DIRECTIONAL SENSITIVITY OF ECHOLOCATION SYSTEM IN BATS PRODUCING FREQUENCY-MODULATED SIGNALS

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INTRODUCTION

For echolocation, bats emit sound and listen to echoes (Griffin, 1958). To investigate the directional sensitivity of their echolocation system it is necessary to measure the directional properties of both the orientation sounds and the ears. The field of the orientation sound around the head has been measured in *Eptesicus* and *Chilonycteris†* (Simmons, 1969), *Rhinolophus* (Schnitzler, 1968) and *Megaderma* (Möhres, 1966). In these measurements the animal with its head unrestrained emitted sounds toward a target. Thus these data might include the effect of head movement. Sokorov & Makarov (1971) fixed the head of *Rhinolophus* and measured the sound field produced by it. Recently, it has been found that sounds very similar to species-specific orientation sounds are elicited by electrical stimulation of the dorsal part of the reticular formation in the midbrain and/or the central grey matter of an unanaesthetized bat. In this case the head was immobilized by cementing it to a nail (Suga & Schlegel, 1972). This technique makes possible accurate measurements of the sound fields produced by bats.

For sound localization at least two types of cues are conceivable: interaural pressure and time (or phase) differences. In man the interaural pressure difference (IPD) is used mainly for location of high-frequency sound, while the interaural time difference (ITD) is used mainly for low-frequency sound (Mills, 1958, 1960; Stevens & Newman, 1936). Since the bats of the genus *Myotis* are small and their orientation sounds are higher than 10 kHz, the IPD may be a primary cue for echolocation. The IPD as a function of azimuth is obtained from the directional sensitivity curve of the auditory system, which can easily be measured by recording summated or single neural activity (Grinnell, 1963; Grinnell & Grinnell, 1965; Neuweiler, 1970; Suga, 1964).

To investigate the directional sensitivity of the echolocation system and the IPD as a function of azimuth, we therefore measured the sound fields produced by bats, and also the directional sensitivity of the auditory system in terms of summated neural activity.

Orientation sounds of *Myotis* are frequency-modulated (FM) so that an ITD can be coded by a group of neurones with different best frequencies on both the left and right sides. Possible roles of the ITD as well as the IPD are also discussed in relation to echolocation.

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† This bat is now called *Pteronotus* by Smith (1972).

MATERIALS AND METHODS

Three grey bats (*Myotis grisescens*) and five little brown bats (*M. lucifugus*) were used. These two species are closely related, and there were no noticeable differences in orientation sounds and audiograms. Under ether anaesthesia a nail 1·5 cm long was mounted on the skull with acrylic adhesive and dental cement. Then the pinnae were carefully relocated to their original position by tightening the skin with sutures. A few hours to a day later the animal (now recovered) was placed on a 7·5 cm diameter vinyl ball floating on water. The head of the animal was fixed by fastening the nail to a metal rod with a set screw. The midpoint of the ears was placed at the centre of the acoustic perimeter and the eye-nostril line was made horizontal. The nail, the rod supporting it, and the floating ball were at least 20° posterior to the animal's mouth.

Without anaesthesia, a small hole was made in the skull through which a double steel electrode with a few megohms resistance was inserted for the electrical stimulation of the midbrain to elicit FM sounds similar to species-specific orientation signals (Suga & Schlegel, 1972). After fixing the electrode in place with dental cement, the micromanipulator used for positioning it was removed. The electrical stimulus applied to the brain was a short train of pulses delivered twice per second. Each train consisted of 10 electric pulses, each having a duration of 0·1 msec and an amplitude of 1–15 V. The inter-pulse interval was 1·7 msec.

The sounds elicited by the bat were recorded with two quarter-inch condenser microphones (Brüel & Kjaer 4135). One, 'reference microphone' pointed toward the bat's mouth and was positioned 5° right, 5° down from the eye-nostril line, and 70 cm anterior to the mouth. The other, 'the scanning' microphone, mounted on a movable aluminium arm in order to scan the bat's perimeter at a 50 cm radius, was also aimed at the mouth. Since the sounds emitted by the bat were frequency-modulated, the interference between the signal directly incident upon the microphones and the echoes was easily detected, because the overlap of the delayed echoes with the signal produced ripples in the envelope of the recorded signal. To minimize these echoes, objects in the sound-proofed room were covered with cotton. An Ampex FR-100 tape recorder (frequency response: 300–300000 Hz at 60 in/sec) simultaneously recorded the following signals: electrical stimuli applied to the brain, bat's sound monitored with the reference and scanning microphones, and electric signals indicating the position of the scanning microphone. At each position of the scanning microphone about 15 FM sounds emitted by the bat were recorded.

The recorded signals were played back at $\frac{1}{32}$ of the original tape speed. A 2 sec square pulse triggered by the electrical stimulus controlled the shutter of a camera, while the pulse synchronized with the onset of the bat's sound triggered the sweep of a cathode-ray oscilloscope. The sound monitored with the reference microphone was fed into the period meter in order to examine the frequency sweep. The output of the period meter and the tape-recorded sounds were simultaneously displayed on the oscilloscope screen and were photographed. A 3125 Hz signal, which corresponds to 100 kHz at the original tape speed was also fed into the period meter prior to the tape-recorded sound and its output was also displayed for purposes of calibration (Fig. 1). In addition, the signal indicating the location of the scanning microphone was
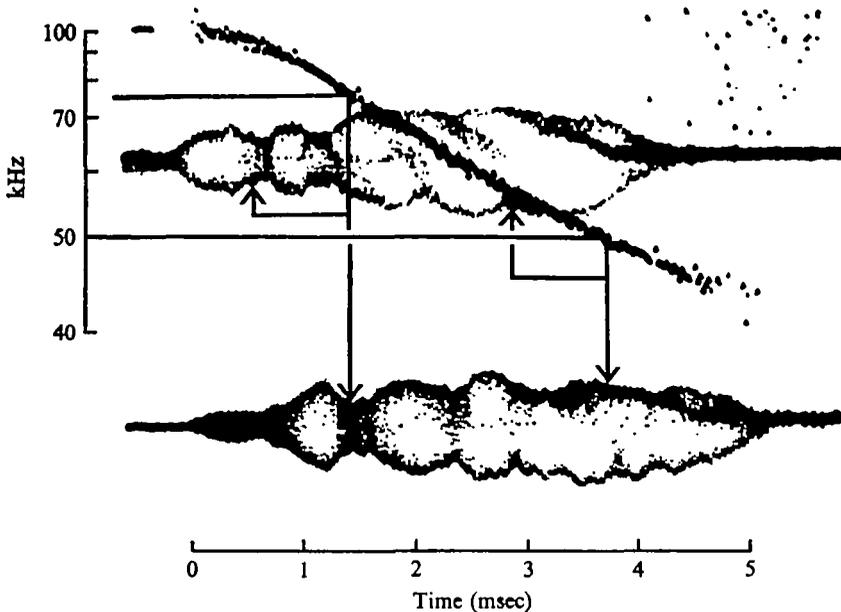
Fig. 1. A photograph used for amplitude measurement of an FM sound emitted by *M. grisescens*. The sound waves monitored with the scanning and reference microphones are shown in the upper and lower traces, respectively. The period meter output is simultaneously displayed by dots with a short calibration signal of 100 kHz on the left. The arrows indicate the corresponding amplitude of either the 50 or 75 kHz component. The frequency scale for the period meter output is given to the left in kilo-Hertz, and the time scale at the bottom in milliseconds.

