In-air hearing of a diving duck: A comparison of psychoacoustic and auditory brainstem response thresholds

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Auditory sensitivity was measured in a species of diving duck that is not often kept in captivity, the lesser scaup. Behavioral (psychoacoustics) and electrophysiological [the auditory brainstem response (ABR)] methods were used to measure in-air auditory sensitivity, and the resulting audiograms were compared. Both approaches yielded audiograms with similar U-shapes and regions of greatest sensitivity (2000−3000 Hz). However, ABR thresholds were higher than psychoacoustic thresholds at all frequencies. This difference was least at the highest frequency tested using both methods (5700 Hz) and greatest at 1000 Hz, where the ABR threshold was 26.8 dB higher than the behavioral measure of threshold. This difference is commonly reported in studies involving many different species. These results highlight the usefulness of each method, depending on the testing conditions and availability of the animals. [http://dx.doi.org/10.1121/1.4948574]

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I. INTRODUCTION

The accurate measurement of auditory sensitivity in animals is an important addition to the body of knowledge of species about which little information concerning sensory biology is available. Furthermore, non-invasive techniques to measure hearing in animals are valuable tools to learn about species that are not typical laboratory animals. When the opportunity arises to study a species in captivity, it is useful to compare techniques to validate non-invasive methods against standard laboratory techniques. Therefore, the aim of this study was to carry out comparisons of an electrophysiological technique that might be utilized in the field, such as the auditory brainstem response (ABR), with psychoacoustic methods that have been more established as the "gold-standard" of laboratory research (Fay, 1988). For this purpose, the lesser scaup (*Aythya affinis*), a species of diving duck that is not commonly kept in captivity, was used.

Psychoacoustic methods involve training an animal to respond to test stimuli with a particular behavior, such as pressing a lever or pecking a key (e.g., Dooling and Okanoya, 1995; Kastak and Schusterman, 1999; Szymanski *et al.*, 1999; Wolski *et al.*, 2003). In contrast, the ABR is an auditory evoked potential, recorded from the scalp, occurring within the first 10 ms following auditory stimulation (Hall, 1992). The recorded series of waves represents synchronized neural discharge during the progressive propagation of auditory neural activity through the ascending auditory pathway (Hall, 1992). The ABR provides a rapid estimate of the shape of the audiogram and range of hearing sensitivity, but thresholds are often 10−15 dB higher than when using behavioral methods (Borg, 1982; Borg and Engström, 1983; Gorga *et al.*, 1988; Brittan-Powell *et al.*, 2002; Wolski *et al.*, 2003; Yuen *et al.*, 2005; Houser and Finneran, 2006; Henry and Lucas, 2008). These elevated thresholds in the ABR can be attributed to differences in stimulus characteristics and measurement techniques between behavioral and electrophysiological methods, and as a result of the lack of synchrony in the neural discharges at lower frequencies (Silman and Silverman, 1991; Hall, 1992; Szymanski *et al.*, 1999; Brittan-Powell *et al.*, 2002; Schlundt *et al.*, 2007; Ladich and Fay, 2013; Sisneros *et al.*, 2016). The major advantages of the ABR are that an entire audiogram can often be constructed after one session of less than 60 min, and no animal training is involved (it can be used on temporarily caught wild animals). By comparison, psychoacoustic methods can often take months for training and testing.

Previous studies on lesser scaup and other diving ducks have focused mainly on foraging and reproductive ecology (e.g., Afton and Ankney, 1991; Cutting *et al.*, 2011; Brady *et al.*, 2013; Warren *et al.*, 2014). They are capable of diving to depths of at least 18 m, for up to 25 s at a time, to forage primarily on mollusks, crustaceans, and aquatic insects (Austin *et al.*, 1998). Both males and females vocalize throughout the year to signal to mates and offspring (Johnsgard, 1965). The lesser scaup is one of the most abundant and widespread species of diving duck in North America, and prefers freshwater, but will winter on brackish bodies of water. Its numbers have been declining in recent years for unknown reasons (Austin *et al.*, 1998). Studies on the sensory biology of this species could elucidate unknown foraging strategies, communication behavior, and habitat selection, and become an important resource in creating an appropriate management strategy if the population continues to decline.

