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Vocally correlated seasonal auditory variation in the house sparrow (*Passer domesticus*)

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SUMMARY

Songbirds exhibit seasonal plasticity in a broad variety of behavioral and morphological traits associated with reproduction. Changes in song production are well described while changes in song reception are not. In the present study, we test for seasonal variation in auditory processing of the house sparrow (*Passer domesticus* L.) using auditory brainstem responses (ABRs) to tone bursts. We measured amplitude and latency of the first ABR peak in spring, summer and autumn at stimulus frequencies from 0.8 to 6.4 kHz and intensity levels from 24 to 80 dB SPL. ABR thresholds were determined at each frequency using cross-correlation. Amplitude was greater in spring than in autumn at frequencies from 3.2 to 6.4 kHz whereas latency and thresholds exhibited no seasonal variation. The results indicate an increase in the number or temporal synchrony of responses from peripheral auditory neurons during the early breeding season. Changes in peripheral auditory processing may enhance temporal coding of the fine structure and envelope of song; thereby, improving assessment of encoded information in both sexes (e.g. individual identity and dominance status) and auditory feedback during song production in males. Peripheral auditory changes may be mediated by reproductive hormones, and could involve changes in hair cell density on the basilar papilla. Our results suggest that peripheral auditory processing of songbirds changes seasonally in parallel with other behavioral and morphological traits, such as song production.

Key words: animal communication, auditory brainstem response (ABR), house sparrow, *Passer domesticus*, seasonal plasticity, sensory ecology.

INTRODUCTION

In songbirds, many of the anatomical structures underlying song production undergo seasonal growth and regression. For example, the syrinx and song control nuclei of the forebrain increase in size during the breeding season in many species. These morphological changes allow increased song output and quality at a time when singing behavior has the greatest impact on reproductive success (Brenowitz, 2004). Outside of the breeding season, regression of song structures appears to conserve metabolic costs when production of numerous, high-quality songs would yield little benefit (Meitzen et al., 2007). Auditory structures responsible for song reception may undergo parallel seasonal changes. Auditory enhancement during the breeding season may improve detection and discrimination of songs when these behaviors have the greatest impact on reproductive success whereas regression of auditory structures outside of the breeding season could conserve metabolic costs [for discussion of sensory costs, see Niven and Laughlin (Niven and Laughlin, 2008)]. However, seasonal variation in auditory performance remains relatively unexplored.

Seasonal auditory changes have been documented in a small number of species from a broad taxonomic range. Single-unit studies of the auditory nerve in plainfin midshipman fish [*Porichthys notatus* (Sisneros et al., 2004)] and auditory midbrain in northern leopard frogs [*Rana pipiens* (Goense and Feng, 2005)] showed seasonal variation in the temporal precision of neural responses to the acoustic structure of artificial calls. In songbirds, Lucas and colleagues found preliminary evidence of seasonal variation in auditory brainstem responses (ABRs) of four species, including the house sparrow (*Passer domesticus*) studied here (Lucas et al., 2002; Lucas et al., 2007). ABRs are voltage waveforms recorded from the scalp that reflect the summed neural onset response of the auditory nerve and brainstem nuclei to sound (Hall, 2007). Responses to clicks and tones were stronger in spring than in winter in Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophyus bicolor*) and stronger in winter than in spring in white-breasted nuthatches [*Sitta carolinensis*, a species that sings in winter (Lucas et al., 2002; Lucas et al., 2007)]. In house sparrows, responses to clicks were stronger in spring than in winter (Lucas et al., 2002) but responses to tones were not studied. Unfortunately, these studies provide an incomplete description of seasonal auditory variation in songbirds because auditory measurements were not made throughout the breeding season (i.e. data were not collected from May to September). Moreover, the studies did not measure ABR thresholds, which provide an indication of audiogram shape. The description of seasonal auditory variation is particularly coarse in the house sparrow, where only responses to broadband click stimuli were evaluated (Lucas et al., 2002).

