Primate communication in the pure ultrasound

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Few mammals— cetaceans, domestic cats and select bats and rodents—can send and receive vocal signals contained within the ultrasonic domain, or pure ultrasound (greater than 20 kHz). Here, we use the auditory brainstem response (ABR) method to demonstrate that a species of nocturnal primate, the Philippine tarsier (Tarsius syrichta), has a high-frequency limit of auditory sensitivity of ca 91 kHz. We also recorded a vocalization with a dominant frequency of 70 kHz. Such values are among the highest recorded for any terrestrial mammal, and a relatively extreme example of ultrasonic communication. For Philippine tarsiers, ultrasonic vocalizations might represent a private channel of communication that subverts detection by predators, prey and competitors, enhances energetic efficiency, or improves detection against low-frequency background noise.

Keywords: ultrasound; sensory ecology; bioacoustics; auditory brainstem response; evoked potential audiogram

1. INTRODUCTION

Human hearing is relatively poor at higher frequencies; our putative high-frequency limit is 20 kHz, and frequencies above this boundary are classified as ultrasound. The hearing of most haplorhine primates is similarly constrained, although some species have ultrasonic. The hearing of most haplorhine primates and frequencies above this boundary are classified as species; our putative high-frequency limit is 20 kHz, audiogram.

Keywords:

2. MATERIAL AND METHODS

(a) Audiograms

Six adult or subadult tarsiers (T. syrichta; figure 1a) were captured by hand or mist net in the vicinity of Motorpool, Surigao del Norte, Mindanao, Philippines (09°38′ N, 125°33′ E). The animals were anaesthetized for ca 1 h (5–8 mg kg−1 Telazol, supplemented with 3 mg kg−1 Telazol or 15 μg kg−1 deamedetomidine) and positioned in a custom-built sound-attenuating chamber (electronic supplementary material, figure S1).

To estimate auditory sensitivities, we used the minimally invasive auditory brainstem response (ABR) method [20] and EVREST software [21,22] operating on a PC with a data acquisition card (NI-USB-6251; National Instruments, Austin, USA). The stimuli were tone pips (sinusoidal, 2-cycle linear rise/fall, 1-cycle plateau) digitally generated within EVREST, converted to analogue (500 kHz, 16-bit), bandpass filtered from 0.02 to 200 kHz (3B series, 24 dB/octave rolloff, Butterworth; Krohn-Hite, Brockton, USA), attenuated (PA5; Tucker-Davis, Alachua, USA), and delivered at a rate of 39.1 s−1 (alternating polarity) for 2048 repetitions per frequency/level step via an electrostatic speaker (ES1; Tucker-Davis) positioned 10 cm from the left ear. Test frequencies were half octaves from 1 to 64 kHz, delivered in steps of 10 dB from ca 60 to 80 dB and decreasing until the response approached residual electroencephalographic background noise (BN) level and was undetectable; we then tested 5 dB steps around the estimated threshold. We calibrated the peak-equivalent levels (dB re SPL re 20 μPA) of the tone pip stimuli by recording 50 ms pure tones via a free-field 0.5 inch condenser microphone (MKH 800, Sennheiser, Old Lyme, USA; frequency response 0.03–50 kHz, 0°) connected to a PC running Raven Pro v. 1.3 (Cornell Laboratory of Ornithology, Ithaca, USA); calibration was periodically cross-checked against an ultrasound condenser microphone (USM 10-2, Laar, Gut Klein Goernern, Germany; frequency response 0.1–140 kHz, 0°) and a Korg MR-1 mobile recorder (Melville, USA).
We recorded the vocalizations of 35 wild tarsiers from the islands of Bohol and Leyte with an ultrasound microphone. We estimated the high-frequency limit by linear extrapolation of thresholds at 45 and 64 kHz. Given that the threshold at 64 kHz was consistently distinct above random fluctuations in BN (figure 1b), we estimated the high-frequency limit by linear extrapolation from the thresholds at 45 and 64 kHz.

Figure 1. Philippine tarsier and its auditory and acoustic capabilities. (a) Tarsius syrichta in its natural habitat, Mindanao, Philippines. (b) Representative ABR waveform series for 45 kHz stimuli. (c) Average audiogram and standard error of six individuals; the high-frequency limit was extrapolated from the thresholds at 45 and 64 kHz. (d) Spectrogram of vocalization shows the call duration (approx. 650 ms) and dominant frequency (approx. 70 kHz); signal intensity is represented by the density of the red–black scale (hear electronic supplementary material, sound file S1, available online).

