 2005). In addition to body size, however, correlative

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data suggest that the acoustic signal space of song and calls may influence auditory sensitivity in some cases. In a comparison of two congeneric sparrows of similar size, Okanoya & Dooling (1988) found that the frequency of maximum sensitivity was 2 kHz in song sparrows, *Melospiza melodia*, and 4 kHz in swamp sparrows, *Melospiza georgiana*, reflecting variation in the dominant frequency of song between these species. Similarly, Langemann et al. (1998) found that the great tit, *Parus major*, is exceptionally sensitive, for its body size, from 6 to 9 kHz, which coincides with the frequency range of its predator alarm calls.

Many vocal signals contain periodic fluctuations in amplitude known as envelope periodicity. Envelope periodicity seems to be a salient feature of communication signals in many vertebrates, including birds. For example, two sympatric dove species in the genus *Streptopelia* rely on envelope cues for species recognition (Beckers & TenCate 2001). Depending on the rate of periodicity, envelope fluctuations may be resolved temporally by the auditory system as discrete changes in intensity over time. A system capable of encoding higher rates of envelope periodicity is said to have greater temporal resolution (Viemeister & Plack 1993). Based on traditional behavioural measurements, temporal resolution seems to be similar among songbirds and between birds and terrestrial mammals (reviewed in Dooling et al. 2000). However, recent experiments using acoustic stimuli similar to natural bird vocalizations find greater temporal resolution in birds than in terrestrial mammals, as well as variation across songbird species (Lohr & Dooling 1998; Dooling et al. 2002; Lohr et al. 2006). Interestingly, a comparative study by Dooling et al. (2002) found that zebra finches, *Taeniopygia guttata*, have greater temporal resolution than canaries, *Serinus canaria*, and use a greater proportion of broadband, harmonic vocalizations with periodic envelopes (Dooling et al. 2002). Studies of a broader diversity of songbirds are needed to assess the extent of coevolution between temporal resolution and envelope periodicity of vocalizations.

Auditory-evoked potentials (AEPs) have emerged over the past several decades as a valuable tool for assessing peripheral auditory performance (reviewed in Hall 1992). AEPs are minute changes in voltage recorded from the scalp surface that reflect the response of the auditory nerve and brain-stem nuclei to sound. AEPs evoked by tone bursts, or auditory brain-stem responses (ABRs), have been used to assess the frequency range of auditory sensitivity in a wide variety of vertebrates including several bird species (Saunders et al. 1973; Dmitrieva & Gottlieb 1992, 1994; Woolley & Rubel 1999; Brittan-Powell et al. 2002, 2005; Brittan-Powell & Dooling 2004; Lucas et al. 2007). ABR waveforms consist of three to five peaks occurring within 10 ms of stimulus onset. The earliest peak is generated by the auditory nerve, whereas peaks of greater latency originate in the brain stem and midbrain (Hall 1992). The ABR threshold at a given frequency is the lowest stimulus intensity that evokes a detectable ABR. ABR thresholds correlate well with behavioural auditory thresholds (Dmitrieva & Gottlieb 1992; Brittan-Powell et al. 2002, 2005), whereas amplitude and latency provide additional indexes of sensitivity. As a general rule, ABR amplitude increases as stimulus intensity increases above threshold, whereas latency decreases (e.g. Dmitrieva & Gottlieb 1994; Brittan-Powell et al. 2002). Hence, comparing ABRs recorded at the same intensity level, amplitude is proportional to sensitivity (the difference in intensity between the stimulus and the threshold levels), whereas latency is inversely proportional to sensitivity.

AEPs evoked by envelope periodicity, or envelope-following responses (EFRs), have been used to assess temporal resolution in several mammals (Kuwada et al. 1986; Dolphin & Mountain 1992, 1994; Dolphin et al. 1995; Supin & Popov 1995; Mann et al. 2005; Cook et al. 2006; Mooney et al. 2006), but not birds. EFR waveforms are phase-locked to envelope periodicity in the stimulus, meaning that peaks in the EFR coincide with times of maximum amplitude in the stimulus after accounting for a delay. The amplitude of the EFR indicates how well envelope periodicity is encoded by the peripheral auditory system. A system with greater temporal resolution is expected to respond to high rates of envelope periodicity with greater amplitude. Indeed, modulation rate transfer functions (MRTFs) plotting EFR amplitude as a function of envelope periodicity rate indicate greater temporal resolution in odontocetes (toothed whales and dolphins) than in terrestrial mammals (references above). This pattern agrees with behavioural data and seems to reflect an adaptation for processing rapid envelope fluctuations of returning echolocation signals (Dolphin et al. 1995).

In this study, we used ABRs and EFRs to assess the frequency range of auditory sensitivity and temporal resolution, respectively, in three songbird species: the tufted titmouse, *Baeolophus bicolor*; house sparrow, *Passer domesticus*; and white-breasted nuthatch, *Sitta carolinensis*. These species are of similar body size, are phylogenetically distinct, and differ in their use of acoustic signal space. Each species is currently placed in one of the three songbird superfamilies. Titmice are in the superfamily Sylvioidea, sparrows the Passeroidea, and nuthatches the Muscicapoidea (Jonsson & Fjeldsa 2006). Based on coevolution between the auditory system and the acoustic signal space, we predicted that (1) the frequency range of auditory sensitivity should vary with the frequency range of vocalizations and (2) temporal resolution should vary with the maximum rate of envelope periodicity found in vocalizations.

As a secondary objective, we estimated the neural generator of the EFR in birds. We used the minimum phase angle technique of Bode (1945) to calculate the group delay, or latency, of the EFR. Latency can be used to infer the point of origin of an AEP.

METHODS

Subjects

We recorded AEPs from 36 wild-caught, adult birds between 16 June 2006 and 5 March 2007. The sample included seven tufted titmice (4 females, 3 males), 18 house

sparrows (7 females, 11 males) and 11 white-breasted nuthatches (2 females, 9 males). We collected the subjects near Purdue University in West Lafayette, Indiana, U.S.A., at two private residences and in the Martel Forest. We captured them in the morning in treadle traps baited with mixed seed. We fitted each subject with a uniquely numbered aluminium leg band. We determined age by plumage in sparrows and nuthatches and mouth colour in titmice (Pyle 1997) and determined sex using plumage in sparrows and nuthatches (Pyle 1997) and wing chord length in titmice (Thirakhupt 1985; Lucas et al. 1993). We transported captured birds to an indoor aviary at Purdue University where they were housed individually in 1-m^3 wire-mesh cages. The light:dark cycle of the aviary was set to local conditions. We provided titmice and nuthatches with sunflower seed, two or three mealworms, grit, and vitamin-treated water daily. We provided sparrows with mixed seed, grit, and vitamin-treated water. Generally, we conducted auditory tests on the afternoon of capture and released the subjects 1 to 2 days later at their capture sites. Mean body mass $\pm$ SD was 21.5 $\pm$ 1.4 g in titmice, 27.3 $\pm$ 2.9 g in sparrows and 20.9 $\pm$ 1.2 g in nuthatches.

Auditory Test Equipment and Procedure

We weighed the birds and then anesthetized them with an injection of ketamine (40–60 mg/kg) and xylazine (8–12 mg/kg) into the breast muscle. Xylazine is a sedative anaesthetic, whereas ketamine is a dissociative. After 1–2 min, we placed the birds in the test chamber on a towel-wrapped, Snugglesafe microwave-heated pad (Pet Supply Imports, South Holland, Illinois, U.S.A.). Internal body temperature was not measured directly during the experiments, but we maintained the temperature between the subject's body and the heating pad at 38 $\pm$ 2 °C by adding or removing layers of towel. After 5 min, we inserted needle electrodes (Nicolet Biomedical, Fitchburg, Wisconsin, U.S.A.) under the scalp high at the vertex (positive electrode), directly posterior to the right auditory meatus (negative electrode) and at the nape of the neck (ground electrode). We maintained interelectrode impedance below 7 K ohms to ensure good electrical contact with the subject's scalp. We gave one or two supplemental injections of ketamine (15–20 mg/kg) and xylazine (2–3 mg/kg) to complete approximately 80 min of auditory tests.

The test chamber consisted of a box, 1.2 m tall by 1.4 m wide by 1.2 m deep, lined with one layer of acoustic tile and one layer of 3-inch (7.7-cm)-thick Sonex foam (Acoustic Solutions, Richmond, Virginia, U.S.A.). We positioned the subjects centrally on the floor of the chamber with the lights off and their right ear facing upwards. Stimulus presentation, AEP acquisition, and data storage were coordinated by a Tucker Davis Technologies System II modular rack-mount system (TDT, Gainesville, Florida, U.S.A.) and Dell PC running TDT SigGen32/BioSig32 software in an adjacent room. Digitally generated stimuli passed through a TDT DA1 digital-to-analogue converter and Crown D75 power amplifier before presentation through a downwards projecting, electromagnetically shielded, dynamic loudspeaker suspended 30 cm above the subject (RCA Model 40–5000; 140- to 20 000-Hz frequency response). Electromagnetic shielding was necessary because AEP waveforms can be contaminated by electromagnetic fields. We calibrated stimuli within $\pm$1 dB relative to 1 μPa across the frequencies required for the experiments using a Bruel & Kjaer Model 1613 precision sound level meter and Model 4131 1-inch (2.6-cm) condenser microphone placed at the approximate location of the bird's ear. Responses were recorded through needle electrodes feeding into a TDT HS4 headstage. They were amplified by a TDT DB4 biological amplifier before passing through an AD1 analogue-to-digital converter to the computer for data storage.