Previously, we conducted a comprehensive study of ABRs to tone burst stimuli in the house sparrow using subjects captured outside of the breeding season (Henry and Lucas, 2008). Specifically, we described the effects of stimulus frequency and intensity on the amplitude and latency of the first ABR peak, and variation in ABR thresholds with stimulus frequency. Here, we test for seasonal variation in these measurements using an expanded dataset, including auditory data collected throughout the breeding season from both sexes. The amplitude of the first ABR peak is positively related to the number of auditory nerve fibers responding to the stimulus and their synchrony while the latency of the first ABR peak is the mean reaction time of the auditory nerve fiber responses (Hall, 2007). The ABR threshold is the lowest stimulus intensity that elicits a detectable ABR waveform. In birds, ABR thresholds are 25–30 dB higher than behavioral auditory thresholds and correlate with ABR latency (Dmitrieva and Gottlieb, 1992; Brittan-Powell et al., 2002; Brittan-

Powell et al., 2005; Henry and Lucas, 2008). ABR thresholds determined by cross-correlation, as in the present study, reflect contributions of the auditory periphery and brainstem.

The house sparrow (*Passer domesticus* L.) is a non-migratory, sexually dimorphic, monogamous songbird species introduced to North America in the mid 19th century (Lowther and Cink, 2006). Individuals are found worldwide in environments modified by humans, including farmland, residential areas and cities. Unlike most songbirds, house sparrows have a prolonged breeding season with multiple broods. Songs range in frequency from 3.2 to 5.4 kHz (Henry and Lucas, 2008). Song rates peak during 3–4 egg-laying stages between late March and early August (Hegner and Wingfield, 1986a; Hegner and Wingfield, 1986b), and decrease gradually until November when activity in almost negligible [although some songs are still produced (Lowther and Cink, 2006)]. We predicted that ABR amplitude would be greater, latency shorter and thresholds lower in spring and summer than in autumn. Moreover, we expected seasonal auditory changes to have the greatest magnitude at stimulus frequencies from 3.2 to 5.4 kHz.

MATERIALS AND METHODS

Subjects and seasons

We analyzed ABRs of 24 adult birds between June 2006 and April 2008. Data were divided into spring (March–May; 7 birds: 4 females and 3 males), summer (June–July; 7 birds: 2 females and 5 males) and autumn (September–November; 10 birds: 4 females and 6 males). Subjects were captured using treadle traps in a residential area, fitted with an aluminum leg band and transported to an indoor aviary at Purdue University (West Lafayette, IN, USA). Species, sex, and age were determined based on plumage (Pyle, 1997). Subjects were housed individually in 1 m × 1 m × 1 m wire-mesh cages and provided with mixed seed, grit and vitamin-treated water. The light–dark cycle of the aviary was set to local conditions and the temperature was held constant at 22°C. Auditory tests were conducted on the afternoon of capture, and subjects were released 1–2 days later at their capture sites. Protocols were approved by the Purdue Animal Care and Use Committee (# 05–058).

Auditory test procedures and equipment

Subjects were weighed and then anesthetized with an injection of ketamine (40–60 mg kg^{-1}) and xylazine (8–12 mg kg^{-1}) into the breast muscle. Body mass ($\bar{X}$±s.d.) was 27.9±2.9 g in males and 26.0±1.9 g in females. Needle electrodes (Nicolet Biomedical, Fitchburg, WI, USA) were inserted subdermally at three well-defined anatomical locations to record ABRs. A positive electrode was positioned high at the vertex of the skull, a negative electrode 3 mm posterior to the right auditory meatus and a ground electrode at the base of the neck. Electrodes were positioned by the same observer throughout the study to ensure consistent placement. One or two supplemental injections of ketamine (15–20 mg kg^{-1}) and xylazine (2–3 mg kg^{-1}) were given in order to complete approximately 80 min of auditory tests.

The test chamber (1.2 m tall × 1.4 m wide × 1.2 m deep) was lined with a layer of 7.7 cm-thick Sonex foam (Acoustic Solutions, Richmond, VA, USA). Subjects were placed on a pre-heated pad (Pet Supply Imports, South Holland, IL, USA) inside the test chamber with the lights off and their right ear facing upwards. Stimulus presentation, ABR acquisition and data storage were coordinated by a Tucker Davis Technologies system II modular rack-mount system (TDT, Gainesville, FL, USA) and a Dell PC running TDT SigGen32/BioSig32 software in an adjacent room. Stimuli were amplified by a Crown D75 amplifier and presented through a downward projecting, electromagnetically shielded, dynamic loudspeaker suspended 30 cm above the subject (RCA model 40-5000; 140–20,000 Hz frequency response). Stimuli were calibrated within ±1 dB SPL using a Bruel & Kjaer model 1613 Precision Sound Level Meter (Norcross, GA, USA) and model 4131 2.6 cm condenser microphone placed at the location of the bird's ear.