The ABR was recorded with 28-gauge subdermal needle electrodes (F-E3; Grass Instruments, West Warwick, USA) positioned in the skin over the cranial vertex (positive), the ipsilateral mastoid (reference) and the contralateral mastoid (ground). The signals were recorded with a biopotential amplifier (P511; Grass Instruments), amplified (×10^5), filtered (0.03–3 kHz bandpass, 60 Hz notch), digitized (10 kHz, 16-bit), input into EVREST (20 ms epochs, 12 μV reject level) and digitally filtered offline [20]. We used a linear regression method [20] to determine the threshold (quietest detectable level) for each frequency. Generally, responses above average BN were included in the regression. We set the criterion at 62 μV (average BN = 40 μV); at this level, the ABR was consistently distinct above random fluctuations in BN (figure 1b and electronic supplementary material, figure S2). For the average audiogram, we calculated two parameters that agree across methods [1,20]: the frequency of best sensitivity and the highest frequency detectable at 60 dB SPL. Given that the threshold at 64 kHz was below 60 dB, we estimated the high-frequency limit by linear extrapolation of thresholds at 45 and 64 kHz.

(b) Vocal recordings
We recorded the vocalizations of 35 wild tarsiers from the islands of Bohol and Leyte with an ultrasound microphone/recording unit (Song Meter SM2BAT; Wildlife Acoustics, Concord, USA; frequency response 0–96 kHz). During fieldwork, we occasionally observed stereotypical vocal behaviours that were inaudible to us; and, for eight individuals, we recorded a call in the pure ultrasound (Sound Meter S1, available online). The call was emitted in two contexts: (i) during human handling and (ii) during unrestrained activity within temporary enclosures. In Raven Pro, we defined the dominant frequency of the call as that with the most energy, and determined the lowest frequency by visual distinctiveness from spectrogram noise. This protocol was approved by the Institutional Animal Care and Use Committee of Texas A&M University (approval no. AUP2008-7).

3. RESULTS
Among six tarsiers, we found two frequency regions of best auditory sensitivity (1.4 and 16 kHz), and an audible range that extended substantially into the ultrasound (figure 1c). The 60 dB high-frequency limit of T. syrichta is estimated at 91 kHz (figure 1c), a value that surpasses the known range of all other primates (figure 2) and is matched by few animals [10–14]. We also recorded a distinctive vocalization in the pure ultrasound (bandwidth 67–79 kHz, dominant frequency, approx. 70 kHz) from eight animals (figure 1d; electronic supplementary material, sound file S1, available online). The minimum frequency of the call (67 kHz) is the highest value for any terrestrial mammal excluding bats and some rodents [10,14]. The distinctive tone-like structure of the call partly resembles the vocalizations of other tarsier species [19]; however, none of these calls was purely ultrasonic. They were contained below 34 kHz and featured strong harmonics less than 20 kHz.

Figure 2. The 60 dB high-frequency limits of strepsirrhine and haplorhine primates. Boxes represent the interquartile range between the first and third quartiles and the line inside represents the median. Whiskers denote the lowest and highest values, excepting Tarsius syrichta. At ca 91 kHz, T. syrichta is substantially higher than other primate species [1,23,24].

4. DISCUSSION
The Philippine tarsier’s estimated high-frequency limit of auditory sensitivity (ca 91 kHz) and call with a dominant frequency of 70 kHz are among the highest values recorded for terrestrial mammals, and an extreme
example of acoustic communication. Vocalizations in the pure ultrasound might confer several selective advantages. For example, although ultrasonic calls are expected to attenuate quickly, they are also expedient private channels of communication with the potential to subvert detection by predators, prey and competitors, enhance energetic efficiency, and improve signal-to-noise ratios in habitats inundated with low-frequency biological noise [15]. Our observation that the tarsiers emitted the call in the proximity of humans suggests a context of alarm. Ultrasonic alarm calls can be advantageous to both the signaller and receiver as they are potentially difficult for predators to detect and localize [13,15].

Yet, tarsiers are themselves specialized predators. They lack conventional visual adaptations to nocturnality, such as a reflective tapetum lucidum in the retina, and possess instead the largest eyes relative to body size of any mammal [25]. Visual predation of arthropod prey is a central element of tarsier foraging behaviour, but it is constrained by the availability of downwelling light in the forest understory. Under the darkest nocturnal conditions—when cloud cover occludes starlight—it is plausible that the exceptional hearing of tarsiers contributes to improved foraging efficiency through acoustic eavesdropping [18]. For instance, tarsiers might attend to ultrasonic signals between prey species (e.g. katydids and moths [26,27]) or broadband cues signifying the presence and location of potential prey, such as rustling leaves [28].

Our findings demonstrate that Philippine tarsiers can send and receive signals in the pure ultrasound. Although the advantages of this specialized sensory adaptation are yet uncertain, additional studies comparing the evolutionary, behavioural and physiological foundations of ultrasonic communication in tarsiers are likely to provide insights into the fundamental properties promoting high-frequency hearing in all vertebrates.

All animals were captured, examined and released unharmed under protocols approved by the Institutional Animal Care and Use Committee of Dartmouth College (approval nos. 10-11-02).

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