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Habitat-related differences in the frequency selectivity of auditory filters in songbirds

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Summary

1. Environmental constraints in woodland habitats favour long-range communication signals with slow modulations of frequency and amplitude, while constraints in open habitats favour faster modulations.

2. Spectral filtering by the peripheral auditory system results in a trade-off between frequency resolution and temporal resolution of modulations. Greater frequency resolution requires integration of acoustic signals over a longer period of time, which in turn decreases responsiveness to temporal modulations.

3. Here, we test the hypothesis in songbirds that woodland habitats have selected for narrowly tuned auditory filters with high frequency resolution of tonal elements, while open habitats have selected for broader auditory filters with greater temporal resolution of rapid modulation.

4. Auditory filter shapes were measured at 2, 3 and 4 kHz in three woodland species, the dark-eyed junco (*Junco hyemalis*), tufted titmouse (*Baeolophus bicolor*) and white-breasted nuthatch (*Sitta carolinensis*), and two open-habitat species, the house sparrow (*Passer domesticus*) and white-crowned sparrow (*Zonotrichia leucophrys*). Auditory filter shapes were derived from auditory brainstem response thresholds in notched noise using Patterson's rounded exponential (roex) auditory filter model.

5. Auditory filters increased in bandwidth with increasing frequency in all species except the dark-eyed junco. Auditory filters were generally narrower in woodland species than open-habitat species as predicted, although auditory filters of the junco were relatively narrow only at 4 kHz, and the difference between white-crowned sparrows and tufted titmice was not significant. Finally, at 4 kHz, open-habitat species had auditory filters with lower signal-to-noise response thresholds than woodland species (i.e. greater response efficiency).

6. The results suggest that environmental constraints on song structure have influenced the evolution of peripheral auditory filters in songbirds, although species using signals not optimized for long-range transmission should be less affected. Differences in filter bandwidth between dark-eyed juncos and white-crowned sparrows are noteworthy because *Junco* and *Zonotrichia* share a recent common ancestor as sister genera within the Emberizidae. Finally, open-habitat species may compensate for inherently lower sensitivity in noise of broad auditory filters with greater response efficiency.

Key-words: acoustic adaptation hypothesis, auditory brainstem response, frequency resolution, notched noise masking, vocal communication

Introduction

The physical characteristics of the environment have long been recognized to constrain the structure of signals used for long-range communication in animals (Morton 1975; Endler 1993; Marchetti 1993). In forested habitats, for example, acoustic signals below 3–5 kHz in frequency with slow modulations of frequency and amplitude are favoured because they are less degraded by reverberation during transmission than higher frequency, more rapidly modulated signals (the acoustic adaptation hypothesis; Morton 1975; Waser & Waser 1977; Wiley & Richards 1978; Naguib 2003). In open habitats, in contrast, higher frequency, rapidly modulated signals are possible due to limited reverberation. Moreover, rapid modulations occurring more than 10–20 times per second are favoured because they are less

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likely to be degraded by added modulations from wind (Richards & Wiley 1980). In songbirds, tests of the acoustic adaptation hypothesis are largely consistent with its predictions. That is, species and conspecific populations inhabiting more open environments tend to sing songs with higher acoustic frequencies and faster modulation rates than counterparts inhabiting woodland environments (e.g. Wiley 1991; Badyaev & Leaf 1997; Kopuchian *et al.* 2004; Nicholls & Goldizen 2006), although other factors contribute to the acoustic structure of bird song (Boncoraglio & Saino 2007).

Songbirds adapted to communication in different environments may require different auditory configurations for optimal processing of long-range signals (songs), as suggested by Wiley (1991). The peripheral auditory system performs a spectral analysis of sound that results in a trade-off between frequency resolution and temporal resolution of changes in frequency and amplitude (Moore 1993; Viemeister & Plack 1993; Bradbury & Vehrencamp 1998). The system acts as a bank of overlapping bandpass filters, or 'auditory filters', which decompose broadband sounds into spectrally tuned channels (Fletcher 1940). Narrower bandwidth auditory filters provide greater frequency resolution because signals of similar frequency are more likely to be processed in separate channels of the system (i.e. they stimulate sufficiently different populations of sensory hair cells on the basilar papilla to be differentiated). However, the high frequency selectivity of narrow auditory filters requires integration of the signal over a relatively long period of time. The long integration period limits temporal resolution of changes in the amplitude or frequency of a signal over time. As a general rule, amplitude modulation (AM; see Table 1 for commonly used abbreviations) frequencies that exceed the bandwidth of the auditory filter cannot pass through, and therefore cannot be processed through a temporal mechanism (i.e. neural phase-locking to AM cycles; Viemeister & Plack 1993). Fewer studies have focused on frequency modulation (FM), but narrow bandwidth auditory filters appear to limit auditory processing of rapid frequency sweeps in humans (Thyer & Mahar 2006). Potentially, songbirds adapted to communication in open environments may benefit from broader auditory filters that trade off frequency resolution for greater temporal resolution of FM and AM, while woodland species may benefit from narrower, more selective filters with finer frequency resolution of tonal elements but less sensitivity to temporal modulations. However, this hypothesis remains unexplored.

Table 1. Commonly used abbreviations and definitions

ABR	Auditory brainstem response
AM	Amplitude modulation
DEJU	Dark-eyed junco
ERB	Equivalent rectangular bandwidth. The bandwidth of the auditory filter containing one-half of its area, equal to four times the centre frequency divided by p
ETTI	Eastern tufted titmouse
FM	Frequency modulation
HOSP	House sparrow
K'	Response efficiency. The signal-to-noise ratio of the auditory filter at threshold expressed in dB
nw	Normalized notch bandwidth of the notched noise masker. Equal to one-half of the notch bandwidth divided by the centre frequency
p	Passband parameter. Determines the slope of the auditory filter function near its centre frequency
r	Range parameter. The minimum value of the auditory filter function
roex(p,r)	The two parameter, rounded exponential auditory filter function
WBNU	White-breasted nuthatch
WCSP	White-crowned sparrow

The peripheral auditory filters of songbirds have been studied in the European starling (*Sturnus vulgaris*) using a behavioural notched noise-masking technique (Marean *et al.* 1998) and single cell recordings at the level of the auditory nerve (Manley *et al.* 1985; Gleich 1994), and in several strains of domestic canary (*Serinus canaria*) using psychophysical tuning curves (Lauer, Dooling & Leek 2009). Moreover, indirect measures of frequency resolution are available for a broader assemblage of species based on critical ratio and band experiments (reviewed in Dooling, Lohr & Dent 2000). Taken together, these studies suggest that songbirds generally have broader auditory filters with less frequency selectivity than humans and other terrestrial mammals. Concomitantly, songbirds appear to have greater temporal resolution. For example, zebra finches (*Taeniopygia guttata*) and, to a lesser extent, canaries (*Serinus canaria*) exhibit greater sensitivity to temporal modulations of fine structure than terrestrial mammals (Dooling *et al.* 2002; Lohr, Dooling & Bartone 2006). Zebra finches and starlings are also more sensitive to temporal gaps in broadband noise at low sound pressure levels than terrestrial mammals, and show a slower decrease in sensitivity to AM with increasing modulation frequency (Dooling, Lohr & Dent 2000).

The notched noise method of deriving auditory filter shape involves measuring auditory thresholds in the presence of notched masking noise. Notched noise is white noise with a band of energy, or notch, filtered out around a specific test frequency. Auditory thresholds at the test frequency are measured as the bandwidth of the notch is increased. The resulting threshold-by-notch bandwidth function is used to derive the shape of the auditory filter based on the power spectrum model of auditory masking (Fletcher 1940; reviewed in Moore 1993). The model assumes that (i) the test frequency is processed within a single filter; (ii) only spectral regions of the noise that overlap with the passband of the filter contribute to masking of the auditory threshold; and (iii) the degree of a masking is proportional to the amount of noise passing through the filter. Auditory thresholds can be measured behaviourally (e.g. Marean *et al.* 1998) or physiologically using the auditory brainstem response (ABR; e.g. Popov, Supin & Klishin 1997) as in the current study. ABRs are voltage waveforms recorded from the scalp in response to transient acoustic stimuli, such as tone bursts, that reflect neural activity in the auditory nerve and brainstem nuclei (Hall 1992). ABR waveforms consist of 3–5 voltage peaks occurring within 10 ms of stimulus onset. The ABR threshold is the lowest stimulus intensity that evokes a detectable waveform. In birds, ABR thresholds are 25–30 dB higher than behavioural auditory thresholds (Dmitrieva & Gottlieb 1992; Brittan-Powell, Dooling & Gleich 2002; Brittan-Powell *et al.* 2005; Henry & Lucas 2008).