Acoustic Signal Space

We reviewed the primary literature and analysed commercially available digital recordings of species-specific vocalizations to characterize properties of acoustic signal space in each species. Parameters of interest included the dominant, minimum and maximum frequencies of song, the maximum frequency of call notes and the maximum rate of envelope periodicity contained in call notes. Songs are generally used as long-distance territory advertisements, whereas calls serve a broader variety of functions. We measured minimum and maximum frequencies from digital scans of published spectrograms in some cases. We conducted acoustic analyses of digital recordings from Elliot et al. (1997; sampled at 44.1 kHz) and the Cornell Lab of Ornithology Macaulay Library (recording no. 53157 of 15 distress calls given by a single titmouse; sampled at 32 kHz) using PRAAT version 4.5.17 (Boersma & Weenink 2007) and Avisoft SASLab Pro version 4.23b computer software (Sprecht 2002). We measured dominant frequencies from long-term average power spectra generated in PRAAT with a bin width of 100 Hz and minimum and maximum frequencies from spectrograms generated in PRAAT with a 10-ms, Gaussian window. We defined minimum and maximum frequencies as the low- and high-frequency points of the spectrogram where amplitude dropped 15 dB below peak amplitude (the dynamic range of the spectrogram was set to 15 dB to identify these limits). To measure envelope periodicity, we extracted the analytic signal with a Hilbert transform in Avisoft. The analytic signal represents the amplitude envelope of the original signal. We generated a spectrogram of the analytic signal in PRAAT to show the rate of envelope periodicity in the signal as a function of time and noted the maximum frequency. To confirm the presence of envelope periodicity, we examined the original signal for periodic fluctuations in amplitude at the indicated rate.

Auditory Sensitivity

ABR stimuli were 5-ms tone bursts with 1-ms $\cos^2$ onset/offset ramps, presented at a rate of 31.1 stimuli per second with alternating phase values of 0.5π and 1.5π radians. We evoked ABRs at stimulus frequencies of 0.8, 1.4, 2.2, 3.2, 4.2 and 6.4 kHz in random order. At each frequency, we recorded ABRs at eight intensity levels ranging from

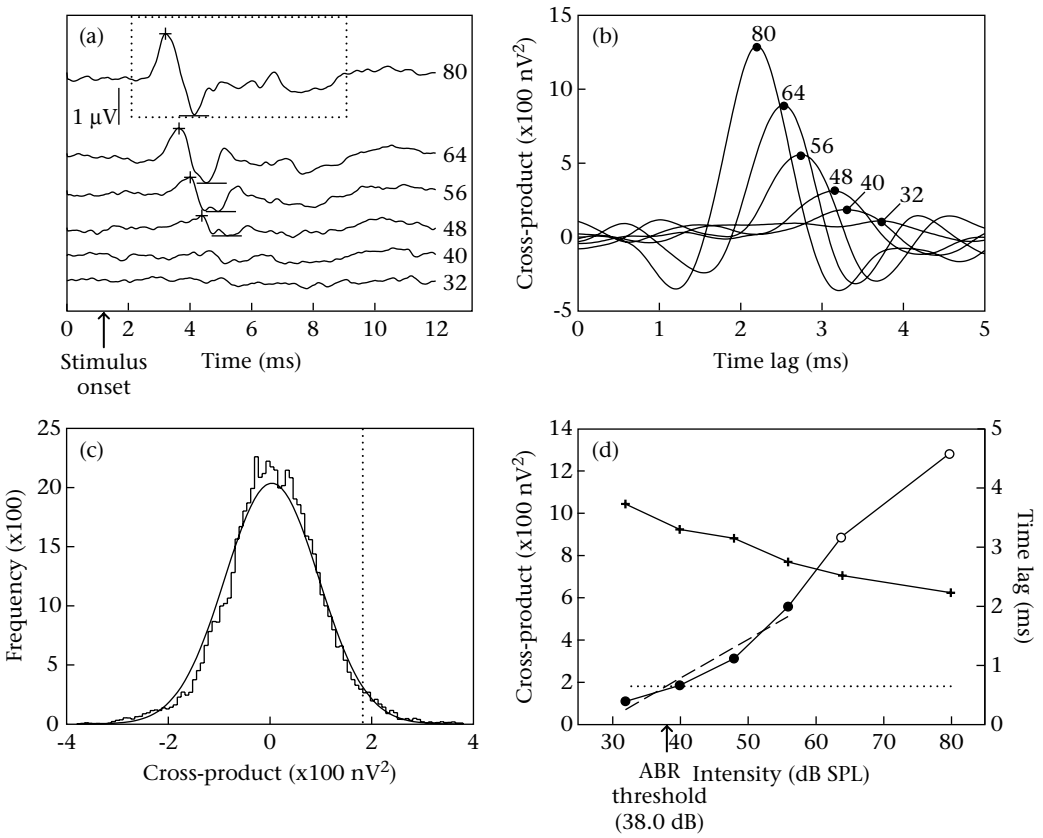

Figure 1. (a) ABR waveforms of a single nuthatch (SXLX) in response to 4.2-kHz tone bursts ranging in intensity from 32 to 80 dB SPL. The 7-ms segment of the 80-dB SPL response enclosed by dotted lines indicates the ABR template, whereas the arrow on the time axis indicates the timing of stimulus onset. '+' symbols indicate the location of ABR peak I, whereas '—' symbols indicate the subsequent trough used for measurement of amplitude (see text). (b) Cross-correlation functions plotting the cross product between each ABR waveform from (a) and the ABR template as a function of time lag from 0 to 5 ms. Filled circles indicate the maximum cross product and time lag of the maximum for each function. (c) Null distribution of cross products between the template and 1.5 s of physiological background noise. Bin width of the histogram is 8 nV^2. The dotted line indicates the 95% criterion for a cross product significantly greater than 0. (d) Maximum cross products (circles; left axis) and respective time lags (crosses; right axis) plotted as a function of intensity along with the 95% criterion (dotted line; left axis). The dashed regression line is fit to a subset of low-intensity cross-product data (filled circles; see text for selection criteria). The arrow on the intensity axis indicates the ABR threshold at which the regression line crosses the 95% criterion.

80 down to 24 dB SPL in 8 dB steps (Fig. 1a). Each ABR was the average response to 1000 stimulus repetitions. We sampled responses at 40 kHz for 12 ms beginning 1.2 ms before stimulus arrival at the ear, amplified 200 K times, band-pass filtered from 0.1 to 3 kHz and notch filtered at 60 Hz.

We calculated ABR thresholds for each subject using cross-correlation analyses conducted in PRAAT. The method is based on techniques described in Cone-Wesson et al. (1997) and Supin et al. (2001). At each frequency, we generated a template from the 80-dB SPL ABR by extracting 7 ms from the waveform beginning 1 ms after stimulus onset. Major peaks of the ABR were clearly visible in the template (Fig. 1a). The template was cross-correlated with the ABR at each intensity level to yield a maximum cross product and respective time lag (Fig. 1b). In addition, the template was cross-correlated with 1.5 s of physiological background noise recorded in the absence of acoustic stimulation to generate a null distribution of cross products (Fig. 1c). The noise recording was a concatenation of 60-ms segments from eight subjects of each species using the same filter setting and number of averages described above. We did not observe consistent differences in noise level between species or individuals. Because the null distribution of cross products was approximately normal with a mean of 0, we calculated the 95% criterion for a cross product significantly different from 0 as the standard deviation of the null distribution times a factor of 1.96. We plotted cross products between ABR waveforms and the template as a function of stimulus intensity along with respective time lags and the 95% criterion (Fig. 1d). In all cases, cross products increased roughly linearly with increasing intensity, whereas time lags decreased. We therefore fit a regression line to the relationship between intensity and cross product and calculated the ABR threshold as the intensity at which the regression line crossed the 95% criterion. Each regression included four data points. In most cases we used the first four data points falling above the criterion, but the first data point below the criterion was included when its time lag was consistent with time lags of points

of above the criterion (e.g. the 32-dB SPL point in Fig. 1d). Finally, we discarded ABR thresholds based on R^2 values less than 0.85.

We measured amplitude and latency of the first ABR peak (Fig. 1a) using manually placed cursors in BioSig32. Amplitude was measured in nanovolts relative to the subsequent trough, whereas latency was measured in milliseconds relative to the time of stimulus onset. We limited analyses of amplitude and latency to intensities of 48 dB SPL and above.

Temporal Resolution

EFR stimuli were sinusoidally amplitude-modulated tones (trace i of Fig. 2a–d). Stimulus waveforms were calculated as

$$A \sin\left(2\pi f_c t\right)\left[0.5 + 0.5 \sin\left(2\pi f_m t\right)\right],$$

where A is the amplitude of the carrier, f_c is the frequency of the carrier in hertz, f_m is the rate of amplitude modulation in hertz (hereafter the modulation frequency), and t is time in seconds. Modulation depth was 100%. Stimuli contained energy at the carrier frequency and two sideband frequencies ($f_c + f_m$ and $f_c - f_m$) but not at the modulation frequency. Stimuli were 53.3 ms long with 3 ms $\cos^2$ onset/offset ramps, presented at a rate of 11.1 stimuli per second with constant starting phase. Carrier frequency and amplitude were held constant at 2.75 kHz and 80 dB SPL, respectively, whereas EFRs were evoked at modulation frequencies of 150, 230, 350, 510, 710, 950, 1230, 1550 and 1910 Hz in random order. The envelopes of the three highest modulation frequency stimuli are difficult to visualize because they contain 1.4–2.3 cycles of the carrier frequency per cycle of amplitude modulation. Nonetheless, these stimuli contain undistorted, sinusoidal amplitude modulation, as revealed by analytic signals plotting envelope amplitude as a function of time (trace ii of Fig. 2a–d; see Viemeister & Plack 1993). Stimuli with as few as 1.1–1.2 carrier cycles per modulation cycle have been used to successfully obtain MRTFs in other species (Dolphin & Mountain 1992; Dolphin et al. 1995). That is, MRTFs obtained using low carrier frequencies (with fewer carrier cycles per modulation cycle) had the same shape as MRTFs obtained with higher carrier frequencies (e.g. compare Figures 4b and 5 of Dolphin & Mountain 1992). Each EFR was the average response to 1000 stimulus repetitions. Responses were sampled at 40 kHz for 65 ms starting 1.2 ms before stimulus arrival at the ear, amplified 200 K times, band-pass filtered from 0.1 to 10 kHz, and notch filtered at 60 Hz.