Auditory brainstem responses

ABR stimuli were 5 ms tone bursts with 1 ms cos^2 onset/offset ramps, presented at a rate of 31.1 stimuli per second with alternating phase values of 0.5 π and 1.5 π radians. We evoked ABRs at frequencies of 0.8, 1.4, 2.2, 3.2, 4.2 and 6.4 kHz in random order and intensity levels from 80 to 24 dB SPL in 8 dB steps. Each ABR was the mean response to 1000 stimulus repetitions. Responses were sampled at 40 kHz for 12 ms, beginning 1.2 ms before stimulus arrival at the ear, amplified 200,000 times, band-pass filtered from 0.1–3 kHz and notch filtered at 60 Hz.

The amplitude of the first ABR peak was measured relative to the subsequent trough, while latency was measured relative to the time of stimulus onset (Fig. 1). ABR thresholds were estimated using a cross-correlation technique described previously by Henry and Lucas (Henry and Lucas, 2008). 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.

A cross-correlation analysis was conducted at each frequency in each subject. Each analysis involved (1) determining an amplitude score for each ABR by cross-correlating it with an ABR template waveform, (2) removing non-significant ABRs, and (3) calculating the ABR threshold by extrapolating from the amplitude score by stimulus intensity function.

(1) The same ABR template waveforms were used for all subjects. An ABR template was generated at each stimulus frequency by averaging together the 80 dB SPL responses of all 24 subjects and extracting 7 ms from the grand mean waveform beginning 1 ms after stimulus onset (Fig. 1). Each ABR was cross-

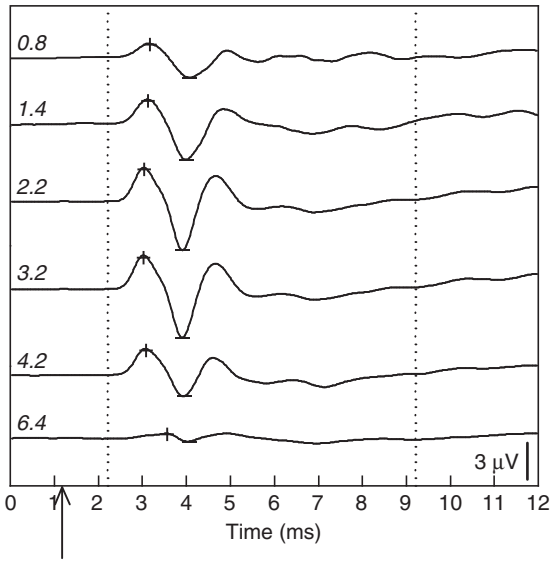

Fig. 1. Grand mean auditory brainstem response (ABR) waveforms (*N*=24 birds) in response to 80 dB SPL stimuli. Stimulus frequency (kHz) is given in italics. The amplitude of peak I (+ symbol) was measured relative to the subsequent trough (– symbol); latency was measured relative to stimulus onset (upward pointing arrow). The portion of the waveform between the dotted lines is the ABR template.

correlated with the ABR template of the same frequency to determine the maximum cross-product. We also cross-correlated the template with 1.5 s of electrophysiological background noise to determine a null distribution of cross-product values. The noise was a concatenation of 60 ms recordings obtained from the subjects under quiet conditions using the acquisition parameters described above. The null distribution of cross-products was approximately normal with a mean of zero. We defined the amplitude score of the ABR as the maximum cross-product value divided by the standard deviation of the null distribution.

(2) ABRs were removed from the dataset 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 less than 1.645. 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 the null expectation of zero at the 95% confidence level.

(3) The ABR threshold was calculated by extrapolating from the amplitude score by stimulus intensity function. Specifically, we defined the ABR threshold as the stimulus intensity level necessary to produce an amplitude score of 1.965 (i.e. greater than the null expectation of zero at the 99% confidence level). The amplitude score by stimulus intensity function was linear at intensity levels within 30–40 dB of the presumed threshold. We therefore calculated the ABR threshold from a linear regression model that included the four lowest-intensity data points remaining in the series after removal of non-significant ABRs (step 2).

Statistical analyses

We used repeated-measures mixed models to analyze the three dependent variables: ABR amplitude, latency and threshold (Proc MIXED; SAS Institute Inc., v. 9.1, Cary, NC, USA). All dependent variables were normalized using the Box-Cox procedure. Optimal lambda values of 0.25 for amplitude, 0.5 for latency and –1 for thresholds were selected using Proc TRANSREG in SAS.

