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ORIGINAL PAPER

A broad filter between call frequency and peripheral auditory sensitivity in northern grasshopper mice (*Onychomys leucogaster*)

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Abstract

Acoustic communication is a fundamental component of mate and competitor recognition in a variety of taxa and requires animals to detect and differentiate among acoustic stimuli (Bradbury and Vehrencamp in Principles of animal communication, 2nd edn., Sinauer Associates, Sunderland, 2011). The matched filter hypothesis predicts a correspondence between peripheral auditory tuning of receivers and properties of species-specific acoustic signals, but few studies have assessed this relationship in rodents. We recorded vocalizations and measured auditory brainstem responses (ABRs) in northern grasshopper mice (*Onychomys leucogaster*), a species that produces long-distance calls to advertise their presence to rivals and potential mates. ABR data indicate the highest sensitivity (28.33 ± 9.07 dB SPL re: 20 µPa) at 10 kHz, roughly corresponding to the fundamental frequency (11.6 ± 0.63 kHz) of long-distance calls produced by conspecifics. However, the frequency range of peripheral auditory sensitivity was broad (8–24 kHz), indicating the potential to detect both the harmonics of conspecific calls and vocalizations of sympatric heterospecifics. Our findings provide support for the matched filter hypothesis extended to include other ecologically relevant stimuli. Our study contributes important baseline information about the sensory ecology of a unique rodent to the study of sound perception.

Keywords Acoustic communication · Auditory brainstem response · Matched filter · *Onychomys*

Introduction

The perceptual world of animals emerges from the tuning of nervous systems faced with an excess of external stimuli (von Uexküll 1934; Wehner 1987; von der Emde and Warrant 2016). The matched filter hypothesis proposes that sensory systems evolve to detect only the most ecologically relevant stimuli (Barlow 1961; Wehner 1987). Efficient allocation of sensory resources enhances signal detection by maximizing signal-to-noise ratios to facilitate behaviors essential for survival and reproduction (Endler 1993; Lucas et al. 2015). Matched filters for economical sensing (von der Emde and Warrant 2016) exist in diverse modalities and taxa, including insect vision and olfaction (Warrant 2016), arachnid mechanoreception (Barth 2016), and fish electroreception (von der Emde and Ruhl 2016).

In the acoustic domain, the matched filter hypothesis specifically predicts a correspondence between peripheral auditory tuning of receivers and properties of species-specific acoustic signals (Capranica and Moffat 1983). In crickets and anurans, matching of the peripheral auditory system with the dominant frequency of male advertisement signals facilitates discrimination of conspecifics from heterospecifics (Gerhardt and Schwarz 2001; Gerhardt and Huber 2002). Similarly, many birds exhibit heightened peripheral auditory tuning for species-specific frequency and temporal parameters to facilitate social communication (Dooling et al. 1979; Gall et al. 2012). The relationship between peripheral auditory tuning and

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species-specific vocalizations is less well described in mammals in part due to a focus on selective encoding of acoustic stimuli in the central auditory pathway that integrates inputs from the brainstem, the auditory cortex, and associated cortical areas (Holmstrom et al. 2010; Portfors and Roberts 2014; Portfors 2018). However, recent evidence in rodents suggests that subcortical auditory nuclei play an important role in mediating behavioral responses to ecologically relevant sounds (Portfors 2018). For example, pup rearing experience shortens maternal auditory brainstem response latencies to promote recognition of infant isolation vocalizations (Miranda et al. 2014). Such findings have contributed to increased interest in the role of the peripheral auditory system to rodent sound perception in ecologically relevant contexts (Kubke and Wild 2018; Portfors 2018).

Although many rodents produce both sonic and ultrasonic vocalizations (USV) to mediate social interactions (Kalcounis-Rueppell et al. 2006; Portfors 2007; Briggs and Kalcounis-Rueppell 2011; Hanson and Hurley 2012), laboratory mice and rats account for most studies of hearing physiology (Dent et al. 2018). In addition, such studies often occur in the context of biomedical applications and are largely divorced from ethologically relevant acoustic signals that mediate social behavior (Bennur et al. 2013). The comparatively few studies of auditory sensitivity in exotic rodents are based on behavioral audiograms (e.g., Webster and Webster 1972; Heffner 1980; Heffner and Heffner 1985, 1990, 1992) and/or did not relate auditory sensitivity to the vocal repertoire of the species (Ralls 1967; Katbamna et al. 1996; Zhou et al. 2006). Broadly, studies are lacking that relate hearing physiology to vocalizations in non-model rodents, thus limiting our ability to identify whether the peripheral auditory filtering applies more broadly across different taxa and contexts.

