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Audiograms of a South Indian bat community

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Summary. 1. Audiograms are recorded from one non-echolocating and nine echolocating sympatrically living bat species of South India. These species are *Cynopterus sphinx* (non-echolocating), *Tadarida aegyptiaca, Taphozous melanopogon, T. kachhensis, Rhinopoma hardwickei, Pipistrellus dormeri, P. mimus, Hipposideros speoris, H. bicolor* and *Megaderma lyra.*

2. In *Rhinopoma hardwickei* a highly sensitive frequency range was found which is narrowly tuned to the frequency band of the bat's CF-echolocation call (32–35 kHz, Fig. 3). In hipposiderids a 'filter' narrowly tuned to the frequency of the CF-part of the CF-FM echolocation sounds (137.5 kHz in *H. speoris* and 151.5 kHz in *H. bicolor*, Fig. 5) could be recorded from deeper parts of IC.

3. In the echolocating species the best frequency of the audiograms closely matched with that frequency range in the echolocation calls containing most energy.

4. In bat species foraging flying prey best frequencies of audiograms and height of preferred foraging areas are inversely related, i.e. bat species hunting high above canopy have lower best frequencies than those foraging close to or within canopy (Fig. 6).

5. A hypothesis is forwarded explaining how fluttering target detection by constant frequency echolocation might have evolved from long distance echolocation by pure tone signals.

Introduction

In the last two decades, the auditory nervous system of echolocating bats, especially the adaptation of the system to echolocation signals, has been studied in great detail (for reviews see Busnel and Fish 1980). In contrast only few studies have dealt with the comparative aspect. Grinnell (1970) and his colleague (Grinnell and Hagiwara 1972a, b) recorded evoked potentials and from single units in five phyllostomatid species and studied audiograms, tuning curves and temporal resolutions in five hipposiderid, two vespertilionid species, and in non-echolocating fruit-eating bats collected during an Alpha Helix Expedition to New Guinea. On a recent expedition to Australia Jen and Suthers (1982) recorded audiograms from different parts of inferior colliculus in one emballonurid, two vespertilionid, one hipposiderid and two rhinolophid species. In each species studied the frequency range of the species' echolocation signals was found to be similar to the 'audible range' defined electrophysiologically. In these studies, the echolocation signals comprising CF-FM and FM sounds were mostly recorded in the laboratory. Many species, however, emit different types of signals when echolocating in open air. Thus it is uncertain, if all sound types used in freely behaving bats were taken into account. Moreover, nothing is known about the foraging behavior and preferred hunting areas of the different bat species studied and thus no conclusions can be drawn on the possible adaptive significance of the specific auditory capacity.

In this paper we report audiograms recorded from inferior colliculus of nine sympatric echolocating bat species most commonly found around the campus of Madurai University in South India.

Abbreviations: BFA best frequency of audiogram; *b.w.* body weight; *CF* constant frequency; *FM* frequency modulated; *IC* inferior colliculus; SPL Sound Pressure Level

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Their nightly foraging behaviour, preferred hunting biotopes and echolocation signals emitted have been thoroughly described by Habersetzer (1983): *Taphozous* and *Tadarida* prefer to hunt well above the canopy in open space, *Rhinopoma* and *Pipistrellus* prefer the open space between trees and bushes or over ponds whereas hipposiderids can skilfully hunt close to obstacles and inside the canopy of bushes and trees. *Megaderma* flies close to the ground and over water surface searching for all kinds of prey. Echolocation signals employed by these bats are species specific but may also vary according to the flight path.

We can thus examine if and how the auditory sensitivity, as expressed in collicular audiograms, correlates with the different foraging areas in these nine sympatric species. This problem became especially relevant since Habersetzer (1983) found that *Taphozous, Rhinopoma* and *Pipistrellus* emit long pure tones with or without harmonics during search flight or in unobstructed flight pathways.

In bats emitting long pure tones we also pay attention to the possible presence of an 'acoustic fovea' which is sharply tuned to the frequency of the pure tone echolocation signal as demonstrated in horseshoe bats (Neuweiler 1970; Neuweiler et al. 1980) for detecting moving prey. For comparison with non-echolocators the audiogram of *Cynopterus sphinx*, a very common fruit-eating species in Madurai, is recorded.

Materials and methods

One megachiropteran species, *Cynopterus sphinx*, and the following nine echolocating Microchiroptera were studied: *Tadarida aegyptiaca, Taphozous melanopogon, Taphozous kachhensis, Rhinopoma hardwickei, Pipistrellus mimus, Pipistrellus dormeri, Hipposideros speoris, Hipposideros bicolor* and *Megaderma lyra*. All species were identified by Dr. Kock, Senckenberg-Museum, Frankfurt.

Unless otherwise stated recordings were made from two specimens of each species. Several audiograms were recorded from each specimen. Due to the remarkable invariance of the audiograms, especially in the range of the most sensitive frequencies we feel confident that the recordings are representative for each species. All three investigators recorded audiograms independently so that possible personal biases could be checked.

Surgery and recording procedures were basically the same as those described in Schuller (1980). During surgery bats were anaesthetized by an intraperitoneal injection of 0.025 mg Nembutal/g body weight. Recordings were made from awake bats. The wounds were locally treated by Novocain. Evoked potentials were recorded from the dorsal surface of the inferior colliculus by chlorated silver-ball electrodes. Glass insulated tungsten electrodes were used for recording from deeper layers of inferior colliculus (IC) in hipposiderids and from the IC of *Cynopterus sphinx*. In a sound shielded room where the temperature was kept around 35 °C an average evoked potential from 32 stimulus presentations was obtained from a Nicolet computer type 1070 and the response thresholds at various frequencies were audiovisually determined in order to construct the audiogram. Threshold was defined as that stimulus intensity (dB SPL) at which the averaged evoked potential was just discernable above neural noise.

