

Songbirds tradeoff auditory frequency resolution and temporal resolution

Kenneth S. Henry · Megan D. Gall ·
Gavin M. Bidelman · Jeffrey R. Lucas

Received: 21 October 2010 / Revised: 17 December 2010 / Accepted: 24 December 2010 / Published online: 12 January 2011
© Springer-Verlag 2011

Abstract Physical tradeoffs may in some cases constrain the evolution of sensory systems. The peripheral auditory system, for example, performs a spectral decomposition of sound that should result in a tradeoff between frequency resolution and temporal resolution. We assessed temporal resolution in three songbird species using auditory brainstem responses to paired click stimuli. Temporal resolution was greater in house sparrows (*Passer domesticus*) than Carolina chickadees (*Poecile carolinensis*) and white-breasted nuthatches (*Sitta carolinensis*), as predicted based on previous observations of broader auditory filters (lower frequency resolution) in house sparrows. Furthermore, within chickadees, individuals with broader auditory filters had greater temporal resolution. In contrast to predictions however, temporal resolution was similar between chickadees and nuthatches despite broader auditory filters in chickadees. These results and the results of a model simulation exploring the effect of broadened auditory filter bandwidth on temporal resolution in the auditory periphery strongly suggest that frequency resolution constrains temporal resolution in songbirds. Furthermore, our results suggest that songbirds have greater temporal resolution than some mammals, in agreement with recent behavioral studies. Species differences in temporal resolution may reflect adaptations for efficient processing of species-specific

vocalizations, while individual differences within species may reflect experience-based developmental plasticity or hormonal effects.

Keywords Auditory brainstem response · Auditory filter · Frequency resolution · Songbird · Temporal resolution

Abbreviations

ABR Auditory brainstem response
AEP Auditory evoked potential
CAP Compound action potential
ERB Equivalent rectangular bandwidth
PSTH Peri-stimulus time histogram

Introduction

A variety of selective pressures are expected to influence the evolution of sensory systems including detection of predators, prey, and communication signals in the environment (Konishi 1973; Feng et al. 2006; Fullard et al. 2010). The response of the sensory system to selective pressures, however, may in some cases be limited by physical tradeoffs. In the visual system, for example, the evolution of greater sensitivity requires an increase in photoreceptor size that, for a given eye size, reduces the spatial resolution of the visual field (Collin et al. 2009). The auditory system faces an analogous physical tradeoff between frequency resolution and temporal resolution. This hypothesis is well supported by theoretical models, but has attracted relatively little empirical research.

The peripheral auditory system of vertebrates performs a spectral decomposition of sound that should result in a tradeoff between frequency resolution and temporal resolution. The cochlea is commonly modeled as a linear system

K. S. Henry (✉) · G. M. Bidelman
Department of Speech, Language, and Hearing Sciences,
Purdue University, 500 Oval Drive, West Lafayette,
IN 47907, USA
e-mail: kshenry@purdue.edu

M. D. Gall · J. R. Lucas
Department of Biological Sciences, Purdue University,
915 West State Street, West Lafayette,
IN 47907-2054, USA

of band-pass auditory filters, each representing a place on the sensory epithelium, that vary in center frequency across the frequency range of hearing (Moore 1993). The frequency bandwidth of the filters determines the frequency resolution, or minimum detectable frequency difference, of the system. Narrower filter bandwidth increases frequency resolution, because signals of closely adjacent frequency are more likely to stimulate different filters. Narrower filter bandwidth, however, also decreases temporal resolution (given a specific model of cochlear biomechanics; see de Boer 1996), or the ability to detect fast changes in sound intensity, because the frequency bandwidth of a linear filter and its time constant are inversely related properties. Narrow filters have longer time constants, and therefore, ring for a prolonged period of time in response to brief stimulation (Viemeister and Plack 1993).

Empirical support for a tradeoff between frequency resolution and temporal resolution is currently equivocal. Studies of damage to the peripheral auditory system, which increases auditory filter bandwidth, have generally not found an increase in temporal resolution. Behavioral estimates of temporal resolution are similar between normal and hearing impaired individuals in humans (Viemeister and Plack 1993), rodents (Walton et al. 2008), and starlings (Marean et al. 1998). Furthermore, studies examining frequency resolution and temporal resolution across auditory nerve fibers have yielded mixed results. In normal hearing cats, auditory filter bandwidth increases with increasing characteristic frequency. For frequencies up to 10 kHz, this increase is accompanied by a concomitant increase in temporal resolution as predicted by theoretical models (Joris et al. 2004). For characteristic frequencies above 10 kHz, however, temporal resolution remains relatively constant. Also, in starlings, auditory filter bandwidth and temporal resolution are unrelated across auditory nerve fibers (Klump and Gleich 1991). In other bird species, a behavioral study of silent gap detection found a positive relationship between temporal resolution and auditory filter bandwidth across stimulus frequencies in zebra finches, but not budgerigars (Okanoya and Dooling 1990). Taken together, these studies suggest that factors other than auditory filter bandwidth limit temporal resolution under some conditions, such as neural refractoriness or adaptation at the synapse between sensory hair cells and auditory nerve fibers.

A variety of studies have used auditory-evoked potentials (AEPs) in response to paired click stimuli to assess the temporal resolution of the peripheral auditory system [e.g., domestic cats (Parham et al. 1996), humans (Ohashi et al. 2005), dolphins (Supin and Popov 1995), and fishes (Wysocki and Ladich 2002)]. AEPs are gross potentials that reflect action potentials generated by the auditory nerve and nuclei of the brainstem and midbrain (Hall 2007). AEP

amplitude is positively related to the number and synchrony of neural responses, and hence, the general sensation level of the stimulus. In paired click experiments, AEPs are recorded in response to two clicks separated in time by a brief inter-click interval. The variable of interest is the amplitude of the response to the second click, or response recovery, which is measured as a percentage of the response amplitude evoked by a single click. The relationship between response recovery and inter-click interval at relatively short inter-click intervals (e.g., <5 ms) provides an index of temporal resolution. Estimates of temporal resolution based on paired clicks may show a closer relationship to auditory filter bandwidth than estimates based on other stimuli (e.g., amplitude modulated tones; silent gaps in noise) because the short initial stimulus minimizes the effects of refractoriness and adaptation.

