

## Hearing Characteristics and Doppler Shift Compensation in South Indian CF-FM Bats

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**Summary.** 1. Echolocation pulses, Doppler shift compensation behaviour under laboratory conditions and frequency response characteristics of hearing were recorded in *Rhinolophus rouxi*, *Hipposideros speoris* and *Hipposideros bicolor*.

2. The frequencies of the constant frequency portions of the CF-FM pulses lie at about 82.8 kHz for *R. rouxi* from Mahabaleshwar, at 85.2 kHz for *R. rouxi* from Mysore. Hipposiderid bats have considerably higher frequencies at 135 kHz in *H. speoris* and 154.5 kHz in *H. bicolor*. The mean sound durations were 50 ms, 6.4 ms and 4.7 ms, respectively.

3. *R. rouxi* compensates for Doppler shifts in a range up to typically 4 kHz of positive Doppler shifts (Fig. 2). The Doppler shift compensation behaviour is almost identical to that of *R. ferrumequinum*.

4. *H. speoris* and *H. bicolor* do not compensate for Doppler shifts under laboratory conditions. Doppler shifts in the echoes induce emission frequency changes which are not correlated to the presented Doppler shifts (Fig. 3).

5. The frequency response characteristics of hearing of *R. rouxi* show characteristic sensitivity changes near the bat's reference frequency as also found in *R. ferrumequinum*. The threshold differences between the low threshold at the reference frequency and a few hundred Hz below are 40 to 50 dB in awake bats (Fig. 5).

6. Frequency sensitivity changes near the emitted CF-frequency of the bats are less pronounced in *H. speoris* or almost absent in *H. bicolor*.

### Introduction

Several species of bats that do not belong to the same taxonomical group (rhinolophids, hipposiderids and the neotropical mormoopids) use echolocation signals composed of a relatively long-lasting constant frequency portion (CF) terminated by a short final frequency modulated sweep (FM) to lower frequencies. Several special adaptations of the hearing system to the distinct pulse design, to the echolocation sound and to the behavioural strategies have been demonstrated in *Rhinolophus ferrumequinum* (Neuweiler, 1970; Schnitzler et al., 1976), *Pteronotus p. parnellii* (Suga, 1978) and hipposiderid bats (Grinnell and Hagiwara, 1972). One of the most striking adaptive features in *Rhinolophus ferrumequinum* and *Pteronotus p. parnellii* is the enhanced frequency sensitivity of hearing in the frequency range coinciding with the frequencies of the CF-portion of the emitted echolocation pulse and poor frequency sensitivity at adjacent lower frequencies (Neuweiler, 1970; Pollak et al., 1972). The other interesting behavioural adaptation in these bat species is the Doppler shift compensation leading to the decrease of the emitted frequency if a positive frequency shift occurs in the echo due to the relative movement between the bat and the reflector (Schnitzler, 1968; Schuller et al., 1974; Simmons, 1974).

Whereas the frequency pattern (CF-FM) of the echolocation signal is roughly the same in the three bat families, the pulses considerably differ in frequency and duration. The duration of the sound as well as the frequency may be important factors for the Doppler shift compensation behaviour, as sampling time and absolute frequency value affect the obtainable accuracy and extent of the compensation. A short stay in the laboratory of the Indo-German Project of Animal Behaviour at the University of Ma-

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*Abbreviations:* CF, constant frequency; FM, frequency modulated

durai, South India, offered the opportunity to investigate the echolocation signals, the Doppler shift compensation behaviour and the hearing capacities of the Indian *Rhinolophus rouxi* and two hipposiderid bat species, *Hipposideros speoris* and *Hipposideros bicolor*.

The results obtained on the sound structure, Doppler shift compensation and the frequency response characteristics of hearing are presented in the following report.

## Methods

The hipposiderid bats (*H. speoris* and *H. bicolor*) were caught in the Kila Kuyil Kudi rocks near Madurai University, the *R. rouxi* came from caves near Mahabaleshwar (about 200 miles south of Bombay) or roosting sites near Mysore.

The echolocation pulses were recorded from the hand-held bat about 30 cm in front of a quarter inch Bruel & Kjaer microphone (type 4135), amplified and stored on a Lennartz analog tape recorder. A double heterodyning technique was used to test the Doppler shift compensation behaviour. This technique has been extensively described in Schuller et al. (1974) and was modified only in selecting the mixing frequency and filter settings appropriate to the higher emitted CF-frequencies of the different bat species. Frequency distributions of the CF-frequencies in individual bats were obtained with a Nicolet 1070 laboratory computer (with plug-in SH 71) used in its frequency distribution mode: the zero-crossings of the bat's echolocation signals were transformed in standard pulses that were counted during count gate times of 2 ms and 10 ms depending on the duration of the echolocation pulses and classified by frequencies. The count times mentioned above determine the frequency resolution to 500 Hz and 100 Hz respectively. As the count time intervals were not synchronized to the pulse emission, those at the beginning and the end of the pulses indicate lower frequencies than actually present in the echolocation pulse. Consequently the lower frequency part of the frequency distribution histograms will be slightly broadened which is insignificant for the evaluation of the Doppler shift compensation behaviour for which the maximum in the frequency distribution histogram is used.