Pure tone stimuli (30 ms duration and 1 ms rise/falltime) were delivered in free field and directed toward the contralateral ear at a rate of 3/s via a custom made ultrasound loudspeaker. Distance between the loudspeaker and the bat was 34 cm. The frequency response of the loudspeaker was flat within ±5 dB from 16 to 92 kHz and the maximum output was 97 dB SPL. The loudspeaker was calibrated by a Brüel and Kjaer Type 2209 Impulse Precision Sound Level Meter and a quarter inch microphone (Brüel and Kjaer 4135) from 1 to 200 kHz. We could not measure harmonic distortions of our loudspeaker in Madurai. However, calibrations of the same type of loudspeaker in our Munich lab show that harmonic distortions are present only for frequencies below 10 kHz at intensities of 90 dB SPL and higher. At sound pressure levels used in our studies, mostly 40–60 dB SPL, in the low frequency range distortions are far less pronounced: for 2 kHz at 50 dB SPL the 4 kHz component is 20 dB below and higher harmonics more than 40 dB below the fundamental component. For an 8 kHz stimulus at 64 dB SPL the harmonic ratio is −20 dB for the first harmonic and drops to even −40 dB for an 8 kHz stimulus of 47 dB SPL. These measurements suggest that our threshold measurements for low frequencies were not influenced by the presence of harmonics. Nevertheless, since the harmonic content of the stimuli was not measured in our Madurai loudspeaker thresholds for frequencies below 5 kHz should be considered as tentative only. For this reason, audiograms for frequencies below 5 kHz are drawn in dashed lines.

Results

Cynopterus sphinx, (b.w.) 43 g (Fig. 1)

In one specimen of this non-echolocating fruit-eating bat evoked potentials were recorded by a tungsten electrode pushed into the inferior colliculus (IC) which does not protrude to the brain surface as in the echolocating species.

Audiograms of *Cynopterus sphinx* were very broad and the best sensitivity occurred around 14 kHz, henceforth this frequency will be called the best frequency of the audiogram (BFA). The frequency band of the audiogram with thresholds within 20 dB above that of the BFA encompassed 6 to 45 kHz. Thus, this non-echolocating bat is sensitive to ultrasound and only from 50 to 70 kHz thresholds of the audiogram rose steeply from 50 to 97 dB SPL. For frequencies lower than 10 kHz, the threshold curve increased by 16 dB/octave. Evoked potentials could still be recorded at 500 Hz but not at 300 Hz.

Tadarida aegyptiaca, b.w. 22–24 g (Fig. 1)

This bat is a strong flier which preferably forages at considerable height (10–20 m above ground),

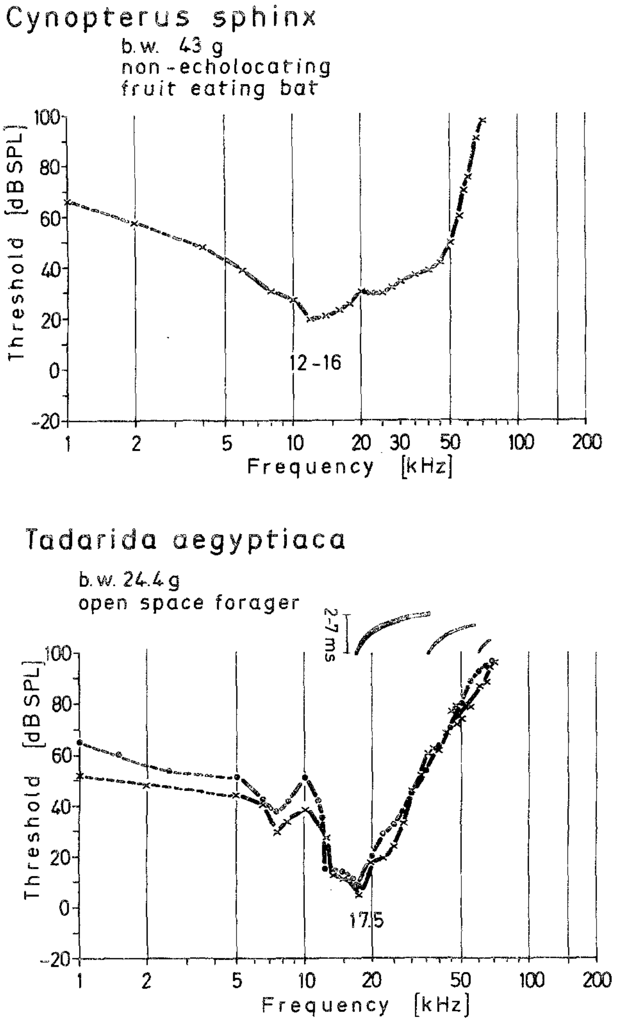

Fig. 1. Audiograms of the non-echolocating megachiropteran bat *Cynopterus sphinx* and the echolocating bat *Tadarida aegyptiaca*, as derived from threshold measurements of evoked potentials in the inferior colliculus. *Explanations for Figs. 1–5:* The audiograms for each species are represented from one specimen. Sonagrams of the species' echolocation sounds are inserted in the upper part of the graphs with identical frequency scale shown on the abscissa. Note: time scale of the sonagrams should be read from top to bottom and sound durations are indicated in ms. Dashed line of the audiogram from 1 to 5 kHz indicates suggestive thresholds due to possible distortions (see Methods). b.w.: body weight

well above canopy and over ponds. In this echolocating species, the BFA was surprisingly low occurring at 16.5 kHz in one and at 17.5 kHz in the other specimen. Below the BFA, thresholds increased rather steeply by 52 dB/octave down to 10 kHz. Further down there was a second BFA at 7.5–5 kHz. However, in the second specimen this second peak at 7.5 kHz was very shallow (not shown in Fig. 1). For frequencies higher than BFA thresholds rose rather steeply by 45 dB/octave up to 97 dB SPL at 70 kHz. This is the same upper frequency limit as in the audiogram of the non-echolocating *Cynopterus sphinx.*