In the current study, we used auditory brainstem responses (ABRs) to paired click stimuli to assess temporal resolution in three songbird species: the house sparrow (*Passer domesticus*), Carolina chickadee (*Poecile carolinensis*), and white-breasted nuthatch (*Sitta carolinensis*). ABRs are a class of AEP recorded from the scalp in response to transient sounds. In birds, ABR waveforms are dominated by a biphasic deflection generated by the auditory nerve that occurs within 5 ms of stimulus onset (Brittan-Powell et al. 2002). Previously in these species, we determined the equivalent rectangular bandwidth (ERB) of auditory filters within the frequency range of best sensitivity (2–4 kHz) using ABRs to tone bursts in notched masking noise (Henry and Lucas 2010a, b; see also Gall and Lucas 2010). The mean bandwidth of auditory filters in this frequency range is the greatest in house sparrows, intermediate in chickadees, and the lowest in nuthatches (Fig. 1). Based on the hypothesized tradeoff between frequency resolution and temporal resolution, we expected temporal resolution to be the greatest in house sparrows, intermediate in chickadees, and the lowest in nuthatches. Furthermore, auditory filter bandwidth in chickadees varies considerably across individuals. Based on the hypothesized tradeoff, we expected individuals with greater auditory filter bandwidth to have greater temporal resolution. Analyses of inter-individual variation were not possible in house sparrows and nuthatches because auditory filter bandwidth and temporal resolution were measured in different individuals. Finally, to generate more specific predictions for our ABR recovery experiment, we used a computational model of the mammalian auditory nerve (Zilany et al. 2009) to determine the expected effect of broadened auditory filter bandwidth on neural responses to paired click stimuli. This model accurately predicts single-unit temporal responses to a broad variety of simple and complex sounds including tones, broadband noise, amplitude modulation, and speech sounds (Bruce et al. 2003; Zilany and Bruce 2006, 2007).

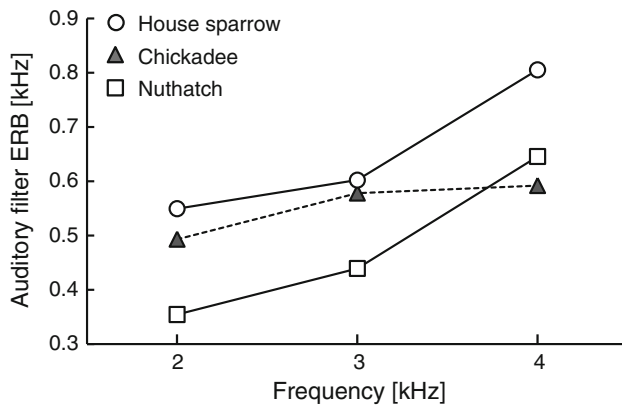


Fig. 1 Mean auditory filter equivalent rectangular bandwidth (ERB) of the study species as a function of frequency, from Henry and Lucas (2010a, b)

Materials and methods

Subjects

We collected auditory data from 25 adult songbirds [12 Carolina chickadees (7 male, 5 female), 8 house sparrows (6 male, 2 female), and 5 white-breasted nuthatches (4 male, 1 female)] between September of 2009 and February of 2010. Sex was determined based on plumage in house sparrows and nuthatches, and wing chord in chickadees. Chickadees with a wing chord of 62 mm or greater were classified as males, whereas chickadees with a wing chord less than 62 mm were classified as females. This method correctly assigns sex in approximately 96% of individuals (i.e., 48 of 50 individuals across two studies; Lucas et al. 2006). Mean body mass \pm SD in grams was 9.76 ± 0.65 in chickadees, 28.65 ± 3.20 in house sparrows, and 21.06 ± 0.91 in nuthatches. Subjects were collected near Purdue University in West Lafayette, IN, USA, from two-wooded areas and three-private residences using elevated treadle traps baited with seed. Each subject was marked with a numbered aluminum leg band and housed individually in a 1 m³ wire mesh cage located in an indoor aviary at Purdue University. The light–dark cycle of the aviary was set to local conditions and the temperature was held constant at 22°C. Subjects were provided with mixed seed, 2–3 mealworms, and vitamin-treated water each day. Auditory tests were conducted within 3 days of capture, and subjects were released at their capture site 1 or 2 days after testing.

General auditory test procedure and equipment

Auditory tests were conducted in a sound-attenuating test chamber (1.2 m tall by 1.4 m wide by 1.2 m deep) lined

with 7.7 cm thick Sonex foam (Acoustic Solutions, Richmond, VA, USA). Subjects were anesthetized with an injection into the breast muscle and placed on a pre-heated pad (Pet Supply Imports, South Holland, IL, USA) with their right side facing upwards. House sparrows and nuthatches were anesthetized with ketamine (50 mg kg⁻¹) and xylazine (10 mg kg⁻¹), whereas chickadees were anesthetized with ketamine (75 mg kg⁻¹) and midazolam (7.5 mg kg⁻¹) because xylazine was not effective. The choice of xylazine or midazolam appears to have a little or no impact on ABR amplitude and latency (Henry and Lucas 2010a). The temperature above the heating pad was maintained at $38 \pm 2^\circ\text{C}$. Needle electrodes (Nicolet Biomedical, Fitchburg, WI, USA) were inserted subdermally to record ABR waveforms. The non-inverting electrode was positioned at the vertex of the skull and the ground electrode was positioned midway down the back. The inverting electrode was positioned behind the right external auditory meatus in house sparrows and nuthatches, and at the intersection of the occipital crest and midline in chickadees. The revised placement of the inverting electrode in chickadees reduced electrophysiological background noise with a little or no impact on the ABR signal.