displayed on an oscilloscope screen. In Fig. 1 the frequency of a bat's sound sweeps from 100–43 kHz. Since there were no noticeable harmonics for the components higher than 50 kHz, the radiation patterns of sounds higher than 50 kHz could be studied by measuring the peak-to-peak amplitudes. In our experiments the amplitude of the 55, 75, and 95 kHz components were measured in FM sounds monitored with the reference and scanning microphones, and the difference in amplitude at the two microphones was expressed in either percentage of, or decibels below, maximum. Assuming sagittal symmetry, each point in our data represents the average of six measurements.

To study the relationship between mouth movement and sound emission a photo-electric displacement transducer was connected to the lower jaw of one animal by a rubber band, and a quarter-inch microphone was placed 10 cm anterior to the bat. The outputs of the transducer and microphone were simultaneously displayed on an oscilloscope screen (Fig. 2).

For the measurement of the directional sensitivity of the auditory system a tungsten electrode was inserted into the nucleus of the lateral lemniscus to record its activity evoked by acoustic stimuli. This is hereafter called the *LL* response (equivalent to N_4). The *LL* response was selected, because it is more directional than the summated neural activity of primary auditory neurones (N_1) as a result of binaural interaction occurring in medullary auditory nuclei (Grinnell, 1963). Instruments for acoustic stimulation and recording were the same as those described in the previous paper (Suga, 1971). A condenser loudspeaker was moved around the head in the horizontal
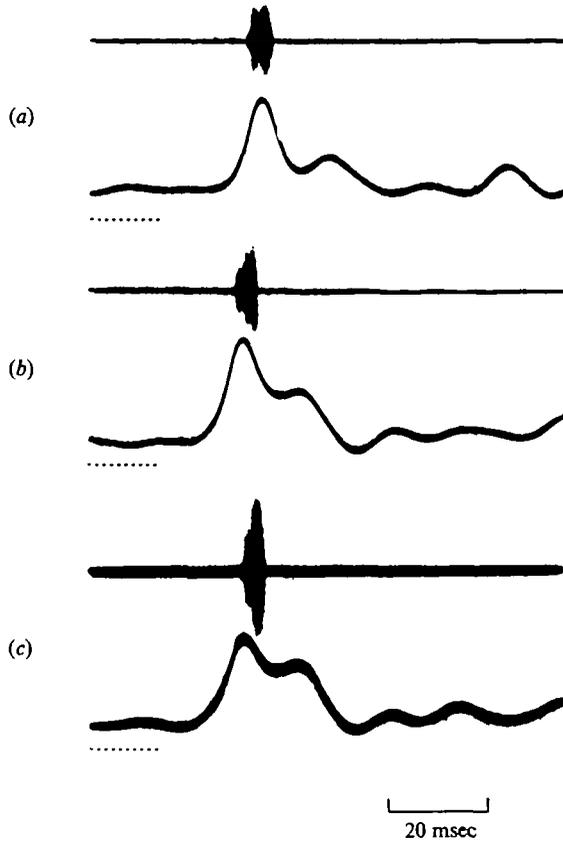
Fig. 2. Relationship between the sound emission (upper trace) and mouth movement in *M. grisescens* (lower trace). The upward deflexion of the lower trace represents the mouth opening. Sounds are emitted around the maximum opening of the mouth. Dots on the left represent the electrical stimuli applied to the midbrain. All three pictures were obtained from one bat under the same stimulus conditions. The time scale is 20 msec.

plane at 66 cm radius, and thresholds of *LL* responses to 35, 55, 75, and 95 kHz sounds were measured as a function of azimuth. These acoustic stimuli had a rise-decay time of 0·2 msec and a duration of 4 msec.