EFR waveforms (trace iii of Fig. 2a–d) contained energy at the stimulus modulation frequency, carrier frequency and sideband frequencies, as indicated by the power spectra of the responses (Fig. 2e–h). We calculated power spectra in PRAAT with a 2552-point fast Fourier transform, resulting in a bin width of 9.76 Hz. EFR amplitude was defined as the magnitude of the peak at the modulation frequency in dBnV. Other peaks were not analysed. Note that peaks at the modulation frequency of the stimulus were readily distinguishable from peaks at the carrier and sideband frequencies. To demonstrate more clearly phase-locking to the envelope of high modulation frequency stimuli, we recorded EFRs from a single house sparrow (XXSK) in response to stimuli with carrier frequencies of alternating phase between 0.5π and 1.5π radians (trace iv of Fig. 2a–d). These derived EFRs contain phase-locking to the modulation frequency but not the carrier or sideband frequencies. Finally, responses less than 3 dB above the noise floor of the power spectrum were deemed nonsignificant and excluded from the analysis.

EFR Group Delay

EFR group delay is equal to the slope of the relationship between stimulus modulation frequency and EFR phase, in radians per hertz, divided by 2π (Bode 1945; as in Kuwada et al. 1986; Dolphin & Mountain 1992; Dolphin et al. 1995; Supin & Popov 1995). Phase measurements must be unwrapped by subtracting integer multiples of 2π to yield the minimum change in phase for each successive increase in modulation frequency. Our original intention was to calculate the EFR group delay based on the complete range of modulation frequencies described above. However, phase shifts below 350 Hz and between 710 and 1230 Hz varied widely between individuals. We therefore restricted our analysis of group delay to modulation frequencies from 350 to 710 Hz and from 1230 to 1910 Hz. Modulation frequencies from 1230 to 1910 Hz were relatively far apart for the unwrapping procedure. To verify that phase measurements above 1230 Hz were unwrapped correctly, we recorded EFRs at modulation frequencies from 360 to 1910 Hz using a smaller, 50-Hz step size in a single house sparrow (N860). Other experimental parameters were the same as described previously.

We measured EFR phase by calculating the complex spectrum of the response waveform in PRAAT after deleting 1.2 ms from the beginning of the recording to correct for the acoustic delay of the stimulus and appending 500 ms of 0-amplitude samples to the end. Increasing the length of the waveform decreased the bin width of the complex spectrum to 1.83 Hz, which was necessary for accurate measurement of phase. We calculated phase as the argument angle of the real and imaginary values of the complex spectrum at the modulation frequency of the stimulus.

Statistical Analysis

Repeated-measures ANOVAs were conducted with Proc MIXED of the SAS statistical analysis program (SAS Institute, Inc., version 9.1). We specified compound symmetry within subject covariance structure for all models. The dependent variables included ABR threshold, ABR amplitude, ABR latency, EFR amplitude, and EFR phase. Independent variables (species, sex, frequency, intensity and modulation frequency, depending on the analysis) were generally treated as discrete variables, except that modulation frequency was treated as

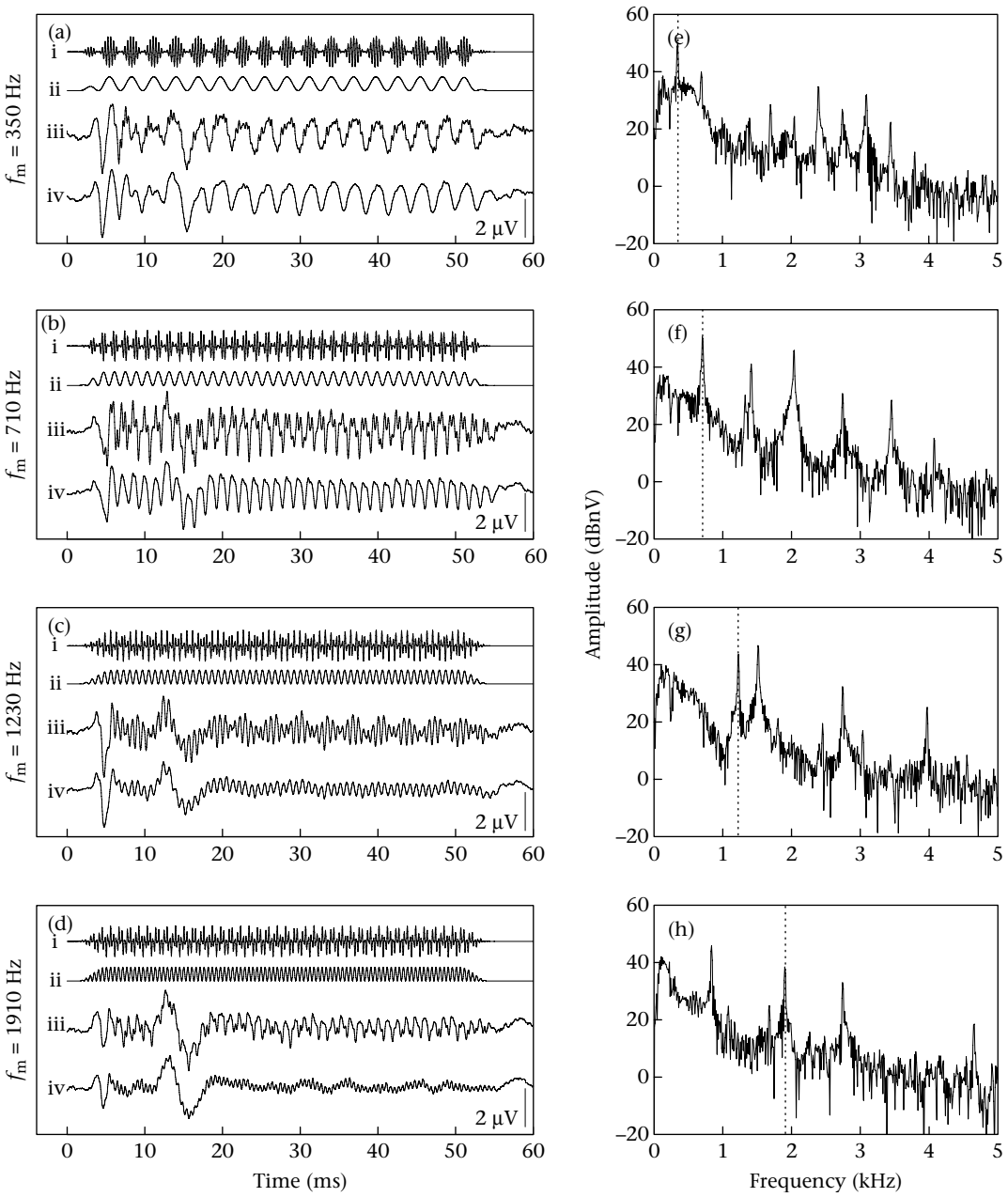

Figure 2. For stimulus amplitude modulation frequencies of 350, 710, 1230 and 1910 Hz, (a–d) show (trace i) the acoustic waveform of the stimulus, (trace ii) the amplitude envelope of the stimulus, (trace iii) the raw EFR waveform containing phase-locking to the modulation, carrier and sideband frequencies of the stimulus and (trace iv) the derived EFR waveform containing phase-locking to the modulation frequency only (see text). (e–h) Power spectra of raw EFR waveforms (trace iii) from (a–d). Dotted lines indicate the modulation frequency of the stimulus. EFR waveforms and power spectra are presented for a single house sparrow (XXSK).

a continuous variable for the analysis of EFR phase. Nonsignificant interaction terms were eliminated in order of decreasing P value. We used Proc UNIVARIATE to test for normality of residuals and homogenous variance. Log transformation of ABR amplitude was necessary to achieve these conditions. We selected dBnV as the unit for amplitude. Sex effects and interactions with sex were not significant for all models ($P > 0.05$ in all cases). We conducted post hoc comparisons between means using t tests generated by the 'LSMEANS/diff' and 'ESTIMATE' commands of Proc MIXED.

Physiological Control

We evoked ABRs with click stimuli before and after every experiment. Each ABR was the average response to 400 clicks of 0.1 ms duration, 90-dB peak-equivalent SPL and alternating polarity, presented at a rate of 31.1 Hz. Responses were sampled at 40 kHz for 12 ms starting 1.2 ms before stimulus arrival at the ear, amplified 200 K times, band-pass filtered from 0.1 to 3 kHz and notch filtered at 60 Hz. If the amplitude of the first peak shifted by more than 10%, or latency shifted by more than 0.1 ms

during an experiment, we discarded the results from that experiment.

