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Echolocation by the Long-eared Bat, *Plecotus phyllotis*

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Summary. The echolocating bat, *Plecotus phyllotis* (Vespertilionidae), uses long-CF/FM and FM sonar sounds in different situations. The CF component in long-CF/FM sounds occurs at 27 kHz and has a duration of 20 to 200 ms. The FM component sweeps down from 24 to 12 kHz, with a prominent second harmonic from 40 to 22 kHz. This second harmonic sweep is interrupted at 28 to 25 kHz, providing a notch in the spectrum of the FM component at the CF frequency. This notch probably permits isolation of CF and FM components in echoes for separate processing, thus avoiding mutual interference with the different kinds of target information the two components convey. The FM component is also used without the CF component as a sonar sound. Two other FM orientation sounds are used when the bat is in a confined space such as a room. One contains only the second and fourth harmonics of the 24 to 12 kHz fundamental sweep, while the other contains only the fifth harmonic. This bat's repertoire of sonar sounds closely matches the hearing capacities of the genus.

Introduction

Echolocating bats in the suborder Microchiroptera use constant-frequency (CF) and frequency-modulated (FM) signals for orientation. These two signals are combined into several different sound patterns by different species of bats (Simmons et al., 1975). CF and FM signals are used for different purposes, and the presence of one or the other in orientation sounds reflects the bat's interest in particular perceptual features of the environment. In very general terms, narrowband CF signals are used to detect targets, to determine target velocity, and probably to determine target direction by interaural intensity comparisons. FM signals, being broad in bandwidth, are used to form a multidimensional acoustic image to identify targets, to determine target range, and to determine target direction probably by interaural intensity, spectrum, and time comparisons (Altes, 1977; Simmons, 1977).

The sound patterns used by bats fall into three basic categories, FM/short-CF, short-CF/FM, and long-CF/FM sounds. The majority of bats apparently use only one type of sound, although some species are exceptions. For any one species using one type of sound, there are also variations in the characteristics of the sounds used in different situations. Echolocation is an adaptive perceptual system both within individuals and across species (Simmons et al., 1975; Pye, 1977).

Bats are a numerous group of animals found throughout the world. Bats using FM/short-CF sounds are widely distributed in both the New and Old World tropics and temperate zones, and short-CF/FM bats are widely distributed in all tropical regions, but bats using long-CF/FM sounds are found primarily in the Old World tropics and in warmer parts of Eurasia (Koopman, 1970; Fenton, 1972). Long-CF/FM sounds are used principally by the horseshoe bats (*Rhinolophidae* and *Hipposideridae*) of the Old World, and *Pteronotus parnellii* (*Mormoopidae*), of the New World tropics. The peripheral auditory systems of these bats are modified by the inclusion of unusually sharp mechanical tuning within the cochlea for frequencies in each bat's CF region (Bruns, 1976; Suga et al., 1975; Schnitzler et al., 1976). It appears likely that long-CF/FM echolocation, with associated auditory adaptations, may have evolved independently in the New World species and in several Old World families. Other Mormoopid bats (*Pteronotus suapurensis*, for example) use short-CF/FM sounds for orientation. Some of the *Emballonuridae*, *Phyllostomatidae*, and *Vespertilionidae*, as well as *Noctilio leporinus*, may use long-CF signal components in certain situations (Pye, 1977; Suthers, 1965).

Long-CF/FM echolocation confers upon bats the capability for perceiving target velocity from echo Doppler shifts and detecting fluttering motions of targets (Schnitzler, 1973; Griffin and Simmons, 1974). The use of long CF signals provides the bat with the basis for different prey detection and tracking strategies than those available to other bats not using such signals (Simmons et al., 1975). It is puzzling that such strategies, which seem to be exploited by so many Old World species, may be used extensively by only one species in the New World. Furthermore, although a number of species of *Rhinolophus* are found in Eurasia, no long-CF/FM bat is known from North America.

We report here observations on echolocation by the long-eared bat, *Plecotus phyllotis*. This species uses long-CF/FM sounds and several kinds of FM sounds in various situations. It may have evolved similar orientation behavior to other long-CF/FM bats without exaggerated mechanical tuning within the cochlea. The sonar signals of *P. phyllotis* are so structured that they themselves may supply the effect produced in other species by peripheral auditory tuning. At least one more previously unknown independent evolution of long-CF/FM echolocation seems to have occurred.

Methods

Bats of the species, *Plecotus (Idionycteris) phyllotis* (*Vespertilionidae*), were observed while foraging for insects at White Rock Spring, Red Rock Canyon, Spring Mountains, Clark Co., Nevada during October, 1975 and August 1976. The sonar sounds of these bats were recorded in several different situations. Mist nets were used to collect specimens for identification.