RESULTS

Sound fields produced by bats. When an electrical stimulus was applied to the dorsal part of the reticular formation in the midbrain, the bat opened its mouth 50–60° and emitted an FM sound with a latency of 30–50 msec. This was very similar to the species-specific orientation sound used in the searching phase of echolocation. The amplitude of the emitted sound ranged from 100–110 dB SPL (sound pressure level referred to 0·0002 dyne/cm² r.m.s.) at 10 cm in front of the mouth. Its duration was between 3 and 5 msec. The frequency always swept downward from 100–ca. 45 kHz. If such an FM sound was emitted at different phases of mouth movement, the sound field measured would show large variations; the relationship between the sound emission and mouth movement was thus first studied. As shown in Fig. 2, the sound emission was not strictly locked to a certain phase of the mouth movement, but it
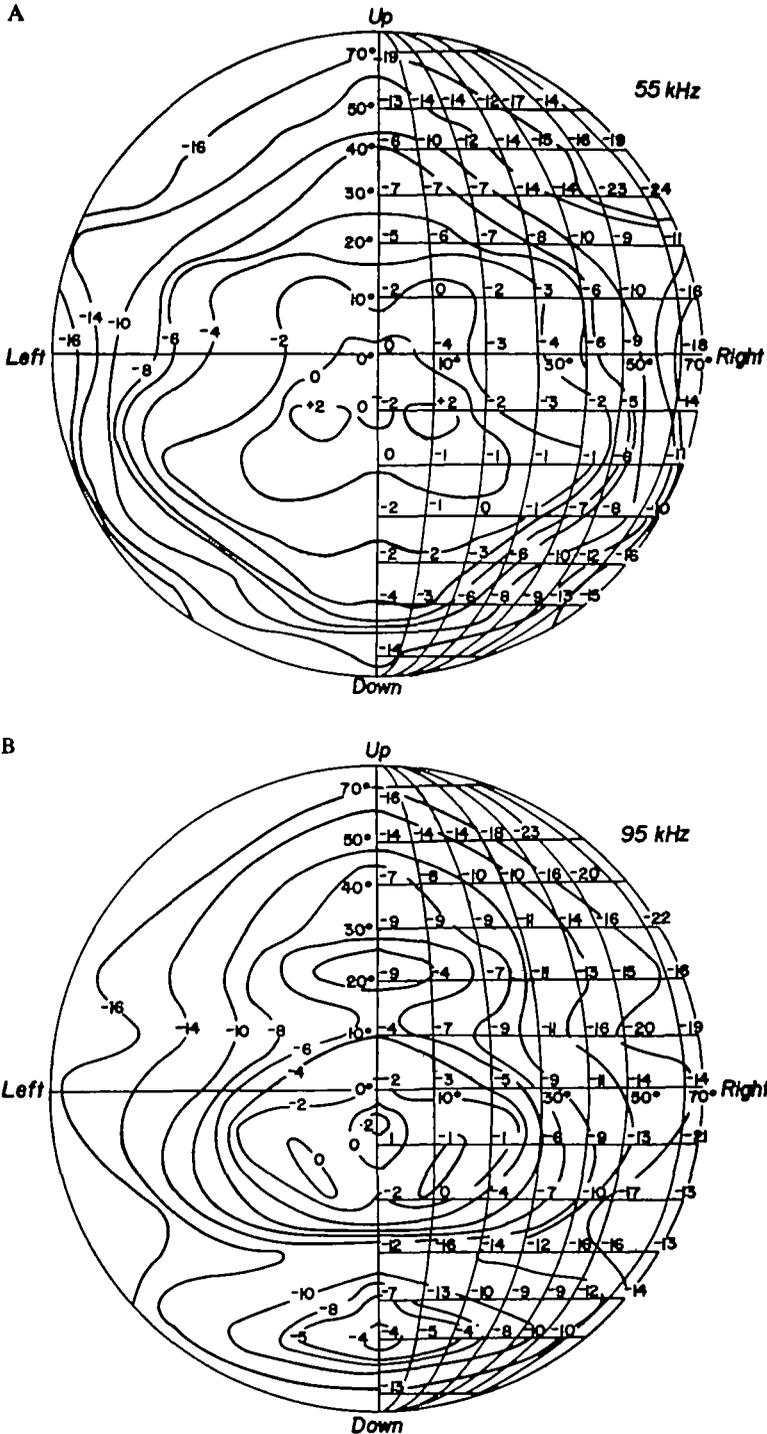
Fig. 3. Radiation patterns of the 55 and 95 kHz components in FM sounds produced by *M. grisescens*. Each number near the ordinate crosspoints represents a sound pressure relative to that at the reference point (5° right and 5° down) in decibels. The contours were drawn by interpolation through these values. Zero degree is defined as the eye-nostril line. A, 55 kHz; B, 95 kHz.