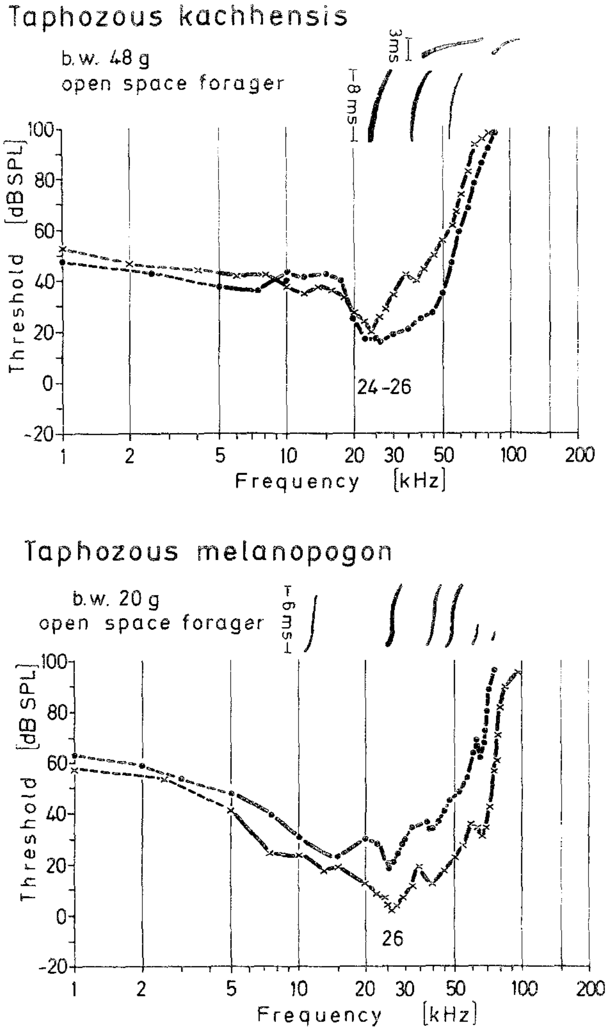

Fig. 2. Audiograms of *Taphozous kachhensis* and *T. melanopogon.* For *T. kachhensis*, sonagrams of both types of echolocation sounds emitted by this species, short FM-sweep and long multiharmonic sound, are shown. Other explanations see Fig. 1

The BFA of the audiogram coincided with the low frequency end of the hyperbolically downward frequency modulated echolocation sounds which comprise 1–2 higher harmonics up to 70 kHz. However, most energy is contained in the fundamental, especially in its shallow modulated low frequency tail.

Taphozous kachhensis, b.w. 48–54 g (Fig. 2)

This is the largest and the most sturdy species among the commonly occurring echolocating bat species in Madurai. It is as fast a flier as *Tadarida* foraging at high speed (10–15 m/s) preferably at 17–30 m above ground in unobstructed areas.

The audiogram of *T. kachhensis* was quite similar to that of *Tadarida* with a slightly higher BFA (24–26 kHz in one and 22.5–24 kHz in the other specimen). Thresholds at frequencies below 15 kHz were relatively low (40–55 dB SPL). The band of lowest thresholds ranged from 15 to 42 kHz. The upper frequency limit was 85 kHz.

The rather broad band of good sensitivity comprises the frequency band of maximal energy emitted in the echolocation sounds. *Taphozous kachhensis* produces either brief steeply modulated FM sweeps from 75–40 kHz or long weakly modulated frequency sweeps with 2 harmonics. The fundamental component sweeping from 30 to 20 kHz contains the most sound energy. Again, as in *Tadarida*, the long and intense low frequency end of the echolocation signal coincides precisely with the BFA.

Taphozous melanopogon, b.w. 20–24 g (Fig. 2)

This species also preferably hunts high above the canopy in open air and in free flight they emit a fairly constant frequency signal with several harmonics.

Audiograms of this very common species were similar to those of *Taphozous kachhensis* with a slightly higher BFA, i.e., at 26 and 28 kHz in the two specimens tested. These BFAs again closely match the frequency of maximal energy in the echolocation sounds emitted, which are 2–3 kHz higher than in *T. kachhensis.*

In one of the two specimens, peculiar and unpredictable sudden shifts of thresholds to highest sensitivities appeared during recording sessions. Frequently, these 'sensitivity bursts' were preceded by fast and high amplitude brain waves lasting for several minutes. We, for instance, measured the threshold for 26 kHz at 18 dB SPL but ten minutes later clear evoked potentials could be recorded at the lowest intensity level available (−13 dB SPL) for frequencies from 24.6 to 30 kHz. Another ten minutes later thresholds had shifted back to 5–0 dB SPL, however, after a brief burst of fast brain activity evoked potentials were again elicited by stimuli at −13 dB SPL. These inconsistently recurring periods of highest sensitivity were limited to stimuli at frequencies of 24–30 and 40–50 kHz. We do not understand the cause of this occasional and unpredictable outburst of extreme sensitivity, except that its appearance is associated with brief periods of fast and high amplitude brain-waves. Unfortunately, we also do not know the cause of these sudden brain activities.