The analyses of ABR amplitude and latency included main effects of stimulus frequency, intensity, season and sex. Intensity was modeled as a continuous variable and an intensity-squared term was included to account for non-linearity. The analyses also included two-way interactions between frequency and intensity, season and frequency, season and intensity, sex and frequency and sex and intensity. The analysis of ABR thresholds included main effects of stimulus frequency, season and sex, and two-way interactions between season and frequency and sex and frequency. Note that interactions between sex and season were not included in any model due to inadequate sample sizes.

Non-significant effects (P>0.05) were dropped from the model in order of decreasing P-value. The remaining factors were explored using tests of simple effects (for two-way interactions) and comparisons of least squares (LS) means. The degrees of freedom for all significance tests were calculated using the Kenward–Roger correction for small samples. LS means ± s.e. are presented throughout the text whereas 95% confidence intervals of back-transformed LS means are presented in the figures.

We selected the within-subject covariance structure for each model based on procedures outlined by Littell et al. (Littell et al., 2006). We fit a variety of potential covariance structures, including compound symmetry, first-order autoregressive, first-order autoregressive with a random subject effect, heterogeneous first-order autoregressive and Toeplitz, and selected the model that yielded the lowest Akaike and Bayesian Information Criteria (i.e. the most parsimonious model). First-order autoregressive covariance with a random subject effect provided the best fit for all analyses.

Visual inspection of the model residuals indicated that they were normally distributed and had constant variance, i.e. normal probability plots were linear and residual variance did not vary with predicted values. Furthermore, residual variance was similar across the levels of interest of the analyses (e.g. combinations of season, frequency and intensity for the analysis of ABR amplitude).

A number of negative results call into question the statistical power provided by the sample sizes of the study (i.e. the probability that differences would be detected given that they exist). We therefore calculated the power to detect biologically reasonable effects of season and sex on ABR amplitude, latency and threshold based on observed levels of variance in LS means (Proc POWER). Hypothesized effects were centered at the global mean of each measurement: 1870 nV, 2.64 ms and 35.1 dB SPL for ABR amplitude, latency and threshold, respectively. The power to detect an amplitude difference of 30% was 74% between seasons and 88% between sexes, the power to detect a latency difference of 0.15 ms was 74% between seasons and 88% between sexes, and the power to detect a threshold difference of 4 dB was 67% between seasons and 83% between sexes.

RESULTS

ABR amplitude

The analysis of ABR amplitude revealed significant effects of frequency (repeated-measures mixed model: $F_{5,367}$=811.24, P<0.001), intensity ($F_{1,641}$=836.58, P<0.001) and the intensity-squared term ($F_{1,634}$=332.55, P<0.001) but no significant frequency × intensity interaction ($F_{5,628}$=0.31, P=0.91). Maximum ABR amplitude was observed at intermediate stimulus frequencies from 2.2 to 3.2 kHz (Figs 2 and 3). Transformed amplitude × intensity functions were similar in slope across frequencies (data not shown) whereas back-transformed functions were greater in slope at intermediate frequencies from 2.2 to 3.2 kHz than at higher and lower frequencies (Fig. 2).

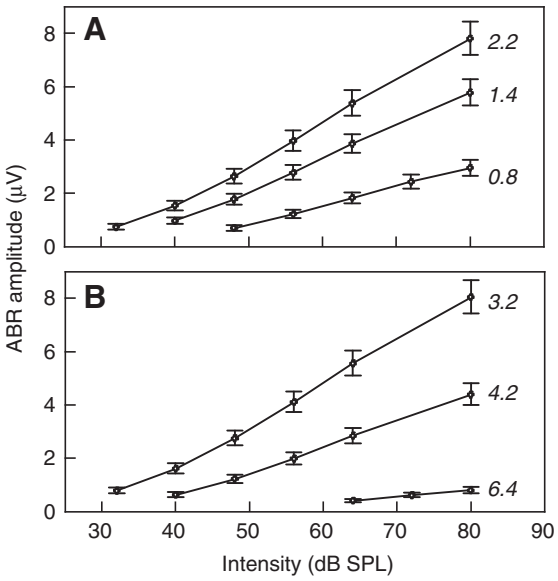

Fig. 2. Back-transformed least squares (LS) mean auditory brainstem response (ABR) amplitude as a function of intensity at (A) 0.8, 1.4 and 2.2 kHz, and (B) 3.2, 4.2 and 6.4 kHz. Stimulus frequency (kHz) is given in italics. Error bars represent 95% confidence intervals.