Here, we report auditory filter shapes of five songbird species at 2, 3 and 4 kHz. Filter shapes were derived from notched noise experiments based on the rounded exponential filter model of Patterson (e.g. Patterson *et al.* 1982; Moore & Glasberg 1983; Marean *et al.* 1998; May, Kimar & Prosen 2006). Masked thresholds were estimated using the ABR. The study species included three woodland species, the dark-eyed junco (*Junco hyemalis*; family Emberizidae), tufted titmouse (*Baeolophus bicolor*; family Paridae) and white-breasted nuthatch (*Sitta carolinensis*; family Sittidae), and two open-habitat species, the house sparrow (*Passer domesticus*; family Passeridae) and white-crowned sparrow (*Zonotrichia leucophrys*; family Emberizidae). Based on physical constraints of the environment on long-range signals, we predicted that the open-habitat species should have broader auditory filter bandwidths than species inhabiting woodland environments.

Materials and methods

SUBJECTS AND ANAESTHESIA

We collected auditory data from five dark-eyed juncos (three males, two females), eight tufted titmice (four males, three females and one individual of unknown sex), twelve house sparrows (eight males, four females), six white-breasted nuthatches (five males, one female) and four white-crowned sparrows (of unknown sex) between May 2008 and February 2009. Sex was determined based on plumage differences in juncos, house sparrows and nuthatches (Pyle 1997), and wing chord in titmice (males: ≥80 mm; females: ≤79 mm; Thirakhupt 1985; Lucas, Peterson & Boudinier 1993). Sex could not be determined in white-crowned sparrows due to limited sexual dimorphism in this species. Subjects were captured near Purdue University in West Lafayette, IN, USA, at three private residences and two wooded areas, the Martel Forest and Ross Biological Reserve, using elevated treadle traps baited with mixed seed. Each subject was fitted with a uniquely numbered aluminium leg band for identification and transported to an indoor aviary at Purdue University. Subjects were housed individually in 1-m^3 wire mesh cages and provided with mixed seed, two to three mealworms, grit and vitamin treated water daily. Auditory tests were typically conducted in the afternoon on the day of capture, and subjects were released at their capture site 1–2 days after testing.

Subjects were weighed and then anaesthetized for the auditory tests with an injection into the breast muscle. Average body mass ± SD in grams was 20·5 ± 1·5 in juncos, 20·9 ± 1·4 in titmice, 27·7 ± 2·3 in house sparrows, 20·7 ± 0·6 in nuthatches and 32·6 ± 2·7 in white-crowned sparrows. House sparrows and nuthatches were anaesthetized with ketamine (60 mg kg^{-1}) and xylazine (12 mg kg^{-1}). Juncos, titmice and white-crowned sparrows were anaesthetized with ketamine (55 mg kg^{-1} in titmice and 75 mg kg^{-1} in juncos and white-crowned sparrows) and midazolam (5·5 mg kg^{-1} in titmice and 7·5 mg kg^{-1} in juncos and white-crowned sparrows) because it was difficult to achieve adequate anaesthesia with ketamine and xylazine in these species. The choice of anaesthetic agent appears to have little impact on ABR amplitude and latency. In tufted titmice, responses to a 90-dB SPL click stimulus were similar between individuals anaesthetized with ketamine and midazolam in the current study (amplitude: 17·6 ± 0·8 μV; latency: 3·32 ± 0·03 ms; $N = 8$) and ketamine and xylazine in previous experiments (amplitude: 20·4 ± 1·5 μV; latency: 3·32 ± 0·03 ms; $N = 9$; two-tailed *t*-test of amplitude: $t_{15} = -1{\cdot}57$, $P = 0{\cdot}14$; two-tailed *t*-test of latency: $t_{15} = 0{\cdot}19$, $P = 0{\cdot}85$). One to two supplemental injections at half the initial dose were given at 20–40 min intervals to maintain anaesthesia for 45 min (the approximate duration of the auditory filter experiments).

AUDITORY TEST EQUIPMENT

Auditory tests were conducted in a 1·2-m tall by 1·4-m wide by 1·2-m deep sound chamber lined with 7·7-cm-thick Sonex foam (Acoustic Solutions, Richmond, VA, USA). Subjects were positioned centrally on the floor of the chamber on a pre-heated pad (Pet Supply Imports, South Holland, IL, USA) with their right ear facing upwards. 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 39 ± 2 °C by adding or removing layers of towel. Needle electrodes (Nicolet Biomedical, Fitchburg, WI, USA) were inserted under the skin of the subject's scalp high at the vertex of the skull (positive), directly posterior to the right auditory meatus (negative), and at the nape of the neck (ground). The electrode leads ran from the subject to a low-impedance headstage also located in the sound chamber [Tucker Davis Technologies (TDT) model HS4, Gainesville, FL, USA]. Inter-electrode impedance was below 7000 ohms. An electromagnetically shielded dynamic loudspeaker (RCA (Indianapolis, IN, USA) model 40–5000; 140–20,000 Hz frequency response) was suspended 30 cm above the subject in the sound chamber.

Stimulus delivery, response acquisition and data storage were coordinated by a TDT system II modular rack-mount system and Dell computer equipped with a signal-processing card (TDT model AP2) in a room adjacent to the sound chamber. Experiments were conducted using two TDT computer programs: SigGen32 for stimulus specification and BioSig32 for stimulus delivery and data acquisition. Stimuli consisted of periodically presented tone bursts and continuous notched masking noise. Tone bursts were generated digitally on the signal-processing card of the computer and converted to analogue with a convertor (TDT model DA3-4). Two analogue waveform generators (TDT model WG1) acted as white noise sources for the notched noise maskers. The first noise source was routed through a highpass filter and the second through a lowpass filter (TDT model PF1 programmable filters); corner frequencies were set to the upper and lower frequencies of the notch respectively. The roll-off rate of the filters was approximately 156 dB per octave based on 26 poles (Fig. 1d, dashed lines). Filtered noise sources were routed through two attenuators (TDT model PA4) to control intensity level and then mixed with the tone bursts in a signal mixer (TDT model SM3). Output from the mixer was passed through a 31-band equalizer (Behringer Ultragraph model FBQ6200, Bethel, WA, USA) to equalize the frequency response of the system before final amplification by a Crown D75 amplifier (Elkhart, IN, USA) driving the RCA loudspeaker in the sound chamber. We equalized the frequency response of the system by generating continuous pure tones of constant amplitude (1 V) on the AP2 card of the computer. Tones were played at the centre frequency of each third-octave band from 0·4 to 10 kHz (15