Preparations of the animals for neurophysiological recordings were made with the conventional techniques as described earlier (Schuller, 1979). Gross silver or tungsten electrodes were used for recording the evoked potentials from surface and deeper layers of the inferior colliculus. The evoked potentials were averaged 32 times to determine the hearing thresholds with the Nicolet laboratory computer (Type 1070, plug-in SD-72/2A).

Anaesthetics (ether, Novocain) were only used during the surgical preparation of the animals but not during the recording sessions so that the recordings were made in the awake animal. During recording the wound margins were treated with local anaesthetics.

The acoustical stimuli consisted of tone bursts with a duration corresponding to the average duration of the echolocation pulses of the bats and had rise-decay times of 1 ms. The tone bursts were delivered under free field conditions to the contralateral ear of the bat. The distance between bat and loudspeaker was 34 cm. The frequency response of the loudspeaker varied by  $\pm 5$  dB in a frequency range from 30 to 150 kHz and the thresholds were corrected accordingly.

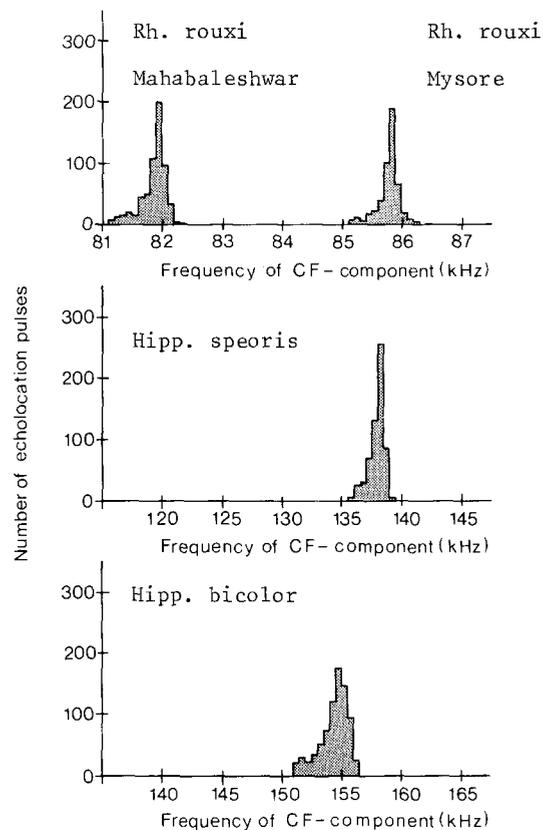
The species were identified following the key given by Brosset in his work on bats of central and western India (1962, 1963).

## Results

### A. Echolocation Pulse Characteristics

The typical echolocation pulses of the three species *R. rouxi*, *H. speoris* and *H. bicolor* consist of a constant frequency portion (CF) with a short final frequency modulated sweep (FM). Frequencies of the CF-portions and duration of the signal are different in the three species.

*R. rouxi* (specimens from Mahabaleshwar) emit a mean interindividual frequency of 82.8 kHz (SD: 1.3; 6 animals) in the CF-portion and the echolocation pulses have a mean duration of 50 ms in resting animals. Bats from the same species, but from a site near Mysore (1,000 km away from Mahabaleshwar) had a higher interindividual mean CF-frequency at 85.2 kHz (SD: 1.0; 6 animals). The difference of the mean emitted CF-frequency in the two groups of bats



**Fig. 1.** Emission frequency in the constant frequency component (CF) of the bats *Rhinolophus rouxi* (upper), *Hipposideros speoris* (middle) and *Hipposideros bicolor* (lower). The histograms show the distribution of frequencies in the CF-portion for individual bats. Two different representative examples of CF-frequency distributions of *Rh. rouxi* from Mahabaleshwar (left) and Mysore (right) are represented in the upper graph

is 2.4 kHz. No difference in echolocation pulse duration could be detected in the two different groups of *R. rouxi*. The CF-frequency produced by the roosting bat is kept with high accuracy at the so called resting frequency. Examples of frequency distributions for two individual bats, one from Mysore and one from Mahabaleshwar, are shown in Fig. 1. The standard deviations in the individual bats ranged typically from 130 Hz to 230 Hz, corresponding to an average frequency accuracy of 0.2%.

