

Hearing in American leaf-nosed bats. I: *Phyllostomus hastatus*

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Abstract

We determined the audiogram of *Phyllostomus hastatus* (the greater spear-nosed bat), a large, omnivorous American leaf-nosed bat native to Central and South America. A conditioned suppression/avoidance procedure with a fruit juice reward was used for testing. At an intensity of 60 dB sound pressure level (SPL re 20 $\mu\text{N}/\text{m}^2$), the hearing range of *P. hastatus* extends from 1.8 to 105 kHz, with a best sensitivity of 1 dB SPL at 20 kHz. Both its high-frequency and low-frequency hearing are not unusual for a small mammal. Despite its use of low-intensity echolocation calls there was no evidence for unusual sensitivity to either the frequencies used for echolocation or to the main frequencies of its communication calls, suggesting no selective ‘tuning’ of the audiogram. Its behavioral pure-tone thresholds are lower than the multi-unit thresholds in the inferior colliculus. © 2002 Elsevier Science B.V. All rights reserved.

Key words: Audiogram; Chiroptera; Echolocation; Evolution; Mammal

1. Introduction

This report is the first in a series examining the passive hearing of New World bats in the highly diverse and successful family, Phyllostomidae. In bats, diet and foraging environment, such as pursuit of insects in the open versus capturing food amid clutter, are known to affect the nature of echolocation (e.g., Schnitzler and Kalko, 2001). However, it is not known whether there are corresponding effects on hearing because behavioral audiograms for relatively few bat species are available. In an effort to reveal any relationship between lifestyle or type of echolocation and hearing, as well as to compare the hearing of bats to mammals in general, we have begun examining basic hearing abilities in a range of bat species.

Only two behavioral audiograms have been attempted for this family, which includes more than 150 species. One, the lesser spear-nosed bat, *Phyllostomus*

discolor, could hear frequencies from 5 to 142 kHz, but the best sensitivity achieved by any of the bats was reported as only 18 dB sound pressure level (SPL re 20 $\mu\text{N}/\text{m}^2$), with most being much less sensitive (Esser and Daucher, 1996). The other, the frog-eating bat, *Trachops cirrhosus*, made unconditioned pinna responses to frequencies from 200 Hz to 15 kHz (the highest frequency examined), but again only limited sensitivities of 35–50 dB could be demonstrated (Ryan et al., 1983). Furthermore, both *P. discolor* and *T. cirrhosus*, as well as other phyllostomids that have been studied, are described as ‘whispering’ bats because their echolocation calls are 40–50 dB less intense than those of bats that pursue aerial prey (Griffin, 1958; Howell, 1974). When compared to the 2.9-dB (± 9.8 S.D.) mean best sensitivity for terrestrial mammals, these two phyllostomids appear insensitive, which seems inconsistent with the use of low-intensity echolocation signals. Thus, it is of interest to explore the hearing of bats in this family.

In this report we present the audiogram of the greater spear-nosed bat, *Phyllostomus hastatus*, a large leaf-nosed bat common in Central and South America. At approximately 60–110 g, it is the second largest bat in the New World, comparable in size to many of the non-

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Abbreviations: SPL, sound pressure level re 20 $\mu\text{N}/\text{m}^2$

echolocating Megachiroptera. *P. hastatus* is omnivorous (Gardner, 1977), and, although it eats fruit and insects, it prefers meat, preying on small vertebrates, including other bats. Like many other bats that forage for fruit amidst leaf clutter or detect live prey against a solid surface (gleaners), it uses relatively low-intensity, brief sonar pulses when foraging (Fenton et al., 1995; Kalko and Condon, 1998; Neuweiler, 1984, 1989). It may also listen passively for sounds generated by the movements of its prey, a behavior thought to be common in bats that take large prey from substrates (Belwood, 1986). As it has been suggested that such passive listening may be associated with good low-frequency sensitivity (Bell, 1982; Brown et al., 1984; Schmidt et al., 1983/1984; Tuttle and Ryan, 1981), the question arises whether *P. hastatus* hears lower frequencies than bats that pursue aerial insects or that eat only fruit.

