

Studies of Auditory Neurophysiology in Non-Echolocating Bats, and Adaptations for Echolocation in One Genus, *Rousettus*

ALAN D. GRINNELL

Department of Zoology, UCLA

S. HAGIWARA

Department of Physiology, UCLA, Los Angeles, California

Received September 14, 1971

Summary. 1. Six species of New Guinea megachiropteran bats have been studied electrophysiologically. Five are non-echolocating, one (*Rousettus amplexicaudatus*) has evolved an echolocation capability independent of echolocating microchiropteran bats. The purpose of the study was to compare auditory responses of non-echolocating bats with those of the echolocating bats studied to date, and to determine what adaptations have occurred in *Rousettus* to permit echolocation.

2. Evoked potentials were recorded from the posterior colliculus and more peripheral levels in anesthetized preparations.

3. Emitted sounds of each species were recorded and are described (Fig. 1). All bats emit sounds at frequencies up to 60 kc/s or higher.

4. All species were found to have similar audiograms, broadly tuned with greatest sensitivity around 45–50 kc/s. *Rousettus* was unexceptional (Fig. 2). No “off”-responses were seen.

5. All species showed capabilities of frequency resolution comparable to that seen in microchiropteran bats emitting FM pulses (Fig. 3). *Rousettus* was not conspicuously different in this respect.

6. The non-echolocating bats showed very slow recovery of responsiveness following an initial sound (Fig. 4) and poor ability to follow trains of stimuli at a high repetition rate compared with echolocating bats. *Rousettus* differed dramatically from its non-echolocating relatives in recovering quickly and in following with little reduction in response amplitude at a frequency of 200/sec. In all species, recovery rate was inversely related to stimulus intensity. In *Rousettus* even stimuli 20–30 db fainter than an initial sound elicited good responses at 2 msec or greater intervals (Fig. 5).

7. *Rousettus* and its non-echolocating relatives showed generally smaller changes in sensitivity with changes in stimulus angle than are seen in microchiropteran bats. Greatest sensitivity was uniformly at 60–80° to one side, with relatively reduced sensitivity to sounds coming from directly in front, consistent with pinna position and with the lack of necessity for hearing sounds from directly ahead. *Rousettus* did not differ in any apparent way from the non-echolocating bats (Figs. 7, 8).

8. It is concluded that non-echolocating bats, like other small mammals, lack several of the auditory adaptations considered to be adaptations for echolocation: sharp restriction of sensitivity to the region of emitted sounds, sensitivity at extremely high frequencies, fast temporal resolution, facilitation of responsiveness to the second of a pair of sounds, and sharply directional hearing in front of the bats.

9. The only conspicuous difference between *Rousettus* and its non-echolocating relatives was in recovery rate. This suggests that fast temporal resolution is perhaps the most important of the necessary neural adaptations for echolocation.

Introduction

Previous studies have revealed many conspicuous neurophysiological adaptations for echolocation in bats of the sub-order Microchiroptera (Grinnell, 1963a-d, 1967, 1970; Grinnell and Grinnell, 1965; Grinnell and Hagiwara, 1971; Henson, 1965, 1967; Suga, 1964a, b, 1965a, b, 1968, 1969, 1970). To date, however, comparisons have been made only with non-echolocating mammals of other orders than bats, principally cats, guinea pigs and man. To better appreciate which adaptations are unique to echolocation, it would obviously be preferable to study auditory responses in non-echolocating bats (sub-order Megachiroptera). Moreover, within the Megachiroptera, one genus is apparently unique in having independently evolved the capacity to echolocate, albeit rather crudely by means of tongue clicks rather than the highly organized emitted pulses of microchiropteran bats (Kulzer, 1956, Griffin, Novick and Kornfield, 1958). It is of major interest to determine whether auditory responses are distinguishably different in *Rousettus* than in closely-related, non-echolocating genera.

A recent *Alpha Helix* expedition provided the opportunity for us to study both echolocating and non-echolocating bats, including *Rousettus*, in New Guinea. This paper describes our findings on *Rousettus* and its non-echolocating relatives of the suborder Megachiroptera. An earlier paper (Grinnell and Hagiwara, 1971) describes findings on New Guinea Microchiroptera.

In the present experiments, we examined four major response parameters: (a) frequency range used, and region of greatest sensitivity; (b) acuity of frequency resolution as judged by evoked potential changes; (c) temporal resolution of the auditory system, that is, ability to respond to the second of two sounds presented close together in time; and (d) the sharpness and pattern of directional sensitivity. It has been found that the non-echolocating bats hear well at ultrasonic frequencies and generally conform to what has been found in other small non-echolocating mammals. *Rousettus* differ conspicuously only in their temporal resolving capability. These results confirm the conclusion that auditory response patterns of echolocating bats do in fact represent major neuro-

physiological adaptations for echolocation. They also provide an insight into the adaptability of certain response patterns of the auditory nervous system, and the apparent preeminent importance of fast temporal resolution for echolocation.

