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# THE ACTIVITY AND FUNCTION OF THE MIDDLE-EAR MUSCLES IN ECHO-LOCATING BATS

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In most vertebrates the visual system plays a dominant role in orientation, allowing animals to orient themselves with respect to their environment and to assess the size, shape, distance, nature and movements of objects. During the past 20 years, largely through the efforts of Donald R. Griffin and co-workers, it has become increasingly apparent that the auditory system of bats is capable of performing these same functions. Indeed, laboratory experiments have shown that bats can perform remarkable feats without the aid of vision. Flying at speeds of 3–4 m/sec they can detect 1 mm diameter wires at a distance of 2 m, fly unhindered through an array of 0·2 mm diameter wires, and capture mosquitoes and fruit flies at rates of up to two/sec (Grinnell & Griffin, 1958; Griffin, Webster & Michael, 1960).

This is accomplished by echo-location, that is, the emission of ultrasonic pulses and the subsequent perception and analysis of echoes. Ordinarily the emitted pulses are frequency modulated with the fundamental frequency sweeping one octave or less downward during each cry. The frequency range usually lies between 150 and 12 kc/sec and the peak-to-peak sound pressures, when measured at distances of 3–10 cm from a bat's mouth, average from 70–80 db (re-0·0002 dyne/cm$^2$) in so-called 'whispering' bats, to values well above 100 db (re-0·0002 dyne/cm$^2$) in loud bats (Griffin & Novick, 1955; Griffin, 1958; Novick, 1958, 1962, 1963*b*). These and other pulse characteristics vary, not only from species to species, but within the same species depending upon the activity of the animal. Indeed, on the basis of changes in the pulse characteristics, different phases of echo-location can be recognized. In the case of *Myotis* hunting fruit flies, echo-location can be divided into a *search* phase, an *approach* phase and a *terminal* phase (Griffin *et al.* 1960; Griffin, 1962).

During the *search* phase each emitted pulse has a duration of 2–3 msec, and the pulse repetition rate is about 10–20/sec. The emitted pulses appear to have peak-to-peak sound pressures of 109 db (at a distance of 10 cm from the bat's mouth) and the fundamental frequency of each pulse sweeps about one octave, from 100 to 50 kc/s. Flying at speeds of 3–4 m/sec, *Myotis* appear to be able to detect 15–30 db echoes from fruit flies at distances ranging from 50 to 100 cm.

After the detection of an insect, the *approach* phase begins. This is characterized by a progressive shortening of the interval between pulses such that the pulse repetition rate increases from approximately 25/sec up to 66/sec. The pulse duration may shorten somewhat but the frequency sweep remains about the same as during the search phase. As the bat approaches to within 10 cm of the insect, the echo intensity is probably 70 db or more.

The *terminal* phase begins when the bat is only a few centimetres from its prey; during this phase the pulse duration shortens to 0·3–0·5 msec and the pulse repetition rate increases to as high as 250/sec. The intensity of the pulses usually decreases during this phase and the frequency sweep also decreases such that each cry contains only a small number of waves having a frequency of about 30 kc/sec.

These different phases have also been studied in *Pteronotus* (Novick, 1963*a*) and *Chilonycteris* (Novick & Vaisnys, 1964) and are basically similar to those described in *Myotis* as far as pulse repetition rates are concerned. *Myotis*, however, appear to shorten their pulses such that no pulse-echo overlap occurs (Cahlander, McCue & Webster, 1964), while *Pteronotus* and *Chilonycteris* seem to regulate the duration of their pulses to assure pulse-echo overlap.

As indicated by neurophysiological studies of Grinnell (1963*a*), the threshold sensitivity of a bat's ear is probably, at best, of the order of zero db (0·0002 dyne/cm$^2$). During the pursuit and capture of insects, however, the conditions would seem to be far from optimal. A bat's ear is only about 1 cm from the mouth and it seems that the high sound pressures of the emitted pulses would reach the ear by air, tissue or bone conduction. As Griffin (1958) and others have pointed out, this raises some rather interesting problems with respect to acoustic physiology. It is known, for instance, that the auditory threshold increases (by as much as 80 db) when the ear is exposed to loud sounds. This has been shown from subjective sensitivity studies on man (Rosenzweig & Rosenblith, 1950; Licklider, 1951) and neuro-physiological studies on bats (Grinnell, 1963*a*; Grinnell & McCue, 1963) and cats (Rosenzweig & Rosenblith, 1950, 1953; Rosenzweig & Amon, 1955; Rosenzweig & Wyers, 1955; Rosenzweig & Sutton, 1958; Peake, 1960; Wigand, 1960). In these studies it was shown that the louder a first stimulus and the shorter the interval between it and a second stimulus, the greater the loss in sensitivity for the second stimulus. Since loud pulses, short intervals and relatively faint echoes are the physical characteristics of stimuli facing an echo-locating bat, how can a bat's auditory system be in a sensitive state for the perception of echoes? In addition, no satisfactory explanation has been offered to account for the ability of bats to detect and analyse overlapping echoes which would seem likely to be masked by the outgoing pulses.