Absolute thresholds of two *P. hastatus* were determined using a conditioned suppression/avoidance procedure. The resulting audiogram was then compared to those of other Phyllostomidae and placed within the context of mammalian hearing. We also compared the behavioral audiogram to thresholds for neural responses to sound recorded in the inferior colliculus (Grinnell, 1970).

2. Methods

The bats were tested using a conditioned suppression/avoidance procedure in which a hungry animal was trained to make continuous mouth contact with a reward spout in order to receive a steady trickle of fruit juice. Pure tones were then presented at random intervals followed by a mild electric shock, delivered via the spout. To avoid the shock, the bat had to break contact with the spout, thereby also indicating that it had detected the signal (Heffner and Heffner, 1995). Absolute thresholds were determined throughout the animals' audible range with the loudspeaker placed at 0° azimuth and elevation.

2.1. Subjects

The colony of *P. hastatus* was group-housed and maintained on a diet of meat (cooked beef steak or Alpo Prime Cuts from Friskies Pet Care Co.) and mixed fruit. The two females used in this study were born in captivity and were 5 years old at the time of testing, which is a relatively young age as bats in this family are known to live 9–18 years in the wild (Barnard, 1995). The bats were individually housed in wood and plastic mesh cages (48×39×95 cm) and allowed to fly daily for 10 min in a flight room (2.55×2.75×

2.05 m). They received the major portion of their diet during the test sessions in the form of fruit juice (a mixture of cantaloupe, pear juice and vitamin supplement; finely blended and sieved). While on test, the bats had free access to water and were given supplements of juice and mealworms as needed to maintain their weights between 85 and 90% of free-feed weights.

2.2. Behavioral apparatus

Testing was conducted in a carpeted, double-walled acoustic chamber (IAC model 1204; 2.55×2.75×2.05 m), the walls and ceiling of which were lined with egg-crate foam. The equipment for stimulus generation and behavioral control was located outside the chamber and the bats were observed via closed-circuit television.

The bats were tested in a cage (50×30×50 cm) constructed of 1-inch (2.54-cm) hardware cloth, and mounted 93 cm above the floor on a tripod (Fig. 1). A reward spout (2.5-mm diameter brass tube, topped with a 9×8-mm oval lick plate that sloped toward the bat at a 45° angle) projected 7 cm above the cage floor

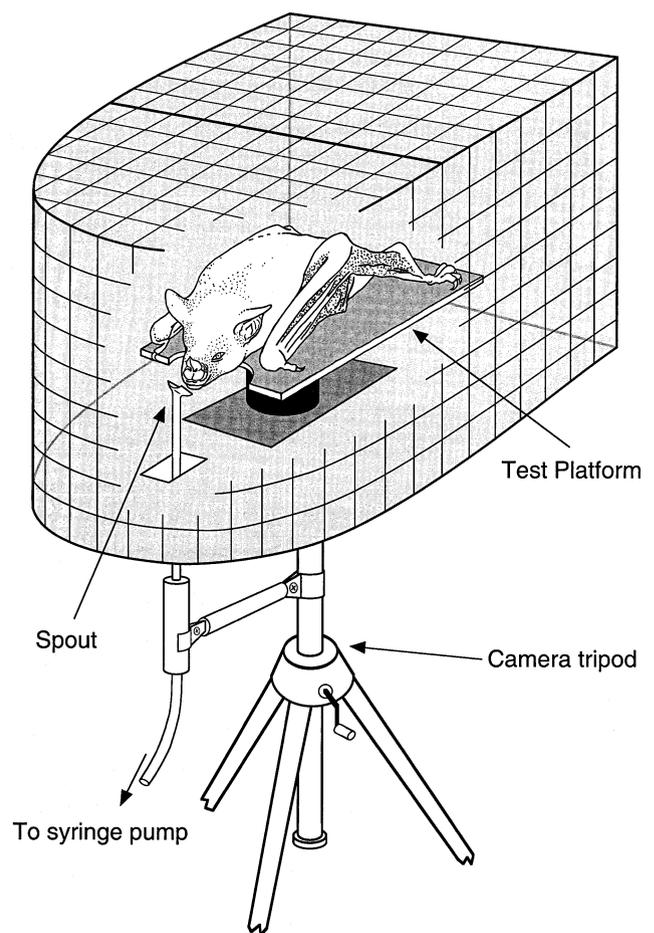


Fig. 1. Cage used for testing showing a greater spear-nosed bat in position on the platform, ready to drink.