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In addition, data on the auditory sensitivity of the lesser scaup will add to current literature on comparative avian hearing. Of the approximately 10 000 extant species of birds, hearing has only been measured in about 50 species (Dooling *et al.*, 2000; Dooling, 2002). Approximately half of all birds for which there are hearing data are from the order Passeriformes (perching birds—includes the songbirds), as well as 13 species of owl and several other non-passerine, non-aquatic birds (Dooling *et al.*, 2000; Dooling, 2002). There are few data on aquatic birds, with only the black-footed penguin (*Spheniscus demersus*, Wever *et al.*, 1969) and the mallard duck (*Anas platyrhynchos*, Trainer, 1946) represented in the literature. Adaptations for living in an aquatic environment may be related to auditory sensitivity.

The goal of this study was to investigate the auditory sensitivity of the lesser scaup in order to contribute both to the biological knowledge of a species in decline and to the overall comparative avian audition literature. Objectives included: (1) use psychoacoustic methods to obtain absolute auditory thresholds, (2) compare these psychoacoustic results to lesser scaup ABR data from Crowell *et al.* (2015), (3) investigate correlations between auditory sensitivity and vocalization parameters, and (4) measure critical ratios. The critical ratio, or the lowest signal-to-noise ratio at which a tone is detected in broadband masking noise, is calculated as the difference between the masked hearing threshold and the spectral level of the masking noise (Fletcher, 1940; Scharf, 1970). Critical ratios have been used to estimate the frequency selectivity of the auditory system in a variety of animals, including several bird species (Dooling and Saunders, 1975; Langemann *et al.*, 1995; Langemann *et al.,* 1998; Lauer *et al.*, 2009; Noirot *et al.*, 2011). Critical ratios also provide a method to verify that ambient noise levels in an experimental setup are not masking absolute thresholds, which is what the data were used for in the present study.

II. METHODS

A. Psychoacoustics

1. Subjects

Three adult lesser scaup, one male and two female, were used for this study. The three birds were hatched in an incubator in June 2010 and raised together at the U.S. Geological Survey Patuxent Wildlife Research Center's seabird colony. Testing began when the birds were 1 year old. Thresholds were measured in both quiet and noise (used to calculate critical ratios) for all subjects. The Institutional Animal Care and Use Committees at both the University of Maryland and U.S. Geological Survey Patuxent Wildlife Research Center approved all of the following procedures.

2. Equipment

Ducks were tested in concrete tanks (2.5 m deep) at the U.S. Geological Survey Patuxent Wildlife Research Center's seabird colony. The testing apparatus consisted of an observation target, report target, automatic mealworm dispenser, and speakers, all at the surface of the water (Fig. 1). Both targets and mealworm dispenser were made of PVC pipe.
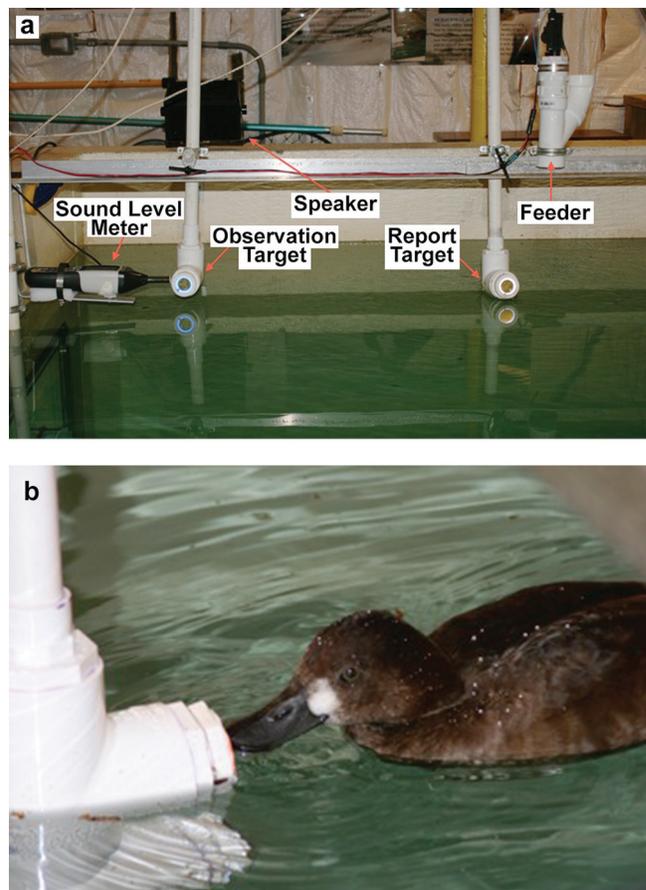