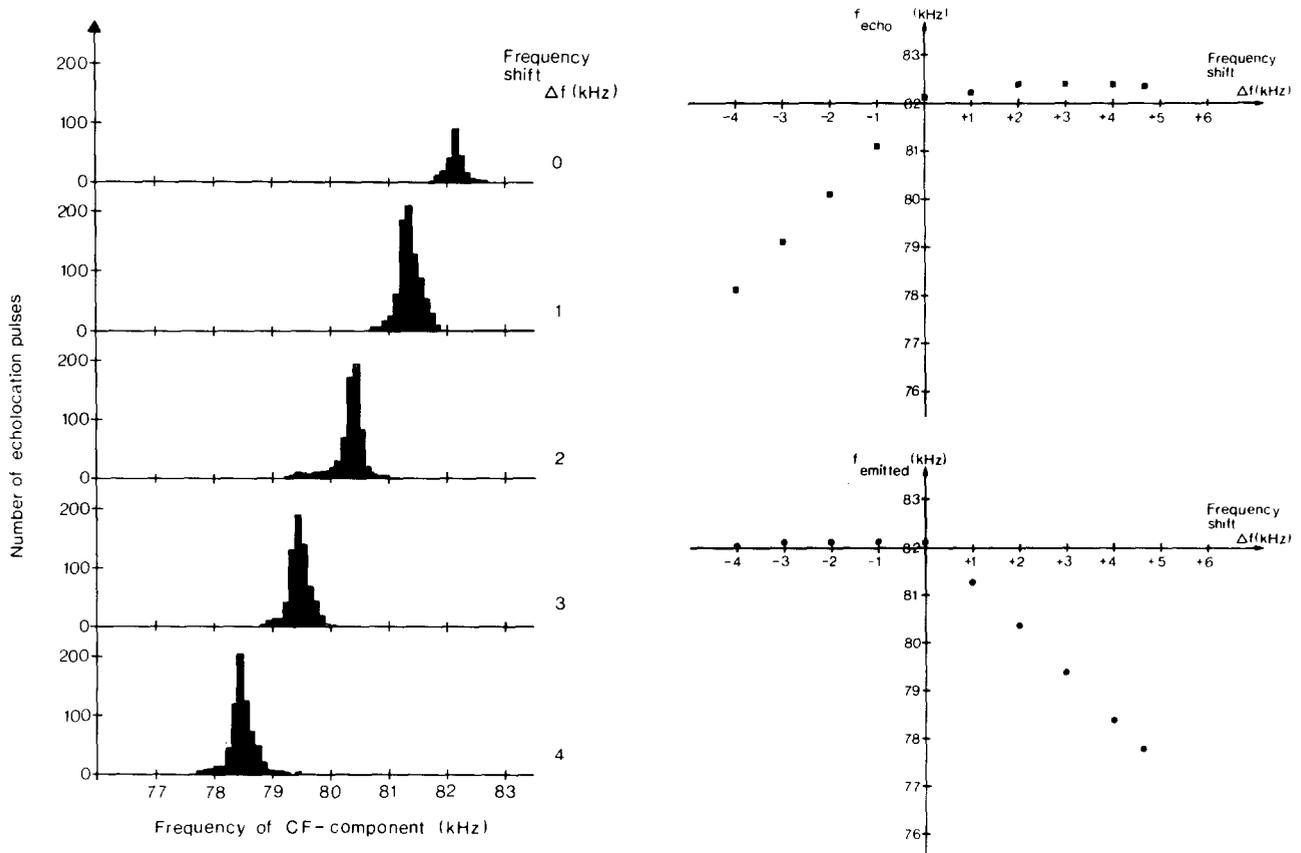
The echolocation pulse of *Hipposideros speoris* and *Hipposideros bicolor* were shorter than those of *R. rouxi* and much higher in frequency. Most sound energy was emitted by *H. speoris* at a frequency of 135 kHz (SD: 2.1; 10 animals) and the CF-portion lasted between 6 and 7 ms. *H. bicolor* maintained its echolocation frequency in the CF-portion at 154.5 kHz (SD: 2.3; 10 animals) and the CF-portion had durations between about 4 and 5 ms. The frequency distributions in Fig. 1 show the accuracy with which the individual bats keep the emitted CF-frequency (*H. speoris*: SD: 660 Hz, *H. bicolor*:

SD: 1.17 kHz). The variations of the CF-frequencies are considerably higher for hipposiderid bats (0.5% and 0.75% respectively) than for *Rhinolophus* (0.2%).