The sounds were recorded with a plastic-diaphragm condenser microphone similar to a previously-described type used for studies on bats (McCue and Bertolini, 1964). The signals were stored on a Pentek Model 110A portable instrumentation tape recorder and analyzed in detail with Fast Fourier transform programs in a Digital Equipment Corp. PDP-11/40 computer. The frequency structure of the sounds was observed in real time in the field with a portable frequency display device which shows frequency sweeps on an oscilloscope. Some additional observations were made of the bat's behavior with a Javelin Model 221 Night Vision Device.

Results

At intervals of 15 min to an hour individuals of the species, *P. phyllotis*, were observed to fly into the study location, forage for insects around Pinyon Pine (*Pinus monophylla*), and then fly out of the area. It was not possible to determine the total number of bats working through the location, although on several occasions at least two individuals were present simultaneously. None were seen until after darkness was complete.

These bats made very audible orientation sounds when approaching across the level canyon floor or when flying near vegetation. These sounds were distinctly tonal in quality, not like the faint "Ticklaute" produced by many species of bats employing entirely ultrasonic frequencies in their sounds (Griffin, 1958). The bats flew slowly and several times hovered when near vegetation and on a few occasions were observed to attack insects on or among the branches. These insects could not be identified but appeared to be small moths.

When flying in the open or near vegetation, *P. phyllotis* emitted predominantly long-CF/FM sounds of a type illustrated in Figure 1. The long-CF signal varied from 20 to 200 ms in duration, the FM signal varied from 2 to 5 ms in duration, and the intervening silent interval was typically 3 to 5 ms long. No initial FM component was observed to precede the CF signal, and one CF harmonic was present, at 27 kHz. In many instances long-CF/FM signals were interspersed with several FM signals; the bat could control the presence or absence of the CF component. In these flight situations the FM signals were all very similar, regardless of the status of the CF component. (Because higher harmonics in the FM signal were recorded when the CF signal was absent, it is unlikely that the CF signal was present but not detected due to the directional acoustical properties of the bat and the microphone.)

The terminal FM signal (or the isolated FM signal) used by flying *P. phyllotis* is shown in Figure 2, and its time-frequency structure is shown in Figure 3. Two harmonics predominate in these FM signals, a first harmonic from 24 to 12 kHz and a second from 40 to 22 kHz. The first harmonic in all of these signals that were recorded begins sweeping several kHz below the CF frequency of 27 kHz, and the sweep of the second harmonic is interrupted when it crosses the CF frequency. Weaker third and fourth harmonic sweeps often occur, too. The interruption of the second harmonic sweep at 25 to 28 kHz was not observed to be accompanied by interruption of the first harmonic, which is still near its maximum amplitude at 13 to 14 kHz (see Fig. 3).

When held in the hand or resting or flying in a closed space (in a room or a cage), the bat emitted purely FM signals of two somewhat different types

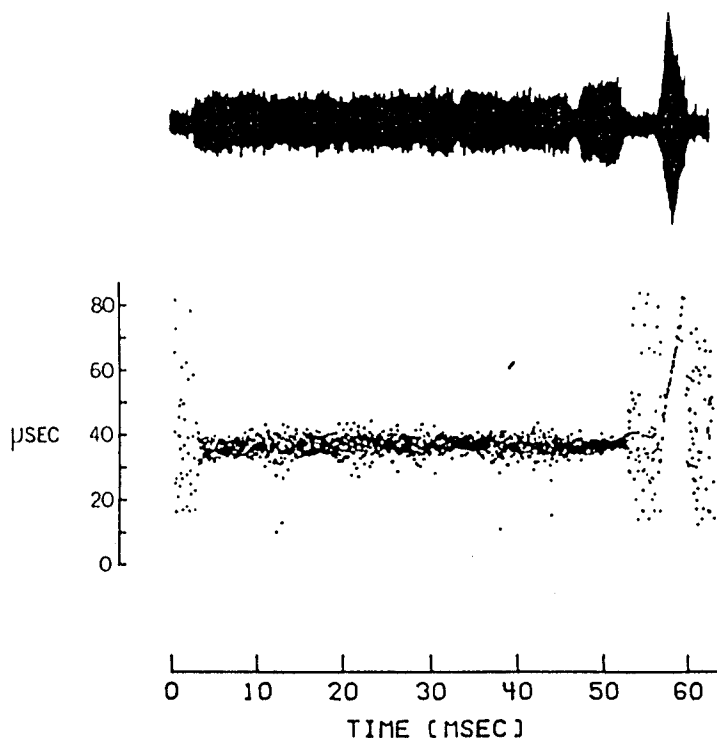


Fig. 1. The waveform and period structure of the long-CF/FM sonar sound of *Plecotus phyllotis*. When present the CF component varies from about 20 to 200 ms long and is separated from the 2 to 5 ms FM signal by a silent interval of several ms. The constant frequency is 27 kHz, and the principal (first) harmonic in the FM signal sweeps down to about 12 kHz. Note that the FM signal does not achieve substantial amplitude until after the sweep has moved down to about 24 kHz, resulting in a gap in the FM sound's spectrum at the frequency of the CF component (see text). The FM signal exhibits linear period modulation. The randomly-spaced dots before and after the signal are displays of zero-crossings from background noise