at the front of the cage and was attached via plastic tubing to a 30 ml glass syringe. The fruit juice was dispensed using a syringe pump enclosed in a high-density polyethylene box (64×21×28 cm). To eliminate noise generated when the pump was activated, the box was lined with egg-crate foam and placed on the floor of the test chamber behind the test cage.

Inside the test cage was a small platform (30×10×7 cm) onto which the bat crawled to drink from the reward spout. The tip of the reward spout was placed 1 cm in front of the platform and at platform height so that it was below the animal's ears and did not interfere with the sound field while it drank from the spout. The platform was covered with a piece of dampened carpet to provide traction and facilitate electrical contact with the bat. A contact circuit connected between the food spout and platform was used to detect when the bat made contact with the spout and to activate the syringe pump. In addition, a shock generator was connected between the reward spout and platform. The shock was adjusted for each individual to the lowest level that produced a reliable avoidance response, which consisted of backing away slightly from the spout or lifting its head from the spout. A 25-W light, mounted 0.5 m below the cage, was turned on and off with the shock to signal a successful avoidance and to indicate when it was safe to return to the spout.

2.3. Acoustical apparatus

Sine waves from 1 to 100 kHz were generated digitally (Zonic A and D 3525); signals of 110 kHz (and 100 kHz for replicating thresholds) were produced using an analog generator (Krohn-Hite 2400). The sine waves were pulsed (400 ms on, 100 ms off) for four pulses, and shaped by a rise–fall gate (Coulbourn S84-04) with a rise–decay time of 10 ms. The electrical signal was then bandpass-filtered (Krohn-Hite 3202, $\pm 1/3$ octave settings, 24 dB/octave rolloff) and attenuated (Hewlett Packard 350D) as needed. Finally, the signal was amplified (Crown D75 or Adcom GFA545), monitored for distortion with an oscilloscope, and routed to a loudspeaker in the test chamber. The loudspeaker was placed approximately 1 m in front of the cage (0° elevation and azimuth) facing directly toward the bat when it was eating from the spout. Care was also taken to produce a homogeneous sound field (within ± 1 dB) in the area occupied by a bat's head and ears when it was drinking from the spout. Various loudspeakers were used to present the tones – for frequencies of 1 to 2.8 kHz either a 15-inch (38-cm), 12-inch (30.4-cm) or 6-inch (15.2-cm) woofer was used; for frequencies from 4 to 110 kHz, a ribbon tweeter (Panasonic EAS-10TH400C or EAS-10TH100A) was used. Thresholds were obtained at 19 frequencies:

1, 1.5, 2, 4, 8, 12.5, 16, 20, 25, 32, 40, 50, 56, 64, 71, 80, 90, 100, and 110 kHz.

2.4. Sound level measurement

The SPL was measured daily with a 1/4-inch (0.64-cm) microphone (Brüel and Kjaer 4135, corrected for free-field with the protection grid on), or a 1/8-in (0.32-cm) microphone (Brüel and Kjaer 4138, again with free-field correction), preamplifier (Brüel and Kjaer 2619), and measuring amplifier (Brüel and Kjaer 2608, set to 22.4 Hz high pass). The output of the measuring amplifier was then sent to a spectrum analyzer (Zonic A and D 3525) to check the acoustic signal for overtones (which can occur when generating pure tones at high intensities). The only measurable harmonics were associated with the 1-kHz signal; subsequent measurements demonstrated that at threshold intensity (88 and 78 dB for bats A and B, respectively), the 1-kHz signal also included 2- and 3-kHz harmonics that were at least 28 and 15 dB, respectively, below the animals' thresholds at those frequencies. Thus, the only measurable harmonics did not contribute extraneous cues.