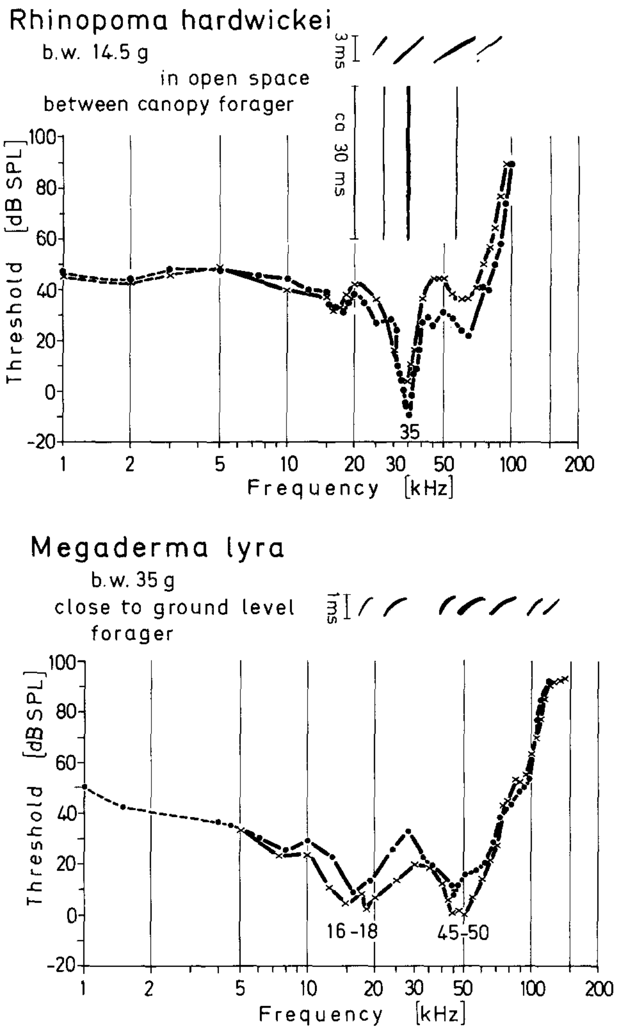

Fig. 3. Audiograms of *Rhinopoma hardwickei* and *Megaderma lyra*. For *Rh. hardwickei*, sonagrams of two types of echolocation sounds are shown above the audiogram. Note matching of the audiogram's BF at 35 kHz with the frequency of the most intense harmonic of constant frequency echolocation signal. Other explanations see Fig. 1

Rhinopoma hardwickei, b.w. 14–15 g (Fig. 3)

Rhinopoma hunts flying insects at medium heights of up to 10 m above ground and always keeps away from dense background. This species produces two entirely different echolocation signals: pure tones (CF-echolocation sounds) of up to 55 ms duration with 3 harmonics and a maximal energy at about 30–35.5 kHz when it is in free flight, and short frequency modulated multiharmonic pulses covering a total frequency range from 90 to 22 kHz when it is approaching a target (Habersetzer 1981). The audiogram discloses a specific adaptation of the auditory system to the frequency range of the CF-echolocation call.

In audiograms of both specimens a narrowly tuned and highly sensitive frequency band was found with a BFA of 35 and 32.6 kHz respectively. This narrowly tuned part of the audiogram is matched to the frequency of the CF-echolocation sound in *Rhinopoma* and thus resembles the 'filter' in the audiogram of horseshoe bats (Neuweiler 1970). In *Rhinopoma* sensitivity at the BFA was mostly below 0 dB SPL and in one recording session potentials could still be evoked with the lowest possible intensity (−13 dB SPL), for frequencies from 32.5 to about 38 kHz. Filterslope at the low frequency side rose steeply by about 130 dB/octave down to 30 kHz, and at the high frequency side by about 250 dB/octave up to 40 kHz. For still higher frequencies, the thresholds continued to increase steeply after a second minor BFA between 50 and 70 kHz. For lower frequencies, thresholds remained remarkably low: 40 dB SPL at 20 kHz and 50 dB SPL at 1 kHz.

Among those species emitting pure tones without FM-parts during free flight, i.e., *Taphozous, Pipistrellus* and *Rhinopoma*, only *Rhinopoma* features a narrowly tuned auditory filter matched to the CF-echolocation signal.

Pipistrellus mimus, b.w. ca. 3 g (Fig. 4)

Pipistrellus mimus forages at low flight speeds in the lower air space, commonly 3–5 m above ground, between trees and bushes, but also steers free from obstacles by a 1–2 m distance. In pursuit of prey it may come down to less than 1 m above ground. This is one of the smallest living mammals and the smallest species of bats in Madurai. Like *Rhinopoma*, it emits long pure tone signals during searching flights and brief hyperbolically downward frequency modulated pulses when approaching targets. Again the frequency of the CF-signal is identical with that of the lowest frequency of the FM-pulse, i.e. 50–55 kHz. However, the frequency of the CF-sound is variable from 48 to 60 kHz (Habersetzer 1983).

As in *Rhinopoma*, the BFA fell in the frequency range of the CF-signal or the low frequency end of the FM-pulses. In four independently recorded audiograms the BFA was invariably 50 kHz. However, the slopes of thresholds for higher and lower frequencies were less steep (83 dB/octave and 105 dB/octave respectively) than those in *Rhinopoma*. The range of frequencies with thresholds up to 20 dB above that of BFA, extended from 49 to 60 kHz, covering the range of frequencies emitted in the pure tone echolocation sounds. In three recordings, a minor peak of sensitivity appeared at 70 kHz, and a third one between 25 and 15 kHz.

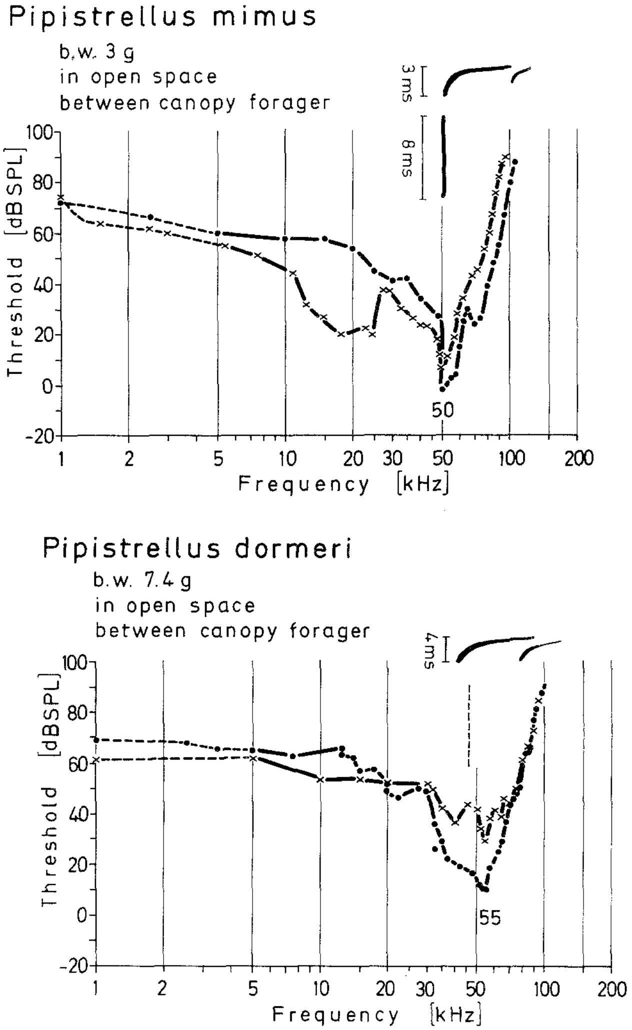

Fig. 4. Audiograms of *Pipistrellus mimus* and *Pipistrellus dormeri*. For *P. mimus*, sonagrams of both types of echolocation sounds, FM and CF, are shown. Note matching of the audiogram's BF at 50 kHz with frequency of the CF-echolocation sound. *P. dormeri*, broken vertical line: this species also emits a CF-signal, however, its frequency is not yet precisely known. Other explanations see Fig. 1