Northern grasshopper mice (*Onychomys leucogaster*) are cricetid rodents of western North America that feed on arthropods and small vertebrates (Bailey and Sperry 1929; Flake 1973). As a consequence of their predatory lifestyle, grasshopper mice have large home ranges (1.72 ± 0.68 ha; Stapp 1999) for their body size (McNab 1963). Like other muroid rodents, grasshopper mice produce USVs (~ 50 kHz) in close-distance mating contexts (Miller and Engstrom 2012; Pasch et al. 2017). However, the genus is unique among mice in their ability to produce audible long-distance advertisement vocalizations to announce their presence to potential mates and competitors (Ruffer 1966; Frank 1989). As females enter receptivity during the summer mating season, both males and females call reciprocally to facilitate localization (Frank 1989). Long-distance calls consist of a fundamental frequency (F_0) and a series of harmonic overtones at integer multiples of F_0 (Pasch et al. 2017; Fig. 1), with populations varying in both call F_0 (9.5–13.5 kHz) and the degree of sexual dimorphism (Hafner and Hafner 1979; Miller and Engstrom 2012; Pasch et al. 2016). In southwestern New Mexico, the species is sympatric with two smaller congeners (Chihuahuan grasshopper mice, *O. arenicola,* and southern grasshopper mice, *O. torridus*) that produce higher frequency species-specific calls (Pasch et al. 2016).

Despite their unique mode of acoustic communication, only two studies have explored auditory sensitivity in grasshopper mice. Conditioned avoidance procedures indicate that northern grasshopper mice ($n = 3$) from western Kansas are most sensitive to 8 kHz tones (Heffner and Heffner 1985) and have an enhanced ability to localize sound relative to other rodents (Heffner and Heffner 1988). However, no studies have simultaneously quantified call characters

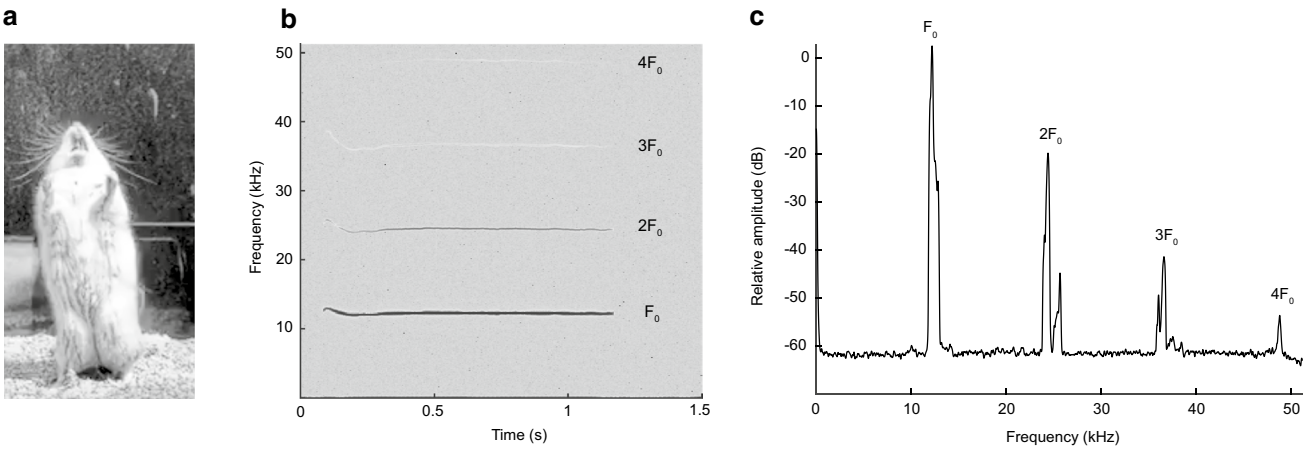

Fig. 1 Long-distance vocalization of a northern grasshopper mice. **a** An illustration of a mouse calling, **b** spectrogram and **c** power spectrum of a long-distance vocalization from a male recorded at 33.3 cm. F_0 fundamental frequency, $2F_0$ 2nd harmonic, $3F_0$ 3rd harmonic, $4F_0$ 4th harmonic. Harmonics are integer multiples of F_0