2.5. Behavioral procedure

A hungry bat was first trained to mount the platform and drink from the spout. Requiring the bat to make mouth contact with the spout also served to fix its head in the sound field and to orient it towards the loudspeaker. A train of four tone pulses was then presented at random intervals, followed at its offset by a mild electric shock (300 ms duration, ≤ 1.25 ma) delivered between the spout and platform. The animal soon learned to avoid the shock by breaking contact with the spout whenever it heard a tone, thus indicating that it had detected the signal. The shock was considered mild as the bats readily returned to the spout after the shock had been delivered.

Test sessions were divided into 2-s trials, separated by 1.5-s intertrial intervals. Approximately 22% of the trial periods contained a pulsing tone (warning signal), whereas the remaining trial periods were silent (safe signal). The contact circuit was used to detect whether an animal was in contact with the spout during the last 150 ms of each trial. If an animal broke contact for more than half of the 150-ms response period, a detection response was recorded. This response was classified as a hit if the trial contained a tone, or as a false alarm if no tone had been presented. The hit and false alarm rates were then determined for each stimulus intensity, with a single intensity presented in a consecutive block of 6–8 warning trials (with approximately 32 associated safe trials). Finally, the hit rate was corrected for false alarms to produce a performance measure (Heffner

and Heffner, 1995) according to the formula: performance = hit rate – (false alarm rate × hit rate). This measure proportionately reduces the hit rate by the false alarm rate associated with each intensity (i.e., each block of trials) and varies from 0 (no hits) to 1 (100% hit rate with no false alarms).

Auditory thresholds were determined by reducing the intensity of the tone by 5 dB in successive blocks of 6–8 warning trials until the bat no longer responded to the warning signal above chance (i.e., the hit and false alarm rates did not differ significantly; $P > 0.01$, binomial distribution). Threshold was defined as the intensity at which the performance measure equaled 0.50, which was usually obtained by interpolation. Testing was carried out at each frequency until thresholds no longer improved (asymptotic performance). For each bat, testing was considered complete at that frequency when the thresholds obtained in at least three different sessions were within 3 dB of each other.

These experiments were approved by the Institutional Animal Care and Use Committee of the University of Toledo.

3. Results

The initial adaptation to the apparatus, learning to respond to sound, and becoming a reliable observer required approximately 2 months. Because *P. hastatus* must eat large volumes of food when their diet consists mainly of fruit, they worked best in two daily sessions, one in the late afternoon and the other in the evening, about 5 h apart. Each session lasted as long as 40 min, during which time a bat consumed up to 15 ml of fruit

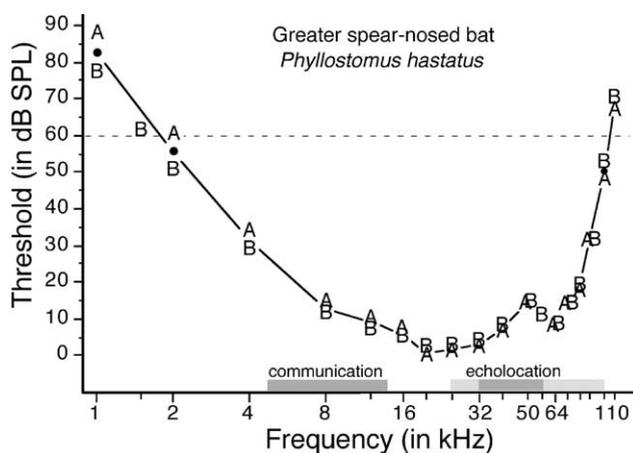


Fig. 2. Audiogram of the greater spear-nosed bat, *P. hastatus*. A and B represent individual animals. Darker bars indicate frequencies used in communication calls and the dominant third harmonic of the echolocation call; lighter bars indicate the additional frequencies encompassed in the weaker second and fourth harmonics of the echolocation call.

juice and received as many as 100 warning trials. Thus, two thresholds could usually be determined daily.