FIG. 1. (a) Experimental setup for hearing test, including two targets and a mealworm feeder, all made of PVC. (b) Lesser scaup in training session pecking at a target.

Each target was equipped with a light emitting diode (LED) and a pressure-sensitive piezo disk that allowed the computer to record the bird's pecking responses. The observation target was lit with a blue LED, signaling to the duck that they can begin a trial. The response target, used by the duck to indicate the presence of a test signal, was lit with a white LED. The speaker (Dynex DX-SP211, Richfield, MN) was mounted on the wall of the tank, approximately 30.5 cm in front of the duck when pecking at the observation target. All experimental events were coordinated by a custom computer system (SEABIRD—Sensory Equipment for Animal Behavior and Integrated Research Data; developed by R. Therrien, U.S. Geological Survey Patuxent Wildlife Research Center), powered by a 12 V battery. Tones were generated as .wav files using Audacity (opensource) software with a 48 k sampling rate. These tones were then stored on an SD card, which was inserted into the SEABIRD hardware. A computer-controlled logarithmic potentiometer attenuated the tones, which were then amplified with a Pyle PLMRMP1A (Brooklyn, NY) before playback. The system was controlled by the user through a touch-screen interface on an Apple iPad (Cupertino, CA).

Calibration of all frequencies and attenuation levels was conducted using a calibrated Earthworks M30 microphone (Milford, NH) at the location where the bird's ear would be, connected to the iPad with an Alesis iO ProAudio Dock

(Cumberland, RI). The iPad was running SignalScope Pro software (Faber Acoustical, Santaquin, UT), which has a fast Fourier transform (FFT) analyzer function to perform real-time spectral analysis in 1 Hz spectral levels. The system was calibrated with a CEM SC-05 sound level calibrator (Shenzhen, China). In addition, a daily calibration was performed, during which a 60 dB re 20 μPa tone was played across all frequencies, measured by a BK Precision 732 A sound level meter (Yorba Linda, CA), which fed back into the SEABIRD hardware to provide voltage adjustments. Daily variation in decibel levels before calibration was $+/-3$ dB re 20 μPa.

Ambient noise in the experimental setup was also measured using the Earthworks M30 microphone connected to the iPad. Ambient spectral levels were visualized using SignalScope Pro on the iPad.

3. Training and testing procedures

An individual duck was transferred to the tank from its outdoor pen before trials began. Ducks were trained using operant conditioning procedures on a go/no-go task. Each duck was trained until reliably performing above 90% accuracy, at which time testing commenced.

At the beginning of a trial, both the observation and response targets were illuminated. To begin a trial, a duck pecked the lit observation target. Each time the bird pecked the observation target, the computer generated a random number from one to 10. When the peck random number was from seven to 10, the trial would go to completion, either with the playback of a tone or a sham trial, and the target lights would shut off. If the peck to the observation target generated a number from one to six, the lights would stay on and the trial would continue, waiting for further pecks. If a tone was played, the duck had to peck the report target within 4 s. If the duck pecked the report target correctly (hit), a variable number of mealworms were delivered as a reward and the target lights shut off for a random interval of 15 s $+/-$ 5 s. If a tone was played and the duck failed to report (miss), no mealworm was delivered and the trial ended with the target lights shut off. If no tone was delivered (sham trial), the duck was to refrain from hitting the report target until the target lights shut off (correct rejection, no mealworm reward). The bird's rate of response during sham trials was used to calculate the false alarm rate. If the duck pecked the report target in the absence of a tone (false alarm), the target lights shut off and the duck received a 10-s "punishment" period when the lights in the building were shut off.