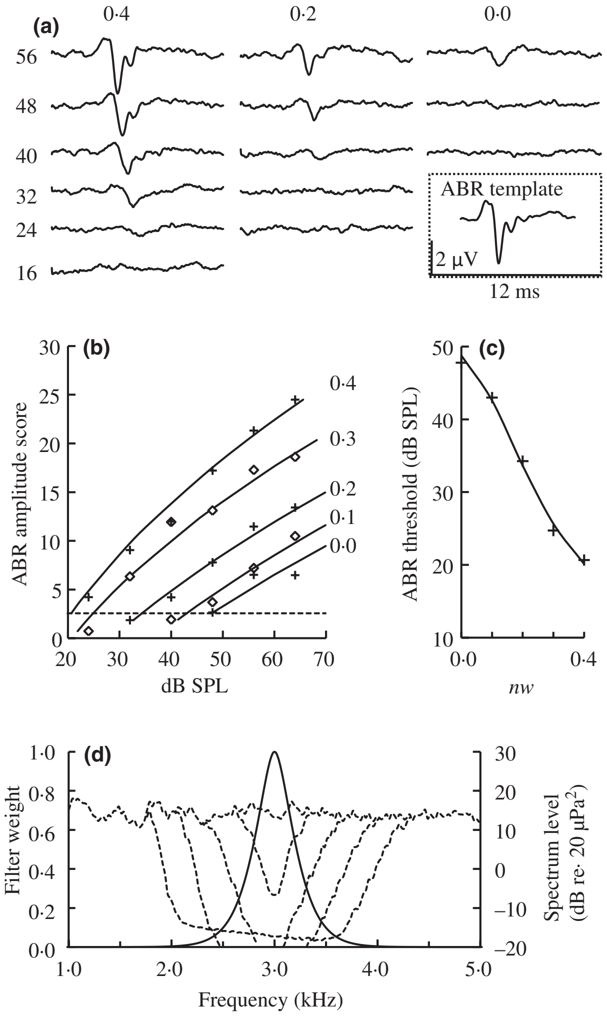

Fig. 1. (a) Auditory brainstem response (ABR) waveforms of a tufted titmouse recorded in response to 3 kHz tone bursts. The intensity level of the tone burst is given in dB SPL to the left of each waveform, while the normalized notch bandwidth (*nw*) of the masking noise is given above. The waveform scale and ABR template used to calculate the amplitude score are drawn in the dotted box (lower right). (b) ABR amplitude score (+ symbols and diamonds) plotted as a function of stimulus intensity for each value of *nw* (right). The solid lines represent the fit of the generalized linear model. The ABR threshold is the dB SPL at the intercept between the function and the dashed line. (c) ABR thresholds (+ symbols) from (b) plotted as a function of *nw*. The solid line represents the fit of the roex(p,r) auditory filter model (p = 23·4, r = 0·000030, K' = 41·7). (d) The shape of the auditory filter derived from the ABR threshold function in (c) (solid line, left axis). Also drawn are the long-term average power spectra (bin width = 25 Hz) of the notched noise maskers (dashed lines, right axis).

bands), and the sound pressure level of the tone was adjusted to 65 ± 1 dB SPL using the gain controls of the equalizer. Sound pressure level was measured at the location of the bird's ear with a Bruel and Kjaer model 1613 Precision Sound Level Meter (Norcross, GA, USA) and model 4131 2·6 cm condenser microphone.

Response waveforms were conducted from the headstage in the sound chamber to a biological amplifier (TDT model DB4) through fiberoptic cables for response amplification and filtering. Filtered, amplified responses were digitized by a convertor (TDT model AD2) prior to averaging and storage on the hard disk of the computer.

NOTCHED NOISE EXPERIMENTS

Notched noise experiments were conducted at test frequencies of 2, 3 and 4 kHz in random order. We were unable to complete notched noise experiments at all test frequencies in every subject due to individual differences in the duration of anaesthesia and low ABR amplitude relative to the level of background noise in some cases. Experiments in which ABR amplitude did not increase consistently with increasing stimulus intensity (due to low ABR signal-to-noise ratio) were excluded from further analysis. Sample sizes at 2, 3 and 4 kHz were respectively 4, 5 and 5 in dark-eyed juncos; 7, 8 and 5 in tufted titmice; 8, 9 and 8 in house sparrows; 5, 6 and 2 (due to low ABR signal-to-noise ratio) in white-breasted nuthatches; and 4, 4 and 4 in white-crowned sparrows.

Each notched noise experiment measured the ABR threshold at the test frequency as the normalized bandwidth of the notch (*nw*, half the bandwidth divided by the centre frequency) was increased from 0 to 0·4 in steps of 0·1. First, ABR waveforms were recorded under each of the five masking conditions in response to tone bursts ranging in intensity from 72 to 16 dB SPL in 8 dB steps (Fig. 1a). Tone bursts were 8 ms long with 2 ms $\cos^2$ onset/offset ramps and an inter-stimulus interval of 11·6 ms (51·1 stimuli per second). The masking noise had a spectrum level of 15·3 ± 2 dB relative to 20 µPa^2 outside of the bandwidth of the notch (Fig. 1d, dashed lines). Responses to 1000 stimulus repetitions of alternating phase (0·5 π and 1·5 π radians) were averaged together to generate each ABR waveform. Responses were sampled for 12 ms at a sampling frequency of 40 kHz. Responses were amplified 200,000 times and bandpass filtered from 0·1 to 10 kHz prior to averaging. Responses that exceeded ± 20 µV (40% of the maximum possible input) were excluded from the averaging process as potential artefacts.

The resulting ABR waveforms were entered into a cross-correlation analysis conducted in PRAAT (Boersma & Weenink 2009) to estimate ABR thresholds. Cross-correlation involves cross-multiplying two waveforms as the first waveform is shifted in time relative to the second. The maximum cross-product of the cross-correlation provides a measure of similarity between the waveforms. Each analysis involved (i) generating an ABR template; (ii) determining the amplitude score of each ABR in the data set by cross-correlation; (iii) removing non-significant ABRs; and (iv) calculating the ABR threshold under each masking condition from the amplitude score by stimulus intensity functions.

1. Auditory brainstem response templates (Fig. 1a, dotted box) were generated by averaging together the ABR waveforms evoked at intensity levels of 72, 64 and 56 dB SPL and *nw* of 0·4. We accounted for the increased latency of the 64 and 56 dB SPL waveforms by subtracting the time shift of the maximum cross-product with the 72-dB SPL waveform, determined by cross-correlation, from the beginning of the waveforms prior to averaging. The first 1·5 ms and last 2·5 ms of the average waveform were deleted to form the final, 8 ms template.
2. We defined the amplitude score of each ABR waveform in the data set as the maximum cross-product with the ABR template divided by the standard deviation of a null distribution of cross-product values. The null distribution was determined by cross-correlating the ABR template with 1·5 s of electrophysiological background noise. The background noise was a concatenation of 60-ms recordings obtained from the subjects under quiet conditions using the acquisition parameters described above. Null distributions were approximately normal with a mean of zero.

3. Auditory brainstem response s were removed from the data set if the timing of the maximum cross-product was inconsistent with the timing of cross-products observed at higher stimulus intensity levels, or if the amplitude score was not $>1{\cdot}645$. Time lags were expected to increase by 0·1–0·4 ms for every 8 dB decrease in stimulus intensity due to increasing latency of ABR peaks. The lower bound of 1·645 corresponds to an amplitude score greater than zero at the 95% confidence level.
4. Auditory brainstem response thresholds were estimated from the amplitude score by stimulus intensity function at each value of *nw* (Fig. 1b). The ABR threshold was defined as the stimulus intensity level necessary to produce an amplitude score of 2·56. An amplitude score of 2·56 is greater than zero at the 99·5% confidence level. Amplitude score by stimulus intensity functions were roughly linear. We calculated ABR thresholds by modelling the effects of *nw* and stimulus intensity on amplitude score using a generalized linear model (PROC GLM; SAS Institute, Inc., Cary, NC, v. 9·1); *nw* was treated as a class level variable while stimulus intensity was treated as a continuous variable. A stimulus intensity squared term and stimulus intensity by *nw* interaction were included in addition to the main effects to account for slight nonlinearity of the amplitude score by stimulus intensity function and variation in slope of the function across values of *nw* respectively.

FILTER SHAPE

Each ABR threshold by notch width function (Fig. 1c) was used to estimate an auditory filter shape (Fig. 1d, solid line). The procedure for deriving auditory filter shapes from notched noise data has been described previously in detail (Glasberg & Moore 1990). In short, the masked threshold for detecting a tone, P_s, in Pa^2 is assumed to equal

$$P_s = K \int_0^\infty N(f)\, W(f)\, df,$$

where K is a constant indicating the minimum signal-to-noise ratio of the auditory filter necessary for signal detection, $N(f)$ is the long-term average power spectrum of the masking noise in $Pa^2\ Hz^{-1}$ and $W(f)$ is the weighting function of the auditory filter ranging from 0 to 1. A lower value of K indicates a lower signal-to-noise threshold of the auditory filter, and therefore more efficient extraction of the signal from noise.

We measured $N(f)$ directly from 2-s recordings of the notched noise maskers made using a Marantz PMD690 digital recorder and Sennheiser K6-ME62 omnidirectional microphone (Mahwah, NJ, USA; 48 kHz sampling frequency). Long-term power spectra of the recordings were generated in PRAAT with a bin width of 25 Hz (Fig. 1d, dashed lines). K and $W(f)$ were solved for using an iterative Gauss–Newton polynomial fitting procedure (PROC NLIN). The mathematical form of $W(f)$ was modelled as the rounded exponential function of Patterson *et al.* (1982); the 'roex(p,r)' auditory filter model) because it generally provides a more stable fit to notched noise data than functions employing more parameters (Unoki *et al.* 2006). The auditory filter was assumed to be symmetric around its centre frequency. Expressed as a function of g, the normalized deviation in frequency from the centre frequency (frequency deviation/centre frequency), the weight of the auditory filter is given by,

$$W(g) = (1-r)(1+pg)e^{-pg} + r.$$

The p parameter indicates the slope of the function near its centre frequency and defines the equivalent rectangular bandwidth (ERB) of the auditory filter provided that the value of r is small. ERB indicates the bandwidth of the auditory filter containing one-half of its area, and is equal to $4/p$ times the centre frequency of the filter in Hertz. The r parameter limits the dynamic range of the auditory filter function by imposing a minimum value on the weighting function.