In *Pipistrellus mimus* we observed 'subthreshold' secondary areas of extreme sensitivity in the frequency range of 49 to 55 kHz. In this range the threshold was commonly reached at about 5–10 dB SPL. However, evoked potentials reappeared a few dB below 'threshold' and remained clearly detectable down to the lowest intensity of our stimulus set up at −13 dB SPL when we slowly decreased the stimulus intensity in 1 dB steps. For instance in a fully awake *Pipistrellus mimus* threshold at 51 kHz was 4 dB SPL and no evoked potentials were detectable for lower intensities. However, at −3 dB SPL the evoked potential recurred and could be clearly elicited down to −13 dB SPL. This phenomenon was also observed for stimulus frequencies of 50.0, 52.5, 53.0, 54.0 and 55.0 kHz but not for higher and lower frequencies. These subthreshold response areas are strikingly similar to the long-latency subthreshold collicular responses recorded by Grinnell and Brown (1978) for the constant frequency components emitted by *Pteronotus suapurensis*. However, no significant latency shifts of the responses were detectable in *Pipistrellus mimus*.

Pipistrellus dormeri, b.w. 7.5 g (Fig. 4)

From this species, complete audiograms were recorded from only one specimen. The audiograms were basically the same as in *Pipistrellus mimus*, but with a slight shift towards higher frequencies, and a broader range of maximal sensitivity covering a band from 35 to 65 kHz with BFA around 55 kHz. No 'subthreshold' responses could be recorded in this species as observed in *Pipistrellus mimus*.

From a recent field study, we know that *Pipistrellus dormeri* also emits pure tones (Vogler, personal commun.). Since these sound recordings have not yet been analyzed, we do not know the precise frequency, but it is in the range of 50–60 kHz. Flight patterns and hunting behaviour are much the same as in *Pipistrellus mimus*.

Hipposideros speoris, b.w. 6.5–7.0 g (Fig. 5)

H. speoris typically forages close to canopy, around bushes and trees and very close to obstacles. The bat sometimes picks up insects even from the ground (Habersetzer 1983). Hipposiderids are CF-FM bats, emitting a high frequency pure tone of 3–6 ms duration terminated by an FM-sweep. *H. speoris* emits CF-pulses of frequencies between 127 and 138 kHz with a downward terminal sweep going down to 110 kHz (Habersetzer 1983).

Schuller (1980) has already recorded audiograms in *H. speoris* and *H. bicolor*. Our results basically confirm his data. The audiogram of *H. speoris* contains three sensitivity peaks. The BFA of lowest threshold was at 20–30 kHz. A second, less distinct BFA was found at about 110 kHz with thresholds of 30 dB SPL corresponding to the lower frequency end in the FM-component of the echolocation signal. In recordings from the surface of the IC, there was occasionally a third minor BFA around the frequency range of the pure tone echo-component. However, thresholds usually were only a few dB lower than for adjacent frequencies.

Having observed the rather precise matching of the pure tone frequency emitted and the BFA of the other species, we were unconvinced from these results and searched for neural responses sensitive to the pure tone frequency in deeper layers of the IC. After several failing penetrations, we hit an area highly sensitive and narrowly tuned to the frequency of 137.5 kHz, about 1,200 µm deep in the caudo-medial part of the IC. In other recordings the BFA of this narrowly tuned sensitivity peak was 131.0 and 132.0 kHz. As in horseshoe bats (Schuller 1980; Neuweiler 1970), the slopes of this auditory filter matched to the pure tone echo frequency are extremely steep: 1200 dB/octave (or 8 dB/500 Hz) to the low frequency side and 1900 dB/octave (7 dB/500 Hz) to the high frequency side. From this result we conclude that *H. speoris* also has a specialized auditory filter matched to its pure tone echo-frequency as described in horseshoe bats (Schuller 1980). However, in *H. speoris*, neurons processing information

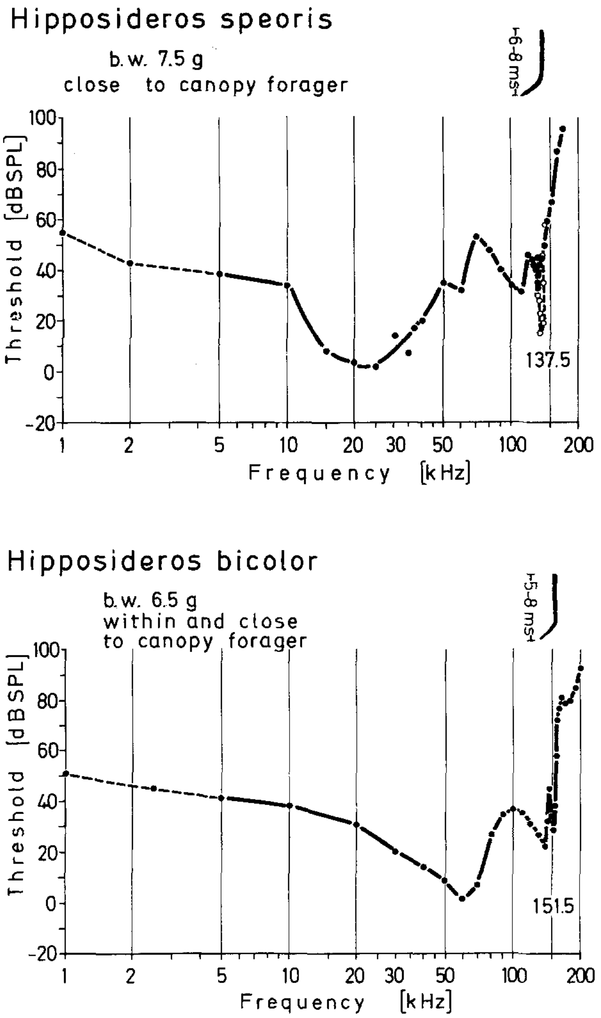

Fig. 5. Audiograms of *Hipposideros speoris* and *H. bicolor*. Open circles: separate recording in a deeper area of IC. Explanations see Fig. 1

in this narrow CF-frequency band are restricted to a more confined and smaller area in the ventral part of the IC, than in horseshoe bats.