Stimulus presentation, response acquisition, and data storage were coordinated by a Tucker Davis Technologies system II modular rack-mount system (TDT, Gainesville, FL, USA) and Dell computer running SigGen32 and Bio-Sig32 TDT software. Stimuli were generated digitally at a sampling frequency of 50 kHz on a signal processing card (TDT model AP2) and converted to analog (TDT model DA3-4 convertor). Stimuli were filtered (Behringer Ultragraph model FBQ6200 31-band equalizer, Bethel, WA, USA), amplified (Crown D75 amplifier, Elkhart, IN, USA), and finally, presented through an electromagnetically shielded dynamic loudspeaker (RCA model 40-5000; Indianapolis, IN, USA) suspended 30 cm above the test subject. We measured the sound pressure level of stimuli with a sound level meter and 2.6 cm condenser microphone (Bruel and Kjaer model 1613/4131, Norcross, GA, USA). Electrophysiological responses were conducted from the subject to a headstage (TDT model HS4) through electrode leads, and from the headstage to a biological amplifier (TDT model DB4) through fiberoptic cables. The headstage and biological amplifier bandpass filtered the signal from 0.1 to 3 kHz and amplified the signal by 100K. Responses were digitized by a converter (TDT model AD2) and sampled by the signal processing card at 40 kHz.

ABR recovery experiment

Acoustic stimuli included (1) paired clicks and (2) single clicks. The period between the onset of one stimulus and

the onset of the next stimulus was 52.4 ms. For paired click stimuli, the first click was presented at 0 ms and the second click was presented after an inter-click interval. Inter-click intervals of 25, 10, 7, 5, 4, 3, 2, 1.5, 1.0, and 0.7 ms were tested in decreasing order. For single click stimuli, a click was presented at 0 ms. Clicks were generated by applying 0.25 ms Blackman onset and offset ramps to a 0.67 ms sinusoid with a frequency of 3 kHz and amplitude of 60 dB SPL. The duration of the click envelope was 0.28 ms between half-intensity time points. The power spectrum of the click had a dominant frequency of 3 kHz, -3 dB bandwidth of 1.7–4.3 kHz, and -10 dB bandwidth of 0.8–5.2 kHz.

Electrophysiological responses were sampled for 40 ms beginning from 1.2 ms prior to stimulus onset. For each inter-click interval, we recorded average responses to (1) 700 paired clicks and (2) 700 single clicks. The system alternated between presentation of paired and single click stimuli, and sorted responses into separate averaging buffers. The responses containing voltage deflections that exceeded ± 40 μ V (40% of the maximum possible input) were excluded from the averaging procedure as potential artifacts.

At inter-click intervals shorter than 2–3 ms, the ABRs to the first and second clicks of paired click stimuli overlapped (Fig. 2). We isolated the ABR to the second click by point-to-point subtraction of the average response to the single click stimulus from the average response to the paired click stimulus. ABR recovery was defined as the peak-to-peak amplitude of the response to the second click divided by the peak-to-peak amplitude of the response to the single click stimulus times 100%.

Auditory nerve model predictions

We used a computation model of the auditory nerve (Zilany et al. 2009) to determine the predicted effect of broadened auditory filter bandwidth on neural responses to paired click stimuli. This phenomenological model represents the latest extension of a well-established model that has been rigorously tested against physiological responses to both simple and complex stimuli including tones, broadband noise, and speech-like sounds (Bruce et al. 2003; Zilany and Bruce 2006, 2007). In its basic implementation, the model accepts the stimulus sound waveform at its input and for a given fiber of specified characteristic frequency, outputs the time-varying neural discharge pattern or the peri-stimulus time histogram (PSTH). Many of the physiological properties associated with nonlinear cochlear tuning are captured by this model including compression, suppression, broadened tuning and best frequency shifts with increases in sound level. Model threshold-tuning curves have been well fit to frequency-dependent variation

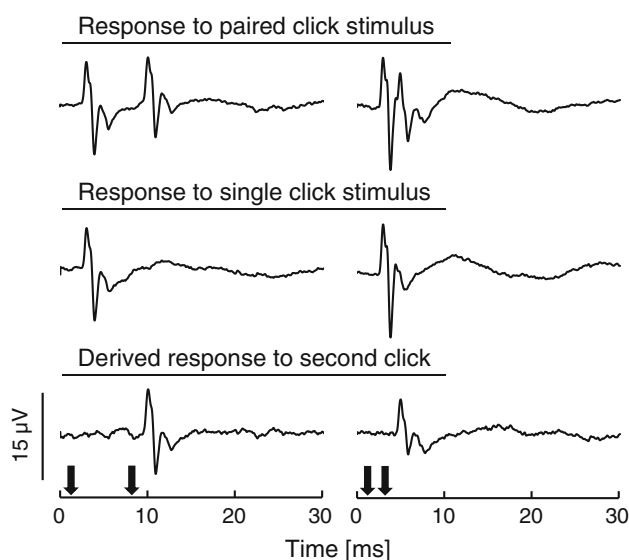


Fig. 2 ABRs to paired click stimuli (*top traces*), single click stimuli (*middle traces*), and derived ABRs to the second click of paired stimuli (*lower traces*). Derived ABRs were generated by point-to-point subtraction of the response to the single click stimulus from the response to the paired click stimulus. *Thick arrows* indicate the timing of clicks, which were separated by time intervals of 7 ms (*left*) and 2 ms (*right*)

in threshold and bandwidth for high-spontaneous rate fibers in normal hearing cats. The stochastic nature of auditory nerve responses is accounted for by a non-homogeneous Poisson process, which includes effects of both absolute and relative refractory periods and captures the major stochastic properties of auditory nerve responses. The current generation of the model also incorporates power law dynamics and long-term adaptation at the synapse between the inner hair cells and auditory nerve (Zilany et al. 2009). These additions have improved temporal encoding allowing the model to more accurately predict results from animal data including neural responses to amplitude modulation and forward masking.