*B. Doppler Shift Compensation Behaviour*

A bat flying at a certain speed towards the target receives echo frequencies that are shifted to higher frequencies due to the Doppler effect. Such echolocation situations can be electronically simulated by the playback of the emitted sounds that are electronically shifted to higher frequencies.

The Doppler shift simulation apparatus is the same as used for the investigations in *R. ferrumequinum* (Schuller et al., 1974). *R. rouxi* emitted its echolocation sounds spontaneously when sitting in front of the microphone-loudspeaker assembly. Its reaction to frequency shifted echoes is illustrated in Fig. 2, where the left graph shows the frequency distributions of the emitted CF-portions for different applied positive frequency shifts. The mean of each frequency distribution is depicted as a function of the Doppler



**Fig. 2.** Doppler shift compensation in *Rhinolophus rouxi* (Mahabaleshwar). Left: Distributions of emitted CF-frequencies for different frequency shifts from 0 to 4 kHz. Upper right: Echo frequencies heard by a bat exposed to Doppler shifts from -4 to +4 kHz. Lower right: Emitted CF-frequencies of the bat when hearing Doppler shifts from -4 to +4 kHz. The dots represent the mean value of the frequency distribution curves for the emitted CF-frequency of the echolocation sounds ( $N \geq 200$  sounds)

shifts played back to the bat in the lower right graph. It can be seen that the bat compensates for the Doppler shifts heard in the echoes by lowering the emitted frequency. The compensation does not reach complete cancellation of the frequency shifts, but is incomplete by a compensation shift offset of about 150–200 Hz. Consequently the echo frequency is slightly higher by this offset than the resting frequency. The frequencies actually heard by the bat after compensation are shown in the upper right graph of the figure. The average echo frequency after compensation has been called reference frequency (Schuller et al., 1974). Negative frequency shifts corresponding to increasing distance between bat and target are not responded to by any change in the emitted frequency of the CF-portion. The general characteristics of compensation for frequency shifts in *R. rouxi* are well described by the example in Fig. 2.

The frequency shift range within which proper compensation occurred varied between 3 and 4.5 kHz and compensation offset ranged from 100 to 300 Hz in the 9 animals tested.

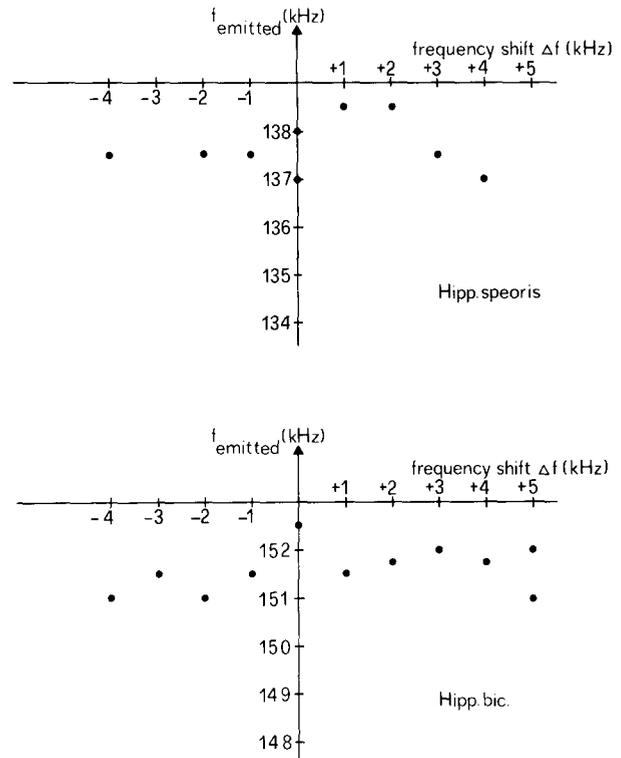
The Doppler shift compensation behaviour in *R. rouxi* can be considered as almost identical to that of *R. ferrumequinum* in all aspects so far investigated.

Six *H. speoris* and seven *H. bicolor* have been exposed to frequency shifted echoes. Most of the bats spontaneously emitted orientation pulses when sitting in the animal holder, others had to be stimulated to emit echolocation pulses by slightly touching their fur. None of the *H. speoris* showed clear compensation of the introduced Doppler shifts. They either did not react at all or emitted the orientation pulses with CF-frequencies different from the resting frequency but not tightly correlated to the Doppler shifts. In general the distributions of emitted frequencies broadened when the Doppler shifts were introduced in the echoes. Figure 3 shows the reaction of one *H. speoris* to Doppler shifts (upper graph).