The thresholds of the two *P. hastatus* (Fig. 2) show good agreement. Beginning with a mean threshold of 83 dB at 1 kHz, sensitivity increased rapidly as frequency increased, showing the best sensitivity at 20 kHz, where thresholds averaged 1 dB. Above 20 kHz, hearing sensitivity gradually declined, reaching a mean threshold of 15 dB at 50 kHz, followed by a slight improvement to 9 dB at 64 kHz. Above 64 kHz, hearing sensitivity rapidly declined, reaching a threshold of 69 dB at 110 kHz, the highest frequency tested. At a level of 60 dB SPL, the audiogram extends from 1.8 to 105 kHz, a range of 5.9 octaves. The mean thresholds for each bat are available in tabular form on the Internet (<http://www.utoledo.edu/psychology/animalhearing/>).

4. Discussion

4.1. Features of the audiogram of the greater spear-nosed bat, *P. hastatus*

4.1.1. High-frequency hearing

For comparisons among species, it is useful to determine (usually by interpolation) the highest frequency audible at a standard intensity of 60 dB (referred to as the high-frequency hearing limit). For *P. hastatus*, this limit is 105 kHz, which is higher than that of most other mammals. However, a comparative analysis indicates that this is not unexpected in a mammal of its size, regardless of whether or not it is an echolocator. Among mammals in general, high-frequency hearing is strongly correlated with functional head size such that mammals with functionally small heads hear higher frequencies than those with larger heads. Functional head size, or interaural distance, is the distance that a sound must travel from one ear to the other and is measured as travel time in the appropriate medium, air or water. It is functional head size that largely determines the magnitude of the interaural-difference cues available for passive sound localization. Specifically, the interaural intensity-difference cue is only effective if an animal can hear frequencies that are high enough to be shadowed by its head so that a sound is more intense at one ear than the other. (Similarly, only relatively high frequencies interact with the dimensions of small pinnae to produce useable pinna cues for locus.) Functional head size is therefore an important source of selective pressure for high-frequency hearing in mammals (Heffner et al., 2001; Masterton et al., 1969).

The 105-kHz high-frequency hearing limit of *P. hastatus* does not deviate from the relationship between high-frequency hearing and functional interaural dis-

tance established for other mammals ($t=1.64$, $P=0.112$, two-tailed). Indeed, its conformity with the relationship is similar to that of humans ($t=-1.42$, $P=0.161$, two-tailed) and cats ($t=1.8$, $P=0.076$, two-tailed). Moreover, all of the bats tested so far have high-frequency hearing within the confidence limits predicted by their interaural distance (cf. Koay et al., 1998). Hence, there is no basis to conclude that bats are atypical in their high-frequency hearing. This conformity with other mammals in a relationship based on passive sound localization supports the idea that bats remain under selective pressure to localize sounds in their environment, as suggested by the importance of prey-generated sound to many species that capture insects from a substrate (cf. Arlettaz et al., 2001; Fuzesery et al., 1993). Furthermore, the finding that high-frequency hearing in bats is typically mammalian and predictable (based on interaural distance) supports the view that echolocation probably evolved as a neural, rather than sensory, adaptation of the use of high frequencies (Neuweiler, 1984). In other words, high frequencies already useful in small mammals for passive sound localization were probably co-opted by early bats for use in echolocation, and high-frequency hearing was not a sensory specialization in bats.

4.1.2. Low-frequency hearing

The low-frequency hearing limit of *P. hastatus* (defined as the lowest frequency audible at 60 dB SPL) is 1.8 kHz, which is better than that of most bats and is exceeded only by the 1.7-kHz low-frequency limit of *Megaderma lyra*, a carnivorous bat (Schmidt et al., 1983/1984). However, a low-frequency hearing limit of 1.8 kHz is still quite restricted when compared to mammals in general, including species that are not carnivorous (as many sounds made by predators and conspecifics also contain low frequencies).