The above equations were combined into the following form to solve for K, p and r from the ABR threshold by notch width function,

$$P_s(nw)' = K' + 10 \times \log_{10} \sum_{i=1}^{N} \frac{\mathrm{PSD}_{nw(i)} \times \int_i \mathrm{roex}(p,r)}{4 \times 10^{-10}},$$

where $Ps(nw)'$ is the masked ABR threshold in notched noise of notch-width nw in dB SPL, K' is the signal-to-noise threshold of the auditory filter expressed in dB (i.e. $10 \times \log_{10} K$), N is the number of 25-Hz bins between 0·2 and 1·8 times the test frequency, $\mathrm{PSD}_{nw(i)}$ is the power spectral density of notched noise of notch-width nw in bin i in $Pa^2\ Hz^{-1}$ and $\int_i \mathrm{roex}(p,r)$ is the integral of the roex(p,r) function evaluated over bin i. The integral of the roex(p,r) function over bin i is given by

$$-(1-r)p^{-1}(2+pa)e^{-pa} + (1-r)p^{-1}(2+pb)e^{-pb} + r(a-b),$$

where a and b are the frequency limits of the bin i in terms of g, and a is the greater value of the two. The value of r was constrained between zero and an upper bound to ensure that the ERB of the filter was accurately represented by p. Specifically, the contribution of the r parameter to the filter weight was constrained to be less than the contribution of the p parameter within g of 0·35. Hence,

$$0 \le r \le (1 + 0{\cdot}35p)e^{-0{\cdot}35p}$$

STATISTICAL ANALYSES

We used repeated-measures ANOVAS (PROC MIXED) to estimate mean ABR thresholds of each species at each notch width. A separate ANOVA was conducted at each stimulus frequency with compound symmetry within-subject covariance structure. Each ANOVA included main effects of *nw* (the within-subject variable) and species, and the interaction between species and *nw*. Notch width was treated as a class variable with five levels. The 95% confidence intervals of ABR thresholds were generated by calculating least-squares (LS) means of the species by notch-width interaction (LSMEANS statement of PROC MIXED). The degrees of freedom of the LS means were calculated using the Kenward–Rogers algorithm. Normal probability plots of the residuals indicated that they were approximately normally distributed for each ANOVA model (PROC UNIVARIATE).

Repeated-measures ANOVAS with compound symmetry within subject covariance structure were used to investigate the effects of species, sex and frequency on auditory filter ERB and K' in separate analyses. Compound symmetry provided a lower Bayesian Information Criterion and similar Akaike Information Criterion to a model with unstructured covariance, suggesting that compound symmetry adequately characterizes within-subject covariance. The models included effects of frequency (the within subject variable), species, sex (nested within species) and the interaction between frequency and species. Frequency was treated as a class variable with three levels, and non-significant interactions were dropped in order of decreasing P-value. We explored significant effects using contrasts and pairwise comparisons of LS means (CONTRAST and LSMEANS statements of PROC MIXED). LS means ± SE are reported throughout unless otherwise noted. Denominator degrees of freedom were calculated using the Kenward–Rogers algorithm. Normal probability plots of the residuals indicated that they were approximately normally distributed for each ANOVA model (PROC UNIVARIATE).

The distribution of r values contained a large number of observations at or near zero. We therefore limited our analysis of the r parameter to calculations of the median and interquartile range for each species at each frequency.

Results

Auditory brainstem response thresholds decreased with increasing notch bandwidth in all subjects at all test frequencies (Fig. 2). The roex(p,r) auditory filter model provided a good fit to the ABR threshold functions. The proportion of variance in ABR thresholds described by the model had a median value of 0·985 and interquartile range from 0·970 to 0·993.

The analysis of auditory filter ERB indicated significant main effects of frequency ($F_{2,46\cdot4} = 22\cdot81$, $P < 0\cdot001$) and species ($F_{4,26\cdot1} = 6\cdot04$, $P = 0\cdot001$), a significant interaction between frequency and species ($F_{8,46} = 3\cdot45$, $P = 0\cdot003$) and no significant effect of sex nested within species ($F_{4,20\cdot5} = 0\cdot34$, $P = 0\cdot85$). The effect of frequency on ERB was similar among tufted titmice, white-breasted nuthatches, house sparrows and white-crowned sparrows ($F_{6,46\cdot9} = 0\cdot25$, $P = 0\cdot96$; Fig. 3a, dashed lines). Within this group, ERB increased by 72 ± 28 Hz from 2 to 3 kHz ($t_{44\cdot7} = 2\cdot54$, $P = 0\cdot015$) and 193 ± 32 Hz from 3 to 4 kHz ($t_{48\cdot9} = 5\cdot97$, $P < 0\cdot001$). Moreover, averaged across frequencies, woodland species tended to have lower ERB than open-habitat species (Fig. 4). ERB was lower in white-breasted nuthatches than white-crowned sparrows (−97 ± 47 Hz; $t_{27\cdot1} = -2\cdot08$, $P = 0\cdot047$) and house sparrows (−170 ± 40 Hz; $t_{34\cdot7} = -4\cdot24$, $P < 0\cdot001$), and lower in tufted titmice than house sparrows (−125 ± 33 Hz; $t_{27\cdot9} = -3\cdot75$, $P = 0\cdot001$). However, the difference in ERB between tufted titmice and white-crowned sparrows was not significant (−52 ± 41; $t_{22} = -1\cdot26$, $P = 0\cdot22$). Finally, ERB did not vary significantly between species from the same habitat, that is, between white-breasted nuthatches and tufted titmice ($t_{31\cdot8} = -1\cdot08$, $P = 0\cdot29$) or house sparrows and white-crowned sparrows ($t_{23\cdot1} = 1\cdot89$, $P = 0\cdot07$).

The effect of frequency on auditory filter ERB differed markedly in dark-eyed juncos from the other study species ($F_{2,43\cdot9} = 12\cdot76$, $P < 0\cdot001$). ERB of dark-eyed juncos did not vary with frequency ($F_{2,43} = 1\cdot06$, $P = 0\cdot35$; Fig. 3a, solid line). Compared to the other species, auditory filters of dark-eyed juncos were relatively broad at 2 kHz, intermediate at 3 kHz and narrow at 4 kHz (Fig. 3a). Specifically, ERB was greater at 2 kHz than in tufted titmice and white-breasted nuthatches, and lower at 4 kHz than in house sparrows, white-crowned sparrows and tufted titmice, but not white-breasted nuthatches (Table 2).

The analysis of the signal-to-noise threshold of the auditory filter (K') indicated a significant main effect of species ($F_{2,24\cdot5} = 4\cdot28$, $P = 0\cdot009$) and interaction between species and frequency ($F_{8,45\cdot9} = 2\cdot79$, $P = 0\cdot013$), but no main effect of frequency ($F_{2,46\cdot4} = 1\cdot47$, $P = 0\cdot24$) or nested effect of sex within species ($F_{4,23} = 0\cdot40$, $P = 0\cdot80$). K' was similar among species at 2 kHz ($F_{4,68\cdot9} = 1\cdot19$, $P = 0\cdot32$) but differed at 3 kHz ($F_{4,68\cdot9} = 2\cdot52$, $P = 0\cdot049$) and 4 kHz ($F_{4,69} = 5\cdot87$, $P < 0\cdot001$; Fig. 3b). At 3 kHz, K' was lower in house sparrows than white-breasted nuthatches and white-crowned sparrows, and lower in tufted titmice than white-breasted nuthatches (note that lower K' indicates more efficient extraction of the signal from noise; Table 3). At