Hipposideros bicolor, b.w. 6.5 g (Fig. 5)

The foraging behaviour of *H. bicolor* is similar to that of *H. speoris* except that *H. bicolor* also forages within the canopy (Habersetzer 1983).

Audiograms in this smaller of the two *Hipposideros* species are basically the same as in *H. speoris* but shifted to higher frequencies. A BF-band ranged from about 30–60 kHz, a second though less sensitive region of low threshold again coincided with the low frequency end of the FM-echo component, i.e. with 130–140 kHz. Finally, a narrowly tuned filter matched to the pure tone echo frequency of 147 to 159 kHz could be recorded only from deep layers of the caudal part of IC. In the audiogram shown in Fig. 5, this frequency was 151.5 kHz. Again as in *H. speoris*, the cluster of neurons processing CF-frequencies appears to be located in a rather restricted and deeply buried part of the IC.

Megaderma lyra, b.w. 31–35 g (Fig. 3)

Megaderma is a carnivorous species scanning the ground and water surfaces for small vertebrates and large insects. They always forage close to the surface, about 0.5–1.0 m above ground. Their echolocation signal consists of multi-harmonic pulses of not more than 1 ms duration covering a frequency band from 130 to 17 kHz. *Megaderma* may also detect and localize prey by listening to noises produced by the target (Fiedler 1979).

Among all the 10 species studied *Megaderma* had audiograms with the broadest frequency range of low thresholds. Thresholds for frequencies from 11 to 65 kHz were below 20 dB SPL with a minor peak of higher thresholds at 30 kHz. Thresholds rose only slowly for frequencies below 16 kHz. From 50 kHz to higher frequencies, thresholds increased more steeply by about 65 dB/octave. Maximal threshold is reached only at 120 to 140 kHz.

Remarkably, evoked potential amplitudes in *Megaderma* diminished only slightly with decreasing sound intensity and at threshold suddenly disappeared within 1 or 2 dB attenuation. Thus thresholds are very clear cut and precisely defined in *Megaderma lyra*.

Discussion

This comparative study on audition is unique in that we employed bat species from a single community around the campus of Madurai University. This area is diversified and comprises cultivated land, paddy fields, numerous ponds, a river, open grassland, scrub jungles and orchards. This biotope offers sumptuous resources for insectivorous, carnivorous and frugivorous bats. From the detailed observations of Habersetzer (1983), we know that the various food resources are divided into preferred foraging biotopes for the different bat species. An inspection of the species' audiograms discloses an interesting correlation between foraging areas and hearing capacity (Fig. 6).

For both *Taphozous* species and *Tadarida aegyptiaca* which preferably hunt with high speed (10 to 15 m/s) at high altitudes (7–30 m above ground), well above canopy, the BFAs in their audiograms are ranging from 17 to 26 kHz. For *Rhinopoma hardwickei* which forages at medium height (up to 10 m above ground) the BFA is somewhat higher (32–38 kHz).

For other species which preferably search for flying insects at lower levels and around bushes, BFAs are even higher. BFAs in *Pipistrellus* species are between 50 and 55 kHz. The BFAs of *Hipposideros speoris* and *H. bicolor* are 135 and 152, respectively and the former flies close to the foliage around bushes and trees, and even picks up insects from the ground, the latter even forages between twigs and inside the canopy.

Thus there appears to be a trend in that species which forage in the higher and less obstructed area (and hence the larger the distance from which echoes can be detected) have lower best frequencies than those which forage in lower altitudes (and hence the shorter the distance from which targets are detected; Fig. 6).

This trend applies to those species hunting for flying insects and not to *Megaderma lyra* which flies low over ground and water surfaces in search of small vertebrates. Its auditory system is broadly tuned not only to high frequencies up to 100 kHz but also to low frequencies in the audible range. This species not only detects prey by its pulse-like, broad-band echoes but also by listening to the rustling noises of potential prey (Fiedler 1979).

Sensitivity of the ear to lower frequencies in high flying, long distance echolocators and to high frequencies in bats echolocating at close range, may be interpreted as an adaptation to maintain acute sense of hearing since there is frequency dependence of sound absorption in air. For instance, a 30 kHz echo is attenuated by 70 dB when returning from a distance of 20 m whereas a 120 kHz echo returns with the same attenuation from a target as near as 6 m (Lawrence and Simmons 1982). Thus it may be highly adaptive for *Tadarida, Taphozous kachhensis* and *Taphozous melanopogon* to