RESULTS

Acoustic Signal Space

Songs were lowest in frequency in white-breasted nuthatches, intermediate in tufted titmice, and highest in house sparrows. Nuthatch songs ranged from 1.5 to 2.5 kHz (Ritchison 1983) with dominant frequencies of 1.9 and 2.4 kHz ($N = 2$ of each from Elliot et al. 1997). Titmouse songs ranged from $\overline{X} \pm \mathrm{SD} = 2.3 \pm 0.3$ to 3.0 ± 0.4 kHz ($N = 13$ from Gaddis 1983 and Schroeder & Wiley 1983) with dominant frequencies of 2.7 ± 0.1 kHz ($N = 7$ from Elliot et al. 1997). Sparrow songs ranged from $\overline{X} \pm \mathrm{SD} = 3.2 \pm 0.2$ to 5.3 ± 0.2 kHz with dominant frequencies of 4.6 ± 0.3 kHz ($N = 15$ from Elliot et al. 1997).

Titmouse calls were higher in frequency than calls of sparrows and nuthatches. Mean frequency ± SD was 9.2 ± 0.5 kHz for titmouse Z notes and 8.9 ± 0.5 kHz for A notes (Owens & Freeberg 2007), whereas 'tseet' alarms ranged from 7.9 to 8.9 kHz ($N = 6$ from Elliot et al. 1997). In contrast, 6.5 kHz was the approximate maximum frequency of sparrow calls (observed in the 'chree' call; Lowther & Cink 2006) and nuthatch calls (observed in 'hit', 'tuck', 'tchup' and 'squeal' notes; Ritchison 1983).

We found higher maximum frequencies of envelope periodicity in titmice and sparrows than in nuthatches (Fig. 3). We observed rates of envelope periodicity up to 1450 Hz in titmouse D notes ($N = 6$ from Elliot et al. 1997; $N = 15$ from the Macaulay Library) and sparrow 'quer' notes ($N = 7$ from Elliot et al. 1997), whereas envelope periodicity of nuthatch 'hit' calls ranged up to 950 Hz ($N = 6$ from Elliot et al. 1997).

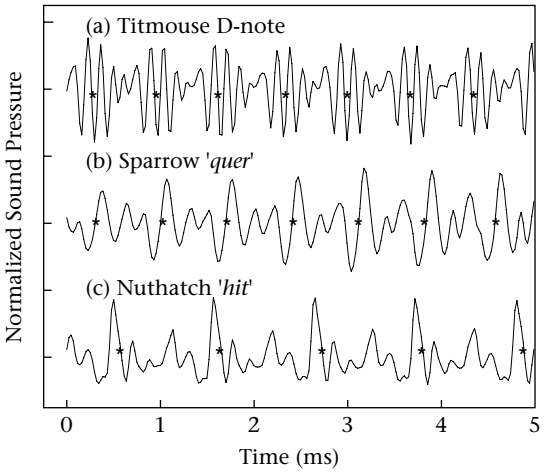

Figure 3. (a–c) Acoustic waveforms of titmouse, sparrow, and nuthatch calls containing rapid envelope periodicity. Amplitude peaks are marked with asterisks. The approximate rate of periodicity is 1450 Hz in the titmouse and sparrows calls and 950 Hz in the nuthatch call.

Auditory Sensitivity

The ANOVA of ABR thresholds found significant effects of frequency ($F_{5,160} = 214.60$, $P < 0.001$), species ($F_{2,33} = 4.59$, $P = 0.018$) and the frequency by species interaction ($F_{10,160} = 7.29$, $P < 0.001$). ABR thresholds were lower from 2.2 to 3.2 kHz than at higher and lower frequencies (Fig. 4). The species effect and frequency by species interaction were driven by species differences in thresholds at high frequencies. At 6.4 kHz, thresholds of titmice were considerably lower than those of sparrows ($\overline{X}_{2-1} \pm \mathrm{SE} = -14.1 \pm 1.9$ dB, $t_{160} = -7.47$, $P < 0.001$) and nuthatches ($\overline{X}_{2-1} \pm \mathrm{SE} = -12.1 \pm 2.0$ dB, $t_{160} = -5.99$, $P < 0.001$), and at 4.2 kHz, thresholds of titmouse were marginally lower than those of sparrows ($\overline{X}_{2-1} \pm \mathrm{SE} = -3.4 \pm 1.8$ dB, $t_{160} = -1.84$, $P = 0.068$) and lower than those of nuthatches ($\overline{X}_{2-1} \pm \mathrm{SE} = -4.7 \pm 2.0$ dB, $t_{160} = -2.33$, $P = 0.021$). Thresholds of nuthatches were lower than those of sparrows at 3.2 kHz ($\overline{X}_{2-1} \pm \mathrm{SE} = -3.4 \pm 1.6$ dB, $t_{160} = -2.13$, $P = 0.034$).

ABR amplitude (in dBnV) was influenced by frequency ($F_{5,165} = 1266.7$, $P < 0.001$), intensity ($F_{3,105} = 798.75$, $P < 0.001$), the frequency by intensity interaction ($F_{15,481} = 7.27$, $P < 0.001$) and the frequency by species interaction ($F_{10,165} = 11.77$, $P < 0.001$). In general, amplitude was greater from 2.2 to 3.2 kHz than at higher and lower frequencies and increased with increasing intensity (Fig. 5a–c). Moreover, curves plotting amplitude as a function of frequency were flatter at high intensities on the logarithmic scale. The frequency by species interaction was driven by species differences in amplitude at high frequencies. At 6.4 kHz, titmice had greater amplitude than sparrows ($\overline{X}_{2-1} \pm \mathrm{SE} = 4.5 \pm 1.1$ dB, $t_{165} = 3.90$, $P < 0.001$) and nuthatches ($\overline{X}_{2-1} \pm \mathrm{SE} = 3.0 \pm 1.2$ dB, $t_{165} = 2.42$, $P = 0.017$). At 4.2 kHz, sparrows had greater amplitude than nuthatches ($\overline{X}_{2-1} \pm \mathrm{SE} = 2.5 \pm 1.0$ dB, $t_{165} = 2.64$, $P = 0.009$).

The ANOVA of ABR latency revealed significant effects of frequency ($F_{5,165} = 483.18$, $P < 0.001$), intensity ($F_{3,99} = 2276.65$, $P < 0.001$), species ($F_{2,33} = 19.86$,

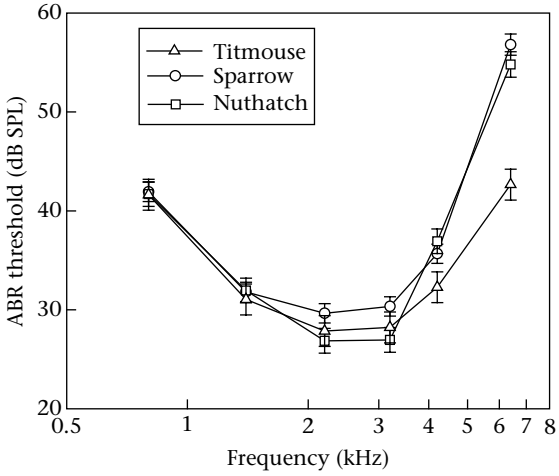

Figure 4. Audiograms plotting mean ABR thresholds ± SE of each species as a function of frequency.

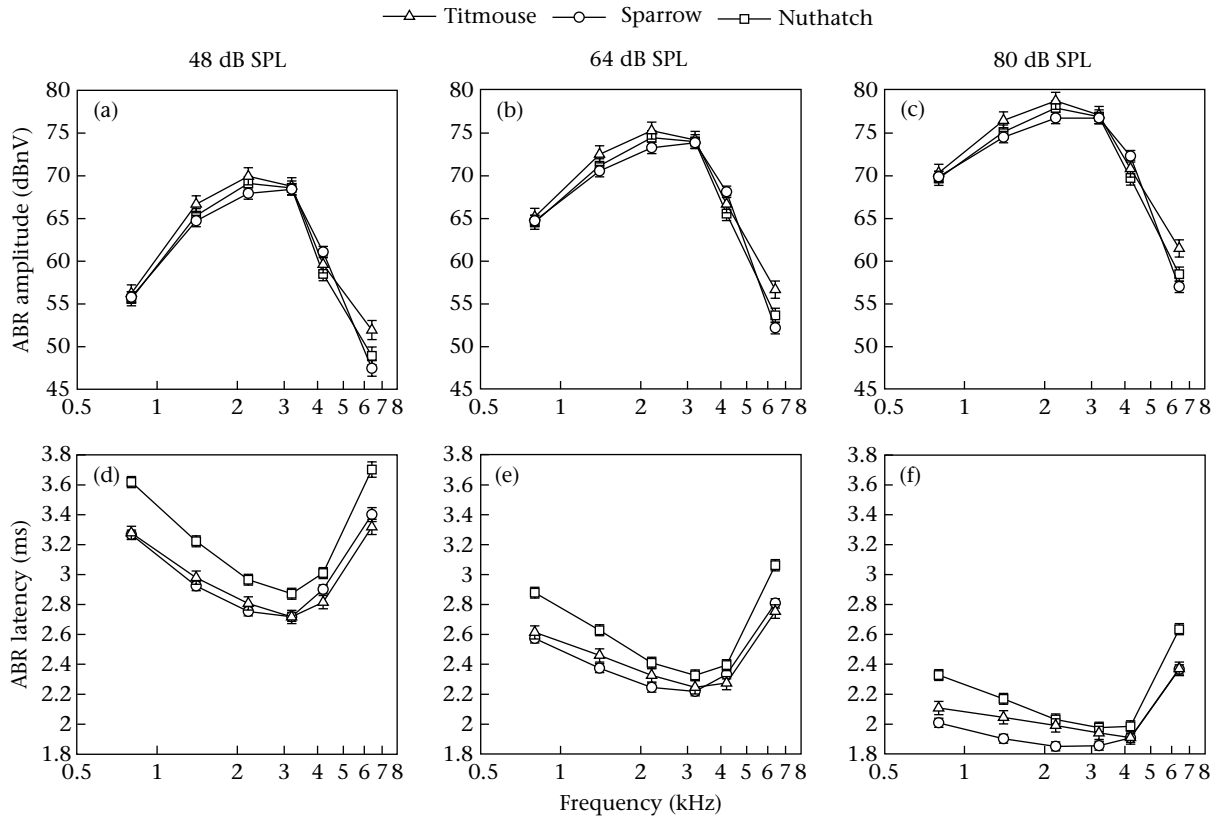

Figure 5. (a–c) Mean ABR amplitude ± SE of each species as a function of frequency at (a) 48, (b) 64 and (c) 80 dB SPL. Note that amplitude has been log transformed to units of dBnV. (d–f) Mean ABR latency ± SE as a function of frequency at (d) 48, (e) 64 and (f) 80 dB SPL.