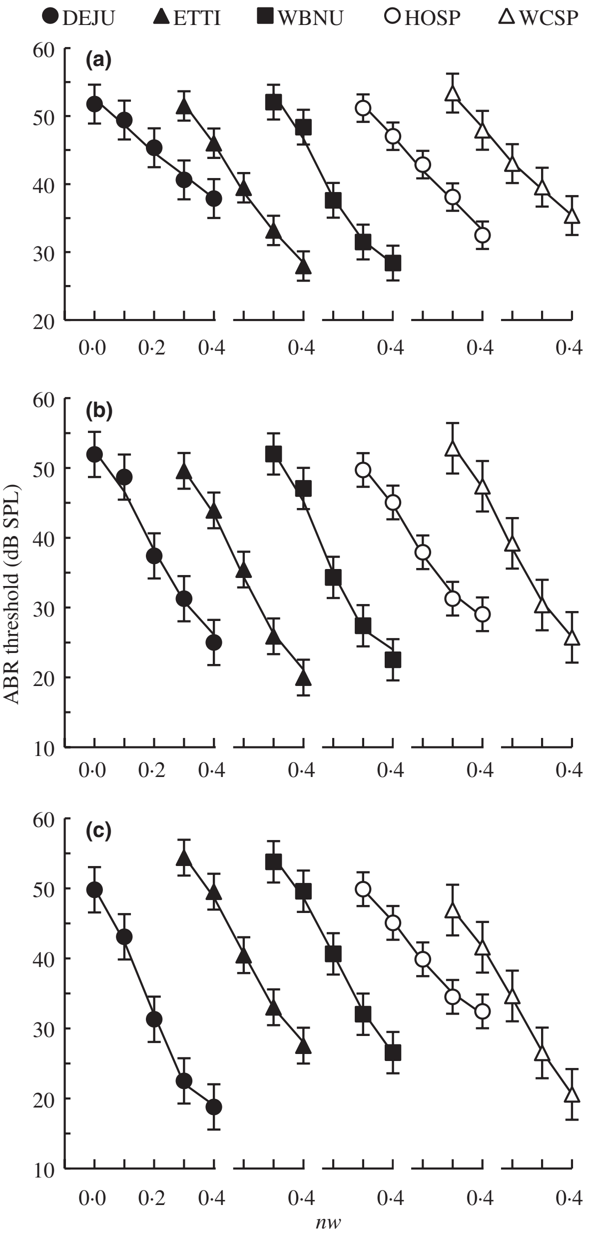

Fig. 2. Auditory brainstem response thresholds (95% confidence intervals of least-squares means) of each species (see legend, top) as a function of nw at test frequencies of (a) 2 kHz, (b) 3 kHz and (c) 4 kHz. Adjacent functions are offset along the nw axis by 0·3 units. See Table 1 for species abbreviations. Note that the closed symbols indicate woodland species and the open symbols open-habitat species.

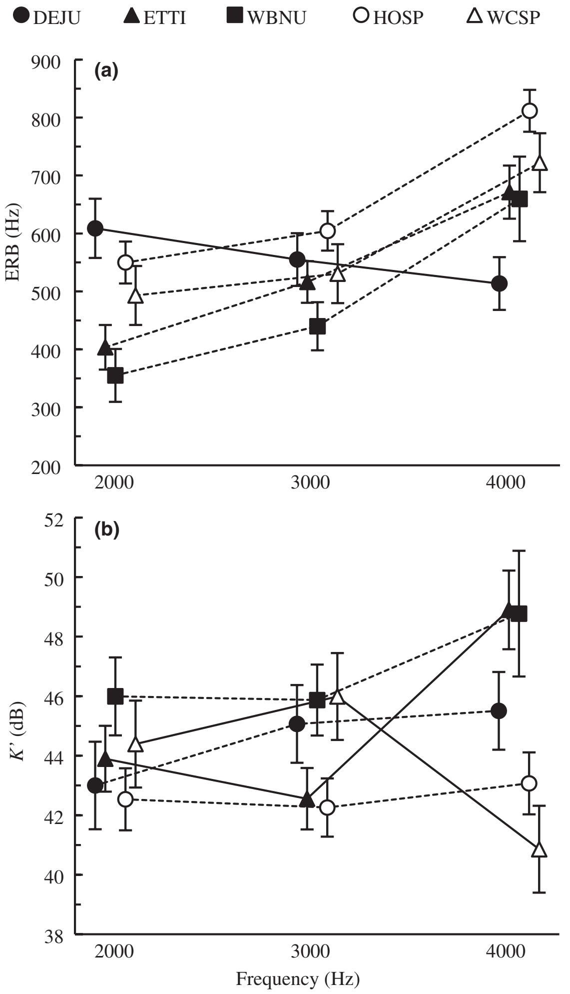

Fig. 3. (a) Equivalent rectangular bandwidth and (b) the signal-to-noise threshold constant (*K*′) of each species (see legend, top) as a function of frequency. Data points represent least-squares means of the species by frequency interaction ± SE. Abbreviations in the figure are given in Table 1.

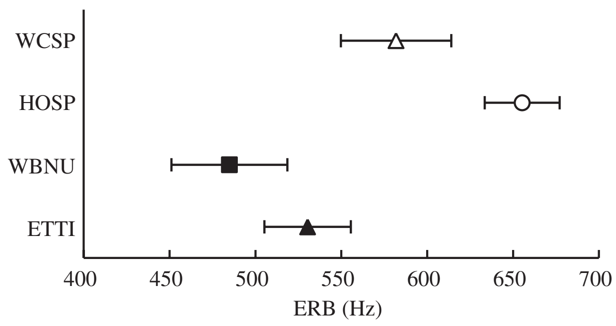

Fig. 4. Differences in equivalent rectangular bandwidth among four of the study species while controlling for the effect of frequency. Data points represent least-squares means of the species effect ± SE. See Table 1 for species abbreviations.

Table 2. Differences in equivalent rectangular bandwidth between dark-eyed juncos and the other study species

Frequency (Hz)	Species	Difference (Hz)	*t*	*P*
2000	ETTI	205 ± 64	3·21	**0·002**
	HOSP	59 ± 63	0·94	0·35
	WBNU	254 ± 68	3·71	**< 0·001**
	WCSP	116 ± 72	1·61	0·11
3000	ETTI	39 ± 58	0·67	0·51
	HOSP	−49 ± 57	−0·87	0·39
	WBNU	115 ± 62	1·87	0·07
	WCSP	24 ± 68	0·36	0·72
4000	ETTI	−158 ± 65	−2·44	**0·017**
	HOSP	−298 ± 58	−5·13	**< 0·001**
	WBNU	−146 ± 86	−1·70	0·09
	WCSP	−209 ± 68	−3·06	**0·003**

Differences are pairwise comparisons of least-squares means of the species by frequency interaction ± SE with 68·5 degrees of freedom. Negative differences indicate lower equivalent rectangular bandwidth in juncos. *P* values in bold indicate statistically significant differences (alpha = 0.05). See Table 1 for species abbreviations.

Table 3. Differences in the signal-to-noise threshold constant (*K*′) among the study species at 3 kHz

Comparison	Difference (dB)	*t*	*P*
DEJU–ETTI	2·5 ± 1·7	1·51	0·14
DEJU–HOSP	2·8 ± 1·6	1·72	0·09
DEJU–WBNU	−0·8 ± 1·8	−0·45	0·65
DEJU–WCSP	−0·9 ± 2·0	−0·47	0·64
ETTI–HOSP	0·3 ± 1·4	0·21	0·84
ETTI–WBNU	−3·3 ± 1·6	−2·10	**0·039**
ETTI–WCSP	−3·4 ± 1·8	−1·92	0·06
HOSP–WBNU	−3·6 ± 1·5	−2·34	**0·022**
HOSP–WCSP	−3·7 ± 1·8	−2·12	**0·037**
WBNU–WCSP	−0·1 ± 1·9	−0·06	0·95

Differences are pairwise comparisons of least-squares means ± SE with 68·8 degrees of freedom. *P* values in bold indicate statistically significant differences (alpha = 0.05). See Table 1 for species abbreviations.