This research was supported principally through NSF grants to the *Alpha Helix* program. Other support was provided by grants USPHS NS06232 to A. D. G. and USPHS NS09012 to S. H.

Methods

Six genera of Megachiroptera were studied: *Dobsonia minor* (average weight, 87 g), *Rousettus amplexicaudatus stresemanni* (weight, 88 g), *Nyctimene albiventer* (29 g), *Paranyctimene raptor* (20 g), *Macroglossus lagochilus* (17 g) and *Syconycteris crassa* (19 g). All were caught in mist nets strung between trees in the bush near the laboratory located about 20 miles north west of Madang, New Guinea. All survived quite well in captivity eating locally-obtained fruit.

Methods of stimulation and recording were the same as those used to study echolocating bats, described in the previous paper (Grinnell and Hagiwara, 1971). Except for their generally larger size, the Megachiroptera introduced only one difficulty not encountered in the Microchiroptera: the posterior colliculi were not visible at the brain surface. After practice dissections, therefore, electrodes were pushed through the cerebellum in a direction determined to be toward the colliculi until good evoked potential responses were obtained. As in the microchiropteran bats studied, the response recorded by a gross electrode in the posterior colliculus consisted of four positive peaks, including activity as far away as the auditory nerve (N_1), summed responses of second (N_2) and third order (N_3) elements in the cochlear nuclear and superior olivary nuclei, and a fourth peak representing input to the posterior colliculi (N_4). This latter peak was usually very much the most prominent. When the electrode was pushed deeper and laterally, more peripheral responses could be recorded at greater amplitude and studied by themselves. No attempt was made to analyze single unit responses at any level. Except where otherwise stated, sound intensities are expressed in db re 0.0002 dyne/cm².

Results

A. Vocalizations

Although none of these bats except *Rousettus* are thought to be able to echolocate, or showed any evidence of such ability, all produce sounds for communication purposes. The range of sounds in communication has been studied extensively in related genera (Nelson, 1965), where the number and variety of communication signals is remarkable. Since the hearing of each bat is probably adapted to the sounds it uses, it is obviously relevant to determine the characteristics of these sounds. No attempt was made to record all of the different types of sounds a given bat could produce. It was very easy, on the other hand, to obtain loud cries of anger or fear as a bat was being held or was squabbling with other bats over food. These provide evidence about the range of frequencies emitted and the patterns of emission of a least certain sounds useful in behavior. From *Rousettus*, echolocation clicks were easily obtained, simply by letting the animal fly in total darkness.