and auditory tuning to explore the degree to which vocalizations are matched to their peripheral auditory sensitivity. In this study, we quantified the F_0 of long-distance vocalizations and hearing thresholds of northern grasshopper mice from southwestern New Mexico using auditory brainstem responses (ABR; Willott 2006). ABRs are a relatively non-invasive method to record auditory-evoked potentials of the cochlear ganglion neurons and nuclei of the central auditory pathway from electrodes on the scalp (Hall 2007). We focused on frequencies (4–32 kHz) surrounding those reported for long-distance vocalizations of *O. leucogaster* (Hafner and Hafner 1979; Miller and Engstrom 2012; Pasch et al. 2017) but below the frequencies of USVs (48.3 ± 2.6 kHz; Pasch et al. 2017). We predicted a correspondence between receiver auditory sensitivity and the F_0 that comprise species-specific long-distance vocalizations.

Materials and methods

Animals

We trapped mice in the San Simon and Animas Valleys, New Mexico, and transferred them to animal facilities at Northern Arizona University, Flagstaff, AZ, USA. Mice were housed individually due to occasional aggression and incompatibility that arises when paired (Pinter 1971; Ruffer 1968), or as breeding pairs in a larger colony room housing conspecifics and heterospecifics (*O. arenicola* and *O. torridus*) from the same geographic area. Mice were maintained on a 14:10 light/dark cycle at 20 ± 3 °C and provided rodent chow and water ad libitum.

Acoustic recording

We recorded the mass and vocalizations of 36 wild-captured mice ($n = 18$/sex). Individual animals in their home cage were placed in a semi-anechoic coolers lined with acoustic foam for overnight (10 h) acoustic recording for three nights. We used 1/4″ microphones (Type 40BE, G.R.A.S.) connected to preamplifiers (Type 26 CB, G.R.A.S.) to obtain acoustic pressure recordings 33.3 cm above the center of the cage of a focal mouse. Microphone response was flat within ± 1.5 dB from 10 Hz to 50 kHz, and pre-amplifier response was flat within ± 0.2 dB from 2 Hz to 200 kHz. Microphones were connected to a National Instruments DAQ (USB 4431) sampling at 102.4 kHz to a laptop computer running MATLAB (Version 2014a). We calculated F_0 and 2 F_0 in Avisoft SASLab Pro (version 4.2.27, Avisoft Bioacoustics, Germany; 256-point Fast Fourier Transform (FFT); Hann window with 50% overlap; frequency resolution 400 Hz, temporal resolution 0.16 ms). For each individual, we calculated averages from the total number of calls recorded ($\bar{x} = 38.3$, range = 1–250). Values are reported as ± standard deviation.

Auditory-evoked potentials

To estimate auditory-evoked potentials, we tested separate captive bred offspring of wild-captured mice ($n = 18$, 9/sex) between the ages of 6–18 month in a shielded semi-anechoic chamber (ETS Lindgren SD-1; internal dimensions 91.4 cm × 91.4 cm × 91.4 cm) lined with acoustic foam. Following measurement of mass, we administered sodium pentobarbital (25 mg/kg; 0.1 mL/40 g) intraperitoneally to anesthetize mice. Occasionally, we injected an additional dose (< 0.05 mL) 10 min after the initial dose to maintain an anesthetic plane. We positioned mice on a gel heating pad (32 ± 5 °C) to maintain body temperature and placed three needle electrodes (27 gauge, 12 mm; Rochester Electro-Medical Inc., Lutz, FL, USA) subdermally behind (1) the left ipsilateral ear receiving the stimulus (reference), (2) at the vertex of the skull (active channel), and (3) behind the contralateral right ear (ground) to obtain monaural ABR signals. Electrodes were connected to a head stage (RA4LI, Tucker Davis Technologies (TDT), Alachua, FL, USA) and preamplifier (RA4RA, TDT) attached to a processor (RZ6, TDT) via a fiber optic cable. Auditory-evoked responses were filtered (high-pass at 100 Hz, low-pass at 3 kHz, and notch-filtered at 60 Hz) and digitized at a sampling rate of 24.4 kHz.

Acoustic stimuli presentation

We created and presented stimuli with SigGenRZ and BioSigRZ (version 5.7.0, TDT), respectively. Stimuli were 2.5-ms tone bursts with 0.4 ms gating with number of averages set to 512. We presented stimuli through a speaker (MF1, Tucker-Davis Technologies) positioned 10 cm away from the left ear of the mouse. Frequency response of the speaker (± 1.5 dB) was calibrated with a Brüel & Kjaer microphone (Type 4939) and preamplifier (Type 2670) connected to a microphone power supply (Type 5935L).