Relevant to the present work, the model's architecture allows for the selective manipulation of inner and outer hair cell integrity via two-scaling coefficients in its control path, C_{IHC} and C_{OHC} , respectively. Both coefficients range from 0 to 1, where 1 simulates normal hair cell function and 0 indicates complete hair cell dysfunction (Bruce et al. 2003). Lowering C_{IHC} elevates fiber response thresholds without affecting frequency selectivity, consistent with physiologic reports. Lowering C_{OHC} , in contrast, causes a decrease in cochlear amplification that both elevates fiber response thresholds and increases auditory filter bandwidth. In our application of the model, we achieved an increase in auditory filter bandwidth of 50% by decreasing C_{OHC} to the point that cochlear amplification was reduced by 10 dB. To compensate for the resulting decrease in the sensation level of stimuli, we increased the overall presentation level by

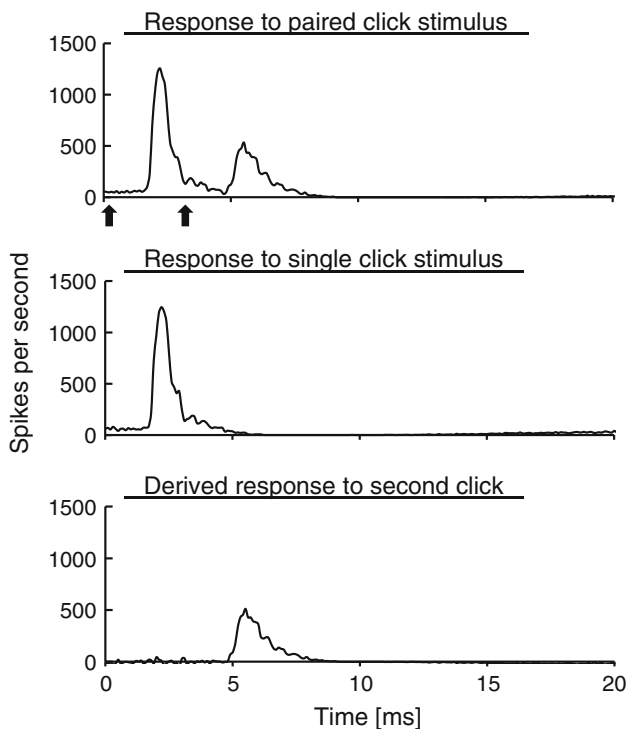


Fig. 3 Mean PSTHs obtained from the auditory nerve model in response to paired (*top panel*) and single (*middle panel*) click stimuli, and the derived response to the second click of the paired stimulus (*bottom*). The derived response was generated by point-to-point subtraction of the response to the single click stimulus from the response to the paired click stimulus. *Thick arrows* indicate the timing of clicks. The interval between clicks was 3 ms

10 dB. Adaptation and refractory effects (Zilany and Carney 2010), which also influence neural responses to paired click stimuli, were left unchanged.

Paired and single click stimuli were presented to the model as in the ABR recovery experiment. An ensemble of 20 high-spontaneous rate (50 spikes/s) fibers was simulated with characteristic frequencies spaced logarithmically between 2 and 4 kHz. PSTHs were computed per fiber based on 500 stimulus repetitions. Individual PSTHs were then averaged across fibers to create a population level response (Fig. 3). As in the ABR experiment, the response to the second click was isolated by subtracting the mean PSTH generated in response to a single click from the mean PSTH generated in response to the paired click stimulus (Fig. 3; bottom panel). Similarly, the extent of auditory nerve recovery was quantified by dividing the peak amplitude of the derived PSTH by the peak amplitude of the PSTH generated by a single click and multiplying by 100.

Statistical analysis

We used repeated measures mixed models (MIXED Procedure; SAS Institute Inc., Cary, NC, v. 9.2) to analyze ABR

recovery in response to paired click stimuli. ABR recovery was arcsine transformed [$\arcsin[(\text{observed value})^{0.5}]$] to normalize the residuals and achieve constant variance. The first analysis, which tested for species differences in ABR recovery functions, contained interval (inter-click interval) and species as categorical independent variables, and the interval \times species interaction. A second analysis, which included chickadees only, tested for a relationship between the ERB of auditory filters, reported previously (Henry and Lucas 2010b), and ABR recovery functions in the same individuals. The analysis contained interval as categorical independent variable, 2 kHz ERB, 3 kHz ERB, and 4 kHz ERB as continuous independent variables, and interval \times 2 kHz ERB, interval \times 3 kHz ERB, and interval \times 4 kHz ERB interactions. A final analysis, also based only on chickadees, contained interval and sex as categorical independent variables and the interval \times sex interaction. We selected compound symmetry within-subject covariance structure over unstructured covariance and heterogeneous compound symmetry based on a lower Bayesian Information Criterion. Non-significant effects ($P > 0.05$) were dropped from the model. Denominator degrees of freedom were calculated using the Kenward-Roger method. Back-transformed least squares mean \pm SE are presented throughout.

Results

Auditory nerve model predictions

In general, auditory nerve recovery increased from approximately 10% at inter-click intervals less than 1 ms to near 100% at intervals greater than 10 ms (Fig. 4). Increasing auditory filter bandwidth by 50% in the model increased auditory nerve recovery by 11–21% points at inter-click intervals from 2 to 7 ms.

ABR recovery

At inter-click intervals longer than 10 ms, ABR recovery was near 100% in all species (i.e., the amplitude of the second click response was similar to the amplitude of a single click response; Fig. 5). At shorter intervals, ABR recovery decreased with decreasing inter-click interval until at 0.7 ms, ABR recovery ranged from 20 to 40%.