Table 1. Seasonal differences in transformed least squares mean auditory brainstem response amplitude [(nV$^{0.25}$–1)/0.25]

Seasons	Frequency (kHz)	$t_{d.f.}$	P	$\bar{X}_{2-1}$±s.e.
Spring–autumn	3.2	$2.78_{34.1}$	0.009	2.33±0.84
	4.2	3.13_{37}	0.003	2.68±0.86
	6.4	$2.78_{40.3}$	0.008	2.43±0.87
Spring–summer	3.2	$2.04_{33.5}$	0.05	1.87±0.92
	4.2	$3.55_{36.5}$	0.001	3.33±0.94
	6.4	$0.96_{39.5}$	0.34	0.92±0.96
Summer–autumn	3.2	$0.55_{33.6}$	0.58	0.46±0.83
	4.2	$-0.76_{36.8}$	0.45	–0.64±0.85
	6.4	$1.75_{39.9}$	0.09	1.51±0.87

Tests for seasonality indicated frequency-dependent seasonal variation in ABR amplitude (season: $F_{2,20.1}$=3.62, P=0.045; season × frequency: $F_{10,397}$=2.61, P=0.005) but no significant changes in seasonality with intensity level (season × intensity: $F_{2,597}$=2.47, P=0.09). Seasonal variation was significant at frequencies of 3.2 kHz and above (simple effect of season at 0.8 kHz: $F_{2,38.3}$=2.14, P=0.13; 1.4 kHz: $F_{2,36.1}$=1.40, P=0.26; 2.2 kHz: $F_{2,35.3}$=1.02, P=0.37; 3.2 kHz: $F_{2,33.7}$=4.03, P=0.027; 4.2 kHz: $F_{2,36.8}$=7.27, P=0.002; 6.4 kHz: $F_{2,39.9}$=4.11, P=0.024). Amplitude was greater in spring than in autumn at 3.2, 4.2 and 6.4 kHz, and greater in spring than in summer at 4.2 kHz (Table 1; Fig. 3).

Finally, the analysis found a significant interaction between sex and intensity ($F_{1,599}$=10.78, P=0.001) but no main effect of sex ($F_{1,38.5}$=0.46, P=0.50) or simple effect of sex at any test frequency (0.8 kHz: $F_{2,37.43}$=0.66, P=0.42; 1.4 kHz: $F_{2,35.3}$=3.55, P=0.07; 2.2 kHz: $F_{2,35.9}$=3.90, P=0.06; 3.2 kHz: $F_{2,33.5}$=3.93, P=0.06; 4.2 kHz: $F_{2,36.8}$=0.36, P=0.55; 6.4 kHz: $F_{2,40.5}$=0.31, P=0.58). The linear component of the slope of the transformed amplitude by intensity function was greater in males (0.847±0.029 transformed units dB^{-1}) than females (0.825±0.029 transformed units dB^{-1}).

ABR latency

The analysis of ABR latency revealed significant effects of frequency (repeated-measures mixed model: $F_{5,544}$=41.31, P<0.001), intensity ($F_{1,661}$=208.88, P<0.001), the intensity-squared term ($F_{1,661}$=12.90, P<0.001) and the frequency × intensity interaction ($F_{5,579}$=17.31, P<0.001). ABR latency was lowest at intermediate frequencies from 2.2 to 3.2 kHz and decreased with increasing intensity (Figs 4 and 5). The slopes of the back-transformed latency by intensity functions became less negative with increasing intensity level and were generally least negative at intermediate frequencies from 2.2 to 3.2 kHz.

Finally, the analysis of latency found no evidence of seasonality (season: $F_{2,20}$=0.24, P=0.79; season × frequency: $F_{10,243}$=0.92, P=0.52; season × intensity: $F_{2,643}$=1.14, P=0.32) or sex differences (sex: $F_{1,20}$=0.01, P=0.93; sex × frequency: $F_{5,245}$=1.76, P=0.12; sex × intensity: $F_{1,642}$=0.18, P=0.67).