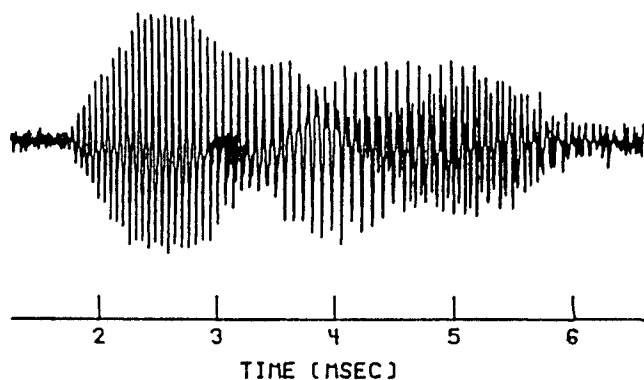


Fig. 2. The waveform of the FM sonar signal used by *P. phyllotis* in flight

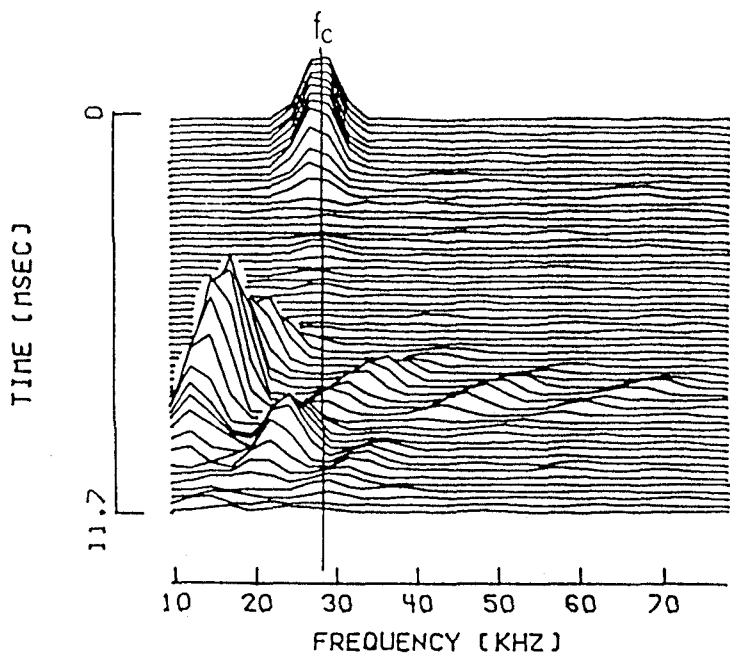


Fig. 3. The time-frequency structure (sound spectrogram) of the terminal FM signal in the long-CF/FM orientation sound of *P. phyllotis*. Note the presence of a first harmonic sweeping from 24 to 12 kHz and a strong second harmonic especially in the latter part of the sweep. A portion of the end of the CF signal (f_c) is shown for reference. Notice the absence of energy in the first and second harmonics in the region of f_c . Third and fourth harmonics sometimes are present but at low amplitudes

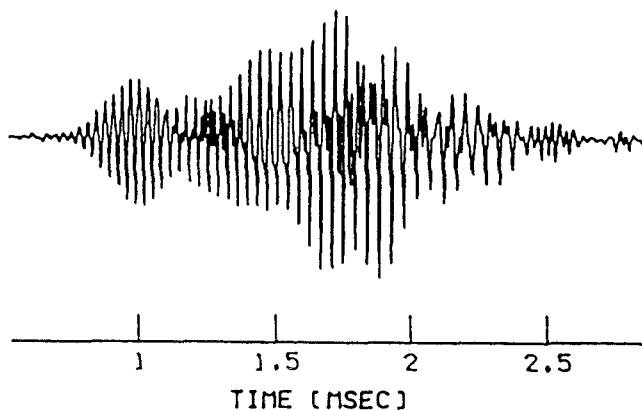


Fig. 4. Waveform of one type of FM sonar sound used by *P. phyllotis* in confined spaces. This signal covers an intermediate range of frequencies from 20 to 60 kHz