The effect of inter-click interval on ABR recovery varied between species (interval $F_{9,196} = 272.28$, $P < 0.001$; species $F_{2,21.9} = 2.61$, $P = 0.096$; interval \times species $F_{18,196} = 3.23$, $P < 0.001$; Fig. 5). ABR recovery was greater in house sparrows than chickadees at intervals of 1 ($t_{79,4} = 2.69$, $P = 0.009$), 2 ($t_{79,4} = 3.25$, $P = 0.002$), 3 ($t_{79,4} = 3.17$, $P = 0.002$), and 4 ms ($t_{79,4} = 2.26$, $P = 0.027$), and greater in house sparrows than nuthatches at intervals of 1 ($t_{79,4} = 2.60$,

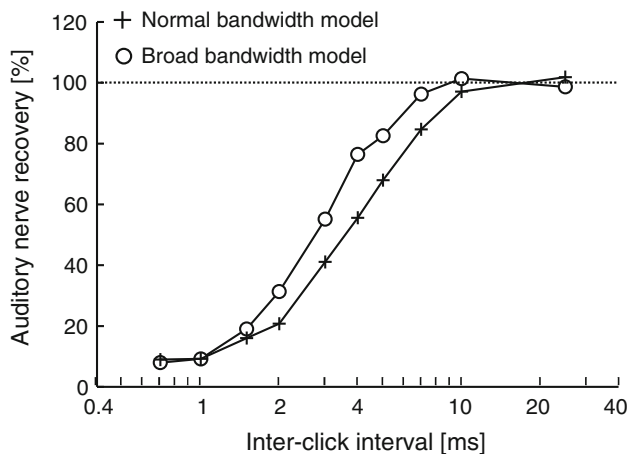


Fig. 4 The percent recovery of auditory nerve fibers predicted from the model as a function of inter-click interval. Auditory filters of the broad bandwidth model are 50% greater in bandwidth than the filters of the normal bandwidth model. Percent recovery is the peak amplitude of the onset response to the second click divided by the peak amplitude of the onset response to a single click times 100

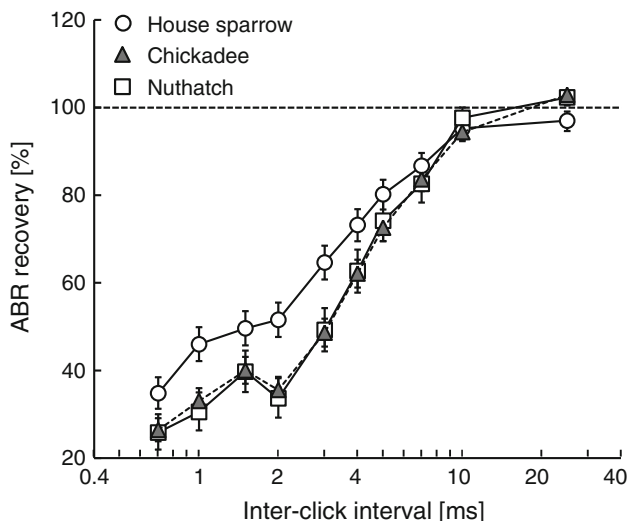


Fig. 5 ABR recovery (least squares mean \pm 1 SE) as a function of inter-click interval in the study species. ABR recovery is the peak-to-peak amplitude of the response to the second click expressed as a percentage of the peak-to-peak amplitude evoked by a single click

$P = 0.011$), 2 ($t_{79,4} = 2.94$, $P = 0.004$), and 3 ms ($t_{79,4} = 2.44$, $P = 0.017$). ABR recovery was similar among all study species at other intervals, and similar between chickadees and nuthatches at all intervals ($P > 0.05$ for all comparisons). The pattern suggests that temporal resolution is greater in house sparrows than chickadees and nuthatches, and similar between chickadees and nuthatches.

Auditory filters in chickadees, reported previously (Henry and Lucas 2010b), range in ERB from 427 to 582 Hz at 2 kHz (mean 489 Hz), 471–731 Hz at 3 kHz (mean 582 Hz), and 396–735 Hz at 4 kHz (mean 585 Hz).

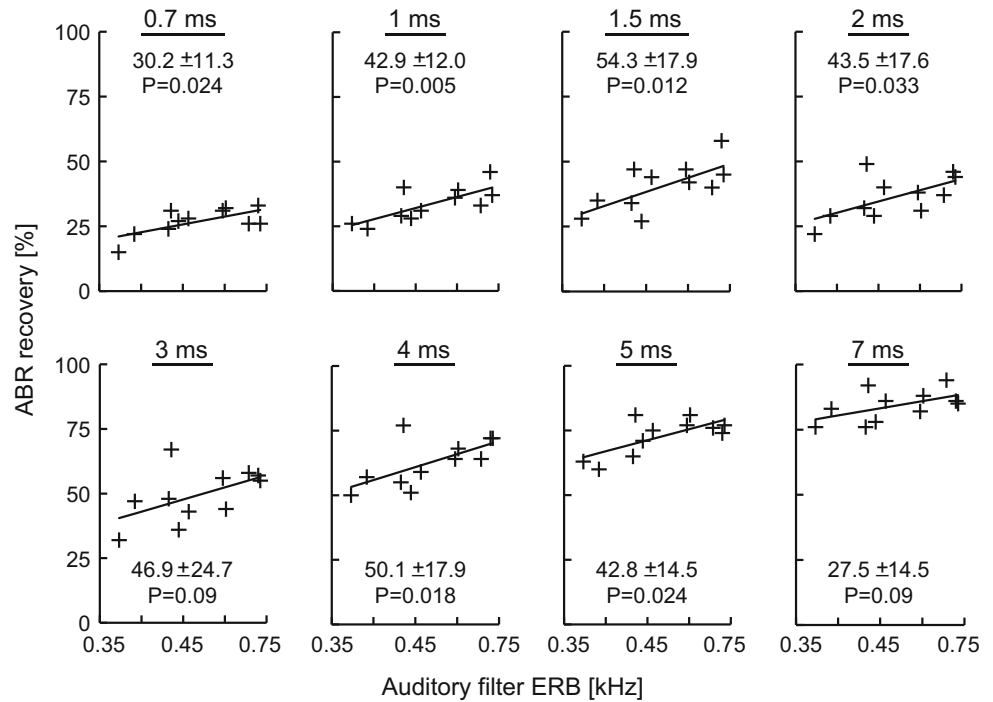
The effect of inter-click interval on ABR recovery varied with ERB at 4 kHz (interval $F_{9,81} = 25.44$, $P < 0.001$; 4 kHz ERB $F_{1,9} = 6.54$, $P = 0.0308$; interval \times 4 kHz ERB $F_{9,81} = 3.28$, $P = 0.002$), but not ERB at 2 kHz (2 kHz ERB $F_{1,5} = 0.37$, $P = 0.57$; interval \times 2 kHz ERB $F_{9,45} = 1.11$, $P = 0.37$) or 3 kHz (3 kHz ERB $F_{1,5} = 0.00$, $P = 0.96$; interval \times 3 kHz ERB $F_{9,45} = 0.34$, $P = 0.96$). ERB at 4 kHz was positively related to ABR recovery at most inter-click intervals shorter than 7 ms (Fig. 6). The pattern suggests that chickadees with lower frequency resolution have a greater temporal resolution. Finally, ABR recovery functions were similar between male and female chickadees (interval $F_{9,90} = 313.84$, $P < 0.001$; sex $F_{1,10} = 0.31$, $P = 0.59$; interval \times sex $F_{9,90} = 0.84$, $P = 0.58$), suggesting similar temporal resolution between sexes.