In each trial, we presented frequencies ranging from 4 to 32 kHz in 2–4 kHz steps at amplitudes ranging from 80 to 10 dB SPL in 10 dB steps. Trials lasted approximately 45 min. After each trial, animals were placed on a flat, clean surface within their home cage over a heating pad. We monitored subjects until fully recovered from anesthesia as defined by upright walking.

Auditory brainstem response analyses

Rodent ABRs typically consist of five voltage peaks within 10 ms of stimulus onset (Willott 2006; Hall 2007), but differences in species or strain identity (Zhou et al. 2006),

methodology (Land et al. 2016), or anesthesia (Ruebhausen et al. 2012) may contribute to variation in waveform shape. To avoid bias, a trained researcher first coded and randomized ABR waveforms so that datasets were analyzed blind to subject identity, stimulus frequency, and stimulus level (dB). We then used three methods to estimate auditory responsiveness. First, we used the visual detection method (Jacobson 1985; Gall et al. 2011; Chen et al. 2016) whereby a researcher determined the lowest stimulus level (dB) per frequency that evoked an ABR response (Fig. 2). Thresholds were operationally defined as the dB level halfway (5 dB) between the last detectable ABR response and next lowest stimulus level. We then measured the amplitude of the ABR response by quantifying the voltage difference between the first detectable positive peak and first negative valley (corresponding to ABR wave II as inferred from robust ABR responses to click stimuli; Supplementary Fig. S1; Blatchley et al. 1987; Hall 2007) for each stimulus frequency at each intensity level (Henry and Lucas 2008; Gall et al. 2011). ABR amplitude reflects the number and synchrony of neural responses (Hall 2007). Finally, we measured the latency from stimulus exposure to the first detectable peak of the ABR, with shorter latencies indicating a faster response to a stimulus (Hall 2007).

Statistical analyses

We used two-sample *t* tests to compare differences in body mass and F_0 between sexes. We analyzed all ABR data using repeated-measures mixed models with individual identity specified as a random effect and sex, stimulus frequency, and their interaction as explanatory variables. For ABR amplitude and latency, stimulus level (dB) and its interaction with stimulus frequency were also included. Because our data did not meet the assumptions of normality (function: shapiro.test, R Core Team 2017), we modeled separately the log of the three continuous response variables (visual detection method, amplitude, and latency) using R (version 3.3.3, GUI 1.69) and R Studio (version 3.3.3; package: nlme, function: lme and anova; Pinheiro et al. 2017; R Core Team 2017). Significant effects ($\alpha = 0.05$) were assessed post hoc using Tukey tests based on the log of the continuous response variables (function: TukeyHSD; R Core Team 2017) adjusted for multiple comparisons.

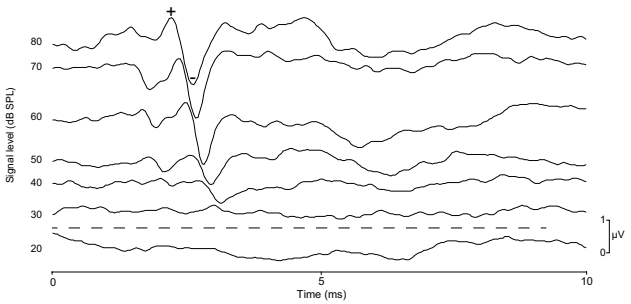

Fig. 2 Auditory brainstem response (ABR) of an individual northern grasshopper mouse in response to a 10 kHz tone. The + and − refer to the peak and valley used to estimate ABR latency and amplitude. The dotted line indicates the hearing threshold estimated from the visual detection method

Results

Body mass and long-distance vocalizations

We found no difference in body mass between female (38.6 ± 4.2 g) and male (41.8 ± 3.6 g; $t_{16} = 1.71$, $p = 0.11$) mice used in our ABR trials. Similarly, we found no difference in mass between females (33.4 ± 5.1 g) and males (35.8 ± 6.1 g; $t_{34} = 1.31$, $p = 0.2$) used in our vocal recording study. The F_0 and $2F_0$ of long-distance calls averaged 11.6 kHz and 23.2 kHz, respectively (range 10.4–12.6 kHz and 20.8–25.2 kHz; Fig. 1) and did not differ between females (11.66 ± 0.67) and males (11.61 ± 0.59 kHz; $t_{34} = -0.23$, $p = 0.813$ for F_0).