Protection of the bat's delicate inner ear from the high sound pressures of the emitted pulses would appear to be necessary. This is indicated by the occurrence of acoustic trauma, permanent hearing losses and serious distortions of the cochlear potentials in experimental animals after exposure of the ear to loud sounds (Stevens & Davis, 1938; Wever & Lawrence, 1954). The means by which bats accomplish this protection has not been resolved. It is known, however, that the middle-ear muscles of these animals are extremely well developed and richly innervated (Staněk, 1933; Henson, 1961; Wever & Vernon, 1961) and their reflex contractions attenuate sound energy reaching the ear (Galambos, 1942; Wever & Vernon, 1961). In fact, Hartridge (1945) has suggested that the sensitivity of the bat's ear may be maintained by contractions of the middle-ear muscles during pulse emission. Griffin (1958), Grinnell (1963*b*) and others, however, have doubted that the middle-ear muscles could contract and relax at the extremely rapid rates at which pulses are emitted. Furthermore, it has not seemed likely that the muscles could function in this manner without adversely affecting the sensitivity of the ear during the silent period between pulses.

In this investigation the physiological responses of the cochlea and middle-ear muscles were monitored in bats actively engaged in echolocation. The results give some indication of the role of these muscles in relation to the auditory problems discussed above.

## METHODS

Mexican free-tailed bats (*Tadarida brasiliensis mexicana*, Saussure) were chosen as experimental animals for this investigation because they adapt easily to captivity and are tolerant of anaesthesia and major surgical procedures. Furthermore, they are well-adapted for terrestrial locomotion and emit loud orientation sounds as they scurry about avoiding obstacles and capturing mealworms placed in their vicinity.

A total of nineteen *Tadarida* collected from New Mexico and Texas were used. In captivity they were kept in small wire cages or lived as part of a colony in a laboratory flight room. They were maintained on a diet of mealworms and 'glop' (equal parts of banana, cream cheese, egg yolk and mealworms).

Anaesthesia was achieved with an intraperitoneal injection of 0·5 mg (0·05 mg/g body weight) of sodium pentobarbitone (Nembutal) in 0·1 ml. of physiological saline. Electrodes were chronically implanted on the round window of the cochlea in all preparations, and in three bats an additional electrode was placed in the stapedius muscle. The exposure of these structures and the implantation of electrodes was accomplished by making a seven-shaped incision over the temporal region. The incision extended along the mid-sagittal line, from the level of the external auditory meatus back to the nuchal crest, and then ventrally to the level of the bulla. The skin flap was reflected, the posterior portion of the temporalis muscle removed and the underlying bone scraped clean and thoroughly dried with the aid of an air jet. The exposed bone was coated with a thin layer of dental cement (Caulk 'Grip' Cement, L. D. Caulk Co., Milford, Delaware). After this an indifferent electrode was placed in the parotid gland and cemented to the base of dental cement; this base layer was used to anchor all subsequently implanted electrodes.

For implanting an electrode in the stapedius muscle a small hole was drilled in the lateral wall of the *cavum m. stapedius* and a platinum wire (0·002 in. diameter) was introduced into the substance of the muscle and sealed in place with dental cement. The round window was exposed by cutting a small flap in the cartilaginous wall of the bulla; after reflecting this an insulated stainless-steel wire (0·05 in. diameter), with the tip melted into a ball, was manoeuvred into the opening and adjusted on the round window until the best microphonic responses elicited by a variety of acoustic stimuli were obtained. The cartilaginous flap was then sealed back in place and the electrode was cemented to the base layer of dental cement. Recovery periods of from several days to a week were generally necessary before the animals became normally active. Of nineteen preparations, eleven were successful and physiological recordings were made over periods of from several weeks to more than a month. All the recordings were made while the animals were scurrying about on a recording platform.

A custom-built condenser loudspeaker (designed after Kuhl, Schödder & Schröder, 1954) was employed for generating high-frequency sounds ranging from 15 to 150 kc/sec. The equipment for recording action potentials from the stapedius muscle consisted of a low-level preamplifier (Grass Instrument Co., Model P-5), a band-pass filter (Krohn-Hite, Model 310-AB) for improving the signal-to-noise ratio, and a dual-beam oscilloscope (Tektronix, Model 502) for displaying the signals. The displayed records were photographed with a high-speed kymograph camera (Grass Instrument Co., Model C-4).

The cochlear microphonic potentials were amplified with a low-level preamplifier (Keithly Instrument Co., Model 103); the signal-to-noise ratio was greatly improved with the aid of band-pass filters. The pulses emitted by the bats were usually detected with a custom-made condenser (Granath) microphone and appropriate amplifier systems. Measurements of sound pressure in db (re-0·0002 dyne/cm$^2$) were made with a microphone amplifier (Bruel and Kjaer, Model 2604) in combination with a calibrated ¼ in. condenser microphone (Bruel and Kjaer, Model 4135). All decibel notations used in this report are relative to 0·0002 dyne/cm$^2$.