Discussion

The results of the current study of ABR recovery in songbirds support a tradeoff between peripheral auditory frequency resolution and temporal resolution. In chickadees, we found greater temporal resolution (i.e., greater ABR recovery at short inter-click intervals) in individuals with greater auditory filter bandwidth at 4 kHz. Across species, we found greater temporal resolution in house sparrows than both chickadees and nuthatches, as predicted based on previous observations of greater mean auditory filter bandwidth in house sparrows. However, temporal resolution was similar between chickadees and nuthatches despite greater mean auditory filter bandwidth in chickadees.

The results of the auditory nerve model simulation, moreover, strongly suggest that the differences observed in temporal resolution are at least in part due to the differences in peripheral auditory filter bandwidth. Increasing auditory filter bandwidth by 50% in the model resulted in an increase in auditory nerve recovery of 11–21% points at inter-click intervals from 2 to 7 ms. This pattern corresponds qualitatively with the patterns observed in our ABR data. Within chickadees, for example, a 50% increase in auditory filter bandwidth at 4 kHz was associated with an increase in ABR recovery of 10–12% points at inter-click intervals from 1 to 5 ms. Similarly, across species, a 28% increase in mean auditory filter bandwidth in house sparrows over nuthatches and chickadees was associated with an increase in ABR recovery of 8–18% points at inter-click intervals from 1 to 4 ms. The lack of precise quantitative agreement between our ABR data and the model predictions can probably be attributed to the fact that our ABR results reflect the activity of neural populations with heterogeneous sensitivity and frequency tuning, while the model results are based on a homogeneous neural population.

Fig. 6 ABR recovery as a function of auditory filter ERB at 4 kHz in chickadees. The inter-click interval is underlined at the top of each panel. The slope \pm SE of the regression line, in percentage points per kHz, and significance of the relationship (*P* value) are also included in each panel



The difference in temporal resolution observed between house sparrows and nuthatches is supported by a previous study of AEPs in response to amplitude-modulated tones. Responses to amplitude-modulation frequencies of 1,550 and 1,910 Hz, but not lower modulation frequencies, have greater amplitude in house sparrows than nuthatches (Henry and Lucas 2008). We were surprised to find similar temporal resolution in chickadees and nuthatches despite a difference in mean auditory filter bandwidth. The pattern may reflect differences in other factors, in addition to auditory filter bandwidth, known to influence auditory temporal resolution. The refractory period of individual neurons, for example, can affect responsiveness to sounds separated by intervals up to 20–30 ms, and adaptation mechanisms within the cochlear synapse can operate over even longer time frames under some conditions (Eggermont and Spoor 1973). Alternatively, the ABR recovery method may assess the temporal resolution of neurons with high-characteristic frequencies relative to frequency bandwidth of the stimulus due to an upward spread of excitation at the shortest inter-click intervals. In this case, similar temporal resolution in chickadees and nuthatches would be expected, because these species have similar auditory filter bandwidth at 4 kHz (Fig. 1). Indeed, it seems possible that at the shortest inter-click intervals, only neurons with the broadest frequency tuning and greatest temporal sensitivity (that is, neurons with high characteristic frequencies) contribute to the ABR to the second click. The tendency for ABR recovery to reflect temporal resolution of high-frequency neurons may also explain why, within chickadees, temporal resolution

was associated with auditory filter bandwidth at 4 kHz but not lower stimulus frequencies. Single-unit or masking studies are needed to test this possibility.

The sensation level of the stimulus (dB above threshold) can also influence estimates of temporal resolution. Higher sensation levels tend to suppress response recovery at short inter-click intervals (Parham et al. 1996), and hence, yield lower estimates of temporal resolution. Estimates of temporal resolution in the current study were probably not overly influenced by differences in sensation level considering that ABR thresholds at 3 kHz, the dominant frequency of the click stimuli, vary by less than 5 dB within and across the study species (Henry and Lucas 2010b).

Ultimately, species differences in temporal resolution may reflect evolutionary adaptations for efficient processing of vocal communication signals. High-temporal resolution in house sparrows, for example, may have evolved to improve temporal coding of vocal fine structure and envelope fluctuations, whereas lower temporal resolution in chickadees and nuthatches may have evolved to permit greater frequency resolution of tonal signals. Consistent with this speculation, house sparrow vocalizations contain rapid modulations of frequency and amplitude (Lowther and Cink 2006), whereas nuthatch vocalizations (Ritchison 1983) and chickadee songs (Lohr et al. 1991) contain mostly tonal elements. Note, however, that many chickadee calls (vocalizations exchanged over shorter distances) contain rapid frequency and amplitude modulation (Lucas and Freeberg 2007). Ultimately, this hypothesis should be explored using a phylogenetic comparative analysis of a larger sample of species.