Frequency sensitivity: auditory thresholds

Similar to body mass and call F_0, we found no effect of sex ($F_{1,16} = 0.0001$, $p = 0.99$) nor the sex by stimulus frequency interaction ($F_{10,160} = 0.5$, $p = 0.9$) on auditory thresholds. However, stimulus frequency was a statistically significant predictor of threshold differences ($F_{10,160} = 19.43$, $p < 0.001$). Auditory thresholds indicated that the frequency range of best sensitivity (operationally defined as the frequency range at which thresholds were < 10 dB greater than the frequency of greatest sensitivity) was wide and did not differ statistically between 8 and 24 kHz (all Tukey HSD post hoc pairwise comparisons adjusted $p > 0.1$; Fig. 3). Frequency sensitivity declined sharply below 8 kHz and above 24 kHz, coincident with the range of F_0 and $2F_0$ produced by senders (8 kHz vs. 10 kHz, adjusted $p = 0.1$; 4 kHz vs. 8 kHz, adjusted $p = 0.001$; 24 kHz vs. 28 kHz, adjusted $p < 0.02$; Fig. 3).

Frequency sensitivity: amplitude and latency

Similar to auditory thresholds, we found no sex differences in ABR amplitude ($F_{1,16} = 0.4$, $p = 0.5$). ABR amplitude was significantly influenced by stimulus frequency ($F_{10,160} = 19.43$, $p < 0.001$), stimulus level ($F_{7,1368} = 422.72$, $p < 0.001$), and the stimulus frequency by stimulus level interaction ($F_{18,1368} = 3.34$, $p < 0.001$). Response amplitudes mirrored auditory threshold measures, with similar amplitudes between 8 and 28 kHz across all stimulus levels (4 kHz

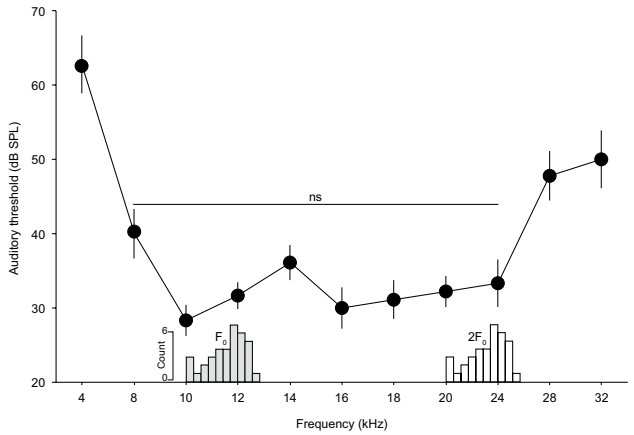

Fig. 3 Audiogram of northern grasshopper mice ($n = 18$) based on the visual detection method relative to histograms depicting the range of fundamental frequencies (F_0; shaded bars) and second harmonics ($2F_0$; open bars) of long-distance vocalizations ($n = 36$). The horizontal line indicates auditory thresholds are not significantly different at $p < 0.05$. Error bars represent ± 1 SE

vs. 8 kHz, adjusted $p < 0.001$; 8 kHz vs. 10 kHz, adjusted $p = 0.71$; 18 kHz vs. 24 kHz, adjusted $p = 0.07$; 18 kHz vs. 28 kHz, adjusted $p = 0.01$; 24 kHz vs. 28 kHz, adjusted $p = 0.99$; Fig. 4). Response amplitudes generally increased with increasing stimulus levels with the largest magnitudes of response within the range of best sensitivity as defined by auditory thresholds (Fig. 4).