4 kHz, *K*′ tended to be lower in open-habitat species than woodland species. That is, *K*′ was lower in white-crowned sparrows than tufted titmice (−8·0 ± 2·0 dB; $t_{68\cdot9} = -4\cdot08$, $P < 0\cdot001$), white-breasted nuthatches (−7·9 ± 2·6 dB; $t_{69} = -3\cdot08$, $P = 0\cdot003$) and dark-eyed juncos (−4·6 ± 2·0 dB; $t_{68\cdot8} = -2\cdot37$, $P = 0\cdot020$), and lower in house sparrows than tufted titmice (−5·8 ± 1·7 dB; $t_{69} = -3\cdot47$, $P = 0\cdot001$) and white-breasted nuthatches (−5·7 ± 2·4 dB; $t_{69} = -2\cdot42$, $P = 0\cdot018$) but not dark-eyed juncos (−2·4 ± 1·7 dB; $t_{68\cdot9} = -1\cdot46$, $P = 0\cdot15$). *K*′ did not vary significantly among species from the same habitat, that is, among dark-eyed juncos, tufted titmice and white-breasted nuthatches ($F_{2,69} = 1\cdot91$, $P = 0\cdot16$), or between house sparrows and white-crowned sparrows ($t_{68\cdot9} = 1\cdot23$, $P = 0\cdot22$). Finally, *K*′ varied with frequency in tufted titmice ($F_{2,45\cdot4} = 7\cdot67$, $P = 0\cdot001$) and white-crowned sparrows ($F_{2,40\cdot4} = 3\cdot36$, $P = 0\cdot045$; Fig. 3b, solid lines) but not dark-eyed juncos ($F_{2,42\cdot7} = 0\cdot93$, $P = 0\cdot40$), house sparrows ($F_{2,51\cdot6} = 0\cdot17$, $P = 0\cdot84$) or white-breasted nuthatches ($F_{2,50\cdot3} = 0\cdot79$, $P = 0\cdot46$; Fig. 3b, dashed lines). From 3 to

Table 4. Summary statistics of the *r* parameter

Frequency (Hz)	Species	Median × 1000	First quartile × 1000	Third quartile × 1000
2000	DEJU	0·858	0·000	3·706
	ETTI	0·142	0·000	0·389
	HOSP	0·000	0·000	0·000
	WBNU	0·117	0·016	0·679
	WCSP	0·172	0·000	3·473
3000	DEJU	0·000	0·000	0·414
	ETTI	0·008	0·000	0·048
	HOSP	0·731	0·599	1·610
	WBNU	0·069	0·000	0·344
	WCSP	0·032	0·009	0·223
4000	DEJU	0·019	0·003	0·039
	ETTI	0·063	0·000	0·148
	HOSP	1·171	0·570	1·688
	WBNU	0·080	0·013	0·147
	WCSP	0·078	0·032	0·204

See Table 1 for species abbreviations.

4 kHz, K' increased by 6·3 ± 1·7 dB in tufted titmice ($t_{48\cdot3} = 3{\cdot}84$, $P < 0{\cdot}001$) and decreased by 5·1 ± 2·0 dB in white-crowned sparrows ($t_{40\cdot4} = -2{\cdot}53$, $P = 0{\cdot}015$).

The r parameter had a median value of $6{\cdot}4 \times 10^{-5}$, interquartile range from 0 to $5{\cdot}19 \times 10^{-4}$ and range from 0 to $6{\cdot}016 \times 10^{-3}$. The value of r tended to be higher in dark-eyed juncos than the other species at 2 kHz, and higher in house sparrows than other species at 3 and 4 kHz (Table 4).

Discussion

The bandwidth of auditory filters increased with increasing frequency in all species except the dark-eyed junco. Auditory filters were generally narrower in woodland species (dark-eyed juncos, tufted titmice and white-breasted nuthatches) than open-habitat species (house sparrows and white-crowned sparrows) as predicted, although auditory filters of the dark-eyed junco were narrower only at 4 kHz and the difference between white-crowned sparrows and tufted titmice was not significant. Finally, at 4 kHz, open-habitat species tended to have auditory filters with lower signal-to-noise response thresholds than woodland species.

Auditory filters increase in bandwidth with increasing frequency in a broad variety of mammals (e.g. Moore & Glasberg 1983; Niemiec, Yost & Shofner 1992; Finneran *et al.* 2002; May, Kimar & Prosen 2006) and other bird species (reviewed in Dooling, Lohr & Dent 2000; Gleich & Manley 2000). In the European starling, auditory filter ERBs based on behavioural thresholds in notched noise are 169, 404 and 550 Hz at 1, 3 and 5 kHz respectively (Marean *et al.* 1998). These values are in the same general range as estimates from the current study but appear to be slightly lower. For example, ERB at 3 kHz ranged from 440 Hz in the white-breasted nuthatch to 605 Hz in the house sparrow. General agreement between the two studies suggests that the ABR method provides a useful approximation of auditory filter shape. Presently, it is not possible to quantify differences between behavioural and ABR-based estimates of auditory filter bandwidth in songbirds because no single species has been tested using both methods. Behavioural estimates of ERB may be lower than ABR estimates because the frequency selectivity of the auditory system tends to increase at higher levels of the auditory pathway through mechanisms such as neural lateral inhibition (e.g. Suga, Zhang & Yan 1997; surprisingly, however, ABR-based filter bandwidths of the bottlenose dolphin (*Tursiops truncatus*) were 75% lower than behaviourally determined values; Popov, Supin & Klishin 1997; Finneran *et al.* 2002). On the other hand, starlings appear to have slightly lower frequency difference limens than red-winged blackbirds, brown-headed cowbirds and several non-passerine birds (reviewed in Dooling, Lohr & Dent 2000), suggesting that they may in fact have relatively narrow auditory filters.

Surprisingly, auditory filters of the dark-eyed junco exhibited little variation in bandwidth across the frequency range of the experiments. Auditory filters that do not increase in bandwidth with increasing frequency are rarely observed, and tend to occur in echolocating species (e.g. Suga, Neuweiler & Moller 1976; Popov *et al.* 2006) and other auditory specialists (e.g. the barn owl, *Tyto alba*; Koppl, Gleich & Manley 1993). Future studies should measure auditory filters of the dark-eyed junco above 4 kHz.

Our results are consistent in part with the hypothesis that environmental constraints on the acoustic structure of song have influenced the evolution of peripheral auditory filters in songbirds. Narrow auditory filters may have evolved in tufted titmice, white-breasted nuthatches and dark-eyed juncos because they provide greater frequency resolution of tonal elements contained in their songs (Fig. 5a), whereas broader auditory filters may have evolved in house sparrows and white-crowned sparrows for greater temporal resolution of rapid FM and AM contained in their songs (Fig. 5b). It must be noted, however, that phylogenetic history may also influence the pattern of auditory filter bandwidth observed across species. Specifically, more closely related species are expected to have more similar filter bandwidths due to shared phylogenetic history. However, the effect of phylogenetic history appears to be relatively weak among the species in the current study based on the observation that the most closely related species in the data set, the dark-eyed junco and white-crowned sparrow (sister genera within the Emberizidae; Carson & Spicer 2003), differed significantly in auditory filter bandwidth in accordance with habitat. Note that the house sparrow is classified in a different family (Passeridae) of the same superfamily (Passeroidea), and the tufted titmouse and white-breasted nuthatch are placed in two other major songbird superfamilies (Sylvioidea and Muscicapoidea respectively; Jonsson & Fjeldsa 2006). Future studies of more closely related species may uncover a stronger phylogenetic signal. Ultimately, the effect of habitat should be estimated using a larger assemblage of songbird species and phylogenetically corrected independent contrasts.

Estimates of temporal resolution in house sparrows, tufted titmice and white-breasted nuthatches (Henry & Lucas 2008)

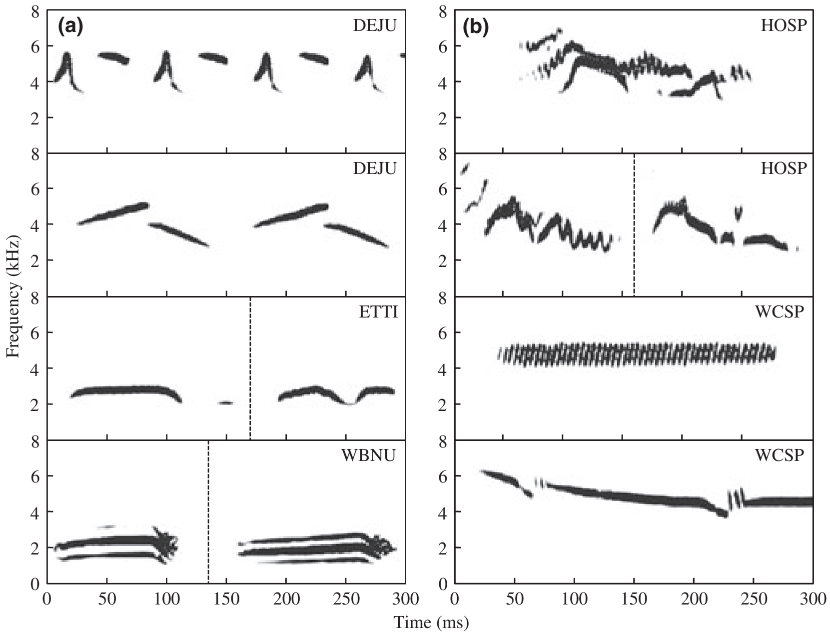

Fig. 5. Spectrograms of song notes from (a) the woodland species and (b) the open-habitat species. Abbreviated species names (see Table 1) are given in the top right corner of each panel. Song notes separated by a dashed line within the same panel are different examples. Spectrograms were generated using a Gaussian spectral analysis window (5 ms) in PRAAT from commercially available recordings (Elliot, Stokes & Stokes 1997; sampling frequency: 44·1 kHz).