Our results indicate a surprising degree of individual variation among chickadees in peripheral auditory processing. The underlying factors responsible for auditory differences are unclear, but could include experience-based developmental auditory plasticity. Indeed, chickadees raised in acoustic isolation are less able to discriminate among contact calls of different individuals (Phillmore et al. 2003). The specific effects of experience on the peripheral auditory system are unexplored in songbirds, but in domesticated ducks and chickens, exposure to music or species-specific vocalizations early in life enhances the anatomical and functional development of auditory brainstem nuclei (Dmitrieva and Gottlieb 1994; Wadhwa et al. 1999). Furthermore, in humans, musical training or experience with tonal language enhances neural processing of speech and music sounds in the brainstem (Musacchia et al. 2007; Krishnan et al. 2010). Individual variation in reproductive hormone levels could also contribute to auditory differences. Previous studies of songbirds indicate the presence of estrogen receptors within the cochlea (Noirot et al. 2009), and differences in peripheral auditory function between sexes and seasons in a variety of species including chickadees (Lucas et al. 2002, 2007; Henry and Lucas 2009, 2010b; Caras et al. 2010). Finally, a small amount of variation across subjects can be attributed to a measurement error. In a single house sparrow tested on two separate occasions, ABR recovery varied by $3.4 \pm 1.9\%$ points (mean absolute difference \pm SD) between days. Note that in this subject, testing was repeated due to excessive background in the ABR recordings on the first day. Hence, the measurement error was probably lower in other subjects.

A comparison of AEP responses to paired click stimuli between songbirds and other taxa suggests that birds may have greater temporal resolution than some terrestrial mammals, but lower temporal resolution than dolphins. In response to click stimuli of 60 dB SPL, ABR recovery in our study species ranged from 30 to 45% at an inter-click interval of 1 ms and from 35 to 50% at 2 ms. Full recovery occurred at intervals greater than about 10 ms. At a similar sensation level of click stimulation (i.e., approximately 30–40 dB above threshold) recovery of the compound action potential (CAP) in cats increases from 30% at an interval of 2 ms to 100% at inter-click intervals greater than 16 ms (Parham et al. 1996). CAP recovery in humans is unknown for inter-click intervals less than 3 ms (at which point CAP recovery ranges from 50 to 65%), but full recovery requires about 70 ms between clicks (Ohashi et al. 2005). Finally, ABR recovery in dolphins, which find prey using echolocation, increases from 50% at an interval of 1 ms to 100% at intervals greater than 5 ms (Supin and Popov 1995). Recent psychophysical studies also suggest sensitive temporal resolution in birds. Zebra finches and budgerigars, for example, can discriminate differences in temporal fine structure

occurring within time intervals as short as 1 ms whereas humans require time intervals greater than 3–4 ms (Dooling et al. 2002; Lohr et al. 2006). Our results provide a potential neural basis for these capabilities.

In conclusion, the results of the current study of songbirds support a tradeoff between frequency resolution and temporal resolution. More generally, our results add to the small body of empirical research on sensory tradeoffs, and highlight their potential importance in the evolution. The adaptive significance of species differences and the ontogeny of individual variation may be rewarding avenues for future research.

Acknowledgments Animal protocols were approved by the Purdue AnimalCare and Use committee (# 05–058). K. S. Henry was supported by a research grant from Purdue University and the A. A. Lindsey Graduate Fellowship in Ecology. We thank R. Krishnan for the use of his auditory test equipment.

References

- Brittan-Powell EF, Dooling RJ, Gleich O (2002) Auditory brainstem responses in adult budgerigars (*Melopsittacus undulatus*). *J Acoust Soc Am* 112:999–1008
- Bruce IC, Sachs MB, Young ED (2003) An auditory-periphery model of the effects of acoustic trauma on auditory nerve responses. *J Acoust Soc Am* 113:369–388
- Caras ML, Brenowitz E, Rubel EW (2010) Peripheral auditory processing changes seasonally in Gambel's white-crowned sparrow. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 196:581–599
- Collin SP, Davies WL, Hart NS, Hunt DM (2009) The evolution of early vertebrate photoreceptors. *Philos Trans R Soc Lond B Biol Sci* 364:2925–2940
- de Boer E (1996) Mechanics of the cochlea: modeling efforts. In: Dallos P, Popper AN, Fay RR (eds) *The cochlea*. Springer, New York, pp 258–317
- Dmitrieva LP, Gottlieb G (1994) Influence of auditory experience on the development of brain-stem auditory evoked potentials in mallard duck embryos and hatchlings. *Behav Neural Biol* 61:19–28
- Dooling RJ, Leek MR, Gleich O, Dent ML (2002) Auditory temporal resolution in birds: discrimination of harmonic complexes. *J Acoust Soc Am* 112:748–759
- Eggermont JJ, Spoor A (1973) Masking of action potentials in the guinea pig cochlea, its relation to adaptation. *Audiology* 12:221–241
- Feng AS, Narins PM, Xu C, Lin W, Yu Z, Qiu Q, Xu Z, Shen J (2006) Ultrasonic communication in frogs. *Nature* 440:333–336
- Fullard JH, ter Hofstede HM, Ratcliffe JM, Pollack GS, Brigidi GS, Tinghitella RM, Zuk M (2010) Release from bats: genetic distance and sensoribehavioural regression in the Pacific field cricket, *Teleogryllus oceanicus*. *Naturwissenschaften* 97:53–61
- Gall MD, Lucas JR (2010) Sex differences in auditory filters of brown-headed cowbirds. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 196:559–567
- Hall JW (2007) *New handbook of auditory evoked responses*. Pearson Education, Boston
- Henry KS, Lucas JR (2008) Coevolution of auditory sensitivity and temporal resolution with acoustic signal space in three songbirds. *Anim Behav* 76:1659–1671
- Henry KS, Lucas JR (2009) Vocally correlated seasonal auditory variation in the house sparrow (*Passer domesticus*). *J Exp Biol* 212:3817–3822