$P < 0.001$), the frequency by intensity interaction ($F_{15,481} = 9.83$, $P < 0.001$), the frequency by species interaction ($F_{10,165} = 12.36$, $P < 0.001$) and the intensity by species interaction ($F_{6,99} = 2.90$, $P = 0.012$). ABR latency was generally shorter from 2.2 to 4.2 kHz than at higher and lower frequencies and decreased with increasing intensity (Fig. 5d–f). Species tuning curves plotting latency as a function of frequency were flatter at high intensity than at low. The species effect was driven by longer latency in nuthatches than in titmice and sparrows ($\overline{X} \pm \mathrm{SE} = 2.55 \pm 0.03$ ms in titmice, 2.52 ± 0.02 ms in sparrows, 2.73 ± 0.03 ms in nuthatches), whereas the frequency by species interaction was driven by diversity in the shape of the latency tuning curves. Nuthatch tuning curves had a deeper U shape than those of titmice and sparrows. Comparing titmice and sparrows, latency of titmice increased at a slower rate above 3.2 kHz. The increase in latency from 3.2 to 4.2 kHz was smaller in titmice than in sparrows ($t_{165} = -2.39$, $P = 0.018$; $\overline{X}_{2-1} \pm \mathrm{SE} = 0.04 \pm 0.03$ ms in titmice, 0.12 ± 0.02 in sparrows), as was the increase in latency from 3.2 to 6.4 kHz ($t_{165} = -2.16$, $P = 0.032$; $\overline{X}_{2-1} \pm \mathrm{SE} = 0.53 \pm 0.03$ in titmice, 0.61 ± 0.02 in sparrows). Finally, the intensity by species interaction was driven by a stronger effect of intensity in sparrows and nuthatches than in titmice. Relative to titmice, latency decreased more from 48 to 80 dB SPL in sparrows ($t_{99} = 2.89$, $P = 0.005$) and nuthatches ($t_{99} = 3.65$, $P < 0.001$; $\overline{X}_{2-1} \pm \mathrm{SE} = 93 \pm 0.03$ ms in titmice, 1.01 ± 0.02 ms in sparrows, 1.04 ± 0.02 ms in nuthatches).

Temporal Resolution

A two-way repeated-measures ANOVA of EFR amplitude revealed significant effects of modulation frequency ($F_{2,236} = 102.77$, $P < 0.001$), species ($F_{2,32} = 5.42$, $P = 0.009$) and the modulation frequency by species interaction ($F_{16,236} = 2.36$, $P = 0.003$). MRTFs of all species showed maximal EFR amplitude from 350 to 710 Hz followed by a marked decrease from 710 to 950 Hz (Fig. 6a). A high-resolution MRTF obtained from a single sparrow indicated a distinct notch in EFR amplitude at 810 Hz. Above 950 Hz, EFR amplitude remained relatively constant up to 1550 Hz in titmice and sparrows and 1230 Hz in nuthatches, followed by a marked decrease. The amplitude of nuthatches at 1550 Hz was weaker than those of titmice ($\overline{X}_{2-1} \pm \mathrm{SE} = -6.8 \pm 2.1$ dB, $t_{236} = -3.26$, $P = 0.001$) and sparrows ($\overline{X}_{2-1} \pm \mathrm{SE} = -7.5 \pm 1.7$ dB, $t_{236} = -4.43$, $P < 0.001$), as was their amplitude at 1910 Hz ($\overline{X}_{2-1} \pm \mathrm{SE} = -7.1 \pm 2.1$ dB compared to titmice, $t_{236} = -3.37$, $P = 0.001$; $\overline{X}_{2-1} \pm \mathrm{SE} = -7.1 \pm 1.7$ dB compared to sparrows, $t_{236} = -4.08$, $P < 0.001$). Finally, the EFR amplitude of sparrows at 150 Hz was greater than those of titmice ($\overline{X}_{2-1} \pm \mathrm{SE} = 4.9 \pm 1.9$ dB, $t_{236} = 2.51$, $P = 0.013$) and nuthatches ($\overline{X}_{2-1} \pm \mathrm{SE} = 3.3 \pm 1.7$ dB, $t_{236} = 1.98$, $P = 0.049$).

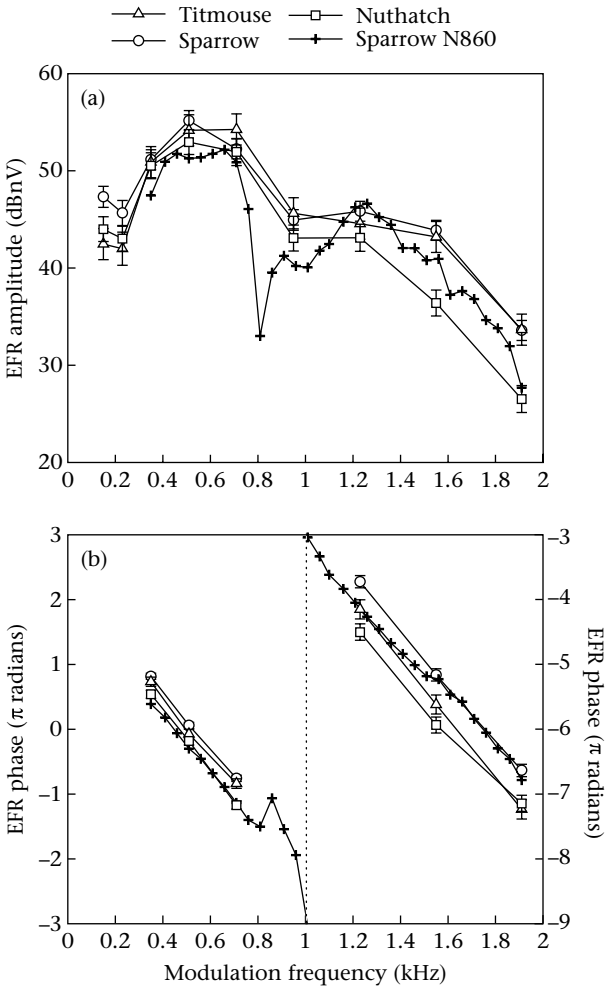

Figure 6. (a) MRTFs plotting mean EFR amplitude ± SE of each species as a function of modulation frequency. Joined crosses plot the MRTF of a single sparrow (N860) using a smaller, 50-Hz step size between modulation frequencies. (b) Mean, unwrapped EFR phase ± SE of each species as a function of modulation frequency. Phase of points to the left of the dotted line is displayed on the left axis. Phase of points to the right is displayed on the right. Joined crosses plot phase measurements of sparrow N860 using the smaller step size.

EFR Group Delay

EFR phase decreased linearly from 350 to 1910 Hz in all species (Fig. 6b). A two-way repeated-measures ANOVA of EFR phase from 350 to 710 Hz found that the modulation frequency by species interaction was not significant ($F_{2,64} = 2.46$, $P = 0.094$). The nonsignificant interaction indicates no diversity in the effect of modulation frequency and hence no difference in group delay (2.17 ± 0.09 ms in titmice, 2.18 ± 0.06 ms in sparrows, and 2.37 ± 0.08 ms in nuthatches). Above 1230 Hz, however, the modulation frequency by species interaction was significant ($F_{2,64} = 5.68$, $P = 0.005$) due to a slightly shorter group delay in nuthatches than in titmice and sparrows ($\overline{X} \pm \mathrm{SE} = 2.27 \pm 0.08$ ms in titmice, 2.14 ± 0.05 ms in sparrows, and 1.93 ± 0.07 ms in nuthatches). Group delay was shorter in nuthatches than in titmice ($t_{64} = -3.25$, $P = 0.002$) and sparrows ($t_{64} = -2.46$, $P = 0.017$). Data collected from a single house sparrow using a smaller, 50-Hz step size between modulation frequencies indicated that phase decreases by approximately 1.5π radians between 710 and 1230 Hz, and measurements above 1230 Hz were unwrapped correctly.