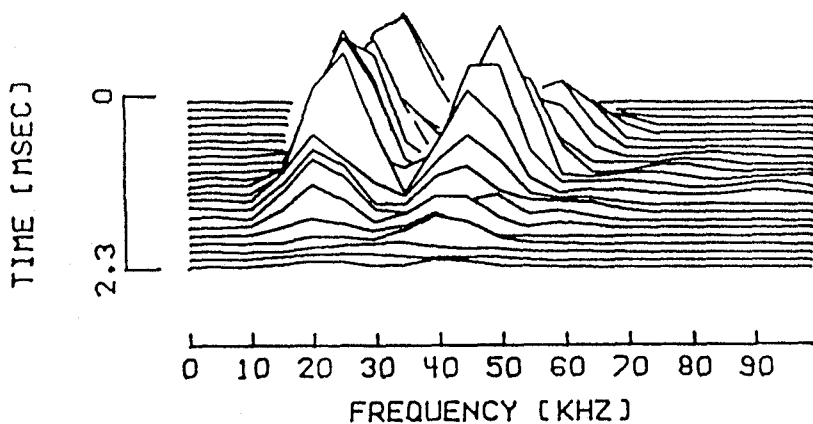


Fig. 5. Time-frequency structure of the intermediate-range signal shown in Figure 4. Note the first harmonic sweeping from 35 to 20 kHz, and the second harmonic sweeping from 60 to 40 kHz. This signal is similar to sonar sounds previously described from the genus *Plecotus*

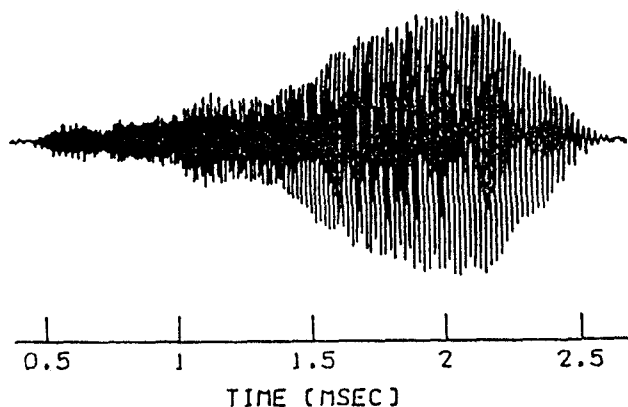


Fig. 6. Waveform of another type of FM signal emitted by *P. phyllotis* in confined spaces. This sound covers frequencies from 50 to 90 kHz

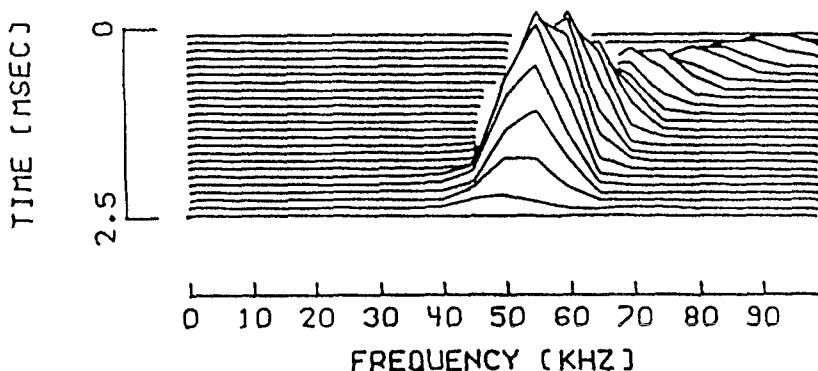


Fig. 7. Time-frequency structure of the FM signal shown in Figure 6. Note the single harmonic in the sweep

than the FM signal used in open flight. Figures 4 and 5 illustrate FM orientation sounds nominally containing a first harmonic from 35 to 20 kHz and a second from 60 to 40 kHz. This FM signal is very much like sounds used by a similar-sized species in the genus, *Plecotus townsendii* (Griffin, 1958; Griffin et al., 1963). It covers a range of frequencies intermediate between the long-CF/FM signal and the FM signal described next.

Occasionally *P. phyllotis* emits a third type of FM signal when in a confined space (Fig. 6). This sound contains a single harmonic sweeping from about 90 kHz down to 50 kHz (Fig. 7). These sounds were emitted with no obvious pattern interspersed among the FM sounds illustrated in Figures 4 and 5.

The intensities of the FM sounds used in confined spaces can be described as moderate, with sound pressures of about 2 to 5 N/m² at distances less than a meter from the bat. The long-CF/FM sounds used by *P. phyllotis* flying in the open were much stronger, with sound pressures often in excess of 10 N/m² for bats several meters away.