- Henry KS, Lucas JR (2010a) Habitat-related differences in the frequency selectivity of auditory filters in songbirds. *Funct Ecol* 24:614–624
- Henry KS, Lucas JR (2010b) Auditory sensitivity and the frequency selectivity of auditory filters in the Carolina chickadee (*Poecile carolinensis*). *Anim Behav* 80:497–507
- Joris PX, Schreiner CE, Rees A (2004) Neural processing of amplitude-modulated sounds. *Physiol Rev* 84:541–577
- Klump GM, Gleich O (1991) Gap detection in the European starling (*Sturnus vulgaris*). III. Processing in the peripheral auditory system. *J Comp Physiol A* 168:469–476
- Konishi M (1973) How owl tracks its prey. *Am Sci* 61:414–424
- Krishnan A, Gandour JT, Bidelman GM (2010) The effects of tone language experience on pitch processing in the brainstem. *J Neurolinguistics* 23:81–95
- Lohr B, Nowicki S, Weisman R (1991) Pitch production in Carolina chickadee songs. *Condor* 93:197–199
- Lohr B, Dooling RJ, Bartone S (2006) The discrimination of temporal fine structure in call-like harmonic sounds by birds. *J Comp Psychol* 120:239–251
- Lowther PE, Cink CL (2006) House sparrow (*Passer domesticus*). In: Poole A (ed) *The birds of North America online*. Cornell Lab of Ornithology, Ithaca
- Lucas JR, Freeberg TM (2007) Information and the chick-a-dee call: communicating with a complex vocal system. In: Otter K (ed) *Ecology and behavior of chickadees and titmice*. Oxford University Press, Oxford, pp 199–213
- Lucas JR, Freeberg TM, Krishnan A, Long GR (2002) A comparative study of avian auditory brainstem responses: correlations with phylogeny and vocal complexity, and seasonal effects. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 188:981–992
- Lucas JR, Freeberg TM, Egbert J, Schwabl H (2006) Fecal corticosterone, body mass, and caching rates of Carolina chickadees (*Poecile carolinensis*) from disturbed and undisturbed sites. *Horn Behav* 49:634–643
- Lucas JR, Freeberg TM, Long GR, Krishnan A (2007) Seasonal variation in avian auditory evoked responses to tones: a comparative analysis of Carolina chickadees, tufted titmice, and white-breasted nuthatches. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 192:201–215
- Marean GC, Burt JM, Beecher MD, Rubel EW (1998) Auditory perception following hair cell regeneration in European starling (*Sturnus vulgaris*): frequency and temporal resolution. *J Acoust Soc Am* 103:3567–3580
- Moore BCJ (1993) Frequency analysis and pitch perception. In: Yost WA, Popper AN, Fay RR (eds) *Human psychophysics*. Springer, New York, pp 58–89
- Musacchia G, Sams M, Skoe E, Kraus N (2007) Musicians have enhanced subcortical auditory and audiovisual processing of speech and music. *Proc Natl Acad Sci USA* 104:15894–15898
- Noirot IC, Adler HJ, Cornil CA, Harada N, Dooling RJ, Balthazart J, Ball GF (2009) Presence of aromatase and estrogen receptor alpha in the inner ear of zebra finches. *Hear Res* 252:49–55
- Ohashi T, Ochi K, Nishino H, Kenmochi M, Yoshida K (2005) Recovery of human compound action potential using a paired-click to stimulus paradigm. *Hear Res* 203:192–200
- Okanoya K, Dooling RJ (1990) Minimum detectable gap in noise as a function of intensity and frequency for two avian species, budgerigars (*Melopsittacus undulatus*) and zebra finches (*Poephila guttata*). *Hear Res* 50:185–192
- Parham K, Zhao HB, Kim DO (1996) Responses of auditory nerve fibers of the unanesthetized decerebrate cat to click pairs as simulated echoes. *J Neurophysiol* 76:17–29
- Phillmore LS, Sturdy CB, Weisman RG (2003) Does reduced social contact affect discrimination of distance cues and individual vocalizations? *Anim Behav* 65:911–922
- Ritchison G (1983) Vocalizations of the white-breasted nuthatch. *Wilson Bull* 95:440–451
- Supin AY, Popov VV (1995) Temporal resolution in the dolphin's auditory system revealed by double-click evoked potential study. *J Acoust Soc Am* 97:2586–2593
- Viemeister NF, Plack CJ (1993) Time analysis. In: Yost WA, Popper AN, Fay RR (eds) *Human psychophysics*. Springer, New York, pp 116–154
- Wadhwa S, Anand P, Bhowmick D (1999) Quantitative study of plasticity in the auditory nuclei of chick under conditions of prenatal sound attenuation and overstimulation with species specific and musical stimuli. *Int J Dev Neurosci* 17:239–253
- Walton JP, Barsz K, Wilson WW (2008) Sensorineural hearing loss and neural correlates of temporal acuity in the inferior colliculus of the C57BL/6 mouse. *J Assoc Res Otolaryngol* 9:90–101
- Wysocki LE, Ladich F (2002) Can fishes resolve temporal characteristics of sounds? New insights using auditory brainstem responses. *Hear Res* 169:36–46
- Zilany MSA, Bruce IC (2006) Modeling auditory-nerve responses for high sound pressure levels in the normal and impaired auditory periphery. *J Acoust Soc Am* 120:1446–1466
- Zilany MSA, Bruce IC (2007) Representation of the vowel (epsilon) in normal and impaired auditory nerve fibers: model predictions of responses in cats. *J Acoust Soc Am* 122:402–417
- Zilany MSA, Carney LH (2010) Power-law dynamics in an auditory-nerve model can account for neural adaptation to sound-level statistics. *J Neurosci* 30:10380–10390
- Zilany MSA, Bruce IC, Nelson PC, Carney LH (2009) A phenomenological model of the synapse between the inner hair cell and auditory nerve: long-term adaptation with power-law dynamics. *J Acoust Soc Am* 126:2390–2412