At the beginning of each testing session, the bird was trained with five to 10 warm-up trials, during which the bird was presented with a pre-selected stimulus level well above threshold. This regular training allowed the bird a daily adjustment period to the task. Birds were tested once per day, and were allowed to test until they lost interest, signified by 5 min passing without pecking the observation target. Sessions of less than 20 trials were discarded. To measure critical ratios, all testing procedures were the same, except with the addition of the broadband noise described below.

4. Stimuli

Stimuli consisted of two pure tone 1000-ms sinusoidal pulses separated by 500 ms, with a 250-ms rise time, a 500-ms steady state peak, and a 250-ms fall time. Hearing sensitivity was measured for frequencies of 0.5, 1.0, 2.0, 2.86, 4.0, 5.7, and 8.0 kHz. The signal frequency was held constant for each session. The order of frequencies tested was random, but was the same across birds. Each block consisted of 10 trials—seven intensity levels and three sham trials. The seven intensity levels were pre-selected in steps of 10 dB. These levels were adjusted until one stimulus intensity was below threshold, the next was near threshold, and the remaining five were above threshold. During each block, the seven intensity levels and three sham trials were presented in random order. Sham trials consisted of playback of a 0 V signal to control for the presence of artifacts associated with playback.

For critical ratio trials, masking noise was played continuously throughout the session. White noise was also generated using Audacity software, filtered to be flat $[+/-5$ dB re $(20\,\mu$Pa$)^2$/Hz] between 0.5 and 8.0 kHz, and integrated into the hardware system with a Behringer MicroMix MX400 (Bothell, WA). The noise was played at two levels [20 dB re $(20\,\mu$Pa$)^2$/Hz and 30 dB re $(20\,\mu$Pa$)^2$/Hz or 55 dB and 65 dB re 20 μPa overall], for each frequency tested. Spectral levels were calibrated using the same microphone/iPad system described above for tone calibration. Masked thresholds were measured at 1.0 and 2.86 kHz.

5. Threshold estimation

The 10-trial blocks were added together across consecutive days until the bird completed 100 trials. Threshold was estimated after each of these 100-trial sets. The birds were tested repeatedly at each frequency until threshold values across these 100-trial sets showed no further improvement (the threshold was within $+/-1/3$ of the step size for three sets of 100 consecutive trials). The final threshold estimate was then defined as the mean threshold estimate from the last 200 trials, at a sound pressure level (SPL) corresponding to a 50% hit rate, determined through linear interpolation. False alarm rate was also calculated for each set of 100 trials. One hundred trial sets with false alarm rates higher than 15% were discarded.

Critical ratios were calculated by subtracting the spectrum level of the noise from the masked threshold.

6. Vocalization analysis

Adult male and female lesser scaup vocalizations were obtained from Cornell University's Macaulay Library collection. Lesser scaup duckling vocalizations were recorded at Patuxent Wildlife Research Center (Sound Devices 702 portable recorder, Reedsburg, WI). Spectrographic analysis of minimum, maximum, and peak frequency (the frequency of the greatest power) was performed using cursor measurements in Raven Lite 1.0 (Cornell Lab of Ornithology; Ithaca, NY). These measurements were then compared to the most sensitive hearing frequency and high-frequency limit of

hearing. Hearing sensitivity was calculated in 100 Hz steps for the range of frequencies tested by fitting the raw audiogram data points to a third-order polynomial (Gleich *et al.*, 2005). The frequency of best hearing was then defined as the lowest 100 Hz point on this curve. The high-frequency limit of hearing was defined as the point on this curve where threshold rises >30 dB above the lowest threshold.

B. ABR

For comparison, we have included data here from an ABR study (Crowell *et al.*, 2015) on lesser scaup. The subjects for ABR study were of the same species, housed at the same facility, but different individuals, as those tested in this psychoacoustic study. Although it would have been valuable to test the same individuals using both methods, the risk of putting the trained psychoacoustics birds under anesthesia to measure the ABR outweighed the benefits to the study. ABR subjects were six adult lesser scaup, raised from eggs at U.S. Geological Survey Patuxent Wildlife Research Center.