The same was found in *H. bicolor*, when hearing Doppler shifted echoes. The bat again did not respond in a correlated way to the frequency shifts introduced in the echoes (lower graph in Fig. 3). However, both species showed larger variations of the emitted frequencies when exposed to Doppler shifts in the echoes compared to the variations of the resting frequency.

One bat was caught that corresponded in its taxonomical characteristics to the *H. bicolor* but differed in the colour of its fur, which was yellowish-orange in contrast to the grey fur of the other bats from this species. Brosset in his work on Indian bats (1962) describes different subspecies of *H. bicolor*, but it could not be determined whether the bat with the different fur colour belonged to another subspecies.

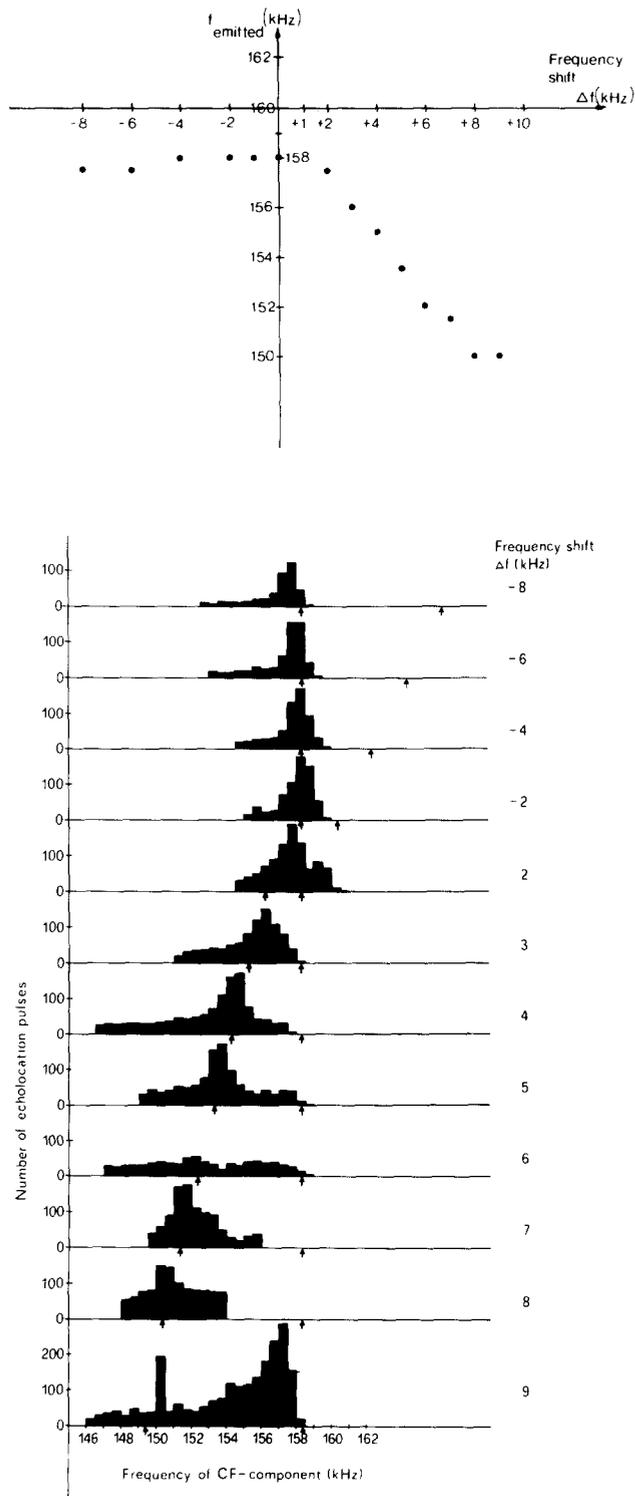
From observations during the captivity of the bat



**Fig. 3.** Doppler shift compensation in *Hipposideros speoris* and *Hipposideros bicolor*. Emitted CF-frequencies of *H. speoris* (upper) and *H. bicolor* (lower) in response to frequency shifts between  $-4$  kHz and  $+5$  kHz. The dots represent the mean value of the frequency distribution curves for the emitted CF-frequency of the echolocation sounds ( $N \geq 200$  sounds)

it was found to be in general more active and more skilled in catching wing beating moths than the grey variety of bats. The frequency of the CF-portion of this bat was 158 kHz, i.e., slightly higher than the means frequency of the *H. bicolor* (154.5 kHz).