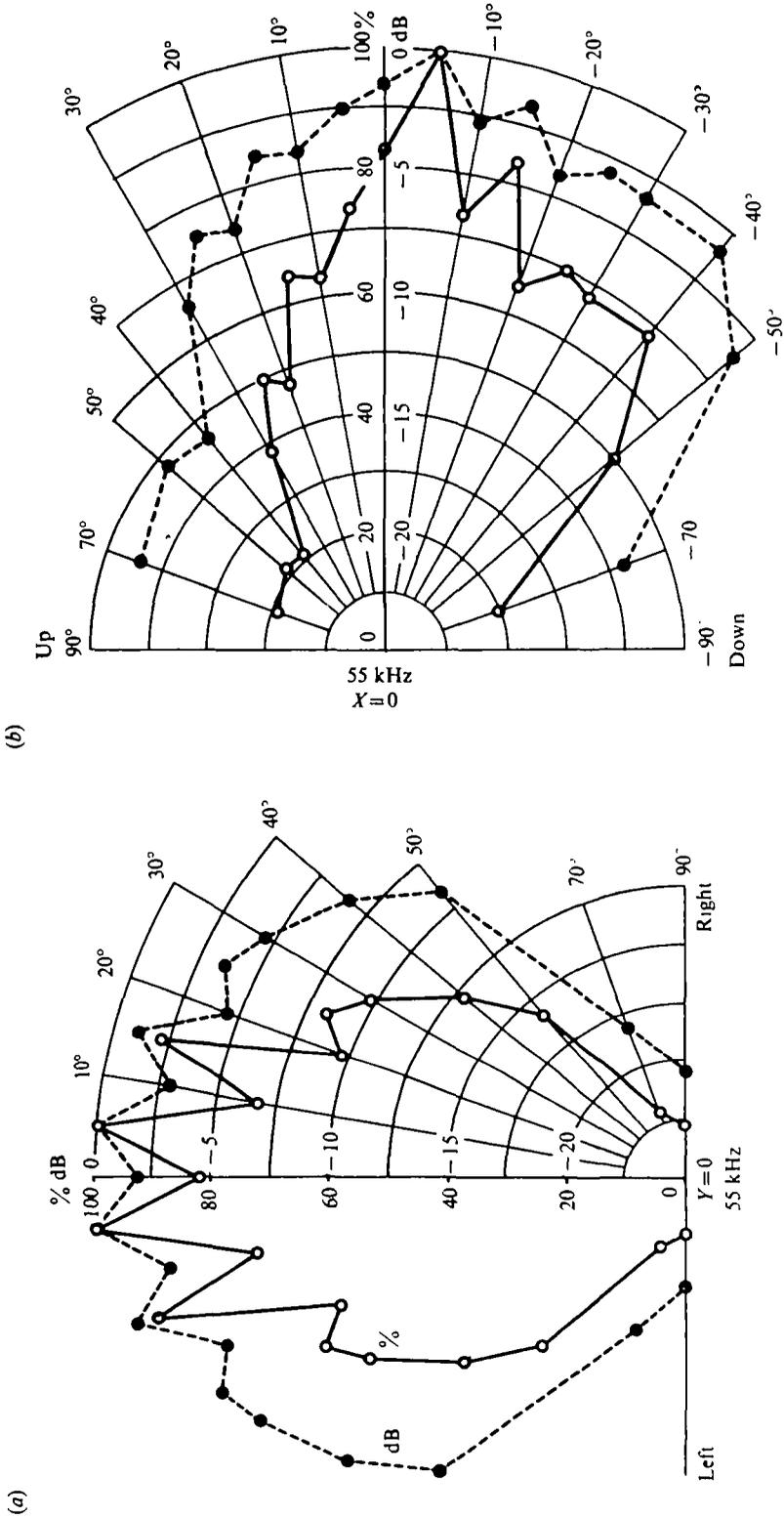
Fig. 4. Radiation pattern of the 55 kHz component of FM sounds emitted by *M. griseus* in the horizontal (*a*) and vertical (*b*) planes in percentage of maximum (solid line and open circles) and in decibels (dashed line and filled circles).
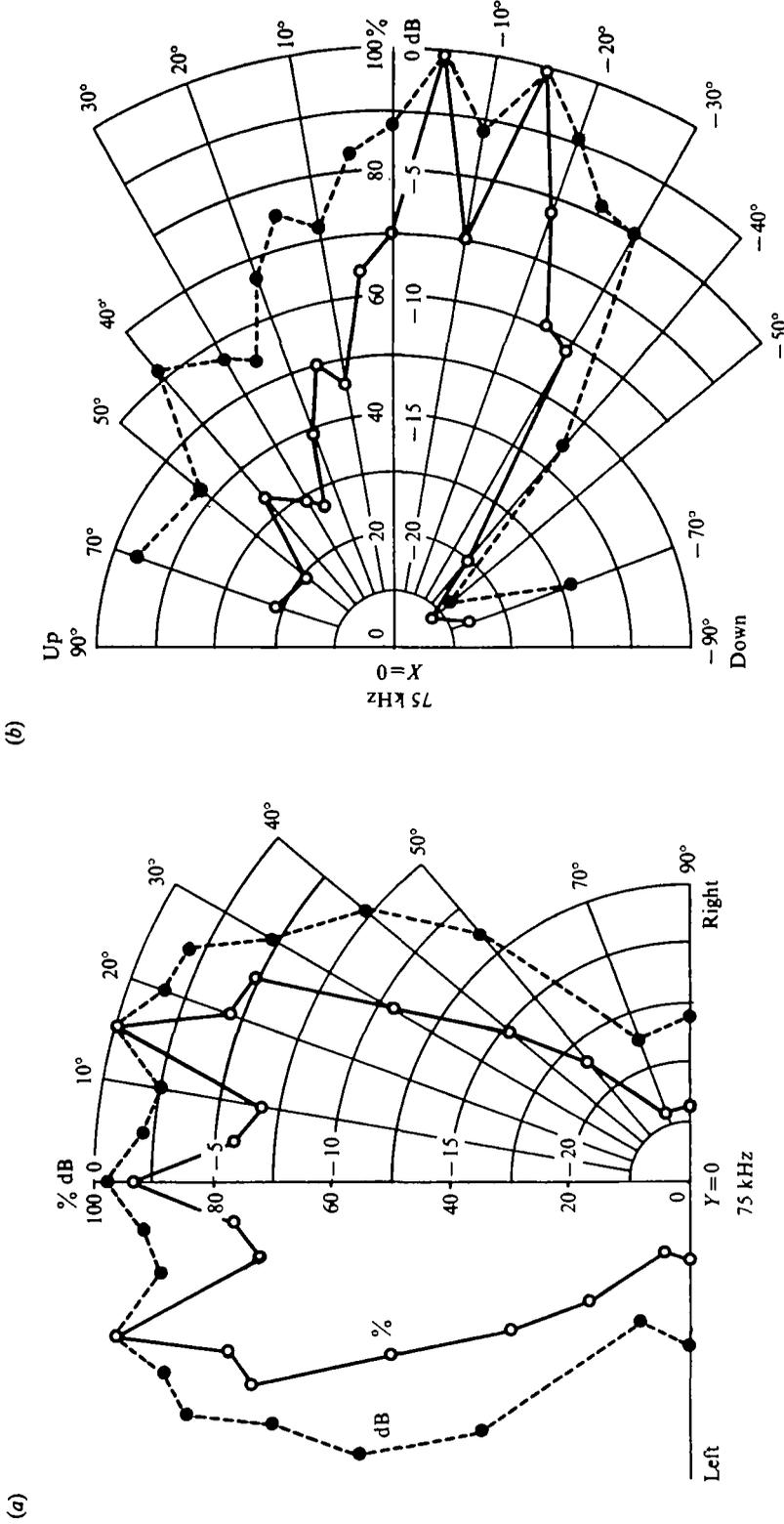
Fig. 5. Radiation pattern of the 75 kHz component of FM sounds emitted by the bat in the horizontal (*a*) and vertical (*b*) planes. All symbols are the same as those in Fig. 4.
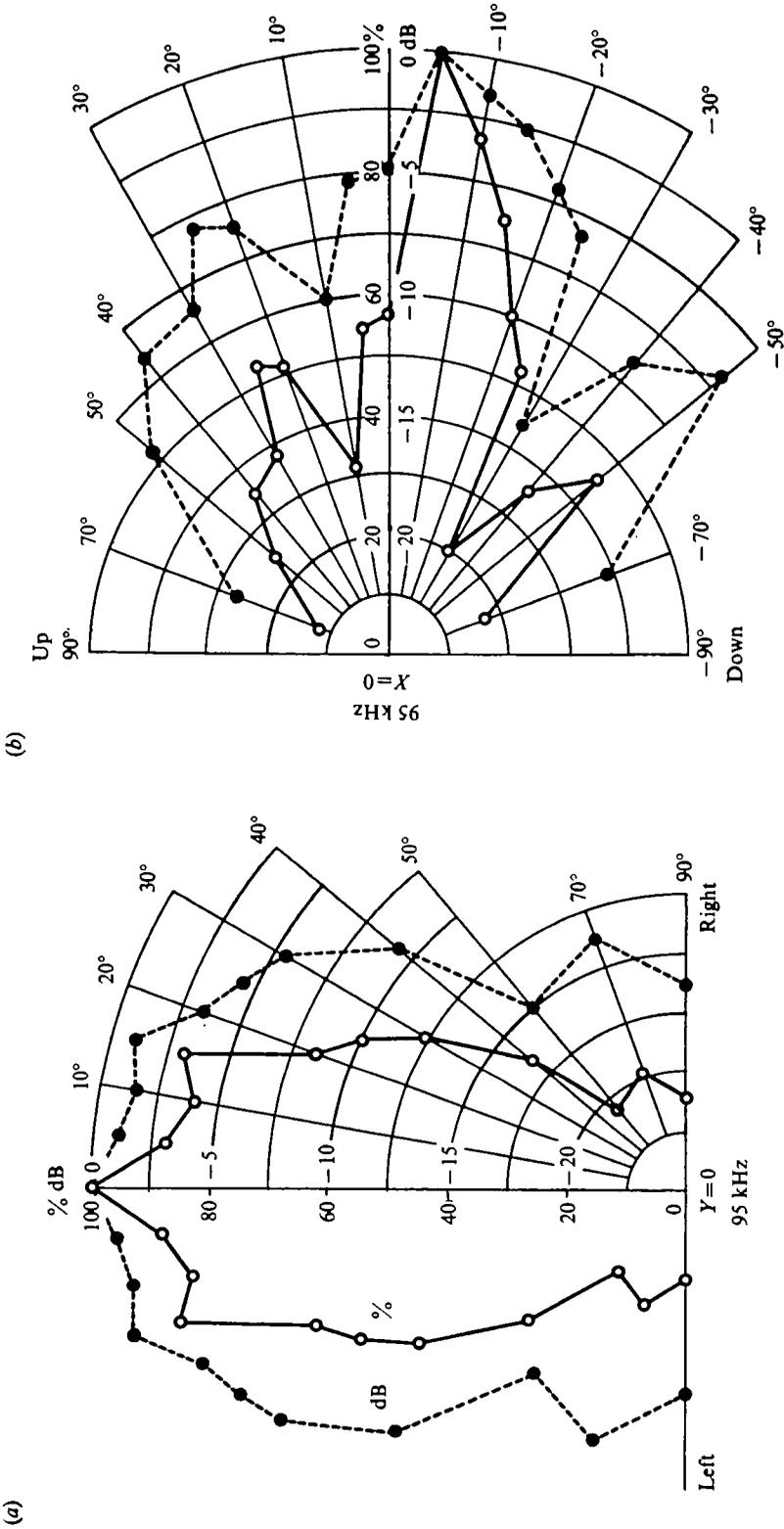
Fig. 6. Radiation pattern of the 95 kHz component of FM sounds emitted by the bat in the horizontal (*a*) and vertical (*b*) planes. All symbols are the same as those in Fig. 4.
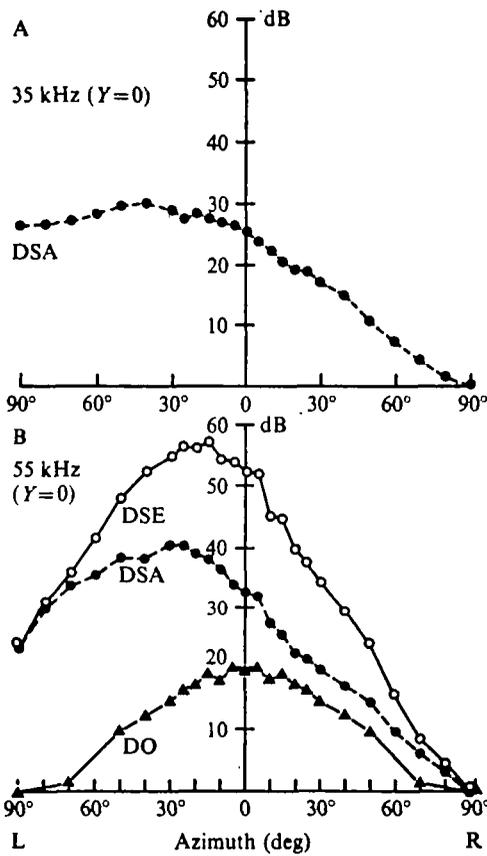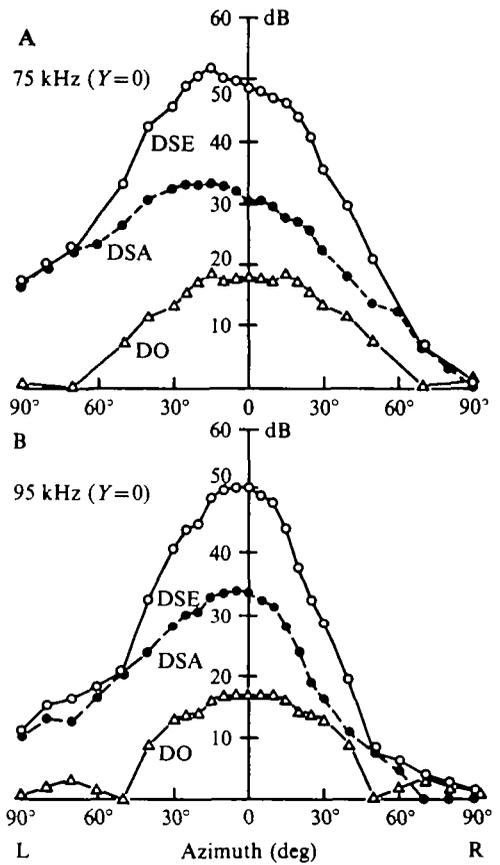
Fig. 7. (A) the directional sensitivity of the auditory system (DSA) at 35 kHz. (B) DSA, directionality of the orientation sound (DO) and directional sensitivity of the echolocation system (DSE) at 55 kHz. Each DSA curve is the average of measurements with 5 bats, while each DO curve is the average of data obtained from 2 bats. The ordinates and abscissae represent sensitivity in decibels and azimuth in degrees, respectively.