1. Experimental procedures

Experimental procedures, including electrode placement and stimulus generation, were described in detail in Crowell *et al.* (2015). ABR testing took place in a veterinary hospital, and ambient noise levels in both the psychoacoustic and ABR testing environments were consistent (within 2 dB re 20 μPa). All birds were sedated with isoflurane (2%−4%; the lowest possible percentage was used to prevent movement in the bird) prior to electrode placement. Subjects were presented with tone burst stimuli and at frequencies between 0.5 and 5.7 kHz (see Crowell *et al.*, 2015; Brittan-Powell *et al.*, 2002; Brittan-Powell *et al.*, 2005; Brittan-Powell *et al.*, 2010). The stimulus presentation and ABR acquisition were coordinated using Tucker-Davis Technologies (Gainesville, FL) hardware and OpenABR software (Edward Smith, University of Maryland).

III. RESULTS

A. Psychoacoustics

1. Audiogram

Using psychoacoustics, three lesser scaup (identified by colored leg bands as Pink, Yellow, and Blue) were tested at frequencies from 0.5 Hz to 8.0 kHz. Less than 10% of sessions for each bird were discarded because of a false alarm rate higher than 15% (0% for Pink bird, 3% for Yellow bird, and 8.8% for Blue bird; false alarm rates given in Table I). Psychometric functions for all three birds at 1.0 kHz are shown in Fig. 2. In this example, at least one stimulus level was well below threshold, one level was slightly above threshold, and four stimulus levels were well above threshold, and responded to close to 100% of the time. Each symbol on the figure represents an average percent correct for the last 20 trials tested at 1.0 kHz. Threshold corresponded to a hit rate of 50%, which was equal to 28 dB re 20 μPa for

TABLE I. Average false alarm rates of each bird (Pink, Yellow, and Blue) for all sessions at each frequency.

Frequency (kHz)	Pink	Yellow	Blue
0.50	0.66	5.50	11.10
1.00	1.10	10.53	12.20
2.00	2.57	7.78	11.10
2.86	3.30	8.33	10.00
4.00	10.00	4.68	10.83
5.70	1.98	4.64	10.46
8.00	5.83	12.2	10.00

Pink bird, 24 dB re 20 μPa for Yellow bird, and 25 dB re 20 μPa for Blue bird.

All three birds tested displayed best sensitivity at 2.86 kHz, with an average threshold of 14 dB re 20 μPa, corresponding to a hit rate of 50%. The high-frequency roll-off above 4 kHz was much steeper than the low-frequency roll-off. Audiograms for all birds are shown in Fig. 3.

2. Critical ratios

Critical ratios were measured at 1.0 and 2.86 kHz. The frequency of test tone, spectrum level of the masking noise, the average masked threshold, and the average critical ratio are reported in Table II. Masked thresholds increased in proportion to noise spectrum level, while critical ratios remained relatively constant.

B. Vocalization analysis

Recorded vocalizations from lesser scaup ducklings and adult males and females were analyzed for several measurements (Table III). Because of limitations on sample sizes, data from males and females were combined for hearing measurements, and therefore the frequency of best hearing and high-frequency limit of hearing were calculated across both sexes. Hearing tests were not conducted on ducklings. Adult female vocalizations were more broadband in nature, spanning a wider range of frequencies, and with a higher peak frequency, than the adult male vocalizations. The peak frequency of the duckling vocalizations was higher than both the male and female vocalizations.
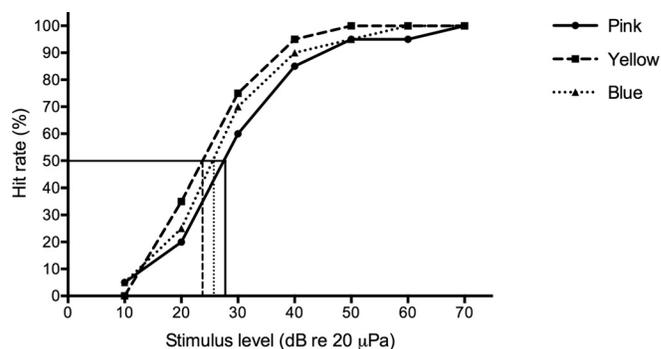