When the bat was tested in the Doppler shift playback apparatus it spontaneously emitted echolocation pulses and compensated frequency shifts up to 8 kHz. In Fig. 4 the Doppler shift compensation response of this bat is shown. The response is not as consistent as in *R. rouxi* and the accuracy of maintaining the lowered frequency at the compensated level is much reduced and consequently the frequency distribution broader. As the bat emits about double the frequency of that of *R. rouxi* the frequency shifts that this hipposiderid bat receives at a given flight speed are also twice as high as that in rhinolophid bats. Assuming that both species cover the same flight speed range, the range for Doppler shift compensation should be two times larger in the hipposiderid as compared to that of the rhinolophid bat. The result strikingly confirms this prediction: the Doppler shift compensation system of the hipposiderid bat covered frequency shifts up to 8–9 kHz. Unfortunately no further speci-



**Fig. 4.** Doppler Shift compensation of one *Hipposideros bicolor* (yellowish-orange fur). Left: Distribution of emitted CF-frequencies in response to Doppler shifts from  $-8$  to  $+9$  kHz. Right: Emitted CF-frequencies of the bat when compensating for Doppler shifts between  $-8$  and  $+9$  kHz

mens of the orange fur type were available, so that these results have to be considered as preliminary.

### C. Frequency Response Characteristics of Hearing as Determined with Evoked Potentials in the Inferior Colliculus

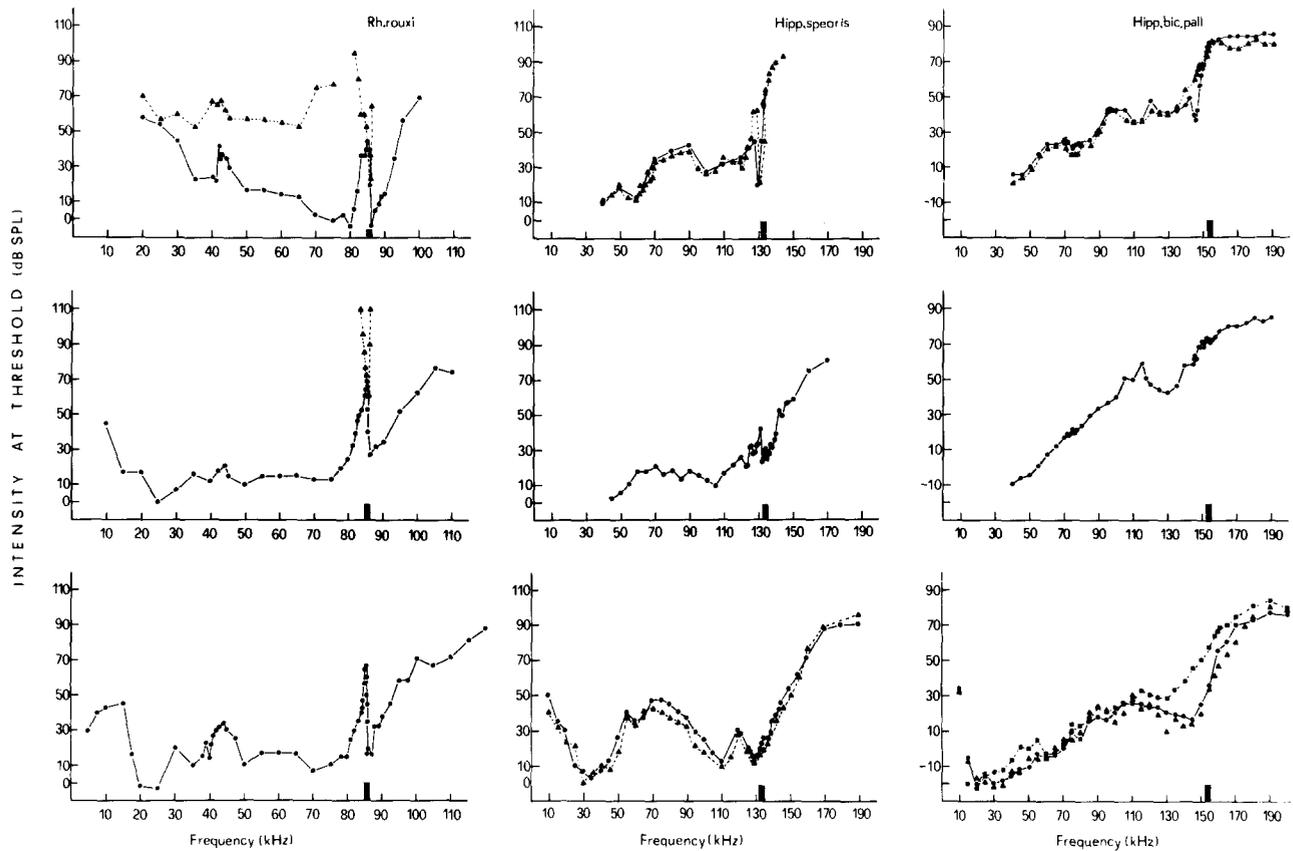
The frequency response characteristics of hearing of *R. rouxi*, *H. speoris* and *H. bicolor* were determined using evoked potential recordings from the surface or from the center of the inferior colliculus. Threshold curves for evoked potential on-responses and off-responses from individual bats are represented in Fig. 5. The on-response threshold curves for *R. rouxi* (Fig. 5, left vertical row) had the characteristic low threshold range at the reference frequency with a steep increase of thresholds to lower frequencies (typically 50 dB/100 Hz) and a less abrupt increase in threshold on the high frequency side of the reference frequency (typically 5 dB/100 Hz). The threshold curve reaches a maximum at a frequency that is between 0.5 to 1.5 kHz lower than the reference frequency and drops back to a threshold level comparable to that at the reference frequency at about 5 kHz below the reference frequency. The difference between the maximum threshold and the threshold at the reference frequency ranges between 40 and 50 dB in awake bats. In *R. rouxi* off-responses were also obtained with stimuli having rise-decay times of 1 ms. The off-response threshold curves had their minimum some hundred Hertz below the reference frequency and coincided with the resting frequency of the bat. The off-response threshold minimum is extremely narrow as can be seen from the graph (Fig. 5, left vertical row, triangles).