DISCUSSION

Auditory Sensitivity

ABRs of tufted titmice, house sparrows, and white-breasted nuthatches to tone-burst stimuli resembled previously published ABRs of the same species to click stimuli (Lucas et al. 2002) and longer duration tones (Lucas et al. 2007). Furthermore, they were similar to ABRs of other birds, including budgerigars (Brittan-Powell et al. 2002; Brittan-Powell & Dooling 2004), owls (Brittan-Powell et al. 2005) and quail (Sheykholeslami et al. 2001). ABR thresholds of the study species, like behavioural thresholds of most songbirds, were lowest from 2.2 to 3.2 kHz and increased at higher and lower frequencies (Fig. 7). However, ABR thresholds were 25–30 dB higher than typical behavioural thresholds. This disparity has been observed in ABR studies of a wide variety of avian species (ducks: Dmitrieva & Gottlieb 1992; finches: Woolley & Rubel 1999; parrots: Brittan-Powell et al. 2002; owls: Brittan-Powell et al. 2005), but not mammals (see Brittan-Powell et al. 2002). The greater disparity between ABR and behavioural thresholds in birds may reflect a smaller absolute number of auditory nerve fibres compared to mammals (e.g. 50 000 in the cat versus 9800 in the budgerigar) and activation of a smaller proportion of fibres at near-threshold levels (Brittan-Powell et al. 2002). Intermediate frequencies and high-intensity levels elicited maximum ABR amplitude and minimum latency, as in other avian studies (e.g. Dmitrieva & Gottlieb 1994; Brittan-Powell et al. 2002). The increase in latency observed at high frequency in birds is not found in mammals, in which latency decreases more consistently with increasing frequency because of phase shifts induced by the peripheral auditory filters (e.g. Neely et al. 1988). The difference between birds and mammals may reflect divergence in the tuning of peripheral auditory filters within the cochlea.

Minimum ABR thresholds, maximum amplitude, and minimum latency were observed from 2.2 to 3.2 kHz in all species, indicating that this is the frequency range of maximum sensitivity. Furthermore, ABR thresholds of titmice were slightly lower at 4.2 kHz than in other species, suggesting a broader frequency range of maximum sensitivity. The match between the frequency range of maximum sensitivity and the frequency range of song was relatively close in titmice and nuthatches. For sparrows, however, maximum sensitivity from 2.2 to 3.2 kHz represents an intriguing mismatch with relatively higher dominant frequency of song ($\overline{X} \pm \mathrm{SD} = 4.6 \pm 0.3$ kHz). Sensitivity of sparrows at 4.6 kHz is predicted to be 9.9 dB worse than sensitivity at 2.2 kHz based on linear extrapolation between points of the audiogram. A cursory inspection of

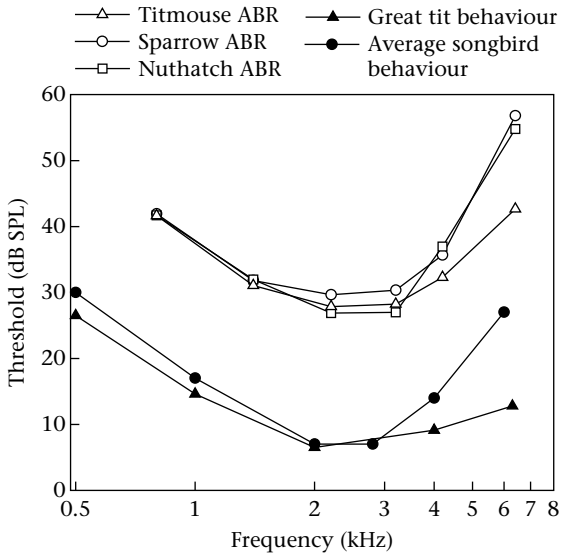

Figure 7. Audiograms plotting mean ABR thresholds of titmice, sparrows and nuthatches along with behavioural auditory thresholds of the great tit (from Langemann 1998) and average songbird (from Dooling et al. 2000).

song recordings from a broad range of geographic locations suggests that this frequency range is typical for house sparrows (e.g. California and Texas, U.S.A.; The Netherlands; Morocco; the Macaulay Library).

The mismatch observed in sparrows may reflect an auditory constraint coupled with selection for high-frequency song and relaxed selection for a close match between sender and receiver. Maximum sensitivity from 2 to 3 kHz has been found in a wide variety of songbirds and suboscine passerines of similar size (reviewed in Dooling et al. 2000; but see Okanoya & Dooling 1988, who found maximum sensitivity at 4 kHz in the swamp sparrow). The source of constraint may be, in part, the avian middle ear (reviewed in Saunders et al. 2000). The avian middle ear relies upon a single ossicle, the columella, to transfer acoustic energy to the cochlea, whereas mammals possess three middle ear ossicles that improve high-frequency efficiency. Several studies of columellar middle ear systems indicate that efficiency is greatest from 2 to 3 kHz and declines sharply above 3–4 kHz (reviewed in Saunders et al. 2000). Note, however, that the columellar ear of the concave-eared torrent frog (*Amolops tormotus*) is capable of transferring ultrasonic frequencies (Feng et al. 2006).

Female preference for song frequency has not been explored in the house sparrow, but studies of sexual selection in other songbirds including the serin (*Serinus serinus*), common blackbird (*Turdus merula*) and white-throated sparrow (*Zonotrichia albicollis*) indicate that females generally prefer high-frequency songs (Hurly et al. 1992; Dabelsteen & Pedersen 1993; Cardoso et al. 2007). Preference for high-frequency songs is thought to arise because high-frequency songs indicate smaller male body size, which is advantageous in aerial fights and displays (see Cardoso et al. 2007 for further discussion). Alternatively, high-frequency songs may be better suited to the sparrow's environment. House sparrows are found almost exclusively in human-modified environments, including farmland, residential and urban areas (Lowther & Cink 2006). High-frequency songs could avoid masking by low-frequency noise sources in these areas (e.g. traffic noise and wind; Brumm & Slabbekoorn 2005) or suffer less distortion during transmission. High-frequency signals are attenuated more during reflection off of objects in cluttered environments, resulting in a cleaner signal with less reverberation at the location of the receiver (Slabbekoorn et al. 2007). Indeed, great tits and dark-eyed juncos (*Junco hyemalis*) sing at higher frequencies in urban settings (Slabbekoorn & Peet 2003; Slabbekoorn et al. 2007). Finally, the short-range nature of house sparrow song may relax selection for a close match between the frequency range of song and the frequency range of maximum sensitivity, thereby allowing the frequency of song to evolve more freely relative to titmice and nuthatches. Effective ranges of song (e.g. the maximum transmission distance to evoke a conspecific, behavioural response) have not been measured in the study species to our knowledge, but should be greater in titmice and nuthatches than in sparrows owing to variation in territory size. Titmice and nuthatches defend territories of 3–8 (Grubb & Pravosudov 1994) and 10–15 Ha (Grubb & Pravosudov 2008), respectively, whereas sparrows defend a small area around the nest (Lowther & Cink 2006).

Finally, the frequency range of maximum sensitivity may shift to match the frequency range of song during the sparrow's breeding season. Evidence of auditory plasticity has been found in seasonally vocal fish (Sisneros et al. 2004), amphibians (Goense & Feng 2005) and birds (Lucas et al. 2002, 2007). We were unable to test this hypothesis in our study species because of insufficient sampling during the breeding season.

The shape of the audiogram above 3 kHz was similar between titmice and great tits (from Langemann 1998), whereas sparrows and nuthatches were more similar to the average songbird (from Dooling et al. 2000) in that thresholds increased more rapidly (Fig. 7). At 6.4 kHz, titmice had lower ABR thresholds and greater ABR amplitude than sparrows and nuthatches. Moreover, the curve plotting latency as a function of frequency was shifted to higher frequency in titmice. The results indicate that titmice are more sensitive to high frequencies, as expected based on the higher maximum frequency of vocalizations in this species. The correlation points to coevolution between the maximum frequency of vocalizations and high-frequency sensitivity, but does not address directly whether signal form has driven the evolution of high-frequency sensitivity or vice versa. We suggest that enhanced high-frequency sensitivity in the titmouse has evolved as a specialization for processing high-frequency communication signals such as alarm calls (i.e. signal form has influenced the auditory system in this case) in light of the high degree of auditory conservation generally observed across songbirds of similar size (Dooling et al. 2000; Gleich et al. 2005). However, we cannot rule out the possibility that a factor other than the maximum vocal frequency or body size (or habitat for the comparison between titmice and nuthatches) may have driven auditory variation.

Regardless of the driving force, enhanced high-frequency sensitivity likely evolved in the common ancestor of Paridae (chickadees, titmice and tits) based on the similar audiogram shapes of titmice and great tits.

Communication at high frequency has several potential benefits. First, high-frequency signals make effective alarm calls because they are difficult for predators to detect and localize (Marler 1955). The great tit, for example, is 30 dB more sensitive than its principal avian predator at the frequency of its alarm call (8 kHz; Klump et al. 1986). A number of other avian species, including titmice, use alarm calls with similar acoustic properties (Marler 1955; Grubb & Pravosudov 1994), suggesting that predator alarms may be a primary selective pressure driving high-frequency communication in birds. Second, high-frequency signals may avoid masking by lower frequency environmental noise such as rustling leaves (Langemann et al. 1998). Ultrasonic communication in the concave-eared torrent frog, for example, avoids broadband masking by fast-running streams (Feng et al. 2006). Given the apparent benefits of high-frequency communication, it is not clear why sparrows and nuthatches do not use high-frequency signals. Indeed, nuthatches are found in mixed-species flocks with titmice and therefore share common predators (Gaddis 1980) and a common acoustic environment.