Fig. 8. The DSA, DO and DSE at 75 (A) and 95 kHz (B). Each DSA curve is the average of measurements with 5 bats, while each DO curve is the average of data obtained from 2 bats. All symbols are the same as those in Fig. 7.

occurred anywhere between slightly earlier and slightly later than the peak opening of the mouth, so that a given component of the FM sound might be emitted at any aperture of the mouth between 30–60°. Thus, the sound field varied for each sound. This variation was within ± 12 % of the mean amplitude.

Fig. 3 shows an example of sound fields produced by *M. grisescens* (Mg 1). The contour map shows that the sound is strongly radiated in a direction of 5–10° downward from the eye-nostril line and the main lobe is sharper at higher frequencies. Figs. 4–6 show radiation patterns of the 55, 75, and 95 kHz components, respectively, in the horizontal and vertical planes produced by Mg 1. All directional patterns were normalized with respect to the maximum amplitude for each component. The radiation angle at half-amplitude of maximum was 38° lateral, 18° up and 50° down at

55 kHz, 34° lateral, 8° up and 32° down at 75 kHz, and 30° lateral, 5° up and 2 down at 95 kHz (Figs. 4–6). Thus, the width of the main lobe becomes narrower with an increase in frequency. At 95 kHz two prominent side lobes were present: one oriented 25° upward and the other 50° downward (Fig. 6). Two other bats showed different values, which were broader in angle at half-amplitude than Mg 1.

Since the measurement of sound pressure was performed in 5° or 10° steps, there was a possibility that sharp lobes which might exist for high frequencies were missed. The fields of 55, 75 and 95 kHz sounds were therefore measured around a loudspeaker with an aperture comparable to that of the bat's mouth. This measurement indicated that the presence of such lobes in addition to those in Fig. 4 was unlikely. The main lobe calculated by Strother & Mogus (1970) is also compatible with our data. Furthermore, there was a possibility that the ball under the bat modified the sound field in the hemisphere in front of the bat. The sound field around the loudspeaker was also measured with and without the ball. The result demonstrated that the sound field in front of the bat was not noticeably different.