Discussion

Taken together, the three types of FM sonar signals used by *P. phyllotis* (Figs. 3, 5, and 7) exhibit a remarkable unity of design. The FM signal used in open flight (Fig. 3) contains a first harmonic terminating in a nearly-constant frequency of about 10 kHz. The structure of the other FM signals corresponds to second, fourth, and fifth harmonics of this first harmonic (Fig. 8). The intermediate-range FM signal contains the second and fourth harmonics, while the high-frequency FM signal contains the fifth harmonic. The FM signal recorded in the field contains first and second harmonics. None of the signals contained a sweep at the third harmonic, centering on 35 to 45 kHz, and this frequency region corresponds to a region of poorer auditory sensitivity in *Plecotus* (see below).

The CF signal occurs at 27 kHz with no prominent higher harmonics present. When the second harmonic of the associated FM signal sweeps through the region of 25-28 kHz, it is interrupted, surrounding the CF frequency with an empty band several kHz wide. This spectral notch corresponds to the range of frequencies in Doppler-shifted CF echoes from biologically relevant targets, moving at relative velocities of less than about 10 m/s. Figure 9 shows the power spectrum of the long-CF signal used by *P. phyllotis*, and Figure 10 shows the power spectrum of its associated FM component (see Fig. 3). The spectrum of the FM signal shows a sharp notch at 27 kHz, the frequency of the CF component. This null in the FM spectrum at the CF frequency is found in every example recorded. The FM signals recorded in confined spaces do not show such a spectral notch at 27 kHz (Fig. 5). The depth of the null is difficult to determine due to tape signal-to-noise ratios and limitations on frequency resolution during analysis.

The functional significance of the narrow empty band of frequencies in the FM signal around the CF frequency reveals the full significance of the discovery of long-CF/FM echolocation in *P. phyllotis* and demonstrates the

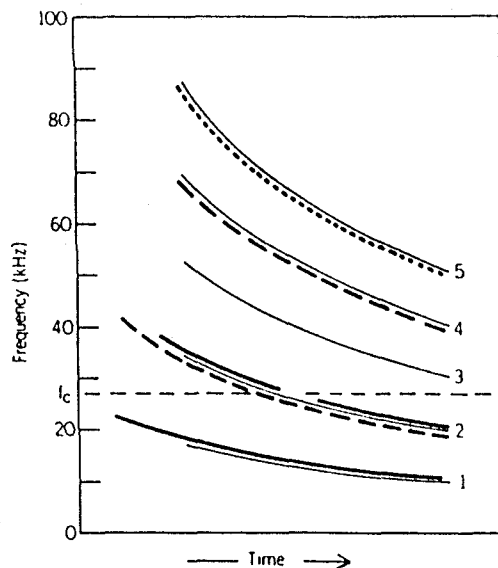


Fig. 8. Composite graph of the harmonic structure of the FM sonar sounds used by *P. phyllotis*. The five harmonic elements shown by light solid lines are numbered at the right, and various combinations of these harmonics appear in three FM sounds observed. Heavy solid lines indicate the first and second harmonics in the FM component of the bat's long-CF/FM sound. Dashed lines indicate the second and fourth harmonics in the intermediate-frequency FM sound, and dotted lines indicate the fifth harmonic in the high-frequency FM sound. None of these sounds contains substantial third harmonics. Note the interruption of the second harmonic in the region of f_c for the FM component of the long-CF/FM sound

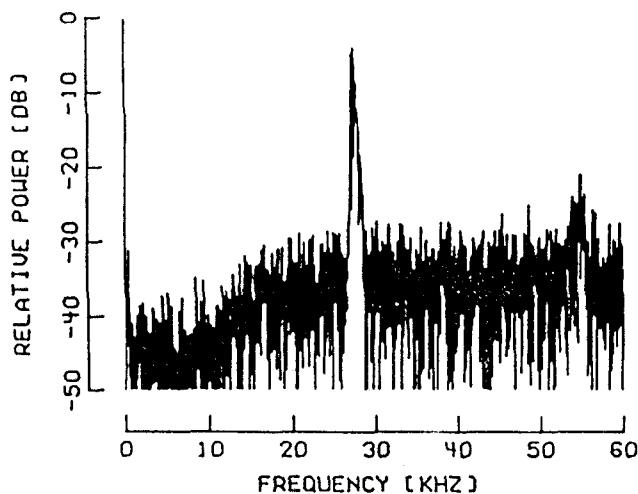


Fig. 9. The power spectrum of the CF component in a long-CF/FM sonar sound emitted by *P. phyllotis*