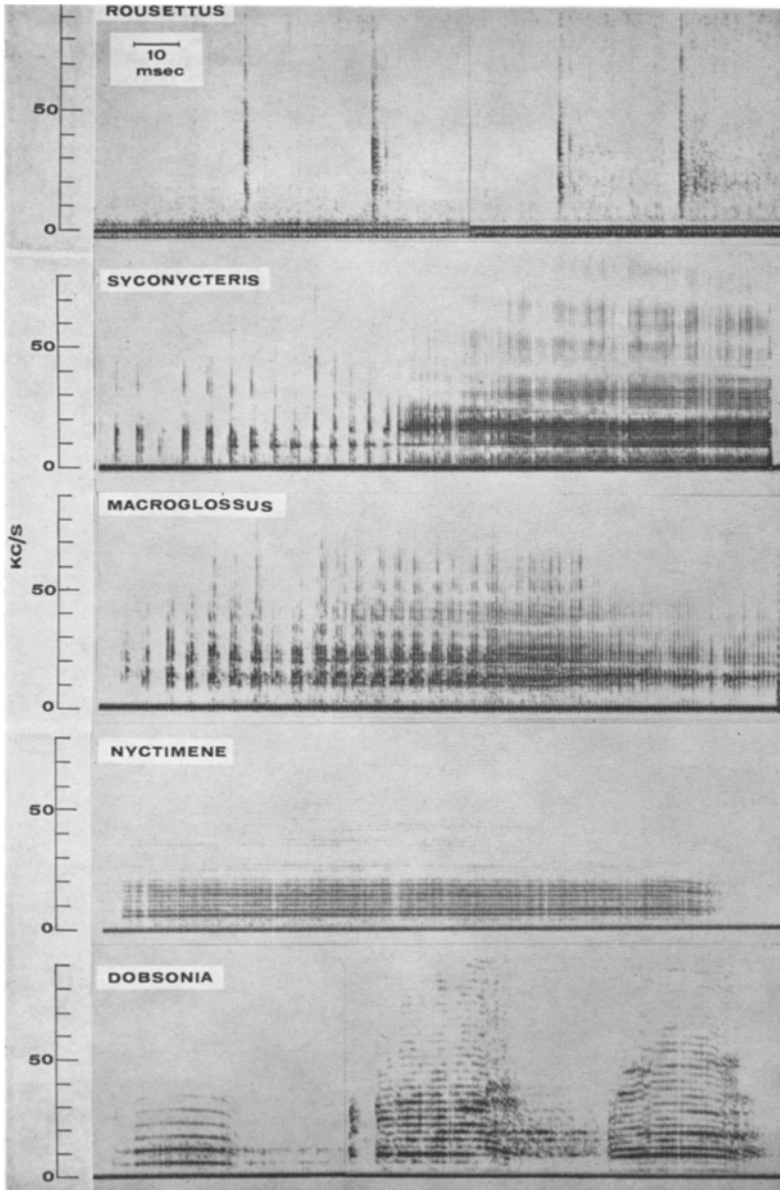


Fig. 1. Sample sonograms of emitted sounds of five of the species studied. The *Rousettus* record consists of two pairs of orientation clicks, without the normal interval between pairs. The clicks in each pair were consistently separated by about 30 msec. Sounds of the other bats were typical screams of anger or frustration. Note that the sounds of *Macroglossus* and *Syconycteris* consist of series of broad band clicks similar to those of *Rousettus*, but at variable repetition rates, up to 1000/sec or even higher. *Nyctimene* and *Dobsonia* cries consist instead of sustained tone pips with large numbers of harmonics

Fig. 1 shows sample sonagram records of sounds emitted by these species. It is apparent that all sounds extend far into the ultrasonic range, with a large fraction of the sound energy between 20 and 60 kc/s. The echolocation sounds of *Rousettus* were unusual in their regular spacing into pairs, approximately 30 msec apart, separated by much longer intervals; but as clicks they did not differ greatly from the click components of the vocalizations of *Syconycteris* and *Macroglossus*, whose screams consisted of a long series of similar, abrupt, click-like bursts of noise, increasing to very high repetition rates and changing slightly in dominant frequency. In *Nyctimene albiventer* and *Dobsonia minor*, on the other hand, emitted sounds were a series of sustained, harmonically-related tones, warbled somewhat in frequency.

B. Sensitivity as a Function of Frequency

Fig. 2 shows average audiograms for all species, indicating the threshold intensity at each frequency necessary to evoke a just detectable positive evoked potential (N_4) from the posterior colliculus. Evoked potentials were seen only to the onset of stimuli, never to the "off". This is in contrast to observations on many echolocating microchiropteran bats (Grinnell and Hagiwara, 1971). In all species, maximum sensitivity was at 45–50 kc/s, with a drop-off of 20–30 db/octave at lower frequencies, of 125–150 db/octave at higher frequencies. Indeed, the similarity is surprising in view of the large range of sizes of the bats involved. The differences in absolute sensitivity are probably due to chance factors, such as electrode location, rather than to real differences between the species.

It is clear from these curves that *Rousettus* is entirely unexceptional in its audiogram. Apparently its adaptations for echolocation do not involve any changes that would be reflected in an evoked potential audiogram. This is not the case in many echolocating microchiropteran bats, where audiograms show extreme specialization (Grinnell, 1963a, 1969, 1970; Grinnell and Hagiwara, 1971). This specialization, when it occurs, can be clearly correlated with the frequency characteristics of the emitted pulses. Since *Rousettus* echolocation sounds are broadband "clicks", covering the same range used for communication by all of the megachiropteran bats studied, lack of such specialization should perhaps not be surprising. It is noteworthy, on the other hand, that in all species the bats' sensitivity in the range of frequencies audible to man is more than 30 db reduced from the peak at 45–50 kc/s. The same is likely to apply to other megachiropterans. Clearly any study of communication in these species should include analysis of emissions at frequencies above the range of human hearing.

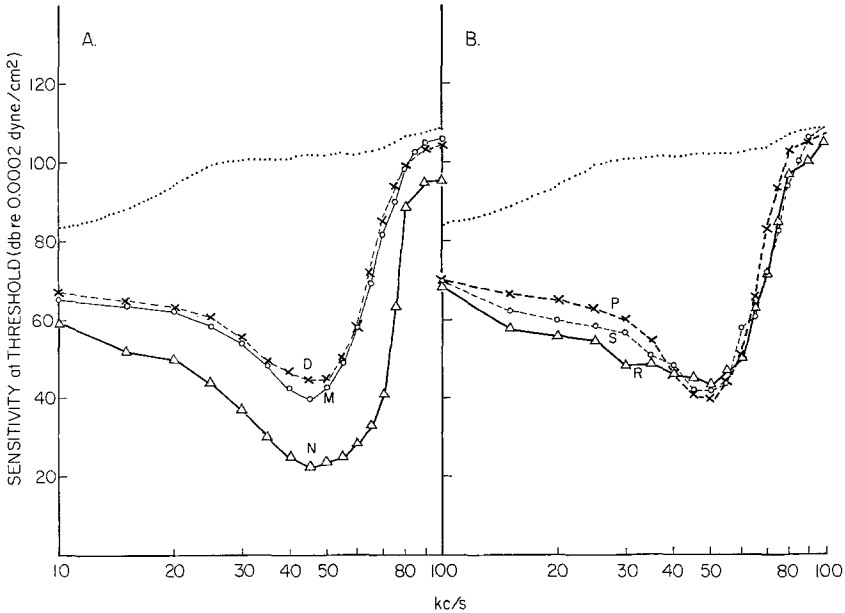


Fig. 2. Average N_1 evoked potential audiograms for the six species studied. Threshold is defined as the intensity necessary to elicit a just detectable evoked potential. *D*, *Dobsonia*; *M*, *Macroglossus*; *N*, *Nyctimene*; *P*, *Paranyctimene*; *S*, *Syconycteris*; *R*, *Rousettus*. Dotted line at top of each graph indicates the maximum intensity available from the stimulating loudspeaker