FIG. 2. Psychometric functions for three lesser scaup (identified by colored leg bands) at 1.0 kHz. Each symbol represents 20 trials.
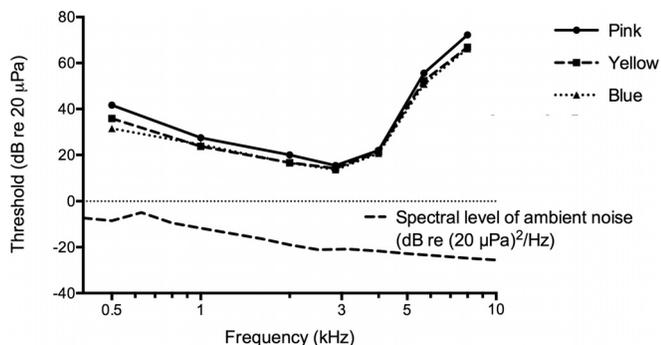
FIG. 3. Audiograms for all three birds tested, corresponding to a hit rate of 50%. Ambient noise spectral levels were measured using SignalScope Pro software on an iPad.

C. ABR

In order to compare the psychophysical audiograms obtained in this study with audiograms obtained in the field from a number of waterfowl species by Crowell *et al.* (2015), we here present ABRs recorded from a similar population of lesser scaup than the birds used to obtain psychophysical audiograms. The typical lesser scaup ABR displayed two to three prominent peaks within 4–5 ms after the stimulus reached the bird's ear canal (Fig. 4, as adapted from Crowell *et al.*, 2015).

The ABR audiogram was U-shaped, and sensitivity peaked between 1.0 and 3.0 kHz, with a steep high-frequency roll-off after 4.0 kHz (see Crowell *et al.*, 2015). Figure 5 compares the visual inspection ABR audiogram to the psychoacoustic audiogram. Both methods produced U-shaped audiograms with similar regions of greatest sensitivity (from 1 to 4 kHz). ABR thresholds were higher than psychoacoustic thresholds at all frequencies tested (ABRs were not measured at 8 kHz). Differences ranged from 11 dB at 5.7 kHz to 27 dB at 1.0 kHz.

IV. DISCUSSION

A. Psychoacoustics

The average lesser scaup behavioral audiogram was U-shaped, with sensitivity peaking at 2.0–3.0 kHz, and an absolute threshold of approximately 14 dB re 20 μPa. Existing data from over 50 species of birds tested to date demonstrate consistency across avian species, with a typical avian pattern of greatest sensitivity between 2000 and 5000 Hz (Dooling *et al.*, 2000; Crowell *et al.*, 2015). The lesser scaup displayed a low-frequency roll-off of approximately 10 dB per octave

TABLE II. Frequency of test tone, masking noise level, masked threshold and calculated critical ratio averaged across all lesser scaup.

Frequency (Hz)	Masking noise level [dB re (20 μPa)^2/Hz]	Masked threshold (dB re 20 μPa)	Critical ratio (dB re 1 Hz)
1000	20	41.5	21.5
1000	30	54.5	24.5
2860	20	41.9	21.9
2860	30	52.9	22.9

TABLE III. The average minimum frequency, maximum frequency, and peak frequency (frequency at greatest power) of male, female and duckling vocalizations, along with the calculated frequency of best hearing, and high-frequency limit of hearing.

	Min freq (Hz)	Max freq (Hz)	Peak (dominant) (Hz)	Best hearing (Hz)	High-freq limit[a] (Hz)
Male	709	2850	1779	2400	5300
Female	391	7594	2736	2400	5300
Duckling	2441	5724	4061		

[a]These two measurements were only calculated for adult lesser scaup, and males and females were not separated.

below 1.0 kHz, and a much steeper high-frequency roll-off above 4.0 kHz (approximately 50 dB per octave). Average avian absolute thresholds in the region of peak sensitivity approach 0 dB, with a loss of sensitivity below 1.0 kHz of about 20 dB/octave and a loss of sensitivity above 4.0 kHz of about 60 dB/octave (Dooling *et al.*, 2000). The only behavioral audiogram available for another non-diving duck species, the mallard duck, also follows this pattern (Trainer, 1946). Despite apparent similarity with other birds tested previously, we note that we did not measure thresholds at the lowest frequencies, where this species might have functional hearing, and where the audiogram may have a slightly flatter roll-off than other bird species. Any differences for a diving bird species would be of great interest.