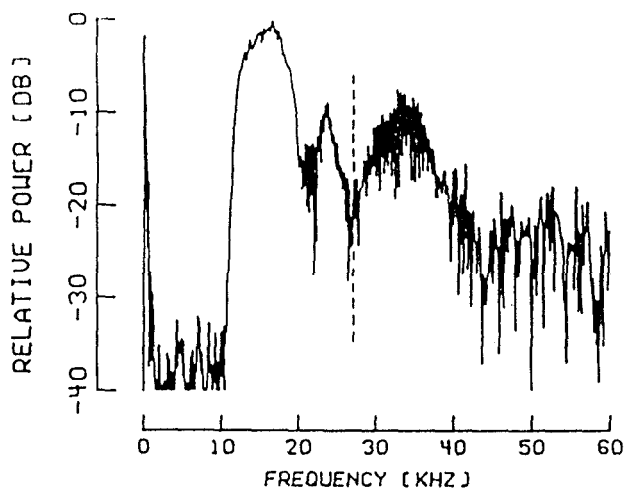


Fig. 10. The power spectrum of the FM component in a long-CF/FM sonar sound. The dashed vertical line indicates the CF frequency (Fig. 9). Note the sharp notch in the FM spectrum at the CF frequency, caused by interruption of the FM sweeps at this point. The fine variations in the spectrum around 20 kHz and 30 to 35 kHz are produced by overlap of harmonic elements at these frequencies

importance of communications theory in sensory science. In general, the FM signal is used to gather information about a number of target features, and salient among these is target range. The CF signal is used for target detection and target velocity determination from echo Doppler shifts (Grinnell, 1973; Schnitzler, 1973; Simmons et al., 1975). The use of FM signals by virtually all echolocating Microchiropteran bats indicates that FM functions such as target ranging must be basic to almost every perceptual situation encountered.

The acuity of target range perception depends upon the characteristics of the FM signal used by the bat; it quantitatively depends upon the nature of the autocorrelation function for the FM signal, or upon signal bandwidth (Simmons, 1973; Simmons et al., 1975). If CF signals associated with the FM sweep are sufficiently long in duration, as apparently is the case for long-CF/FM bats but not for short-CF/FM bats, the poor bandwidth of the CF component can degrade the bandwidth of the sonar sound, reducing the acuity of perception of target range. It becomes vital to perception of target features with FM echoes to separate the CF and FM components into distinctly different sonar receivers for processing. In bats this means that separate groups of neurons must be used to extract information from CF and FM echo components. The action of such a filtering mechanism in preserving good target range resolution in the long-CF/FM bat, *Rhinolophus ferrumequinum*, has been demonstrated behaviorally (Simmons, 1973).

Figure 11 shows the autocorrelation functions for the FM component and for the entire long-CF/FM sound used by *P. phyllotis*. These functions can be considered to be impulses with time-interval resolving power equal to that

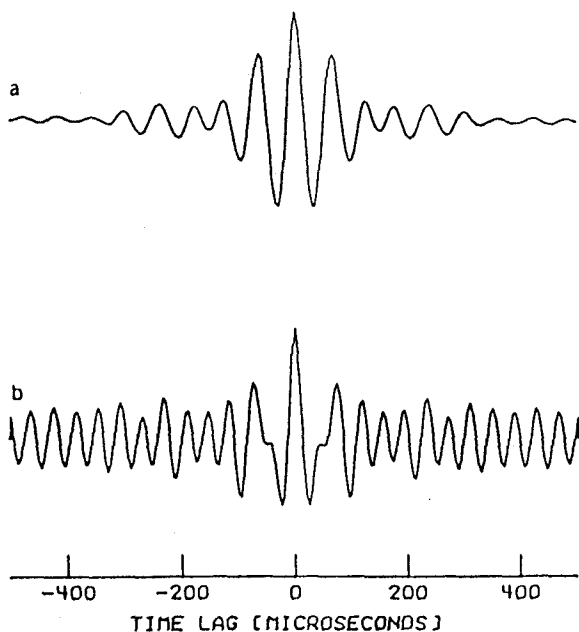


Fig. 11 a and b. Autocorrelation functions for the FM component (a) and the entire long-CF/FM sound (b) used by *P. phyllotis*. The vertical axis shows the magnitude of correlation (between ± 1.0) at each time lag on the horizontal axis. These graphs indicate the temporal resolving power of the sonar signals (see text). Inclusion of the CF component greatly widens the region of peaks in the autocorrelation function, degrading temporal resolution

of the original FM or long-CF/FM sounds. The process of determining the time-of-arrival of returning echoes (and, hence, target range; Simmons, 1973) depends upon detecting the region of peaked waves in the vicinity of zero time lag on these autocorrelation functions. If the time region containing substantial peaks is wide, time-interval and target range resolution will be poor. Notice in Figure 11 that the peaks in the autocorrelation function for the FM component alone (a) are sharply concentrated around $\pm 100 \mu\text{s}$, while the region of substantial peaking in the autocorrelation function of the long-CF/FM signal extends beyond the $\pm 500 \mu\text{s}$ scale of the graph. This means that *P. phyllotis* could detect target range differences as small as $\pm 2 \text{ cm}$ with the FM signal alone, but it could not detect range differences smaller than $\pm 10 \text{ cm}$ with the entire long-CF/FM signal.