C. Frequency Resolution

Since single unit behavior was not studied in these species, satisfactory evidence of the limits of frequency resolution are not available. However, a useful measure that was obtained was the effectiveness of different frequencies in masking response to a signal of a given frequency. Sample curves for *Rousettus* are shown in Fig. 3. In these experiments a tone of constant intensity was presented at different frequencies, and the intensity of the signal necessary to reach threshold was measured. All curves are similar in showing a fast drop in masking effectiveness on either side of the signal frequency. This drop is sharpest for masking tones higher than the signal, and little different from one species to another. All show drops of 15–25 db in the first 5 kc/s, and masking effectiveness is essentially gone (–25 to –40 db) at 10 kc/s separation. On the low frequency side, there was more variability. In *Rousettus* the drop in effectiveness was essentially as sharp at lower frequencies as at higher.

In other species, the change in effectiveness was approximately the same near the signal frequency, but subharmonics were sometimes more

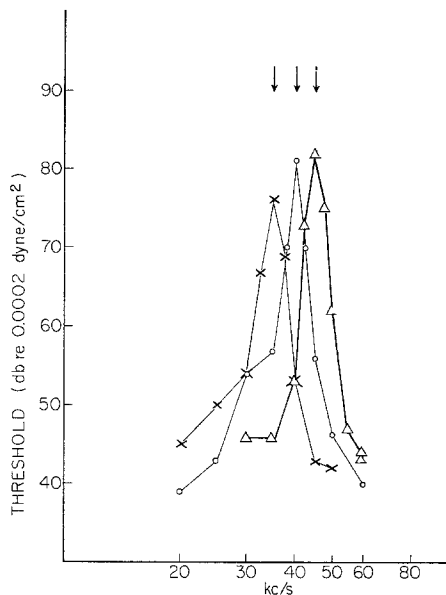


Fig. 3. Frequency resolution in *Rousettus*. For signals of three different frequencies, 35, 40, and 45 kc/s (indicated by arrows), the threshold signal intensity is plotted as a function of the frequency of a background masking tone of constant 90 db intensity. Threshold for each signal in the quiet was 42 db at 35 kc/s, 39 db at 40 kc/s, and 43 db at 45 kc/s. Signal duration 2 msec, 0.2 msec rise and fall times

effective (*Dobsonia* and *Macroglossus*), and the drop in masking effectiveness was in some cases less steep on the low frequency side of the signal than in *Rousettus* (*Nyctimene*). The curves for different species are nevertheless sufficiently similar that, while *Rousettus* may show some superiority in frequency resolution, further experimentation would be necessary to satisfactorily establish the fact. Comparable measurements on echolocating microchiropteran bats show drop-offs closely similar to those of *Rousettus*, with changes of 25–50 db/10 kc/s on either side of the signal frequency.

D. Recovery of Responsiveness Following Stimulation

Extraordinarily fast recovery of responsiveness is perhaps the most dramatic auditory adaptation for echolocation in microchiropteran bats. It was of great interest, therefore, to find that recovery was quite slow in most of the megachiropterans studied, resembling recovery in other mammals, while recovery of responsiveness in *Rousettus* was essentially as fast as in most microchiropteran bats studied. In the non-

Table 1. Average recovery times for evoked potential responses at level of N_2 to N_4 , at 40–50 kc/s, and between 20 and 50 db of threshold. Recovery is expressed as amplitude to the second of two identical 0.2 msec pulses, compared with the amplitude of the response to the first of the pair. Intervals were measured between onsets of the stimuli

	First detectable recovery (msec)	50 % (msec)	100 % (msec)
<i>Rousettus</i>	0.6	0.9	2.3
<i>Macroglossus</i>	0.8	1.5	5
<i>Syconycteris</i>	0.8	2.3	7.5
<i>Paranyctimene</i>	1.2	1.9	5.7
<i>Nyctimene</i>	2.2	4.4	12
<i>Dobsonia</i>	1	2.2	7.7

echolocating species, using pairs of identical brief (0.5 msec) tone pips within 50 db of threshold, initial recovery of response to the second was seen at about 1–1.5 msec, 50% response to the second was reached at separations of about 2–3 msec, and full recovery required 7–10 msec. In *Rousettus*, initial recovery was evident at signal separations of 0.5 to 0.6 msec, 50% recovery was reached in about 1 msec, and full recovery took only about 2 msec. These differences were consistently observed. Table 1 summarizes average values for several tests in each species, and Fig. 4 shows typical recovery curves for *Dobsonia*, *Syconycteris*, and *Rousettus*.