Near 42–43 kHz, i.e. half of the reference frequency of the bat, is another maximum of the hearing threshold which is much broader in frequency and less pronounced compared to the neighboring thresholds (threshold differences about 20 dB).

The frequency response characteristics of hearing of *R. rouxi* correspond in all details and fine structural elements to that of the European *R. ferrumequinum*.

*H. speoris* (Fig. 5, middle row) showed much less characteristic threshold differences near its resting frequency. The largest threshold difference found between the minimal and maximal threshold over a narrow frequency band around the resting frequency was at the most 20 dB compared to 50 dB in *R. rouxi*. The narrow range of low threshold separating the CF-hearing area from the rest of the audiogram is far less pronounced in hipposiderids.

Furthermore the minimum threshold in the audiogram did not coincide with the resting frequency but



**Fig. 5.** Frequency response characteristics of hearing of three CF-FM bat species. On-response threshold curves for *Rhinolophus rouxi* (left row), *Hipposideros speoris* (middle row) and *Hipposideros bicolor* (right row). Bars on the abscissa: resting frequencies of the bats. Triangles in the first row: off-response threshold curves. Different symbols in the second and third row: threshold curves from different depths in the inferior colliculus

was always about 5 kHz below (Fig. 5). The threshold curves of *H. bicolor* (Fig. 5, right vertical row) are even less structured and show a shallow low of thresholds for frequencies 20 to 30 kHz below the resting frequency. In our sample of *H. bicolor* no threshold curve exhibited a narrowly tuned area around the resting frequency of the bat.

In *H. speoris* and *H. bicolor* no off-responses were obtained with stimulus rise-decay times of 1 ms and intensity levels of up to 100 dB SPL.

Unfortunately we could not obtain any threshold curves from the *H. bicolor* with the orange fur that compensated for Doppler shifts as the animal died and no further specimen were available.

## Discussion

*Rhinolophus rouxi*, a species found in South India but having its distribution also in West and North India (Brosset, 1962, 1963), was found to possess an almost identical echolocation system to that of the European

*Rhinolophus ferrumequinum*. The structure of the echolocation signal, consisting of a long CF-portion with a final frequency modulated component, corresponds in duration and frequency to that of *Rhinolophus ferrumequinum*. There may be slight differences in the frequency of the CF-portion within a range of a few kHz, which is even found among individuals of each species.

Both species are very vocal and spontaneously emit echolocation pulses when sitting in small but comfortable animal holders. In *R. rouxi* playback of Doppler shifted echoes to the bat induces Doppler shift compensation with the same characteristic range of about 4 kHz, the same accuracy in the frequency distributions and the same compensation offsets as found for *R. ferrumequinum* (Schuller et al., 1974). In this respect no differences in Doppler shift compensation behaviour as tested in the laboratory could be found in the two different species.

Determining the hearing characteristics of *R. rouxi* yielded curves that strikingly resemble those of *R. ferrumequinum* (Neuweiler, 1970). The threshold

curves exhibit the characteristic low thresholds at the reference frequency with the extremely sharp slope of threshold increase within a few hundred Hz below and above the reference frequency (50 dB/100 Hz and 5 dB/100 Hz respectively). The acoustical filter effect near the reference frequency is therefore a consequence of the steep increase of thresholds at both sides of the threshold minimum near 83 kHz.