are partially consistent with auditory filter data from the current study. Modulation rate transfer functions plotting the amplitude of the envelope following response (a measure of temporal processing) as a function of AM frequency suggest that house sparrows and tufted titmice have greater temporal resolution than white-breasted nuthatches. Greater temporal resolution in house sparrows than white-breasted nuthatches is consistent with the broader auditory filters observed in this study, whereas greater temporal resolution in tufted titmice than white-breasted nuthatches is surprising in light of similar auditory filter bandwidths between these species. The discrepancy may reflect differences in stimulus frequencies and statistical power between the two studies. Modulation rate transfer functions were obtained at a single frequency, 2·75 kHz, whereas auditory filters were measured at 2, 3 and 4 kHz. Moreover, factors other than auditory filter bandwidth may limit temporal resolution to a greater degree in white-breasted nuthatches. For example, temporal resolution may be limited by properties of hair-cell synapses and the refractory period of peripheral auditory neurons, especially at high frequencies where auditory filter bandwidth is broad and unlikely to be limiting (Viemeister & Plack 1993). Future studies should compare auditory filter bandwidths and temporal resolution across a greater number of species to better characterize the relationship.

Contrary to predictions, auditory filters were relatively broad at low frequency in dark-eyed juncos and did not differ between tufted titmice and white-crowned sparrows. These results may reflect several factors. First, auditory filters can be expected to match predictions based on the environment only to the extent that species-specific songs conform to the acoustic adaptation hypothesis. A recent meta-analysis of the acoustic adaptation hypothesis in birds concluded that habitat structure weakly predicts the acoustic structure of songs, and other factors should be included in models of bird song evolution (Boncoraglio & Saino 2007). Specifically, costs associated with signal production and eavesdropping by predators and brood parasites may favour shorter range, more rapidly degraded songs in some species. Moreover, models should incorporate perch heights and a gradient of habitat-based reverberation characteristics rather than a simple dichotomy between woodland and open habitats (Wiley 1991). Among the species from the present study, songs of the dark-eyed junco contain surprisingly high acoustic frequencies in light of their woodland habitat. Limited spectral energy present in songs below 3 kHz (Titus 1998) may relax the selection for narrow auditory filters, thus explaining the broad auditory filters observed at 2 kHz. Second, the auditory filters of some woodland species may be configured to process shorter-range, rapidly modulated signals rather than long-range songs subject to greater environmental constraint. Tufted titmice and other Parids (e.g. chickadees) have simple tonal songs but relatively complex calls used in close-range interactions between individuals (Hailman 1989). The 'chick-a-dee' call of the tufted titmouse, for example, contains four main note types that are combined into different call variants (Owens & Freeberg 2007). Z and A notes contain rapid FM, whereas D and D-h notes contain broadband AM structure. Relatively rapid modulations may favour broader auditory filters than would be expected based on the acoustic structure of song.

The differences in auditory filter bandwidth found in this study most likely reflect underlying differences in cochlear morphology and physiology. Presently, the relationship between cochlear morphology and function is poorly understood in birds. In general, differences in auditory filter bandwidth between species may reflect differences in the electrical or micromechanical tuning of sensory hair cells along the basilar papilla (reviewed in Gleich & Manley 2000). Electrical tuning arises from the properties of the hair-cell membrane whereas micromechanical tuning arises from the structural characteristics of hair-cell stereovillar bundles, mass and stiffness of the tectorial membrane, and active movement processes of hair cells. Studying cochlear morphology and active processes in the species from this study may help elucidate the relative contributions of these tuning mechanisms to frequency selectivity in songbirds.

Estimates of auditory filter bandwidth have also been found to vary with the sensation level of masking noise (i.e. noise level relative to the absolute threshold). Specifically, lower masking sensation levels tend to decrease estimates of auditory filter bandwidth in humans (dependent on centre frequency; Moore 1993) and marine mammals (Finneran *et al.* 2002). Auditory sensitivity below 4 kHz does not vary appreciably among the study species, but higher thresholds above 4–5 kHz in house sparrows and white-breasted nuthatches compared to the other species (by approximately 5–10 dB; see Konishi 1969 for single-unit audiograms of the dark-eyed junco and house sparrow; see Henry & Lucas 2008 for ABR audiograms of the house sparrow, white-breasted nuthatch, and tufted titmouse; white-crowned sparrow audiogram based on unpublished ABR data) may decrease the sensation level of high frequency noise. Hence, auditory filter bandwidths in house sparrows and white-breasted nuthatches at 4 kHz may be slight underestimates.

The environment has also been shown to affect auditory tuning in the cricket frog (*Acris crepitans*). Greater attenuation and degradation of mating calls in pine forest habitats than grassland habitats has favoured the evolution of calls that transmit with greater efficiency and a more narrowly tuned basilar papilla that is more effective at filtering out background noise (Witte *et al.* 2005). Calls and auditory tuning do not appear to be locally adapted to habitat conditions, as we suggest may occur in songbirds, but instead appear to reflect stronger selection for increased signal transmission and detection in woodland habitats compared to open habitats. Indeed, calls and auditory tuning of the pine forest population were more effective than calls and auditory tuning of the grassland population in either habitat (Witte *et al.* 2005).

Species differences in signal-to-noise threshold (K') indicate that the response efficiency of the auditory filters is generally greater in open-habitat species than woodland species at 4 kHz. That is, the auditory filters can detect a signal while more noise is passing through the filter. Greater response efficiency (i.e. lower K' or signal-to-noise threshold) may have evolved to compensate for limitations associated with broad auditory filters. The sensitivity of the auditory system to a signal in noise depends on both the response efficiency and bandwidth of the auditory filter tuned to that signal. A broader auditory filter decreases sensitivity in noise because more noise is allowed to enter the auditory filter during the detection process. Greater response efficiency of the filters should help counteract this effect, thereby restoring auditory sensitivity in noise. Additionally, response efficiency decreased from 3 to 4 kHz in tufted titmice and increased from 3 to 4 kHz in white-crowned sparrows. Similarly, response efficiency increases by 10–15 dB in the European starling (Marean *et al.* 1998). Variation in the response efficiency with frequency highlights problems associated with comparisons of filter bandwidth based on critical ratios and critical bands (reviewed in Dooling, Lohr & Dent 2000), which assume that the response efficiency of the auditory filters does not vary with frequency. Such comparisons are biased by frequency-dependent response efficiency, which appears to be common (e.g. Niemiec, Yost & Shofner 1992; Moore 1993; Marean *et al.* 1998).

In conclusion, results from the current study were consistent in part with the hypothesis that environmental constraints have favoured slowly modulated songs and narrow auditory filters in woodland species and rapidly modulated songs and broad auditory filters in open-habitat species. Differences is auditory filter bandwidth between dark-eyed juncos and white-crowned sparrows are noteworthy because *Junco* and *Zonotrichia* are sister genera. Exceptions should be expected in species with songs or other vocalizations that do not conform to the acoustic adaptation hypothesis. Finally, open-habitat species may compensate for inherently lower sensitivity in noise of broad auditory filters with greater response efficiency.

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References

Badyaev, A.V. & Leaf, E.S. (1997) Habitat associations of song characteristics in Phylloscopus and Hippolais warblers. *Auk*, **114**, 40–46.

Boersma, P. & Weenink, D. (2009) *PRAAT: Doing Phonetics by Computer v. 5.1.07* (computer program). Available at: http://www.praat.org/

Boncoraglio, G. & Saino, N. (2007) Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis. *Functional Ecology*, **21**, 134–142.

Bradbury, J.V. & Vehrencamp, S.L. (1998) *Principles of Animal Communication*. Sinauer Associates, Sunderland, MA.