Directional sensitivity of the auditory system (DSA). When a tungsten-wire electrode was inserted into the lateral lemniscus, the *LL* response (lateral lemniscal evoked potential) to a tonal stimulus was 1–2 mV in amplitude. The loudspeaker was then moved in the horizontal plane including the eye-nostril line, and the threshold of the *LL* response to the sound was measured as a function of azimuth angle. The DSA was expressed by the reciprocal of the threshold. Figs. 7, 8 show DSA curves measured with either 35 and 55 kHz or 75 and 95 kHz tones. Each curve is the average of measurements with 5 different bats. The *LL* response was most sensitive to sounds delivered from the contralateral side, so that impulses for the lateral lemniscus mainly originated from the contralateral ear. The maximum sensitivity appeared at $38 \pm 7.5°$ azimuth to the midline for 35 kHz, $27 \pm 9.0°$ for 55 kHz, $18 \pm 7.5°$ for 75 kHz and $5.0 \pm 8.1°$ for 95 kHz. The slope of the DSA curve toward and beyond the midline was 0.28 ± 0.03, 0.43 ± 0.03, 0.42 ± 0.03 and 0.58 ± 0.03 dB/degree for 35, 55, 75, and 95 kHz, respectively. Since higher-frequency sounds were more directional, it was expected that the slope of the DSA curve would increase with frequency, but it was not anticipated that the maximally sensitive direction would move medially with increasing frequency.

Directional sensitivity of the echolocation system (DSE). The DSE was obtained by adding the two curves for the directionality of the orientation sound (DO) and the DSA. As shown in Figs. 7, 8, the slopes of the DSE curve on both sides of its peak are about 0.6 dB/degree at 55 kHz, 0.8 dB/degree at 75 kHz, and 1.0 dB/degree at 95 kHz. These results confirm that the DSE increases in sharpness with frequency. The peak of the DSE curve is 15° lateral for 55 kHz, 15° lateral for 75 kHz, and 2.5° lateral for 95 kHz. It was noticed that the peak for a 95 kHz sound was very close to the midline.

Interaural pressure difference (IPD). Since the IPD appeared to be the essential cue for echolocation in bats of the genus *Myotis*, it was calculated as a function of azimuth angle for 35, 55, 75, and 95 kHz. We assumed sagittal symmetry of the auditory system. The DSA or DSE curves in Figs. 7, 8 were inverted at zero degrees. The IPD curves in Fig. 9 were then obtained by subtracting the inverted curves from the non-inverted ones. The IPD for a 35 kHz sound changed linearly with
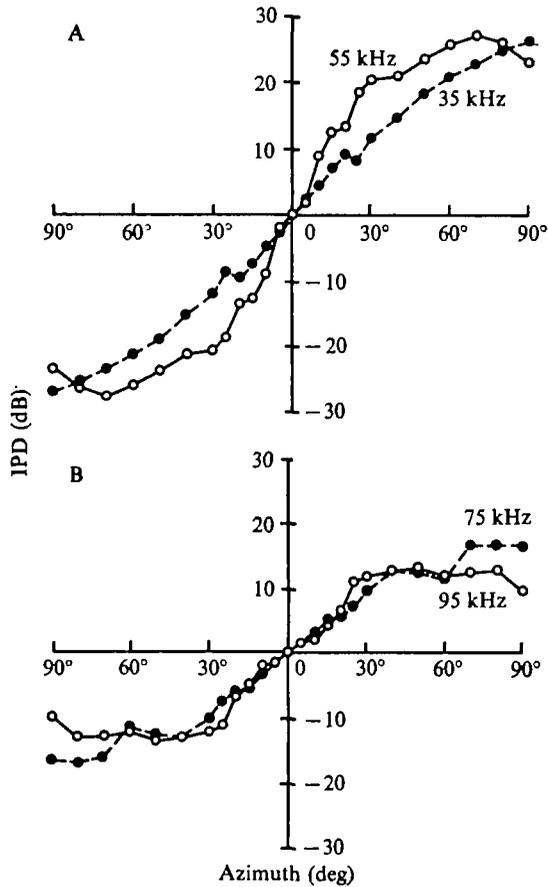
Fig. 9. Interaural pressure differences (IPD) as a function of azimuth at either 35 and 55 kHz (A) or 75 and 95 kHz (B). The ordinates and abscissae represent the IPD in decibels and azimuth in degrees, respectively. These curves were obtained from the data presented in Figs. 7, 8.

azimuth between 0–50° at a rate of 0·4 dB/degree. Beyond 60° it changed at a rate of 0·2 dB/degree. For a 55 kHz sound the slope of the IPD curve was 0·7 dB/degree between 0–30° lateral, and 0·2 dB/degree beyond 30°. For 75 and 95 kHz sounds the slope of the IPD curve was 0·3–0·4 dB/degree between 0° and 30°–40° lateral, but it becomes nearly zero beyond 40°. These data indicate that a 55 kHz sound gives a larger IPD cue than do 35, 75, and 95 kHz sounds and that the IPD cue for sounds higher than 75 kHz is very poor at positions more lateral than 30°.

DISCUSSION

Sound fields. Sound fields produced by different species of bats have been measured by Möhres (1966), Schnitzler (1968), Simmons (1969), and Sokolov & Makarov (1971). Except for Sokolov & Makarov's extensive study, the animals did not have a head-holding device when they emitted orientation sounds toward a target. The azimuth angle at half-amplitude of maximum is 23° at 28–30 kHz for *Eptesicus fuscus*

and *Pteronotus parnellii rubiginosus* (previously called *Chilonycteris rubiginosa*) which
emit sounds through the mouth (Simmons, 1969), and 21–23° at 83 kHz for *Rhino-
lophus ferrumequinum* which emits signals through the nostrils (Möhres, 1966;
Schnitzler, 1968), and 35° at 60–80 kHz for *Megaderma lyra* (Möhres, 1966). Accord-
ing to Sokolov & Makarov (1971) who fixed the head of *Rhinolophus*, the azimuth angle
at a half-amplitude is 28°, but it is 30° after amputating the nose-leaf. Thus, the effect
of the nose-leaf on horizontal radiation is very small. This is unexpected data for us,
because we had the impression that *Rhinolophus* emitted an orientation sound in a
narrower beam than that of *Myotis* and *Eptesicus*, since *Rhinolophus* emits a high-
frequency sound through nostrils which are surrounded by the nose-leaf.

In our data on Mg 1, the horizontal angle at a half of maximum amplitude is 34°
at 75 kHz and 30° at 95 kHz, which are comparable to the data obtained by Sokolov &
Makarov (1971). Conversely, the azimuth angle at half-amplitude at 55 kHz in Mg 1
(38°) is much wider than that at 28–30 kHz in *Eptesicus* and *Pteronotus* (Simmons,
1969).