In the case of *Rousettus*, recovery curves are shown for both the collicular positive evoked potential (N_4) and the cochlear nucleus response (N_2) recorded at a single electrode position. Note that recovery is considerably faster at N_4 than at N_2 . This is characteristic of many microchiropteran bats, but not of other mammals that have been studied. In the other bats examined in this study, recovery was slower at higher neural levels, except in *Macroglossus* where again recovery was significantly accelerated between the first two neural levels and the N_4 . *Macroglossus* also showed faster recovery rates than any of the other non-echolocating bats. In none of the bats, including *Rousettus*, was greater responsiveness to the second than to the first of two identical sounds seen. This is in contrast to observed behavior in many echolocating bats, tested with stimuli within 50 db of threshold.

In all bats studied, both echolocating and non-echolocating, recovery has been found to take progressively longer as the stimulus intensity is increased beyond about 40–50 db above threshold (Grinnell, 1963b,

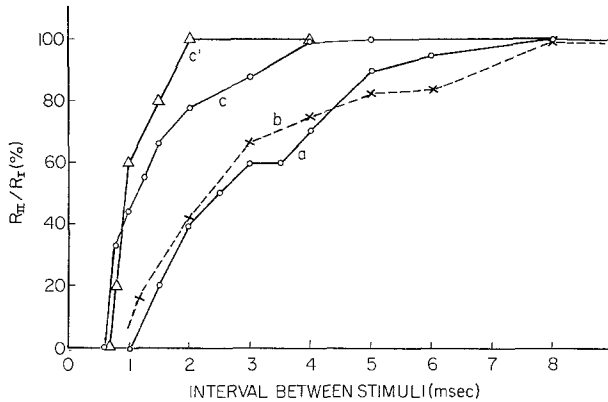


Fig. 4. Recovery curves in *Rousettus*, *Syconycteris* and *Dobsonia*. Responses to the second of a pair of identical tone pips as a percent of the response to the first of the pair, at different intervals between stimuli. *a*, *Syconycteris*; *b*, *Dobsonia*, *c* and *c'* *Rousettus*. *a*, *b* and *c'* were recorded in the colliculus of each species. Curve *c* shows the recovery curve of the cochlear nucleus evoked potential (N_2) recorded at the same time as the N_4 (*c'*). Note the faster overall recovery rate of *Rousettus*, and the exaggeration of recovery in N_4 compared with N_2 .

1970). For this reason, only experiments employing stimuli within 50 db of threshold are used in comparing recovery in different species.

Another criterion of temporal resolution capability is the ability of a response to follow a long train of stimuli without decreasing in amplitude. When such tests were run in the species examined in this study, all at essentially the same anesthesia level, *Rousettus* again was seen to be adapted for much faster following. At 100/sec, the *Rousettus* N_4 was still undiminished in amplitude, while responses in all other species showed depression with a repetition of 50/sec or fewer; at 200/sec, the *Rousettus* responses were only 15% depressed, while the next fastest following was in *Macroglossus* and *Syconycteris*, where responses were nearly 50% reduced.

Rousettus must be able to respond to echoes much fainter than the outgoing sound, and arriving after only brief intervals. Fig. 5 shows the results of measurements of N_4 responsiveness when the second of a pair of sounds was made fainter than the first. The depression of responsiveness was slight, even when the second was 25 db fainter than the first. At -35 db, responsiveness was 60% recovered after 5 msec. Such behavior is quite similar to that seen in echolocating microchiropteran bats (Grinnell, 1963b, 1970).

In one of the three *Syconycteris* studied, a curious repetitive synchronous firing was seen to a tone pip of any frequency in their audible

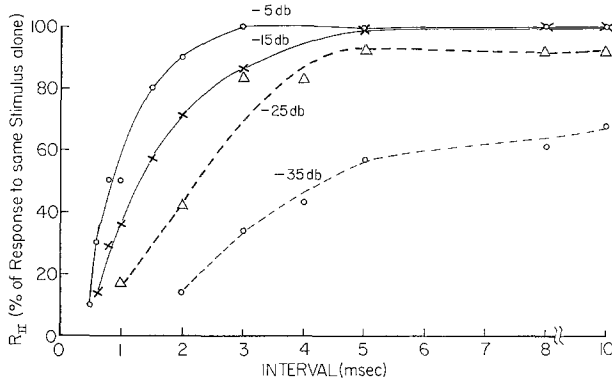


Fig. 5. *Rousettus*. Recovery of N_4 responsiveness at different intervals after a louder first stimulus. The first stimulus was held constant at 50 db above threshold, while the second was made 5, 15, 25, and 35 db fainter. Both were 40 kc/s, 0.3 msec in duration, with 0.1 msec rise and fall times