ABR thresholds

ABR thresholds varied with frequency (repeated-measures mixed model: $F_{5,92.5}$=142.95, P<0.001). Thresholds were lowest from 2.2 to 3.2 kHz [back-transformed LS mean threshold followed by the 95% confidence interval in dB SPL at 0.8 kHz: 40.2 (37.9, 42.8); 1.4 kHz: 31.4 (30.1, 32.9); 2.2 kHz: 29.7 (28.5, 31.0); 3.2 kHz: 28.9 (27.8, 30.2); 4.2 kHz: 35.6 (34.0, 37.5); 6.4 kHz: 60.3 (55.4, 66.2)] (Fig. 6).

Finally, the analysis of ABR thresholds found no evidence of seasonality (season: $F_{2,20.2}$=0.54, P=0.59; season × frequency:

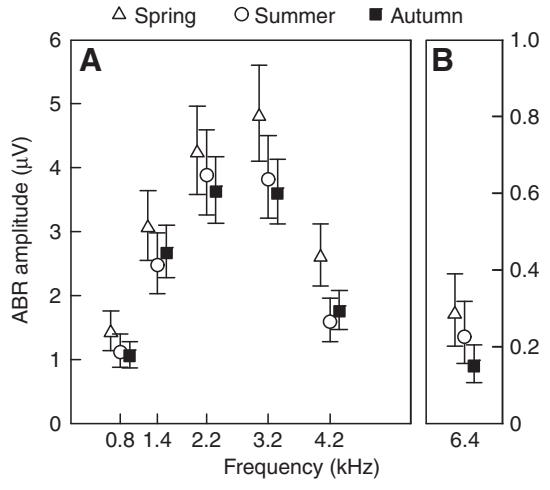

Fig. 3. Back-transformed least squares (LS) mean auditory brainstem response (ABR) amplitude in spring, summer and autumn (see legend) at frequencies of (A) 0.8–4.2 kHz and (B) 6.4 kHz. Error bars represent 95% confidence intervals. Note that spring data are offset –150 Hz, autumn data are offset +150 Hz, and amplitude scales differ between panels.

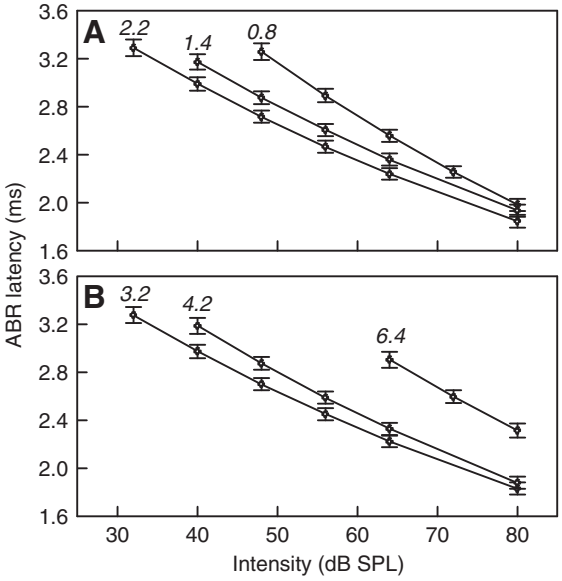

Fig. 4. Back-transformed least squares (LS) mean auditory brainstem response (ABR) latency as a function of intensity at (A) 0.8, 1.4 and 2.2 kHz, and (B) 3.2, 4.2 and 6.4 kHz. Stimulus frequency (kHz) is given in italics. Error bars represent 95% confidence intervals.

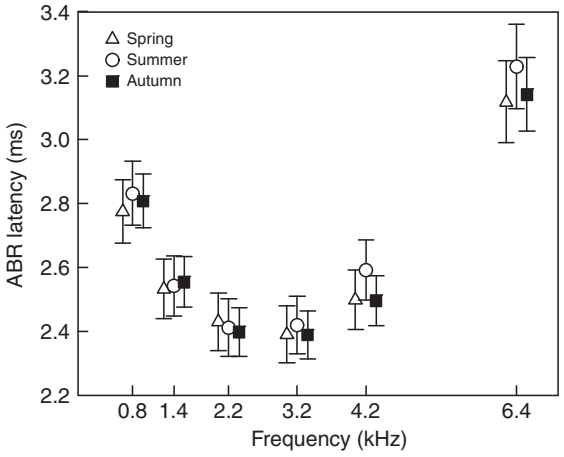

Fig. 5. Back-transformed least squares (LS) mean auditory brainstem response (ABR) latency in spring, summer and autumn (see legend) as a function of frequency. Error bars represent 95% confidence intervals. Note that spring data are offset –150 Hz and autumn data are offset +150 Hz.