We also found no sex differences in latency to the first positive peak of the ABR ($F_{1,16} = 0.0001$, $p = 0.1$). However, there were significant main effects of stimulus frequency ($F_{10,160} = 10.81$, $p < 0.001$) and stimulus level ($F_{7,1368} = 1175.1$, $p < 0.001$). The interaction between stimulus frequency and stimulus level was marginally statistically significant ($F_{18,1368} = 1.82$, $p = 0.05$). Generally, latencies decreased as stimulus levels increased. Similar to the ABR amplitudes, latency was shortest at frequencies within the

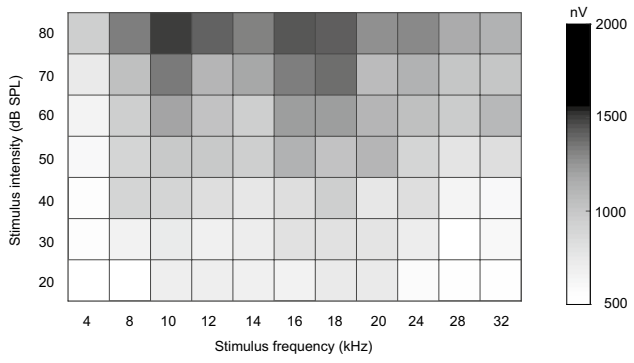

Fig. 4 Heat map depicting auditory brainstem response (ABR) amplitude as a function of stimulus frequency (kHz) and stimulus level (dB SPL) in northern grasshopper mice ($n = 18$)

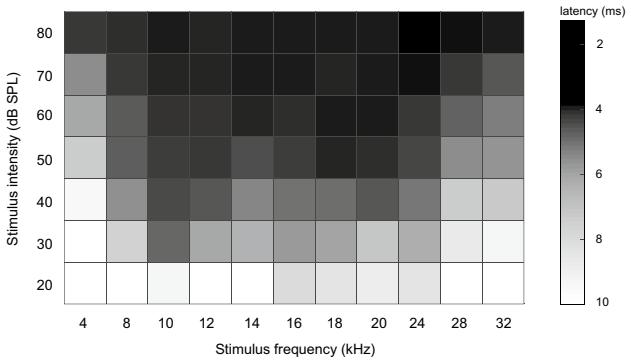

Fig. 5 Heat map depicting auditory brainstem response (ABR) latency as a function of stimulus frequency (kHz) and stimulus level (dB SPL) in northern grasshopper mice ($n = 18$)

range of best sensitivity as defined by auditory thresholds (Fig. 5).

Discussion

Our findings indicate that northern grasshopper mice exhibit selective tuning to frequencies that comprise their long-distance advertisement calls at the level of the peripheral auditory system. Frequency sensitivity is consistent with behavioral audiograms described for the species (Heffner and Heffner 1985), and the absence of sex differences in ABRs correspond to sexually monomorphic size and call frequencies in the population (Pasch et al. 2016; herein). However, ABR thresholds spanned a broader frequency range surrounding F_0 then predicted from a precise definition of a matched filter. We discuss our findings in relation to the unique biology of grasshopper mice.

The electrophysiological data presented herein are consistent with the shape and frequency of northern grasshopper mouse behavioral audiograms. In particular, behavioral audiograms indicate peak hearing at 8 kHz with extended sensitivity to 16 kHz (Heffner and Heffner 1985). Compared to laboratory rats (*Rattus*), house mice (*Mus*; Ralls 1967; Dent et al. 2018), brush mice (*Peromyscus boylii*), and white-footed mice (*P. leucopus;* Ralls 1967), grasshopper mouse ABRs have a similar shape but exhibit sensitivity to lower frequencies as predicted from the spectral properties that comprise their long-distance calls. In rodents, such low-frequency sensitivity is surpassed only by fossorial rodents whose subterranean environments selectively attenuate high frequencies (Heffner and Heffner 1992; Gerhardt et al. 2017). However, ABR levels found herein (20–30 dB) were higher than values reported for behavioral audiograms in grasshopper mice (9 dB; Heffner and Heffner 1985). In general, behavioral methods and compound action potentials provide lower thresholds than ABRs (Ohlemiller et al. 2010;

Kobrina and Dent 2016). Such a discrepancy is commonly attributed to a lack of temporal integration and anesthesia-driven suppression of cortical processes that may enhance acoustic sensitivity by 10–30 dB (Heffner and Heffner 2003; Dent et al. 2018). Thus, while the shape of audiograms tend to be similar across methods, absolute threshold levels differ, and the ABR thresholds reported herein represent a conservative estimate of hearing ability in grasshopper mice.