The vertical distribution of an orientation sound has been measured only with
Rhinolophus. The vertical angular width at a half-amplitude of maximum at 83 kHz
is 43° according to Schnitzler (1968) and 73° according to Sokolov & Makarov (1971).
The large angular width obtained by Sokolov and Makarov is due to the fusion of the
main and side lobes. Interestingly, the dissection of the nose-leaf greatly reduces the
vertical width down to 46° because of the reduction in the side lobes. *Rhinolophus*
moves the nose-leaf during echolocation, probably to control the vertical distribution
of orientation sounds. In our data with Mg 1, the vertical angular width of the main
lobe at half-amplitude was 68° at 55 kHz, 40° at 75 kHz and 30° at 95 kHz.

Interaural pressure difference (IPD). Since the DSE curves showed sharp slopes
(0·6 dB/degree at 55 kHz and 1·0 dB/degree at 95 kHz), the amplitudes of echoes at
the ears greatly decrease as echo sources move away from the maximally sensitive
direction. Accordingly, clatter from irrelevant sources at the ears is greatly reduced.
If the peaks of the DSA curves were more lateral than those in Figs. 7, 8, the IPD
and the dynamic ranges of the IPD curves would increase, but the peaks of the DSE
curves would decrease and move laterally. In other words, the IPD and the DSE are
mutually dependent. For echolocation the peak of the DSA curve should be thus
neither too lateral nor too medial. The dynamic ranges of the IPD curves greatly
depend on the difference between the slopes of the DSA curves toward the ipsi- and
contralateral sides. To increase the dynamic range, the slope lateral to the peak of
the DSA (or DSE) curve should be smaller than that on the medial side. This was
found true for lower frequencies but not for higher ones.

For comparison with the present data, a DSA curve (Neuweiler, 1970) and a
directionality curve of orientation sound (Schnitzler, 1968) of *Rhinolophus ferru-
mequinum* are replotted in Fig. 10A. The frequency of sound used for these measure-
ments was 83·3 kHz. The slope of the DSE curve is 0·5–0·6 dB/degree. The IPD
varies linearly with azimuth angle from 0–30° lateral at a rate of 0·5 dB/degree. It
does not, however, change as the azimuth angle increases beyond 30° (Fig. 10B).
The IPD curve of *Rhinolophus* is thus similar to that of *Myotis* (whether the difference
between the two curves in Fig. 10B is significant or not is subject to future
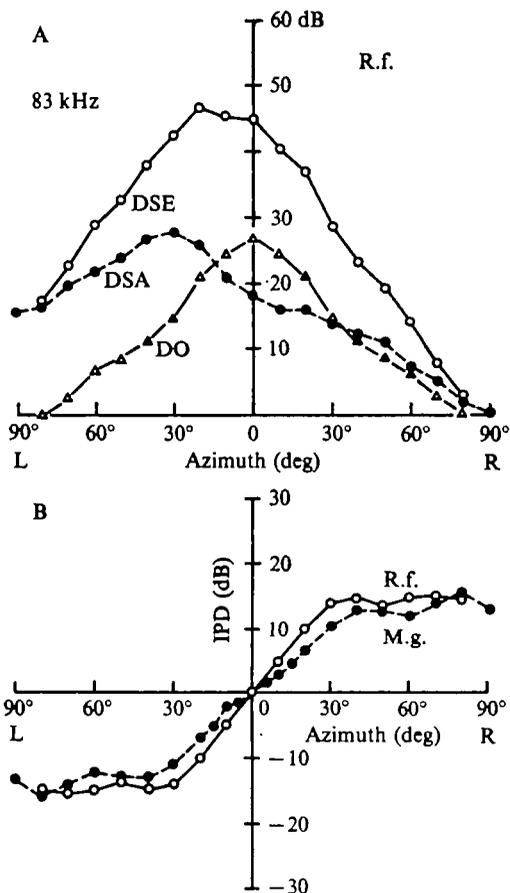experimentation).

Fig. 10. DSA, DO, DSE and IPD of *Rhinolophus* (R.f.) as a function of azimuth at 83 kHz. For comparison, the IPD curve of *Myotis* (M.g.) is also shown, which is the average of the curves for 75 and 95 kHz in Fig. 9. All symbols are the same as those in Figs. 7, 9.

Rhinolophus moves the pinnae synchronously with vocalization and does not change the frequency of CF–FM (constant-frequency plus frequency-modulated) sound more than a few kHz during echolocation (Schnitzler, 1968), while *Myotis* does not move the pinnae during vocalization and greatly drops the frequency of FM sounds when hunting insects and when landing (Griffin, 1958). Thus, the dynamic range of the IPD curve may alternately shift left or right in *Rhinolophus*, while it broadens in *Myotis*.

Both the narrow dynamic range of the IPD curve for higher frequencies and the decrease in frequency of FM orientation sounds during the approach and terminal phases appear to be disadvantageous for echolocation and target characteristics. However, *Myotis* may have not only this disadvantage, but also some advantage. During a searching phase *Myotis* emits FM sounds sweeping from 100–45 kHz. At these frequencies, the slope of the DSE curve toward a lateral side is very sharp, so that any clatter which may be produced by irrelevant objects and/or other bats more lateral than 30° is greatly attenuated. Since the distance to a target is long in the search phase,

a wide dynamic range for echolocation may not be needed by the bats, so the narrow dynamic range may not necessarily be disadvantageous for echolocation. The bats can efficiently find small objects in front of them with a sound of such a high-frequency, although higher-frequency sounds are attenuated by the air more than lower-frequency sounds. The target characteristics may be performed during and/or just before the approach phase. During the terminal phase and the latter part of the approach phase *Myotis* emits FM sounds sweeping down about one octave between 50–15 kHz (e.g. from 40–20 kHz) at a high repetition rate. In these phases tracking of the target may be most important. Since the distance to the target is short, the direction of the target may quickly change, so that a wide dynamic range for echolocation and the frequent emission of orientation sounds may be more important to the bat.