In this study, critical ratio measurements allowed us to verify that the estimated thresholds in quiet actually approached absolute levels. Critical ratios for the lesser scaup were estimated at two frequencies, one of which was the frequency of most sensitive hearing (2.86 kHz). The average critical ratio at 2.86 kHz was 22.5 dB re 1 Hz, very similar to that reported for the budgerigar (*Melopsittacus undulatus,* 19.9 dB re 1 Hz) and canary (*Serinus canaria domestica*, ~20 dB re 1 Hz) (Dooling and Saunders, 1975; Lauer *et al.*, 2009). Background noise in the tanks at Patuxent Wildlife Research Center was quieter than one critical ratio below the threshold at 2.86 kHz, suggesting that the absolute thresholds reported in this study were not masked by ambient noise. Furthermore, any noise in the test enclosure was likely to be co-modulated. Detection of
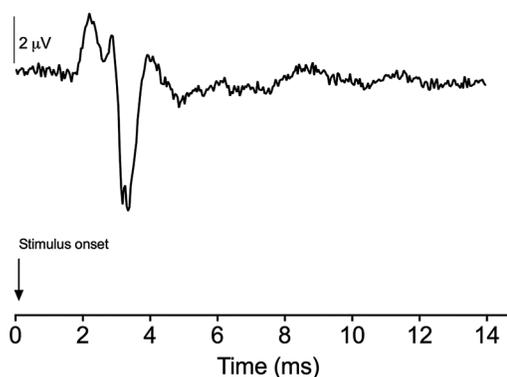

FIG. 4. A typical ABR from a lesser scaup with a 2.86 Hz, 90 dB re 20 μPa (measured at the ear) tone pip as the stimulus, average of 600 responses. Adapted from Crowell *et al.* (2015).

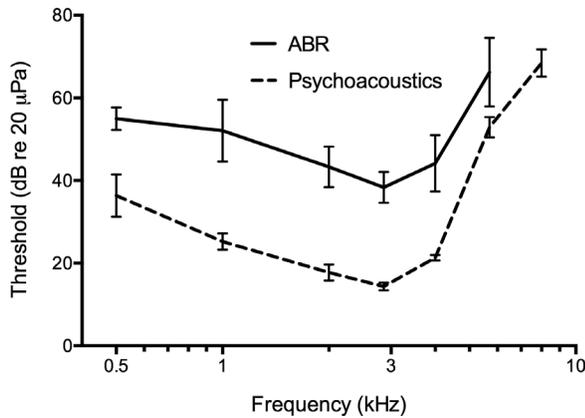J. Acoust. Soc. Am. **139** (5), May 2016

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FIG. 5. A comparison of audiograms using the ABR and psychoacoustics. Mean thresholds for all birds tested are represented ($n = 3$ for psychoacoustics and $n = 6$ for ABR), and vertical bars represent $+/-1$ standard deviation. The ABR was not measured at 8 kHz. ABR audiogram adapted from Crowell et al. (2015).

signals is easier in co-modulated noise when compared to white noise, which support the conclusion that thresholds were unmasked (Langemann and Klump, 2001).