Temporal Resolution

EFR waveforms were similar among titmice, sparrows and nuthatches. EFRs have not been recorded previously in birds, but responses from the study species followed a phase-locked pattern to amplitude modulation that was qualitatively similar to mammalian EFRs (Kuwada et al. 1986; Dolphin & Mountain 1992, 1994; Dolphin et al. 1995; Supin & Popov 1995; Mann et al. 2005; Cook et al. 2006; Mooney et al. 2006). MRTFs of the study species showed maximum EFR amplitude from 350 to 710 Hz. In contrast, EFR amplitude is greatest below 100 Hz in gerbils (Dolphin & Mountain 1992) and 55 Hz in humans (Kuwada et al. 1986) and between 500 and 1500 Hz in odontocetes (Dolphin et al. 1995; Supin & Popov 1995; Cook et al. 2006; Mooney et al. 2006). The intermediate maxima of MRTFs from this study suggest that songbirds have greater temporal resolution than many terrestrial mammals, but lower resolution than odontocetes. This is consistent with recent behavioural findings (Lohr & Dooling 1998; Dooling et al. 2002; Lohr et al. 2006), but with an important caveat. Estimates of group delay in the study species were near 2 ms, suggesting an origin in the auditory nerve, whereas estimates of group delay in gerbils and humans point to an origin in the auditory cortex and midbrain (Kuwada et al. 1986; Dolphin & Mountain 1992). Because central auditory nuclei such as the cortex have a lower upper limit of phase-locking than peripheral auditory nuclei (reviewed in Joris et al. 2004), comparisons of temporal resolution between birds and mammals based on the EFR are probably biased. Recording directly from the auditory nerve, Frisina et al. (1990) found that 370 Hz was the optimum modulation frequency of phase-locking in gerbils, with a few axons phase-locking best at 800 Hz. These values are more similar to (but still lower than) the phase-locking to amplitude modulation observed in our study.

The marked reduction in EFR amplitude from 710 to 950 Hz was apparently driven by the presence of a deep notch (at 810 Hz in sparrow N860). Notches have been observed in MRTFs of gerbils (Dolphin & Mountain 1992) and odontocetes (Dolphin et al. 1995; Supin & Popov 1995; Mooney et al. 2006) and seem to reflect destructive interference between multiple neural generators (Dolphin et al. 1995). For a modulation frequency of 810 Hz, for example, generators separated by a 0.62-ms time lag (half the period of the modulation frequency) are expected to interact destructively in a scalp-recorded AEP. This time lag corresponds roughly to the time difference between peaks I and II of click-evoked ABRs in these species (see Figure 1 of Lucas et al. 2002). Peak I is attributed to the auditory nerve, whereas the origin of peak II is less clear, but may be the intracranial portion of the auditory nerve (which would make peak I the distal portion; see Brown-Borg et al. 1987).

Titmouse and sparrow MRTFs showed greater EFR amplitude from 1550 to 1910 than nuthatches, suggesting that these species have greater temporal resolution. Although we measured temporal resolution at a single frequency, 2.75 kHz, other studies generally find little variation in temporal resolution across frequencies (e.g. Dolphin & Mountain 1992; Dolphin et al. 1995; Supin & Popov 1995). Temporal resolution seemed to reflect the maximum rate of envelope periodicity observed in vocalizations of the study species, suggesting coevolution between these characters. Broader comparative studies and studies of closely related species are needed to distinguish the underlying selective pressures driving these species differences. Moreover, envelope periodicity of vocalizations should be studied in greater detail. Although we attempted to analyse a broad variety of note types for each species, some note types may not have been present in our sample.

The potential selective benefits of rapid envelope periodicity are relatively unexplored in birds. Rapid envelope periodicity does not seem to increase the effective range of signals. In the cluttered habitats occupied by the study species (deciduous forest for titmice and nuthatches and farmland, residential and urban areas for sparrows), modulation rates above 10–20 Hz are rapidly degraded by reverberation off leaves and branches during propagation (Bradbury & Vehrencamp 1998). Furthermore, field observations indicate that vocalizations with the greatest rates of envelope periodicity (the titmouse D note, house sparrow 'quer' and nuthatch 'hit') are generally exchanged between individuals over short distances (Ritchison 1983; Grubb & Pravosudov 1994; Lowther & Cink 2006).

Envelope periodicity can also be processed in the frequency domain (e.g. via resolution of the sideband and carrier frequencies of a sinusoidally amplitude-modulated tone). One implication of this study and others (Lohr & Dooling 1998; Dooling et al. 2002; Lohr et al. 2006) is that birds may rely on temporal resolution to process envelope periodicity to a greater extent than some

terrestrial mammals. Moreover, some avian species, such as the sparrows and titmice of this study, may rely more heavily on temporal resolution than others, such as nuthatches. This raises the question of whether taxa with lower temporal resolution compensate for this with greater frequency resolution. Indeed, theoretical models of cochlear tuning predict a trade-off between temporal resolution and frequency resolution (see Joris et al. 2004). Measurements of frequency resolution in these -species will be a valuable next step for future research.

Concluding Remarks

In conclusion, it appears that the auditory system of songbirds has coevolved with the acoustic signal space of species-specific vocalizations, but its capacity to do so has been limited by auditory constraints. Coevolution is supported by correlations observed in this and other studies between (1) high-frequency auditory sensitivity and the maximum frequency of the vocal repertoire (Langemann et al. 1998) and (2) temporal resolution and the maximum rate or extent of envelope periodicity in the repertoire (Dooling et al. 2002). Moreover, enhanced high-frequency sensitivity of the tufted titmouse and closely related species such as the great tit may reflect a specialization for processing high-frequency communication signals such as alarm calls. Auditory constraints are suggested by conservation of the frequency range of maximum sensitivity observed in this and other studies (Dooling et al. 2000) and the mismatch with song in house sparrows. Identifying selective pressures responsible for this mismatch and examining frequency resolution in all three species may be rewarding directions for future research.

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References

Beckers, G. J. L. & TenCate, C. C. 2001. Perceptual relevance of species-specific differences in acoustical signal structure in *Streptopelia* doves. *Animal Behaviour*, **62**, 511–518.

Bode, H. W. 1945. *Network Analysis and Feedback Amplifier Design*. Toronto: Van Nostrand.

Boersma, P. & Weenink, D. 2007. *Praat: Doing Phonetics by Computer, version 4.5.17*. Computer program retrieved July 2007 from http://www.praat.org/.

Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Sunderland, Massachusetts: Sinauer Associates.

Brittan-Powell, E. F. & Dooling, R. J. 2004. Development of auditory sensitivity in budgerigars (*Melopsittacus undulatus*). *Journal of the Acoustical Society of America*, **115**, 3092–3102.

Brittan-Powell, E. F., Dooling, R. J. & Gleich, O. 2002. Auditory brainstem responses (ABR) in adult budgerigars (*Melopsittacus undulatus*). *Journal of the Acoustical Society of America*, **112**, 999–1008.

Brittan-Powell, E. F., Lohr, B., Hahn, D. C. & Dooling, R. J. 2005. Auditory brainstem responses in the eastern screech owl: an estimate of auditory thresholds. *Journal of the Acoustical Society of America*, **118**, 314–321.

Brown-Borg, H. M., Beck, M. M. & Jones, T. A. 1987. Origins of peripheral and brainstem auditory responses in the white leghorn chick. *Comparative Biochemistry and Physiology, A: Physiology*, **88**, 391–396.

Brumm, H. & Slabbekoorn, H. 2005. Acoustic communication in noise. *Advances in the Study of Behavior*, **35**, 151–207.

Cardoso, G. C., Mota, P. G. & Depraz, V. 2007. Female and male serins (*Serinus serinus*) respond differently to derived song traits. *Behavioral Ecology and Sociobiology*, **61**, 1425–1436.

Cone-Wesson, B. K., Hill, K. G. & Liu, G. 1997. Auditory brainstem response in tammar wallaby *(Macropus eugenii)*. *Hearing Research*, **105**, 119–129.

Cook, M. L. H., Varela, R. A., Goldstein, J. D., McCulloch, S. D., Bossart, G. D., Finneran, J. J., Houser, D. & Mann, D. A. 2006. Beaked whale auditory evoked potential hearing measurements. *Journal of Comparative Physiology, A*, **192**, 489–495.

Dabelsteen, T. & Pedersen, S. B. 1993. Song based species discrimination and behaviour assessment by female blackbirds (*Turdus merula*). *Animal Behaviour*, **45**, 759–771.

Dmitrieva, L. P. & Gottlieb, G. 1992. Development of brainstem auditory pathway in mallard duck embryos and hatchlings. *Journal of Comparative Physiology, A*, **171**, 665–671.

Dmitrieva, L. P. & Gottlieb, G. 1994. Influence of auditory experience on the development of brain stem auditory-evoked potentials in Mallard duck embryos and hatchlings. *Behavioral and Neural Biology*, **61**, 19–28.

Dolphin, W. F. & Mountain, D. C. 1992. The envelope following response: scalp potentials elicited in the Mongolian gerbil using sinusoidally AM acoustic signals. *Hearing Research*, **58**, 70–78.

Dolphin, W. F. & Mountain, D. C. 1994. Comparison of the envelope following response in the Mongolian gerbil using two-tone and sinusoidally amplitude-modulated tones. *Journal of the Acoustical Society of America*, **96**, 2225–2234.

Dolphin, W. F., Au, W. W., Nachtigall, P. E. & Pawloski, J. 1995. Modulation rate transfer functions to low-frequency carriers in three species of cetaceans. *Journal of Comparative Physiology, A*, **177**, 235–245.

Dooling, R. J., Lohr, B. & Dent, M. L. 2000. Hearing in birds and reptiles. In: *Comparative Hearing: Birds and Reptiles* (Ed. by R. J. Dooling, A. N. Popper & R. R. Fay), pp. 308–359. New York: Springer-Verlag.

Dooling, R. J., Leek, M. R., Gleich, O. & Dent, M. L. 2002. Auditory temporal resolution in birds: discrimination of harmonic complexes. *Journal of the Acoustical Society of America*, **112**, 748–759.

Elliot, L., Stokes, D. & Stokes, L. 1997. *Stokes Field Guide to Bird Songs: Eastern Region*. New York: Time Warner Audio Books (compact disc).