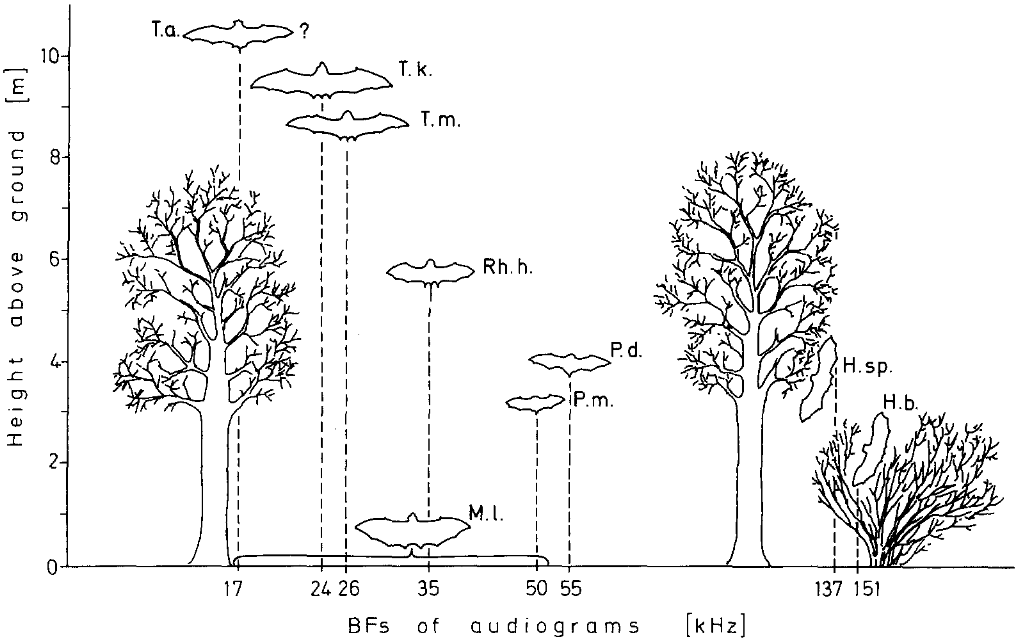

Fig. 6. Relationship of the best frequency of species specific audiogram and preferred foraging area (ordinate) for echolocating bats of Madurai. Hipposiderids (*H.sp., H.b.*) forage close to or within foliage. H.b.: *Hipposideros bicolor;* H.sp.: *Hipposideros speoris;* M.l.: *Megaderma lyra;* P.d.: *Pipistrellus dormeri;* P.m.: *Pipistrellus mimus;* Rh.h.: *Rhinopoma hardwickei;* T.a.: *Tadarida aegyptiaca*; T.k.: *Taphozous kachhensis;* T.m.: *Taphozous melanopogon.* ?: indicates that the preferred foraging area of T.a. is not precisely known

emit 17, 24 and 26 kHz signals respectively for long range echolocation high up in the air where higher frequencies are not needed for target resolution as in the more clutter environments.

In many species, the BFAs conspicuously matched the lower frequency end of the FM-signal emitted in echolocation. One may ask if this correlation to the low frequency end of echolocation sounds is real or is due to the way of recording. Evoked potentials are conventionally recorded by a silver ball electrode placed on the surface of the IC (Grinnell and Hagiwara 1972a, b). Thresholds measured in this way reflect both the overall frequency sensitivity of the ear and the number of neurons in IC synchronously activated by the stimulus frequency. Thus thresholds measured by surface electrodes indicate the relative importance of different frequency bands for the species studied. However, IC in mammals are tonotopically organized, with lower frequencies represented dorsally and higher frequencies ventrally. Sensitivity to lower frequencies may be overrated relative to that to higher frequencies due to the proximity of the surface electrode to neurons tuned to low frequencies. This assumption seems to be supported by the fact that in *Hipposideros speoris* and *H. bicolor* high frequency filters matched to the emitted CF-frequency could be detected only by electrodes placed into the ventral part of IC. On the other hand, in *Rhinopoma, Pipistrellus mimus, P. dormeri* and *Megaderma lyra* the audiograms have BFs at 35, 50, 55 and 45–50 kHz respectively. These frequency bands are not represented at the surface of the colliculus and yet the specific sensitivity to these frequencies clearly shows up in the audiograms. Moreover, in horseshoe bats (Long and Schnitzler 1975) and in *Megaderma lyra* (Türke, in preparation) the behavioral audiograms and the audiograms obtained by collicular surface electrodes have the same shape as well as identical BFAs. In fact, in all audiograms, recorded in various specimens and from various positions of the electrode on the collicular surface, the frequency of minimal threshold was the most invariable component of the audiogram. All these facts suggest to us that the correlation between the minimal auditory threshold and the lowest frequencies emitted in FM-echolocation sounds is real. However, one has to admit, that small and narrowly tuned frequency areas of special sensitivity situated in the ventral most parts of IC may be not detected by the surface recording method.

The above correlation seems to be a consequence of the fact that the best frequencies of audiograms closely match the peak spectral energies in the echolocation calls. When approaching a target, *Tadarida, Taphozous, Pipistrellus* and *Rhinopoma* emit brief frequency modulated echolocation signals which often are hyperbolically modulated and terminate in a constant frequency tail. The peak energy of the echolocation pulses is contained in the low frequency end of the sound. During the searching phase of the flight, the 'open space foragers' (*Taphozous, Pipistrellus* and *Rhinopoma*) emit loud and long-lasting pure tones without any frequency modulated components (Habersetzer 1983). The frequency of the pure tone is again identical with the low frequency end of the FM-pulses. Therefore it is highly advantageous for the auditory system to be most sensitive to the low frequency end of the emitted echolocation sounds which is also identical to that of the pure tones emitted by each species. This is precisely what we have observed in the audiograms of the species emitting FM- and CF-sounds. In hipposiderids where most sound energy is contained in the rather invariable CF-part of the sound, best auditory frequency matches this frequency (135 and 152 kHz) which is situated at the high frequency margin of the spectrum emitted.

In summarizing the results and the arguments presented above, we propose the following hypothesis: the best frequency in echolocating bats is generally narrowly matched to the frequency of the emitted echolocation sounds containing the most energy. In open space foragers which have to detect prey at long distances, the maximal sensitivity is shifted towards lower frequencies, e.g. *Tadarida* 17.5 kHz, *Taphozous kachhensis* 24 kHz and *T. melanopogon* 26 kHz. As the space to be probed by echolocation becomes more restricted, sensitivity and echolocation signals gradually shift to higher frequencies, e.g. *Rhinopoma hardwickei* to 35 kHz, *Pipistrellus mimus* to 50 kHz and *P. dormeri* to 55 kHz. These species are foraging in open space at and below tree level. Bats hunting within and close to foliage and obstacles may possess ears matched to very high frequencies (*Hipposideros speoris* 135 kHz and *H. bicolor* 152 kHz).