Unlike mammalian high-frequency hearing, which is approximately normally distributed, mammalian low-frequency hearing falls into two distinct groups with no apparent overlap (Heffner et al., 2001). Of the 63 species of terrestrial mammals tested so far, approximately two-thirds hear below 125 Hz, whereas the remaining species, including all of the bats, hear no lower than 500 Hz (Heffner et al., 2001). Nevertheless, high- and low-frequency hearing limits are related in both groups such that species with relatively good high-frequency hearing usually have relatively poor low-frequency hearing (Heffner et al., 2001). Although *P. hastatus* has relatively good low-frequency hearing compared to other bats, it does not deviate significantly from the regression line for its group ($t=-1.26$, $P=0.224$, two-tailed). Thus, there is no indication that its low-frequency hearing is unusual. Indeed, none of the bats deviates significantly from

the regression line linking low- and high-frequency hearing.

Although all of the bats with established low-frequency hearing limits fall among the 25% of mammals with the poorest low-frequency hearing (cf. Heffner et al., 2001), it has been suggested that there are some species of bats that have much more extensive low-frequency hearing. Specifically, neural recordings in the common vampire bat (*Desmodus rotundus*) revealed responses to breathing sounds likely to include low frequencies (Schmidt et al., 1991), and frog-eating bats (*T. cirrhosus*) were reported to make unconditioned orientations to tape-recorded tones as low as 200-Hz (Ryan et al., 1983). Conditioned behavioral responses to well-characterized low frequencies will be especially important for these species.

4.1.3. Absolute sensitivity

Because *P. hastatus* uses echolocation calls of relatively low intensity (60–80 dB) compared to bats that detect and track aerial prey (110 dB or greater; Fenton et al., 1995), we might expect it to be especially sensitive to the frequencies in its echolocation calls. In its echolocation calls the dominant harmonic sweeps from about 55 to 32 kHz, with weaker harmonics encompassing frequencies down to 25 kHz and up to 100 kHz (Gould, 1977; Grinnell, 1970; Kalko and Condon, 1998; Pye, 1966). This species also uses vocal signals for communication, and those calls are louder and of lower frequency than its echolocation calls (between 5 and 15 kHz, with the main energy concentrated between about 6 and 12 kHz; Boughman and Wilkinson, 1998; Wilkinson and Boughman, 1998). As can be seen in Fig. 2, the 1-dB best sensitivity of *P. hastatus* is at 20 kHz, a frequency that is not exclusively associated with either its echolocation or its communication frequencies. Indeed, *P. hastatus* has thresholds of 20 dB or better throughout most of the frequency range of both its communication and echolocation calls.

When compared to other bats, the 1-dB best sensitivity of *P. hastatus* does not appear unusual. The best sensitivities of the five other bats with behavioral audiograms extend from –16 dB for *M. lyra* (Schmidt et al., 1983/1984) to 10 dB for *Myotis lucifugus* (Dalland, 1965), and the 1-dB sensitivity of *P. hastatus* is well within that range. It should also be noted that 1 dB is near the mean of best sensitivities for terrestrial mammals, which is 2.9 dB. Thus there is no indication of unusual sensitivity associated with the low-intensity echolocation calls of *P. hastatus*.

4.1.4. Secondary peak of sensitivity

A decrease in sensitivity in the midrange of the audiogram (at 50 kHz) followed by improvement (at

64 kHz) has been seen in other mammals and is evident in most bats (e.g., Koay et al., 1997, 1998; Long and Schnitzler, 1975; Schmidt et al., 1983/1984). Often characterized as a secondary peak of sensitivity (at 64 kHz), it may with equal justification be described as a slight decrease in sensitivity (at 50 kHz). Regardless of whether we attend to the increase or decrease in sensitivity, in most species the irregularity appears to be due to the directionality of the pinnae (Jen and Chen, 1988; Koay et al., 1998). In other bats, such as *Eptesicus fuscus*, the pinnae have been shown to induce spectral notches in the sound reaching the ear (Wotton et al., 1995). The selective filtering of sound by the pinnae in bats plays a major role in localization in the vertical plane (Lawrence and Simmons, 1982; Wotton and Simmons, 2000), and may also provide cues for azimuthal localization as it does in non-echolocators (Huang and May, 1996; Humanski and Butler, 1988; Middlebrooks and Green, 1991).