Like other birds, hearing in lesser scaup may align with species-specific vocalizations. The vocalization peak power in several avian species, including the downy woodpecker (*Picoides pubescens*), hairy woodpecker (*Picoides villosus*), and budgerigar, corresponds well to the most sensitive hearing range (Dooling and Saunders, 1975; Lohr et al., 2013). Henry and Lucas (2008, 2010) suggested that in several songbird species (Carolina chickadees, *Poecile carolinensis*, tufted titmice, *Baoelophus bicolor*, house sparrows, *Passer domesticus*, and white-breasted nuthatches, *Sitta carolinensis*), the high-frequency limit of sensitive hearing may have co-evolved with the maximum frequency of vocalizations. Male and female vocalizations of lesser scaup are dimorphic in nature. Males are generally quieter, but emit a whirring, kazoo-like "whew," or "whee-ooo," often referred to as a coughing call, during courtship (Johnsgard, 1965). Female scaup are louder and more frequently vocal. They produce a noisy "purrr" during courtship, in the presence of predators, and also to inform mates and ducklings when they are returning to the nest (Johnsgard, 1965). Both sexes primarily vocalize while sitting on water, and rarely while flying (Austin et al., 1998). The average peak frequency of both the male (1.779 kHz) and the female (2.736 kHz) vocalizations align with the region of greatest sensitivity on the audiogram, and the calculated frequency of best sensitivity (2.4 kHz). The range of frequencies in lesser scaup duckling vocalizations (2.441–5.724 kHz) also aligns well with both the frequency of best sensitivity as well as the high-frequency limit of sensitive hearing (5.3 kHz). Thus, it would appear that the lesser scaup has hearing abilities that correspond well to both the adult and duckling vocalizations, leading to improved chances for cooperative foraging and predator detection, courtship, and nest success.

B. Comparison of ABR and psychoacoustic audiograms

Both ABR and psychoacoustic measures yielded audiograms with similar U-shapes and regions of greatest

sensitivity. However, ABR thresholds were higher than psychoacoustic thresholds at all frequencies. This difference was least at the highest frequency tested using both methods (5.7 kHz) and greatest at 1.0 kHz, where the ABR threshold was 27 higher. This difference may have been due to the well-known lack of precision in measuring ABR thresholds at low frequencies (see Brandt et al., 2009). Measures of temporal dispersion are on the order of 150–300 μs for pigeon auditory nerve fibers with best frequencies of 400–600 Hz (Hill et al., 1989), and about 1 ms for 150 Hz, and almost 400 μs for 250 Hz barn owl auditory nerve (Köppl, 1997). Thus ABRs by their nature may not provide accurate measures of thresholds for very low-frequency sounds, because of the large temporal dispersion at these sound frequencies. Differences between ABR and psychoacoustic measures have also been attributed to a variety of other factors. These include stimulus characteristics, since ABR stimuli are brief and psychoacoustics stimuli are longer, increasing the possibility that "multiple looks" at the stimuli could decrease thresholds. Other factors include the physiological state of the subjects (anesthetized for the ABR and awake for psychoacoustics), individual differences in hearing abilities (different subjects were used for each method), and the nature of the two methods.

Disparities between psychoacoustics and the ABR have been documented in many animal groups, but differences between the two methods appear to be greatest in avian species, including screech owls (*Megascops asio*), budgerigars, tufted titmice, house sparrows, white-breasted nuthatches, and finches (Woolley and Rubel, 1999; Brittan-Powell et al., 2002; Brittan-Powell et al., 2005; Henry and Lucas, 2008). The only other data available for a duck species, the mallard, displays a similar disparity (Trainer, 1946; Dmitrieva and Gottlieb, 1992). This difference may be a consequence of the ability to detect responses in mammals vs birds, since mammals on average have a greater absolute number of auditory nerve fibers than birds, and a greater proportion of fibers activated at threshold (Brittan-Powell et al., 2002).

C. Conclusions

Used in conjunction, psychoacoustics and the ABR were complementary methods to test hearing in lesser scaup. Audiograms produced maintained the same shape and region of greatest sensitivity, regardless of method used. The ABR is therefore a valuable tool to provide a rapid (under 1 h) estimate of hearing, especially with animals that cannot be trained. For most animal species, the total number of individuals tested is such a small fraction of the population that there is no real consensus on individual variation of hearing and how this variation may affect current assumptions about a species-specific audiogram. The ABR should continue to be used to increase sample size and better characterize hearing abilities across individuals and species, especially in animals that are not typically kept in captivity. It should be noted that there are limitations inherent in ABR testing, such as difficulty in accurate measurement of low-frequency thresholds. In birds, psychoacoustics may remain the "gold standard" for measuring hearing, and should continue to be

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used when possible to verify results obtained with other methods.

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