Endler, J. A. 1992. Signals, signal conditions, and the direction of evolution. *American Naturalist*, **139**, S125–S153.

Feng, A. S., Narins, P. M., Xu, C., Lin, W., Yu, Z., Qiu, Q., Xu, Z. & Shen, J. 2006. Ultrasonic communication in frogs. *Nature*, **440**, 333–336.

Frisina, R. D., Smith, R. L. & Chamberlain, S. C. 1990. Encoding of amplitude-modulation in the gerbil cochlear nucleus. 1. A hierarchy of enhancement. *Hearing Research*, **44**, 99–122.

Gaddis, P. K. 1980. Mixed flocks, accipiters, and antipredator behavior. *Condor*, **82**, 348–349.

Gaddis, P. K. 1983. Differential usage of song types by plain, bridled, and tufted titmice. *Ornis Scandinavica*, **14**, 16–23.

Gleich, O., Dooling, R. J. & Manley, G. A. 2005. Audiogram, body mass, and basilar papilla length: correlations in birds and predictions for extinct archosaurs. *Naturwissenschaften*, **92**, 595–598.

Goense, J. B. M. & Feng, A. S. 2005. Seasonal changes in frequency tuning and temporal processing in single neurons in the frog auditory midbrain. *Journal of Neurobiology*, **65**, 22–36.

Grubb, T. C. & Pravosudov, V. V. 2008. White-breasted nuthatch (*Sitta carolinensis*). In: *The Birds of North America Online* (Ed. by A. Poole), Ithaca, New York: Cornell Lab of Ornithology. doi:10.2173/bna.54.

Grubb, T. C. & Pravosudov, V. V. 1994. Tufted titmouse (*Baeolophus bicolor*). In: *The Birds of North America Online* (Ed. by A. Poole), Ithaca, New York: Cornell Lab of Ornithology. doi:10.2173/bna.86.

Hall, J. 1992. *Handbook of Auditory Evoked Responses*. Boston: Allyn & Bacon.

Hauser, M. D. & Konishi, M. 1999. *The Design of Animal Communication*. Cambridge, Massachusetts: MIT Press.

Hurly, T. A., Ratcliffe, L., Weary, D. M. & Weisman, R. 1992. White-throated sparrows (*Zonotrichia albicollis*) can perceive pitch change in conspecific song by using the frequency ratio independent of the frequency difference. *Journal of Comparative Psychology*, **106**, 388–391.

Jonsson, K. A. & Fjeldsa, J. 2006. A phylogenetic supertree of oscine passerine birds (Aves: passeri). *Zoologica Scripta*, **35**, 149–186.

Joris, P. X., Schreiner, C. E. & Rees, A. 2004. Neural processing of amplitude-modulated sounds. *Physiological Reviews*, **84**, 541–577.

Klump, G. M., Kretzschmar, E. & Curio, E. 1986. The hearing of an avian predator and its avian prey. *Behavioral Ecology and Sociobiology*, **18**, 317–323.

Kroodsma, D. E. & Miller, E. H. 1996. *Ecology and Evolution of Acoustic Communication in Birds*. Ithaca, New York: Cornell University Press.

Kuwada, S., Batra, R. & Maher, V. L. 1986. Scalp potentials of normal and hearing-impaired subjects in response to sinusoidally amplitude-modulated tones. *Hearing Research*, **21**, 179–192.

Langemann, U., Gauger, B. & Klump, G. M. 1998. Auditory sensitivity in the great tit: perception of signals in the presence and absence of noise. *Animal Behaviour*, **56**, 763–769.

Lohr, B. & Dooling, R. J. 1998. Detection of changes in timbre and harmonicity in complex sounds by zebra finches (*Taeniopygia guttata*) and budgerigars (*Melopsittacus undulatus*). *Journal of Comparative Psychology*, **112**, 36–47.

Lohr, B., Dooling, R. J. & Bartone, S. 2006. The discrimination of temporal fine structure in call-like harmonic sounds by birds. *Journal of Comparative Psychology*, **120**, 239–251.

Lowther, P. E. & Cink, C. L. 2006. House sparrow (*Passer domesticus*). In: *The Birds of North America Online* (Ed. by A. Poole), Ithaca, New York: Cornell Lab of Ornithology. doi:10.2173/bna.12.

Lucas, J. R., Peterson, L. J. & Boudinier, R. L. 1993. The effects of time constraints and changes in body mass and satiation on the simultaneous expression of caching and diet-choice decisions. *Animal Behaviour*, **45**, 639–658.

Lucas, J. R., Freeberg, T. M., Krishnan, A. & Long, G. R. 2002. A comparative study of avian auditory brainstem responses: correlations with phylogeny and vocal complexity, and seasonal effects. *Journal of Comparative Physiology, A*, **188**, 981–992.

Lucas, J. R., Freeberg, T. M., Long, G. R. & Krishnan, A. 2007. Seasonal variation in avian auditory evoked responses to tones: a comparative analysis of Carolina chickadees, tufted titmice, and white-breasted nuthatches. *Journal of Comparative Physiology, A*, **192**, 201–215.

Mann, D. A., Colbert, D. E., Gaspard, J. C., Casper, B. M., Cook, M. L. H., Reep, R. L. & Bauer, G. B. 2005. Temporal resolution of the Florida manatee (*Trichechus manatus latirostris*) auditory system. *Journal of Comparative Physiology, A*, **191**, 903–908.

Marler, P. 1955. Characteristics of some animal calls. *Nature*, **176**, 6–8.

Marler, P. & Slabbekoorn, H. 2004. *Nature's Music: the Science of Birdsong*. San Diego, California: Elsevier Academic Press.

Mooney, T. A., Nachtigall, P. E. & Yuen, M. L. 2006. Temporal resolution of the Risso's dolphin (*Grampus griseus*) auditory system. *Journal of Comparative Physiology, A*, **192**, 373–380.

Neely, S. T., Norton, S. J., Gorga, M. P. & Jesteadt, W. 1988. Latency of auditory brain-stem responses and otoacoustic emissions using tone-burst stimuli. *Journal of the Acoustical Society of America*, **83**, 652–656.

Nelson, D. A. & Marler, P. 1990. The perception of birdsong and an ecological concept of signal space. In: *Comparative Perception. Vol. 2: Complex Signals* (Ed. by W. C. Stebbins & M. A. Berkley), pp. 443–478. New York: J. Wiley.

Okanoya, K. & Dooling, R. J. 1988. Hearing in the swamp sparrow (*Melospiza georgiana*) and the song sparrow (*Melospiza melodia*). *Animal Behaviour*, **36**, 726–732.

Owens, J. L. & Freeberg, T. M. 2007. Variation in chick-a-dee calls of tufted titmice (*Baeolophus bicolor*): note type and individual distinctiveness. *Journal of the Acoustical Society of America*, **122**, 1216–1226.

Pyle, P. 1997. *Identification Guide to North American Birds*. Bolinas, California: Slate Creek Press.

Ritchison, G. 1983. Vocalizations of the white-breasted nuthatch. *Wilson Bulletin*, **95**, 440–451.

Saunders, J. C., Coles, R. B. & Gates, G. R. 1973. The development of auditory evoked responses in the cochlea and cochlear nuclei of the chick. *Brain Research*, **63**, 59–74.

Saunders, J. C., Duncan, R. K., Doan, D. E. & Werner, Y. L. 2000. The middle ear of reptiles and birds. In: *Comparative Hearing: Birds and Reptiles* (Ed. by R. J. Dooling, A. N. Popper & R. R. Fay), pp. 308–359. New York: Springer-Verlag.

Schroeder, D. J. & Wiley, R. H. 1983. Communication with repertoires of song themes in tufted titmice. *Animal Behaviour*, **31**, 1128–1138.

Sheykholeslami, K., Kaga, K., Tsuzuku, T. & Mizutani, M. 2001. Electrophysiological measures of auditory function in the neurofilament-deficient mutant quail (Quv). *Hearing Research*, **153**, 115–122.

Sisneros, J. A., Forlano, P. M., Deitcher, D. L. & Bass, A. H. 2004. Steroid-dependent auditory plasticity leads to adaptive coupling of sender and receiver. *Science*, **305**, 404–407.

Slabbekoorn, H. & Peet, M. 2003. Birds sing at a higher pitch in urban noise. *Nature*, **424**, 267.

Slabbekoorn, H., Yeh, P. & Hunt, K. 2007. Sound transmission and song divergence: a comparison of urban and forest acoustics. *Condor*, **109**, 67–78.

Sprecht, R. 2002. *Avisoft–SASLab Pro version 4.23b*. Berlin: Avisoft Bioacoustics.

Supin, A. Y. & Popov, V. V. 1995. Envelope-following response and modulation transfer function in the dolphin's auditory system. *Hearing Research*, **92**, 38–46.

Supin, A. Y., Popov, V. V. & Mass, A. M. 2001. *The Sensory Physiology of Aquatic Mammals*. Boston: Kluwer Academic.

Thirakhupt, K. 1985. Foraging ecology of sympatric parids: individual and populational responses to winter food scarcity. Ph.D. thesis, Purdue University, West Lafayette, Indiana.

Viemeister, N. F. & Plack, C. J. 1993. Time analysis. In: *Human Psychophysics* (Ed. by W. A. Yost, A. N. Popper & R. R. Fay), pp. 116–154. New York: Springer-Verlag.

Woolley, S. M. N. & Rubel, E. 1999. High-frequency auditory feedback is not required for adult song maintenance in Bengalese finches. *Journal of Neuroscience*, **19**, 358–371.