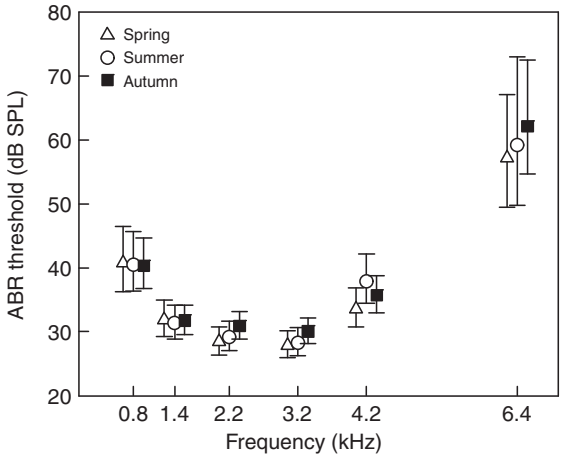

Fig. 6. Back-transformed least squares (LS) mean auditory brainstem response (ABR) thresholds in spring, summer and autumn (see legend) as a function of frequency. Error bars represent 95% confidence intervals. Note that spring data are offset –150 Hz and autumn data are offset +150 Hz.

$F_{10,81}$=0.79, P=0.64) or sex differences (sex: $F_{1,20}$=0.05, P=0.83; sex × frequency: $F_{5,81.5}$=0.17, P=0.97).

DISCUSSION

As predicted, the amplitude of the first ABR peak was greater in spring than in autumn across the frequency range of song. Amplitude in summer, however, was neither greater than in autumn nor less than in spring, and ABR latency and thresholds exhibited no seasonal variation.

Greater amplitude of the first ABR peak in spring indicates an increase in the number or temporal synchrony of responses from neurons of the auditory nerve (Hall, 2007). These changes, in turn, may provide a more faithful neural representation of the temporal features of song. Temporal features of song include the fine structure and envelope of the acoustic signal. Fine structure describes relatively rapid fluctuations in sound pressure contained in the signal (i.e. the signal frequency) whereas envelope modulations describe slower changes in the overall amplitude (Viemeister and Plack, 1993). Behavioral studies indicate that birds rely on both classes of temporal structure to discriminate signal variants, and generally rely on temporal cues more than mammals (Dooling et al., 2002; Lohr et al., 2006). Temporal features are encoded in the relative timing of action potentials at the level of the auditory nerve (Gleich and Manley, 2000; Joris et al., 2004). A greater number of neurons improves temporal processing because errors in the temporal firing pattern of each neuron tend to average out when integrated across an increasingly large number of neurons whereas greater neural synchrony improves temporal processing because action potentials of each neuron are more precisely timed to temporal features of the signal (Joris and Smith, 2008). The upper frequency limit for temporal processing of fine structure ranges from 4 to 6 kHz in songbirds (Gleich and Manley, 2000).

Precise temporal processing of song in spring may aid in assessment of information from song. Males sing up to 12 song variants characterized by complex patterns of frequency and amplitude modulation (Lowther and Cink, 2006). The biological significance of variation in song has not been studied in house sparrows but the acoustic structure of song may encode information important to both sexes such as individual identity, dominance status, parasite load, fighting and parenting abilities and genetic quality, as in other songbirds (Collins, 2004). Females may use this information to choose social mates or partners for extra-pair copulations, as shown in black-capped chickadees [*Poecile atricapillus* (Mennill et al., 2002)]. In house sparrows, 40% of males in an Oklahoma population were found to be cuckolded, and 20% of offspring could be attributed to extra-pair fertilizations (Whitekiller et al., 2000). Greater temporal processing in males may provide more accurate auditory feedback necessary for production of high quality songs or aid in discrimination of intruders from neighbors. Indeed, songbirds may rely more on auditory feedback during song production than previously suspected (Sakata and Brainard, 2008).