Remarkably, in all the bat species, thresholds at 1–5 kHz were at medium level between 40 and 70 dB SPL. Even in *Hipposideros bicolor* with the highest best frequency at 152 kHz and an upper hearing limit of 200 kHz, thresholds for frequencies from 10 to 1 kHz increase by only 13 dB reaching 50 dB SPL at 1 kHz. From behavioral observations (Habersetzer 1983) it is obvious that echolocating bats may listen to sounds produced by prey and are attracted to such sound sources. Precise sound localization without echolocation has been experimentally shown in *Megaderma lyra* (Fiedler 1979). For this species which forages close to surface, auditory sensitivity is broadly tuned to both high and low frequencies. Behavioral studies (Türke, in preparation) as well as our collicular measurements show that *Megaderma* hears up to 140 kHz and, on the other hand, also easily detects 1 kHz signals.

This comparative study clearly demonstrates that audition in bats is not shifted to ultrasonic frequencies at the expense of low frequency hearing. On the contrary, the auditory range is extended to high frequencies only in those echolocating bats which emit high frequencies. For instance, the audiograms of the echolocating *Tadarida aegyptiaca* and the non-echolocating fruit-eating bat *Cynopterus sphinx* are hard to tell apart. Both reach the upper frequency limit of hearing at 70 kHz and both are maximally sensitive to frequencies between 12 and 20 kHz. This again indicates that the capacity to hear high frequencies is not a prerequisite for echolocation (Grinnell and Hagiwara 1972b). Specific adaptations of audition to echolocation have to be looked for in temporal processing of echo signals.

One of the surprising findings in our study was the rather narrowly tuned auditory filter at 35 kHz which corresponds to the frequency of the most intense harmonic in the long CF-signal emitted during search flights of *Rhinopoma hardwickei*. The slopes for both the lower and the higher frequencies around this region are much steeper than for other frequency bands, thus the frequency region of the CF-sound is clearly differentiated in the audiogram. In other bat species emitting pure tones without FM-components (*Pipistrellus* and *Taphozous*), no such narrow filtering of the CF-frequency is detectable with the exception of perhaps *Pipistrellus mimus*. In the latter species, sensitivity to the CF-frequency of ca. 50 kHz is also narrowly tuned but the slopes of thresholds are less steep and more continuous for higher and lower frequencies than in *Rhinopoma*. The question then arises if the narrowly tuned sensitivity to the emitted pure tone frequency in *Rhinopoma* is similar to the specialized filter in *Rhinolophus* which allows the latter to detect fluttering prey (Neuweiler et al. 1980). However, the basilar membrane in *Rhinopoma hardwickei* does not show morphological specializations which are associated with the CF-filter in horseshoe bats (Bruns, personal communication). Habersetzer (1983) found no evidence for Doppler-compensation in *Rhinopoma*, an important feature of the specialization for movement detection, by echolocation, in horseshoe bats. Nevertheless a narrow tuning of the auditory system to the CF-frequency in *Rhinopoma* may imply sensitivity of the auditory system for movement detection though in a less refined way as in horseshoe bats. Single unit studies are required to show if the '35 kHz-filter' in the audiogram is based on an overrepresentation of neurons in IC narrowly tuned to this echo-frequency.

Emission of CF pulses during searching flight in open spaces has been interpreted as an adaptation to long range echolocation (Miller and Degn 1981). Sound energy emitted is channeled into one frequency band and increases the detectability of long range echoes. This interpretation is supported by the fact that pure tone frequencies correspond to the low frequency end of the sounds emitted which minimizes sound absorption in air and that the minimal thresholds in audiograms occur at the same frequencies.

But why then is the audiogram sharply tuned to the pure tone frequency only in *Rhinopoma* and not in the other species as well (e.g. *Pipistrellus* and *Taphozous* species)? Perhaps these gradual differences in auditory adaptation reflect an evolutionary trend. One might speculate that from pure tone echolocation for detecting prey at long range, sensitivity for movement detection has evolved. Wing beats of flying insects are inevitably encoded onto pure tone echoes as frequency and amplitude modulations, due to the rhythmical change of speed and wing position relative to the impinging echolocation sound. These rather shallow modulations caused by wing beats of the prey may be detected by the auditory system as more sensitive and narrowly tuned to the pure tone echo frequency it is. The chance to specifically detect fluttering prey by pure tones may have induced an evolutionary trend to a narrow tuning to the pure tone frequency emitted in those bats which emit CF signals. *Rhinopoma* could then be regarded as an intermediary form on the way from long-range echolocation to specialization for fluttering prey detection as we find it in horseshoe bats.

This speculation on evolution becomes more attractive if one includes hipposiderids into consideration. *Hipposideros speoris* and *H. bicolor* both have auditory filters narrowly tuned to the frequency of the CF-part of their specific echolocation signals. Like horseshoe bats they have conspicuous morphological specializations in the basal part of the inner ear where high frequencies are analyzed (Bruns, personal communication). They also emit CF-FM-signals but of shorter duration than in horseshoe bats. Both hipposiderids may compensate for Doppler shifts of the complete echo signal induced by their own flight speed, but they do this far less consistently than the horseshoe bats (Habersetzer 1983). Both hipposiderids forage flying insects close to or within foliage. Thus hipposiderids might feature an echolocation system specialized for movement detection good enough to detect wing beating insects in cluttering echoes. However, the system of the hipposiderids is not yet as specialized as that of the horseshoe bats. The assumption that auditory specialization matched to the CF-echofrequency is not as detailed in hipposiderids as in horseshoe bats is supported by the fact, that in both hipposiderids the specific filter could be discovered only by placing the electrodes into the ventral part of IC. This suggests that only a small part of IC is analyzing CF-signals whereas in horseshoe bats a tremendous majority of IC-neurons is tuned to the CF-frequency (Neuweiler et al. 1980). Narrow auditory filtering tuned to the pure tone frequency allows selective detection of wing beating insects even in a dense clutter of echoes reflected, for instance, from foliage. By this specialization in echolocation, horseshoe bats and hipposiderids might have tapped a new resource for food, i.e. insects flying close to or within foliage.

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