range when the electrode was advanced into the region of the cochlear nuclei. A compound evoked potential was seen, with a positive component at 1 msec latency (auditory nerve response), and a negative potential at 2 msec latency. The earlier potential was a typical evoked potential, present only at the onset of a stimulus. The later potential, however, which probably represents the activity of a large population of cochlear nuclei cells, was followed by a series of similar negative peaks, at intervals of 2.5 msec. Fig. 6 shows sample records from this experiment. If the stimulus was a 1 msec tone pip, there were three or four following negative peaks. If the pulse was prolonged for 20–50 msec, the synchronized negative peaks recurred at the same frequency (400 peaks/sec) as long as the stimulus was present and for 5–10 msec afterward. The synchrony of response was eventually lost, but for relatively long periods of constant stimulation, the response resembled that to a stimulus of 400 tone pips/sec. The responses to 400/sec and 200/sec tone pips were essentially indistinguishable. If brief stimuli were presented at 300/sec, on the other hand, the responses were rapidly desynchronized, leaving no obvious repetitive firing. A 400 cycle pure tone elicited no response. Apparently the units near this electrode tip responded with highly synchronous firing at a rate of 400/sec. The function or adaptive value of such responsiveness is not apparent.

E. Angular Sensitivity and Auditory Localization of Signals

Echolocating bats typically have elaborate external ears, directed forward in such a way that maximal sensitivity is seen near or just

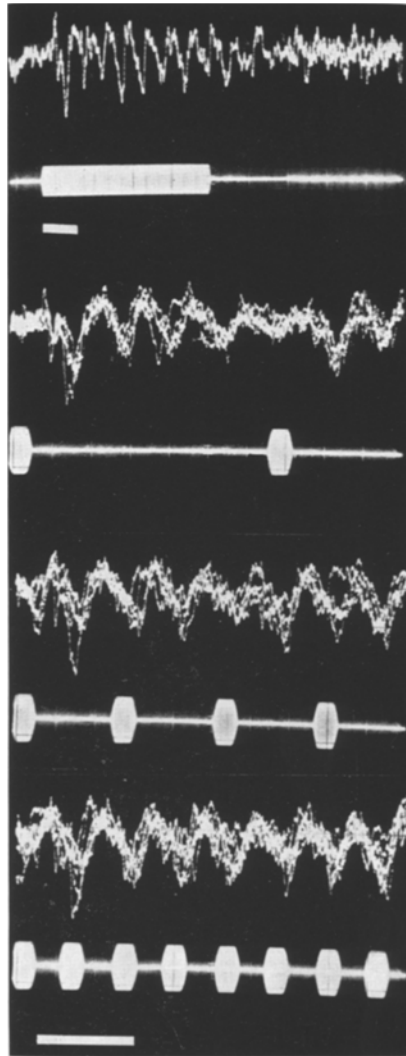
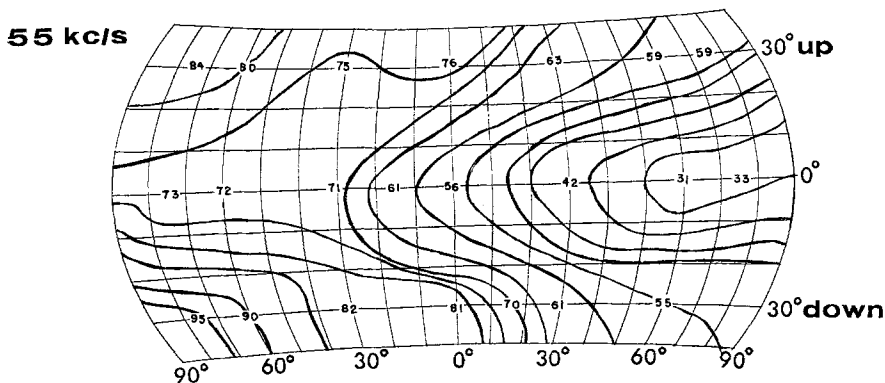
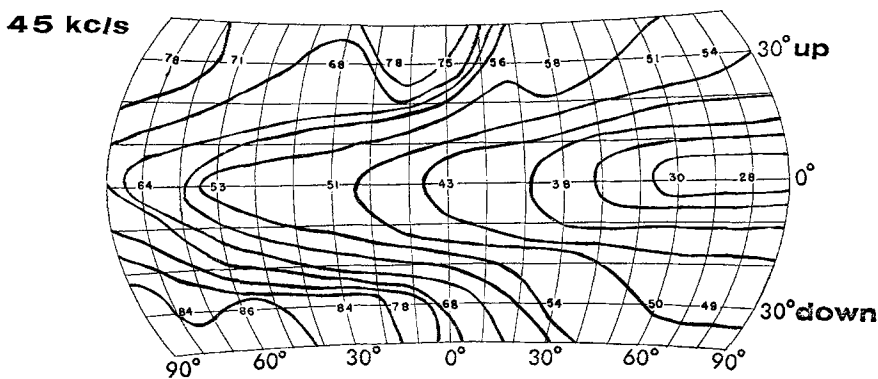
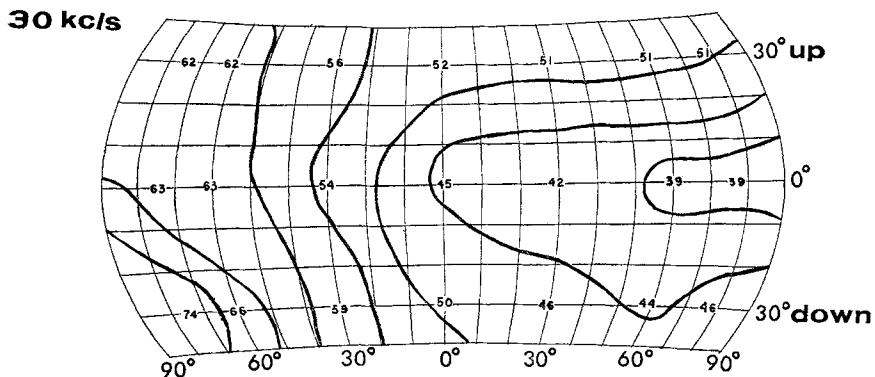