The peripheral auditory system in *Plecotus townsendii* appears to be similar to that of the FM bat, *Myotis* (Grinnell, 1963), and different from that of other long-CF/FM bats such as *Rhinolophus* and *Pteronotus* (Suga et al., 1975; Schnitzler et al., 1976; Suga et al., 1976). In FM bats first- and second-order single auditory neurons that code frequencies used for echolocation exhibit moderately sharp tuning, with $Q_{10\text{dB}}$ values ranging from about 5 to 20. Neurons

found in long-CF/FM bats for FM frequencies also have Q_{10dB} values averaging about 10. These values reflect a fairly uniform degree of mechanical tuning at points along the basilar membrane corresponding to FM frequencies in echolocating bats. Neurons so far found in long-CF/FM bats for frequencies in the region of the CF signals are very sharply tuned, with Q_{10dB} values from 50 to 200. These neurons convey information from points on the basilar membrane, corresponding to CF frequencies, where mechanical specialization has led to unusually fine frequency resolution (Bruns, 1976). In long-CF/FM bats that have been studied previously, the extremely sharp tuning of neurons to CF frequencies presumably provides for good frequency discrimination to perceive Doppler shifts and to isolate CF and FM signals into separate populations of neurons for processing.

In *P. townsendii* there is no evidence for unusually sharp tuning in neurons with best frequencies around 27 kHz (Grinnell, 1963). However, *P. phyllotis* may exhibit sharper tuning at these frequencies; it could only be determined conclusively through electrophysiological studies on this species. *Pteronotus suaveurensis* shows less tuning of this kind than *P. parnellii*, for example (Grinnell, 1973). If *P. phyllotis* is similar to *P. townsendii* and bats in the genus *Myotis*, the mutual isolation of CF and FM signals would be accomplished not by finely distinguishing CF and FM components in the cochlea, but by separating CF and FM bands in the transmission (Fig. 10). The notch in the FM spectrum around 26 to 28 kHz is wide enough to contain the CF transmission as well as biologically reasonable Doppler-shifted echoes.

Can *P. phyllotis* determine target velocities from CF echo Doppler shifts? The CF components are certainly sufficiently long (20 to 200 ms) to provide good frequency determination as the basis for perceiving Doppler shifts (Simmons et al., 1975). However, in the absence of extremely sharply-tuned neurons ($Q_{10dB} = 100$) at 26 to 28 kHz, neural place coding of the magnitudes of Doppler shifts may not be sufficiently precise. For targets at reasonable ranges (up to perhaps 10 m) the CF transmissions and echoes will overlap, generating difference frequencies (beats) in the auditory system. From most moving targets beats might occur at any frequencies from zero to several kHz, and there is abundant evidence that phase-locked discharges in peripheral auditory neurons of long-CF/FM bats can code information about such difference-frequency beats as well as about amplitude and frequency modulations from insect wing-beats (Schuller, 1974; Suga et al., 1975; Vasiliev, 1976). The animal's capability for discrimination of beat frequencies may be sufficiently acute to detect small changes in echo Doppler shifts, although it is not now clear how the direction of the Doppler shift would be determined. Since relative velocities of significance would most probably involve the bat closing in on a slower target, the direction of Doppler shifts may in practice always be positive.

Besides the utility of long-CF/FM signals for acquiring target velocity information, they are useful for the fundamental task of detecting the presence of targets at all. The relatively great energy concentrated in a narrow frequency band can overcome noise interference or echo weakness if targets are small or far away and result in successful detection when FM echoes alone are not