4.2. Comparison with other Phyllostomidae

Estimates of hearing are available for two other species of Phyllostomidae, *P. discolor* (the lesser spear-nosed bat, Esser and Daucher, 1996) and *T. cirrhosus* (the frog-eating bat, Ryan et al., 1983). The thresholds for *P. discolor* depict it as insensitive, with the lowest threshold achieved by any of the bats being 18 dB. However, this appears to be an underestimation of its sensitivity, most likely resulting from the difficulty of the task. Evidence of task difficulty was shown in the marked variation both between and within individuals, and in the unreliable asymptotic performances with tones that should have been easily audible. Thus, even a composite audiogram based on the best thresholds may not represent the true auditory sensitivity of *P. discolor*.

The hearing estimate of *T. cirrhosus* is based on a study of unconditioned responses in the field to tape-recorded tones (Ryan et al., 1983). The thresholds obtained by this study also showed large individual variation and poor hearing sensitivity, with the lowest average threshold being approximately 50 dB SPL. Although these data have been used to support the conclusion that *T. cirrhosus* is anatomically specialized for the reception of low frequencies and is able to distinguish the calls of frogs based on their low-frequency components (Bruns et al., 1989; Ryan and Tuttle, 1983), such conclusions are probably premature. Considering both the likelihood that the hearing of *P. discolor* and *T. cirrhosus* is more sensitive than depicted, and the good sensitivity of *P. hastatus* reported here, we believe that bats in the family Phyllostomidae have hearing sensitivity comparable to the average for mammals (cf. Heffner et al., 2001).

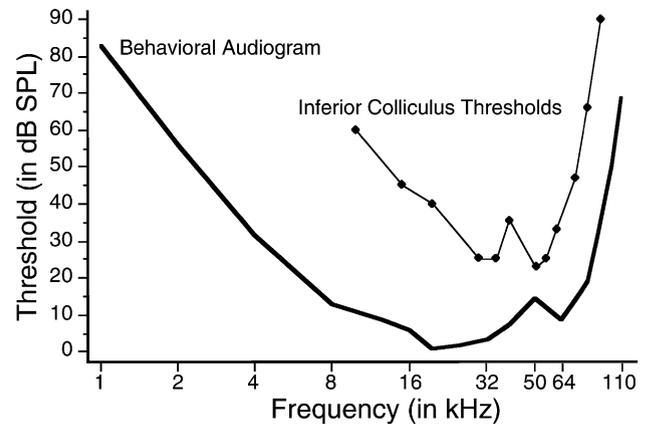


Fig. 3. Behavioral audiogram of *P. hastatus* compared to thresholds for multi-unit responses in the inferior colliculus.

4.3. Relationship to physiological estimates of hearing

Multi-unit response thresholds are available from the inferior colliculi of *P. hastatus* (Grinnell, 1970), and can be compared to the behavioral measure of hearing. For the electrophysiological recordings, tones of varying durations and rise–decay times were presented free-field to determine the best stimulus parameters for cells in the inferior colliculus. Physiological thresholds (defined as the lowest intensity eliciting any neural response) are shown in Fig. 3 together with the behavioral thresholds (mean 50% detection). Although the physiological thresholds reflect the general shape of the behavioral audiogram, they underestimate the absolute sensitivity and frequency range of this species, especially at the lower frequencies. There are many physiological factors that could raise the neural thresholds including the effects of body temperature, anesthesia, and respiration. On the other hand, the typically short rise–decay times of the acoustic stimuli used in electrophysiological studies (compared to the longer rise–decay times used in behavioral studies) tend to lower thresholds. Finally, the nature of the processing in the inferior colliculus may not require responses to low-intensity sounds, whereas the animal as a whole is likely to be under selective pressure to detect sound sources with as much sensitivity as possible. Thus, although the sensitivity of neural responses are of interest for understanding processing in the nervous system, they should not be expected to indicate the sensitivity of the whole animal.

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