Fig. 6. *Syconycteris*. Evoked potentials recorded near the cochlear nuclei, showing sustained repetitive negative response peaks. Top: response to a 20 msec tone pip of 50 kc/s, +80 db. Lower traces: responses to 1 msec, 50 kc/s tone pips of +80db intensity, at repetition rates of 80, 200, and 400/sec.
Time calibration, 5 msec

above the horizontal axis and about 30–45° to the side. In addition, there is conspicuous binaural interaction, sharpening sensitivity to changes in signal angle at neural levels central to the auditory nerve



contra ipsi

Fig. 7. *Macroglossus*. Angular sensitivity maps showing N_1 thresholds (db re 0.0002 dyne/cm²) to tone pips of 30, 45, and 55 kc/s at points from 80° ipsilateral to 80° contralateral in the plane of the lower jaw and 30° above and below this plane. Lower numbers represent greater sensitivity. Equal sensitivity contour lines are drawn at 5 db intervals. Note the sharp increase in directionality from 30 kc/s to 45 kc/s. Maximum sensitivity at all frequencies was on the horizontal axis and at 60–80° to the side

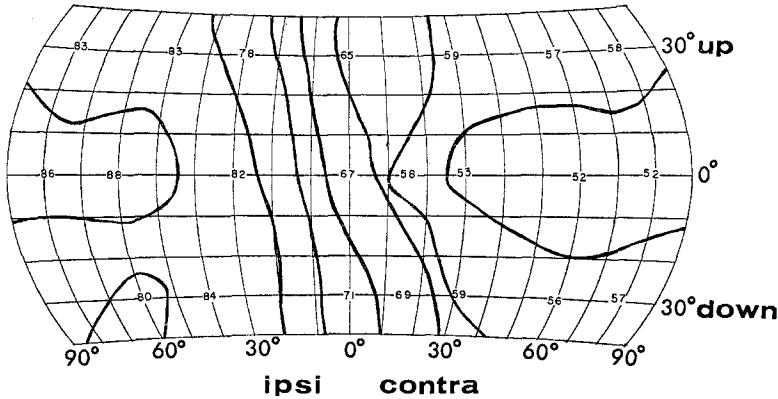


Fig. 8. *Roussettus*. Characteristic record showing directionality of sensitivity at 45 kc/s, plotted as in Fig. 7

(N_1) (Grinnell, 1963c, d; Grinnell and Grinnell, 1965). The non-echolocating bats studied in New Guinea all had relatively simple pinnae pointing approximately 60° laterally. Maximum sensitivity at the level of either auditory nerve was uniformly seen at 60 – 75° to the side, with a drop-off of 15 – 20 db directly ahead. Second order neural responses (N_2) recorded in the medulla reflected the mixing at the superior olive of inputs from cochlear nuclei on both sides of the brain. Sensitivity was often bimodal, high at 60 – 75° on either side, low directly in front of the animal. At the level of input to the colliculi (N_4), the directional sensitivity curve was approximately a mirror image of the N_1 pattern. At both levels, changes were generally less sharp than in equivalent measurements on microchiropteran bats. Maximum rates of change in sensitivity with signal angle were 0.5 db/degree over short arcs, and maximum differences between angles of greatest and least sensitivity from one side of the bat to the other seldom exceeded 40 db. As in echolocating bats, directionality of sensitivity increased with frequency. Fig. 7 shows maps of N_1 sensitivity at different angles at 30 , 45 , and 55 kc/s in *Macroglossus*. This preparation was unusual both in its relatively great sensitivity to change in signal angle and in the fact that sensitivity fell off more sharply above and below the horizon than across the midline. More characteristic of all of the species is the record of Fig. 8 showing N_4 sensitivity at 45 kc/s in *Roussettus*. Generally, there were no obvious differences between *Roussettus* and the non-echolocating bats studied. None showed any conspicuous adaptations for analyzing sounds coming preferentially from in front of the bat, or for sharpening sensitivity to signal angle by increasing binaural interaction.

Discussion

The evoked potential response patterns of non-echolocating megachiropteran bats are essentially like those of other small mammals not specialized for echolocation. The frequency of greatest sensitivity is higher than in other mammals of equivalent or smaller size, such as mice (Ralls, 1967), but in most other respects, the differences are slight. This strengthens the conclusion that the auditory adaptations of echolocating bats that appear useful for echolocation (sharpened audiogram in the range of echolocation frequencies, general high frequency sensitivity, extremely fast temporal resolution, facilitation of response to "echoes", and sharply directional hearing) are in fact adaptations for echolocation, rather than a characteristic of bats in general.