In man the just-detectable IPD is 0·5 dB at 2–3 kHz and 50 dB above the sensation level which corresponds to a 1·2–2·5° lateral shift of a sound source from the midline (Mills, 1960). In our data on *Myotis* the slope of the IPD curve around the midline was 0·4, 0·7, 0·3, and 0·4 dB/degree for 35, 55, 75, and 95 kHz sounds, respectively. If one assumes that the just-detectable IPD of *Myotis* is 0·5 dB, the bat may be able to detect a 0·7–1·7° azimuth difference around the median plane. Harrison & Downey (1970) measured the IPD with *Phyllostomus hastatus* and obtained the minimum detectable angular difference of 2·0° at 10 kHz and 2·3° at 20 kHz. They assumed the just-detectable IPD to be 0·5 dB. Behavioural experiments with bats indicate that *Eptesicus fuscus* with an interaural distance of 14 mm can detect a 6–8° azimuth difference and *P. hastatus* with an interaural distance of 22 mm can detect a 4–6° difference with their orientation sounds (Peff & Simmons, 1971). These behavioural data can be explained by the IPD cue without assuming that the bat can detect a much smaller IPD than can man. There is no doubt that the IPD is the essential cue for echolocation. Since *Myotis* can catch two separate *Drosophila* within a half second (Griffin, Webster & Micheal, 1960), the minimum detectable azimuth difference in *Myotis* may be smaller than the behavioural values cited above.

Pumphrey (1948) stated that sound localization is accomplished by the binaural comparison of intensity ratios at least at three different frequencies to which the ear shows different polar diagrams of sensitivity. As a matter of fact, the polar diagrams of the ears of owls (Payne, 1961) and bats (Neuweiler, 1970; Grinnell & Grinnell, 1965) change extensively with the frequency of sound and also with the position of the external ear. This is also true in man (Sivian & White, 1933), so that the spectrum density of a complex sound differs at the two ears (Nordland & Fritzell, 1963). The source of a complex sound is thus more easily located than that of a pure tone. Thus, FM sounds are apparently better signals for echolocation than CF sounds.

Responses of auditory neurones vary not only in discharge pattern, but also in latency with stimulus amplitude. In *Myotis* the difference in latency between the left and right LL responses to a tonal stimulus due to the IPD appears to be much larger than the ITD and may greatly contribute to the information processing for sound localization. Since this interaural latency difference is due to the IPD, it is not included in the following discussion about the ITD.

Interaural time difference (ITD). In man, the just-detectable ITD is at best 5 μsec (9 μsec on the average) at a 75% correct point for a noise with a band width of 0·15–17 kHz and 60–80 dB above the sensation level (Klumpp & Eady, 1956). This ITD

corresponds to placing a sound source 1·1° lateral from the median plane (Fedderson *et al.* 1957). Fedderson *et al.* (1957) calculated the ITD as a function of azimuth for a sphere with a diameter of 17·5 cm, which is equal to the interaural distance in man, and found that the calculated values (9 μsec/degree) are very similar to the values measured with microphones placed in the ears of human subjects. In *Myotis grisescens* and *M. lucifugus*, the interaural distance is *ca.* 9 mm. The ITD for *Myotis* as a function of azimuth angle can be obtained by multiplying the ITD for man by the ratio between the interaural distances, 0·05. The calculated ITD curve showed a slope of about 0·45 μsec/degree from the median plane to 40° lateral. If one assumes that the just-detectable ITD in *Myotis* is 5 μsec as in some human subjects, the theoretical limit for the just-detectable azimuth difference would be 11°. In order to detect a 0·7–1·7° azimuth difference with the ITD cue, the just-detectable ITD should be at least 0·3–0·8 μsec or less. The just-detectable ITD of *Myotis* should therefore be assumed to be 8–17 times smaller than that of man, if the ITD cue is to be considered equally important to the IPD cue for echolocation. No data have been obtained yet to indicate whether the above assumption is reasonable or not. According to the above assumption the minimum time-pressure trading ratio is 0·6–1·6 μsec/dB, which is much smaller than the value for man, 9–11 μsec/dB (Hershkowitz & Durlach, 1969; Gilliom & Sorkin, 1972).

In *Eptesicus* and *Phyllostomus* the just-detectable azimuth difference is 6–8° and 4–6°, respectively (Peff & Simmons, 1971). Since the interaural distance is about 14 mm for *Eptesicus* and 22 mm for *Phyllostomus*, the ITD at the just-detectable azimuth difference is about 5 μsec. Thus, the ITD cannot be ruled out as a cue for sound localization, although it is apparently inferior as a cue to the IPD.

Primary auditory neurones of mammals commonly show phase-locked responses to sounds lower than 5 kHz (Rose *et al.* 1967). In bats, orientation sounds are higher than 10 kHz, so that phase-locked responses may not play any role in echolocation. Since the orientation sound of *Myotis* is always frequency-modulated by about one octave, the ITD is coded by many neurones tuned at different frequencies within the sound. If the ITD plays an important role in echolocation, FM sounds are much better signals than CF sounds or noise bursts.

SUMMARY

1. Radiation patterns of the 55, 75 and 95 kHz components in frequency-modulated sounds emitted by the grey bat (*Myotis grisescens*) were studied. FM sounds similar to species-specific orientation sounds were elicited by electrical stimuli applied to the midbrain while the head of the animal was immobilized by a nail cemented to its skull. The main beam was emitted 5–10° downward from the eye-nostril line. The radiation angle at one half of maximum amplitude was 38° lateral, 18° up and 50° down at 55 kHz, 34° lateral, 8° up and 32° down at 75 kHz, and 30° lateral, 5° up and 25° down at 95 kHz. At 95 kHz, two prominent side lobes were present.

2. The directional sensitivity of the auditory system (DSA) measured in terms of the potential evoked in the lateral lemniscus was studied with the grey bat (*M. grisescens*) and the little brown bat (*M. lucifugus*). The maximally sensitive direction moved toward the median plane with the increase in frequency from 35–95 kHz. The slope of the DSA curve increased from 0·3–0·6 dB/degree with frequency.

3. The directional sensitivity of the echolocation system (DSE) was calculated using both the DSA curve and the radiation pattern of the emitted sound. The maximally sensitive direction of the echolocation system was 15° lateral to the median plane at 55 kHz and 2·5° lateral at 95 kHz. The slope of the DSE curve increased from 0·6 to 1·0 dB/degree with frequency. Thus, the higher the frequency of sound, the sharper was the directional sensitivity of the echolocation system.

4. The interaural pressure difference (IPD), which appeared to be the essential cue for echolocation in *Myotis*, changed linearly with the azimuth angle from 0–30° lateral regardless of the frequency of sound, at respective rates of 0·4, 0·7, 0·3 and 0·4 dB/degree for 35, 55, 75 and 95 kHz sounds. Beyond 30°, the change in IPD was quite different depending on frequency. For 75 and 95 kHz sounds, the IPD stayed nearly the same between 30° and 90°. Thus, the 75–95 kHz components in FM orientation sounds were not superior to the 35 and 55 kHz components in terms of the IPD cue for echolocation.

5. Assuming the just-detectable IPD and ITD to be 0·5 dB and 5 μsec respectively, as in man, the just-detectable azimuth difference of *Myotis* around the median plane would be 0·7–1·7° with the IPD cue and 11° with the ITD cue.

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