The threshold curves correspond in all details to those of *R. ferrumequinum* if the position of resting and reference frequency in relation to the hearing threshold curve is considered. The reference frequency always coincides with the minimum of the threshold curve, whereas the resting frequency (100 to 300 Hz lower than the reference frequency) falls into the steep slope of rising threshold curve and in the minimum of the threshold curve for the off-responses. The species *R. rouxi* can be considered as having an echolocation system that is identical in its properties of echolocation signal, Doppler shift compensation and frequency response characteristics of hearing to that of *R. ferrumequinum*.

One interesting difference between the two groups of *R. rouxi* caught at different locations (Mahabaleshwar and Mysore) seems to be noteworthy. The resting frequencies of the two bat groups were significantly different by 2.4 kHz which is quite large compared with the individual variation of resting frequency. All audiograms in this paper were measured in bats from Mysore and had their threshold minimum around 85.2 kHz. It can be expected that bats from Mahabaleshwar would have the threshold minimum at about 82.8 kHz. The second group of species of CF-FM bats investigated in this study, *H. speoris* and *H. bicolor* use a much shorter echolocation pulse at considerably higher frequencies. With the exception of one bat, no hipposiderid bat could be induced to Doppler compensate for frequency shifts presented with the Doppler shift simulation device. The North African hipposiderid bat, *Asellia tridens* (CF: 104 kHz) has been shown to compensate for flight induced Doppler shifts (Gustafson and Schnitzler, 1979). No other tests of Doppler shift compensation in hipposiderid bats are known. On the basis of the present laboratory experiments it cannot be completely excluded that hipposiderid bats do compensate for Doppler shifts when they are flying. Although the bats in our experiments emitted orientation sounds and received shifted echoes, some other factors such as the lack of flight movement or the lack of any change in delay time between the shifted echo and the outgoing pulse may prevent if from compensating properly in the Doppler shift simulation device. Further tests on flying bats must be performed to clarify this question.

One theoretical consideration may be given here:

in *R. ferrumequinum* it was found that Doppler shift compensation only functions properly if the echo had a minimum duration of about 10 ms (Schuller, 1977). During the 10 ms the bat hears about 800 cycles of the echo signal. Assuming that for the fine frequency analysis for Doppler shift compensation purposes the bat would need about 800 cycles in the returning echo, the minimum pulse length should be 5 ms in *H. bicolor* and 5.9 ms in *H. speoris*. The respective mean pulse durations are 4.7 ms and 6.4 ms, so that the bats would operate at the lower limit of Doppler shift compensation performance. In *Asellia tridens* the minimum necessary pulse length would be 6.6 ms. This bat emits echolocation pulses during search flight of 8–10 ms (Gustafson and Schnitzler, 1979) and lie therefore well above the postulated pulse duration minimum for Doppler shift compensation.

In *H. speoris* an increase in frequency sensitivity and corresponding low in the audiogram near the emitted CF-frequency of the bats occurred at frequencies below the resting frequency. This is in contrast to the location of the threshold low in *R. rouxi*, where the frequency of the minimum is always a few hundred Hz higher than the resting frequency.

*H. bicolor* showed no pronounced frequency sensitivity changes which were tightly correlated to the CF-frequency of the bats. The frequency characteristics of hearing of *H. speoris* and *H. bicolor* correspond to those found in other hipposiderid bats (Grinnell and Hagiwara, 1972). In contrast to the findings of Grinnell and Hagiwara we did not commonly find off-responses in hipposiderid bats which is probably due to rise-decay times of at least 1 ms of the tone bursts used in this study. Grinnell and Hagiwara indicate that off-responses are not detectable if the rise-decay time is 1.5–2 ms.

One exception to the lack of Doppler shift compensation in hipposiderid bats under laboratory conditions was found, i.e., a *H. bicolor* that had a yellowish-orange fur instead of a grey fur and a CF-frequency of 158 kHz. At this frequency and a given speed to the target this bat receives about double the shifts in the echo frequency as *Rhinolophus* does under the same conditions (CF: 83 kHz). Assuming that both species fly and hunt at about the same flight speeds, the hipposiderid bats should have a range of Doppler shift compensation about double that of a rhinolophid bat. The striking result was that in this bat (yellowish-orange hipposiderid) the Doppler shift compensation range was 8–9 kHz, indeed, double that of *Rhinolophus* (4–5 kHz).

The results on Doppler shift compensation behaviour in *H. speoris* and *H. bicolor* are not yet conclusive and need further elucidation by behavioural experiments. The echolocation system of the hipposiderid

bats seems to be less adapted to Doppler shift compensation because of the short duration of the echolocation pulses and the little or absent specialization in the frequency characteristics of hearing around the resting frequency.

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