Given the expected importance of auditory precision in summer when house sparrows are still actively breeding, we were surprised to find that ABR amplitude was generally not greater than in autumn. This result may reflect variation in the duration of the breeding season across individuals due to resource limitation, and hence the duration of the enhanced auditory phenotype. Female body mass, fat reserves and protein reserves decline throughout the breeding season and appear to regulate the termination of reproduction (Hegner and Wingfield, 1986b). Alternatively, the net benefit of enhanced auditory precision may be less in summer than in spring. This scenario seems less likely, however, given that rates of singing, nest intrusions and extra pair paternity are similar across egg-laying stages within a breeding season (Hegner and Wingfield, 1986a; Hegner and Wingfield, 1986b; Vaclav et al., 2003). Finally, if auditory performance closely mirrors reproductive behavior, greater asynchrony of later egg-laying stages due to nest failures in some pairs could result in a smaller proportion of individuals with the breeding season auditory phenotype in summer. Covariance of reproductive behavior and auditory performance on such a fine scale may or may not be possible depending on underlying auditory mechanism, but would be surprising considering that most morphological changes associated with reproduction persist throughout the breeding season [e.g. beak colour, testis mass, length of cloacal protuberance (Hegner and Wingfield, 1986a)]. Finally, studies focusing on the response properties of individual neurons may be sensitive to auditory changes not immediately apparent based on the ABR method (e.g. changes in response properties limited to a small number of neurons).

The lack of seasonal variation observed in ABR thresholds and latency may reflect no seasonality in auditory thresholds and, consequently, no variation in the maximum distance at which conspecific vocalizations can be detected under quiet conditions.

Increased detection of distant songs may have relatively little selective benefit in house sparrows due to the short range nature of song in this semi-colonial species. Breeding pairs defend only a small area around their nest site, which is often in close proximity to nest sites of conspecifics (Lowther and Cink, 2006). Note, however, that it is unclear whether thresholds under more realistic, noisy conditions vary seasonally, because absolute thresholds do not necessarily predict thresholds in noise (Langemann et al., 1998; Lohr et al., 2003). Previous studies of seasonal auditory plasticity found no variation in thresholds of the plainfin midshipman and northern leopard frog (Sisneros et al., 2004; Goense and Feng, 2005) or in ABR latency of Carolina chickadees, house sparrows and tufted titmice (Lucas et al., 2002; Lucas et al., 2007). White-breasted nuthatches, however, had shorter ABR latency in winter than in spring, suggesting possible seasonal variation in auditory thresholds. Finally, seasonal differences in auditory thresholds may be too small to detect based on the sample sizes of our study (7–10 birds per season), or may occur in an insufficient number of neurons for detection based on the ABR.

Seasonal auditory variation in the house sparrow may be mediated by reproductive hormones given the effects of hormones on auditory performance observed in fish and mammals. In house sparrows, males and females show peaks in circulating levels of testosterone and estradiol, respectively, during each egg-laying stage of the breeding season (Hegner and Wingfield, 1986a; Hegner and Wingfield, 1986b). The plainfin midshipman, mice, rats and humans all have estrogen receptors in the inner ear (Sisneros et al., 2004; Hultcrantz et al., 2006). In the midshipman, injection of females with testosterone or 17β-estradiol induces the enhanced auditory phenotype outside of the breeding season (Sisneros et al., 2004) whereas in mammals, supplemental estrogen reduces the severity of hearing loss associated with Turner's syndrome in humans and mice (chromosomal abnormalities involving estrogen deficiency), menopause in humans and ovariectomy in rats (Hultcrantz et al., 2006). The morphological differences underlying changes in auditory performance are not clear in these species, but hair cell turnover on the basilar papilla is one possibility in house sparrows based on observations of hair cell regeneration in a wide variety of avian and other non-mammalian vertebrates (Stone and Cotanche, 2007). Natural cycles of hair cell turnover have been found in the vestibular organ of adult birds but generally not on the basilar papilla of the cochlea, where regeneration occurs in response to acoustic trauma or ototoxic drugs. In Coturnix quail (*Coturnix japonica*), however, Ryals and Westbrook found evidence of a low level of hair cell production on the basilar papilla of untraumatized adult birds (Ryals and Westbrook, 1990).

In summary, our finding that ABR amplitude of the house sparrow increases during the early breeding season across the frequency range of song raises a number of questions for future study regarding the functional significance of seasonal auditory plasticity and its mechanism. Do seasonal changes in the ABR in fact translate into seasonal differences in temporal processing of song and, ultimately, behavioral differences in song discrimination? What information is gleaned from the acoustic structure of song and how does this information guide reproductive decisions? Future research may also focus on the relationship between auditory feedback during song production and song quality in songbirds. Finally, the morphological changes underlying seasonal differences in the ABR and regulatory mechanism require further exploration.

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LIST OF ABBREVIATIONS

ABR	auditory brainstem response
LS	least squares

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