The independently evolved auditory specializations of *Rousettus*, the only megachiropteran known to echolocate, reinforce this conclusion. *Rousettus* shows no obvious external morphological adaptations for echolocation (enlarged or front-directed pinnae, modified mouth or nasal structures); and in most neurophysiological response parameters *Rousettus* is not different from nonecholocating relatives. In one important respect, however, *Rousettus* is dramatically different: recovery of responsiveness following an initial sound (such as an echolocation click) is essentially as rapid as in echolocating microchiropterans, with full recovery in just over 2 msec, compared with 5–12 msec in other megachiropteran bats studied. Clearly the ability to respond sensitively to frequencies as high as 50–60 kc/s does not automatically permit fast temporal resolution. This seems to require adaptation in central processing mechanisms. *Rousettus* appeared also to have slightly sharper frequency resolution than other megachiropterans, but this difference was slight and could have been the result of inadequate sampling.

The echolocation clicks of *Rousettus* are not greatly different from the clicks produced at a high repetition rate in the "screams" of *Macroglossus* or *Syconycteris*. It would be of interest to determine whether these species might be able to obtain some information from echoes, especially if forced to live in total darkness for some time.

References

- Griffin, D. R., Novick, A., Kornfield, M.: The sensitivity of echolocation in the fruit bat, *Rousettus*. Biol. Bull. **115**, 107–113 (1958).
- Grinnell, A. D.: The neurophysiology of audition in bats: Intensity and frequency parameters. J. Physiol. (Lond.) **167**, 38–66 (1963a).
- The neurophysiology of audition in bats: Temporal parameters. J. Physiol. (Lond.) **167**, 67–96 (1963b).
- The neurophysiology of audition in bats: Directional localization and binaural interaction. J. Physiol. (Lond.) **167**, 97–113 (1963c).

- Grinnell, A. D.: The neurophysiology of audition in bats: Resistance to interference. *J. Physiol. (Lond.)* **167**, 114–127 (1963d).
- Mechanisms of overcoming interference in echolocating animals. In: *Animal sonar systems*, ed. R-G. Busnel, p. 451–481. Jouy-en-Josas. Imprimerie Louis-Jean (Gap) 1967.
- Comparative auditory neurophysiology of neotropical bats employing different echolocation signals. *Z. vergl. Physiol.* **68**, 117–153 (1970).
- Grinnell, V. S.: Neural correlates of vertical localization by echo-locating bats. *J. Physiol. (Lond.)* **181**, 830–851 (1965).
- Hagiwara, S.: Adaptations of the auditory nervous system for echolocation; studies of New Guinea bats. *Z. vergl. Physiol.* **76**, 41–81 (1971).
- Henson, O. W. Jr.: The activity and function of the middle ear muscles in echolocating bats. *J. Physiol. (Lond.)* **180**, 871–887 (1965).
- The perception and analysis of biosonar signals by bats. In: *Animal sonar systems*. (R. G. Busnel, ed.) tome II, p. 949–1003. Jouy-en-Josas. Lab. Physiol. Acoust. 1967.
- Kulzer E.: Flughunde erzeugen Orientierungslaute durch Zungenschlag. *Naturwissenschaften* **43**, 117–118 (1956).
- Nelson, J. E.: Behavior of Australian Pteropidae (Megachiroptera). *Anim. Behav.* **8**, 544–557 (1965).
- Ralls, K.: Auditory sensitivity in mice: *Peromyscus* and *Mus musculus*. *Anim. Behav.* **15**, 123–128 (1967).
- Suga, N.: Recovery cycles and responses to frequency modulated tone pulses in auditory neurons of echolocating bats. *J. Physiol. (Lond.)* **175**, 50–80 (1964a).
- Single unit activity in cochlear nucleus and inferior colliculus of echo-locating bats. *J. Physiol. (Lond.)* **172**, 449–474 (1964b).
- Analysis of frequency modulated sound by auditory neurones of echolocating bats. *J. Physiol. (Lond.)* **179**, 26–53 (1965a).
- Functional properties of auditory neurons in the cortex of echolocating bats. *J. Physiol. (Lond.)* **181**, 671–700 (1965b).
- Analysis of frequency-modulated and complex sounds by single auditory neurones of bats. *J. Physiol. (Lond.)* **198**, 51–80 (1968).
- Echo-ranging neurons in the inferior colliculus of bats. *Science* **170**, 449–452 (1970).
- Vasiliev, A. G.: A comparative description of the auditory system of bats: *Vespertilionidae* and *Rhinolophidae* (electrophysiological data). *Dokl. Akad. Nauk SSSR* **175**, 1414–1417 (1967).

Dr. A. D. Grinnell
 Department of Zoology, UCLA
 Los Angeles, California 90024
 U.S.A.