Brittan-Powell, E.F., Dooling, R.J. & Gleich, O. (2002) Auditory brainstem responses in adult budgerigars (*Melopsittacus undulates*). *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.

Carson, R.J. & Spicer, G.S. (2003) A phylogenetic analysis of the emberizid sparrows based on three mitochondrial genes. *Molecular Phylogenetics and Evolution*, **29**, 43–57.

Dmitrieva, L.P. & Gottlieb, G. (1992) Development of brain-stem auditory pathway in mallard duck embryos and hatchlings. *Journal of Comparative Physiology A. Sensory, Neural, and Behavioral Physiology*, **171**, 665–671.

Dooling, R.J., Lohr, B. & Dent, M. (2000) Hearing in birds and reptiles. *Comparative Hearing: Birds and Reptiles* (eds R.J. Dooling, R.R. Fay & A.N. Popper), pp. 309–359. Springer, New York.

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 (compact disc)*. Time Warner Audio Books, New York.

Endler, J.A. (1993) Some general comments on the evolution and design of animal communication systems. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, **340**, 215–225.

Finneran, J.J., Schlundt, C.E., Carder, D.A. & Ridgway, S.H. (2002) Auditory filter shapes for the bottlenose dolphin (*Tursiops truncatus*) and the white whale (*Delphinapterus leucas*) derived with notched noise. *Journal of the Acoustical Society of America*, **112**, 322–328.

Fletcher, H. (1940) Auditory patterns. *Reviews of Modern Physics*, **12**, 47–65.

Glasberg, B.R. & Moore, B.C.J. (1990) Derivation of auditory filter shapes from notched-noise data. *Hearing Research*, **47**, 103–138.

Gleich, O. (1994) Excitation patterns in the starling cochlea: a population study of primary auditory afferents. *Journal of the Acoustical Society of America*, **95**, 401–409.

Gleich, O. & Manley, G.A. (2000) The hearing organ of birds and crocodilian. *Comparative Hearing: Birds and Reptiles* (eds R.J. Dooling, R.R. Fay & A.N. Popper), pp. 70–138. Springer, New York.

Hailman, J.P. (1989) The organization of major vocalizations in the Paridae. *Wilson Bulletin*, **101**, 305–343.

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

Henry, K.S. & Lucas, J.R. (2008) Coevolution of auditory sensitivity and temporal resolution with acoustic signal space in three songbirds. *Animal Behaviour*, **76**, 1659–1671.

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

Konishi, M. (1969) Hearing, single-unit analysis, and vocalizations in songbirds. *Science*, **166**, 1178–1181.

Koppl, C., Gleich, O. & Manley, G.A. (1993) An auditory fovea in the barn owl. *Journal of Comparative Physiology A. Sensory, Neural, and Behavioral Physiology*, **171**, 695–704.

Kopuchian, C., Lijtmaer, D.A., Tubaro, P.L. & Handford, P. (2004) Temporal stability and change in a microgeographical pattern of song variation in the rufous-collared sparrow. *Animal Behaviour*, **68**, 551–559.

Lauer, A.M., Dooling, R.J. & Leek, M.R. (2009) Psychophysical evidence of damaged active processing mechanisms in Belgian Waterslager canaries. *Journal of Comparative Physiology A. Sensory, Neural, and Behavioral Physiology*, **195**, 193–202.

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.

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.

Manley, G.A., Gleich, O., Leppelsack, H.J. & Oeckinghaus, H. (1985) Activity patterns of cochlear ganglion neurons in the starling. *Journal of Comparative Physiology A. Sensory, Neural, and Behavioral Physiology*, **157**, 161–181.

Marchetti, K. (1993) Dark habitats and bright birds illustrate the role of the environment in species divergence. *Nature*, **362**, 149–152.

Marean, G.C., Burt, J.M., Beecher, M.D. & Rubel, E.W. (1998) Auditory perception following hair cell regeneration in European starling (*Sturnus vulgaris*): frequency and temporal resolution. *Journal of the Acoustical Society of America*, **103**, 3567–3580.

May, B.J., Kimar, S. & Prosen, C.A. (2006) Auditory filter shapes of CBA/CaJ mice: behavioral assessments. *Journal of the Acoustical Society of America*, **120**, 321–330.

Moore, B.C.J. (1993) Frequency analysis and pitch perception. *Human Psychophysics* (eds W.A. Yost, A.N. Popper & R.R. Fay), pp. 58–89. Springer-Verlag, New York.

Moore, B.C.J. & Glasberg, B.R. (1983) Suggested formulas for calculating auditory filter bandwidths and excitation patterns. *Journal of the Acoustical Society of America*, **74**, 750–753.

Morton, E.S. (1975) Ecological sources of selection on avian sounds. *American Naturalist*, **109**, 17–34.

Naguib, M. (2003) Reverberation of rapid and slow trills: implications for signal adaptations to long-range communication. *Journal of the Acoustical Society of America*, **113**, 1749–1756.

Nicholls, J.A. & Goldizen, A.W. (2006) Habitat and density influence vocal signal design in satin bowerbirds. *Journal of Animal Ecology*, **75**, 549–558.

Niemiec, A.J., Yost, W.A. & Shofner, W.P. (1992) Behavioral measures of frequency selectivity in the chinchilla. *Journal of the Acoustical Society of America*, **92**, 2636–2649.

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.

Patterson, R.D., Nimmo-Smith, I., Weber, D.L. & Milroy, R. (1982) The deterioration of hearing with age: frequency selectivity, the critical ratio, the audiogram, and speech threshold. *Journal of the Acoustical Society of America*, **72**, 1788–1803.

Popov, V.V., Supin, A.Y. & Klishin, V.O. (1997) Frequency tuning of the dolphin's hearing as revealed by auditory brainstem response with notch-noise masking. *Journal of the Acoustical Society of America*, **102**, 3795–3801.

Popov, V.V., Supin, A.Y., Wang, D. & Wang, K.X. (2006) Nonconstant quality of auditory filters in the porpoises, *Phocoena phocoena* and *Neophocaena phocaenoides* (Cetacea, Phocoenidae). *Journal of the Acoustical Society of America*, **119**, 3173–3180.

Pyle, P. (1997) *Identification Guide to North American Birds*. Slate Creek Press, Bolinas, CA.

Richards, D.G. & Wiley, R.H. (1980) Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. *American Naturalist*, **115**, 381–399.

Suga, N., Neuweiler, G. & Moller, J. (1976) Peripheral auditory tuning for fine frequency analysis by CF-FM bat, *Rhinolophus ferrumequinum*. 4. Properties of peripheral auditory neurons. *Journal of Comparative Physiology*, **106**, 111–125.

Suga, N., Zhang, Y.F. & Yan, J. (1997) Sharpening of frequency tuning by inhibition in the thalamic auditory nucleus of the mustached bat. *Journal of Neurophysiology*, **77**, 2098–2114.

Thirakhupt, K. (1985) *Foraging ecology of sympatric parids: individual and populational responses to winter food scarcity*. PhD thesis, Purdue University, West Lafayette, IN.

Thyer, N. & Mahar, D. (2006) Discrimination of nonlinear frequency glides. *Journal of the Acoustical Society of America*, **119**, 2929–2936.

Titus, R.C. (1998) Short-range and long-range songs: use of two acoustically distinct song classes by dark-eyed juncos. *The AUK*, **115**, 386–393.

Unoki, M., Irino, T., Glasberg, B., Moore, B.C.J. & Patterson, R.D. (2006) Comparison of the roex and gammachirp filters as representations of the auditory filter. *Journal of the Acoustical Society of America*, **120**, 1474–1492.

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

Waser, P.M. & Waser, M.S. (1977) Experimental studies of primate vocalization – specializations for long-distance propagation. *Journal of Comparative Ethology*, **43**, 239–263.

Wiley, R.H. (1991) Associations of song properties with habitats for territorial oscine birds of eastern North America. *American Naturalist*, **138**, 973–993.

Wiley, R.H. & Richards, D.G. (1978) Physical constraints on acoustic communication in atmosphere – implications for evolution of animal vocalizations. *Behavioral Ecology and Sociobiology*, **3**, 69–94.

Witte, K., Farris, H.E., Ryan, M.J. & Wilczynski, W. (2005) How cricket frog females deal with a noisy world: habitat-related differences in auditory tuning. *Behavioral Ecology*, **16**, 571–579.

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