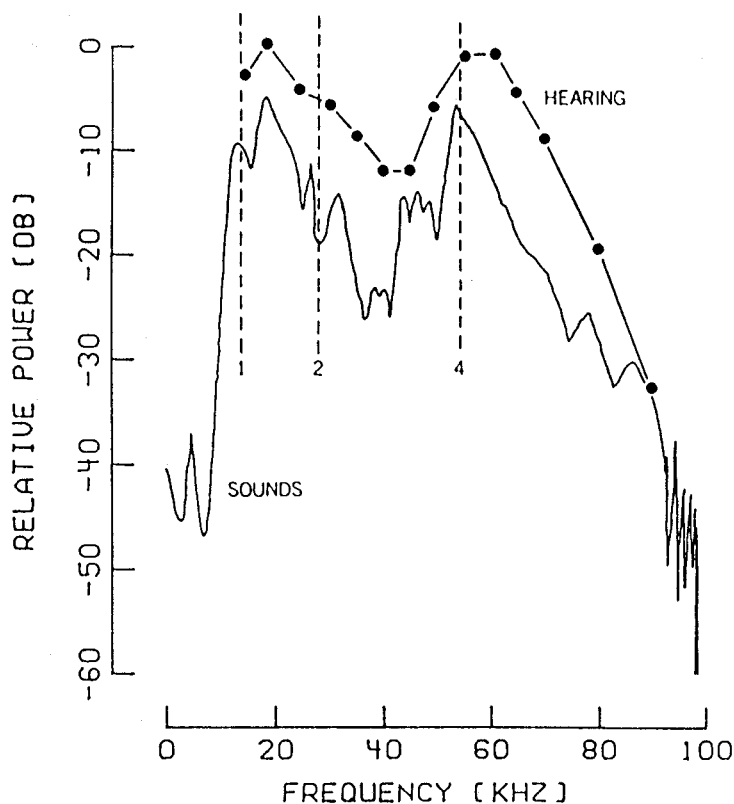


Fig. 12. Graph comparing the composite power spectrum of the sonar sounds of *P. phyllotis* with the N_4 -audiogram of a closely-related species, *P. townsendii*. The curves reveal a close relationship between vocal repertoire and hearing. For the audiogram, the vertical scale represents decibels of hearing loss for frequencies different than the frequency of maximum sensitivity. The dashed lines indicate the frequency of maximum amplitude in the first harmonic (1), the CF frequency and frequency of maximum amplitude in the second harmonic as it occurs in intermediate-range sounds (2), and the frequency of maximum amplitude in the fourth harmonic (4)

audible (Grinnell, 1973; Simmons et al., 1975). Although temporal summation of stimulus energy has not been studied in bats, the influence of stimulus duration upon absolute thresholds in mice (Ehret, 1976) suggests that CF durations up to several hundred milliseconds are appropriate for target detection. *P. phyllotis* uses a rather low frequency for its CF component compared to other long-CF/FM bats, and it might obtain relatively greater maximum operating ranges for echolocation than other long-CF/FM bats, due to the smaller amounts of atmospheric attenuation at lower frequencies (Griffin, 1971).

Long-duration CF signals can convey information about fluttering motions of interesting targets such as moths. Amplitude and frequency modulations imposed upon CF echoes by moving targets may be useful to the bat as criteria for identifying prey. *Rhinolophus* can detect small amounts of target flutter in this way (E. Fliieger, personal communication), and such motions are clearly

represented in the bat's nervous system (Schuller, 1972; Johnson et al., 1974). *P. phyllotis* may be able to recognize prey from amplitude and frequency modulation of CF echoes. Again, in the absence of very sharply-tuned neurons around 27 kHz, beat frequencies between outgoing and returning signals may be important in detecting frequency shifts.

The power spectra for the different orientation sounds recorded from *P. phyllotis* were superimposed to form a composite spectrum for the bat's repertoire of sonar emissions. This composite spectrum is shown in Figure 12, together with the hearing sensitivity of another, closely-related species in the genus *Plecotus*. The auditory thresholds are represented by an audiogram derived from N_4 evoked potentials (Grinnell, 1963). As Figure 12 indicates, the hearing of *Plecotus* seems to match very closely the spectral composition of the sonar sounds. Assuming that the species within this genus do not differ significantly in echolocation behavior, it appears as though the vocal emissions and auditory capabilities of these bats have been closely coupled during evolution of the genus.

The observations reported here do not clarify exactly what aspects of the acoustic environment and the bat's perceptual interests determine which of the different sonar sounds will be emitted. They also do not give any indication that the sounds may be systematically alternated or that there is structure to the trains of emitted signals used by *P. phyllotis* as it goes through a particular echolocation task. Data are needed from the field on this bat's insect pursuit behavior and sonar sounds, and data are needed from the laboratory on this bat's ability to perceive CF echo Doppler shifts and to adapt to acoustic interference. Furthermore, observations of other species which may glean insects from surfaces or vegetation (*Macrotus* and *Antrozous*, for example) are needed to determine whether long-CF/FM echolocation without mechanical specialization of the cochlea may be widespread among bats. Clearly, laboratory observations cannot be trusted to reveal the entire repertoire of echolocation signals by bats. Finally, neurophysiological investigations should begin to elucidate the mechanisms for processing CF echo information in *P. phyllotis*, unless this species' survival would be endangered by collection of subjects for research.

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