Although mice produced advertisement calls with F_0 between 10.4–12.6 kHz, their peripheral auditory systems were most sensitive to frequencies between 8 and 24 kHz. In anurans, imprecise or complete mismatches between sender signals and receiver sensitivity may be due to allometric constraints (Ryan et al. 1992), phylogeny (Wilczynski et al. 2001), abiotic and biotic background noise (Moreno-Gómez et al. 2013; Zhao et al. 2017), or selection to simultaneously stimulate distinct auditory organs with different sensitivities (Zhu et al. 2016). In birds, similar mismatches may reflect a sensory mechanism that mediates preferences for certain signal properties (Vélez et al. 2015). In mice, such broad tuning may be a general feature of the auditory periphery (e.g., the mammalian coiled cochlea permits a greater frequency range; Manley 1971, 2000) relative to the more selective tuning that emerges in the inferior colliculus (Portfors et al. 2011; Woolley and Portfors 2013). Electrophysiological recordings of auditory midbrain neurons are thus needed to better understand how peripheral filter output is processed to decode social vocalizations.

If central auditory processing areas exhibit similar or enhanced tuning compared to the ABR, then mice could readily detect higher frequencies that include the harmonics found in conspecific vocalizations (Fig. 3). Higher frequencies have smaller wavelengths that attenuate more rapidly in the environment compared to lower frequencies (Wiley and Richards 1978; Peters et al. 2012). Thus, sensitivity to the second harmonic ($2F_0$) may enable distance estimation, or ranging, with detection of harmonics indicating a shorter distance between sender and receiver (Nelson 2000). Indeed, Carolina wrens estimate the distance to a sender based on the amplitude of harmonics relative to F_0 (Naguib 1995, 1997). Such distance estimation may facilitate avoidance of potentially costly interactions or promote aggressive responses when rivals are nearby (Naguib 1995). In grasshopper mice, long-distance calls facilitate conspecific localization, with male–female encounters leading to reproductive behaviors and male–male encounters leading to antagonism (Frank 1989). Since males and females do not exhibit sex differences in call parameters (Pasch et al. 2016; herein), distance estimation may provide a cue to switch to alternative modalities (e.g., olfaction) as individuals approach one another. Playback experiments are needed to assess how grasshopper mice respond behaviorally to varying amplitudes of F_0 and $2F_0$ (Lohr and Dooling 1998).

Similarly, if the broad ABR tuning found herein is represented higher in the auditory processing system, animals would likely be able to detect sympatric heterospecifics (*O. arenicola* and *O. torridus*) that produce slightly higher F_0 (15 kHz and 13 kHz, respectively; Hafner and Hafner 1979; Pasch et al. 2016). Animals used in our study were captured and derived from a population that co-occurs with both heterospecifics and raised in a colony room housing all three species. Although mice and bats can distinguish behaviorally among acoustic signals of ecologically similar species (Schuchmann and Siemers 2010; Pasch et al. 2013), auditory recognition mechanisms remain less clear. In dendrobatid frogs, the recognition space—or range of values that receivers treat as valid conspecifics (Ryan and Rand 1993)—extends beyond conspecific frequencies but is constrained by heterospecifics to reduce interference (Amézquita et al. 2011, Simmons 2013). While the peripheral auditory system exhibits plasticity in response to auditory experience (Gall and Wilczynski 2015), disentangling the relative contributions of learning and genetic differences that shape recognition space will necessitate sampling replicate allopatric and sympatric populations with and without exposure to heterospecific vocalizations. In closely related neotropical singing mice (*Scotinomys*), expansion of sensory sensitivity in the central auditory system appears to mediate competitor recognition and interspecific aggression in sympatry (Pasch et al. 2016). In either case, alternative physiological (e.g., critical ratios; King et al. 2015) and behavioral measures (e.g., operant conditioning; e.g., Neilans et al. 2014; Klink et al. 2006) will be necessary to refine estimates of sensitivity and frequency discrimination.

In summary, our data indicate that northern grasshopper mice exhibit broad tuning in the peripheral auditory system that overlaps with both the F_0 and $2F_0$ found in conspecific and heterospecific vocalizations. Our study contributes important baseline information about the sensory ecology of a unique rodent to the study of sound perception. Such findings will facilitate future comparative experiments on hearing abilities of other non-model species to broaden our understanding of the ecology, evolution, and mechanisms of sound production and perception in the most diverse lineage of mammals.

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Compliance of ethical standards

Conflict of Interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in studies involving animals were in accordance with the ethical standards and approval of the Institutional Animal Care and Use Committee at Northern Arizona University (#15-014 and #16-001) and guidelines of the American Society of Mammalogists (Sikes et al. 2016). Founder animals were captured with a permit from the New Mexico Department of Game and Fish (# 3562).

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