## RESULTS

### *Stapedius muscle activity during vocalization*

Simultaneous recordings of stapedius-muscle action potentials and cochlear microphonic potentials were used to assess the activity of the stapedius muscle during vocalizations. A typical record showing the muscle action potentials and their time of appearance in relation to cochlear potentials elicited by a bat's own cry is shown in Fig. 1*A*. This and several hundred similar records showed that stapedius muscle activity always preceded the emission of each orientation pulse. The beginning of this activity, however, seemed to vary with pulse duration and pulse repetition rate. When *Tadarida* emitted 3–4 msec pulses at repetition rates of 50/sec or less, the action potentials either began or there was a notable increase in their amplitude and number, about 10 (6–15) msec before each pulse was emitted. With shorter pulses and at pulse repetition rates of 60–80/sec the appearance of action potentials preceded the beginning of each pulse by approximately 6 (4–8) msec. At still higher pulse repetition rates, at least up to 100/sec, the potentials were more or less continuous, or an increase in their number and amplitude occurred just before the emission of each pulse. Regardless of the pulse rate the potentials normally ceased within one or two msec of the beginning of each pulse.

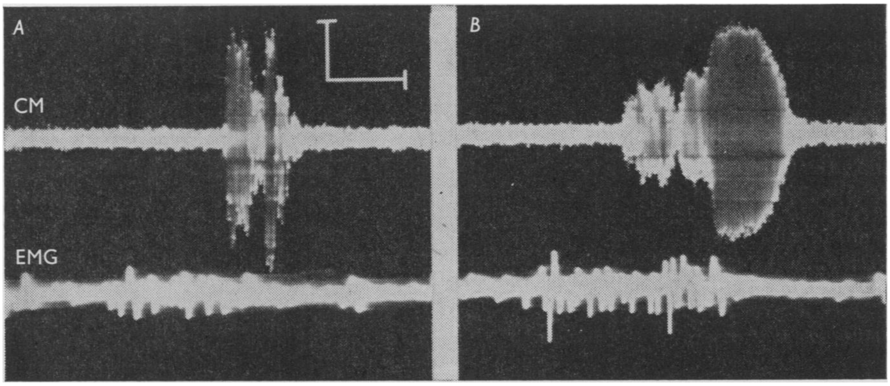

Fig. 1. Cochlear microphonic potentials (CM) elicited by a bat's own orientation pulse (*A*), and by a loud screech (*B*). The lower record (EMG) shows action potentials from the stapedius muscle. Horizontal bar represents 5 msec interval, and vertical bar 30 $\mu$V.

When stapedius muscle potentials were recorded in association with loud 'audible' screeches (Fig. 1*B*) or other non-orientation sounds with long durations (10–30 msec), the potentials again began in advance of each sound, in some cases by as much as 30 msec. The potentials ceased, however, either just before or up to 10 msec after the completion of each cry.

In another set of experiments the bats were placed in pure tone (16–60 kc/sec) sound fields and changes in the amplitude of the cochlear potentials elicited by the tone were used to assess the degree of muscle contraction and relaxation. Under these conditions the amplitude of the cochlear potentials was attenuated before pulse emission, but rapidly restored to the original value within 10 msec of the beginning of each pulse (Fig. 2*B*), again showing that muscle contractions occurred before pulse emission. In one bat the stapedius muscle was removed and the bat recovered sufficiently to emit a few pulses. In this bat there was no attenuation of the microphonic potentials (Fig. 2A) which suggests that only the stapedius, and not the tensor tympani, was responsible for the observed attenuations. Attempts to repeat this experiment were unsuccessful as the bats either refused to emit pulses or died from excessive bleeding.

Many records, including those in Fig. 3, showed that contractions of the stapedius muscle attenuated microphonic potentials elicited by frequencies normally included in the orientation cries of *Tadarida*. These records also indicated that as the pulse repetition rate increased above 50 pulses/sec there was less and less time available for the muscle to build up tension and attenuate the microphonic potentials; similarly, the time available for relaxation was reduced. When the pulse repetition rate reached 140/sec (the highest rate recorded from *Tadarida*) little or no change in the amplitude of the microphonic potentials was observed before or after the emission of each pulse (Fig. 3*D*). It should be noted, however, that when the pulse repetition rate was 100/sec (Fig. 3*C*) the microphonic amplitude often diminished as the series of pulses was emitted, and at 140 pulses/sec the potentials were attenuated well in advance of the first pulse in the series. In the latter case complete muscle relaxation did not occur until about 40 msec after the last pulse. Thus, at fast pulse repetition rates the stapedius muscle appears to be, at least in part, in a state of tonic contraction.

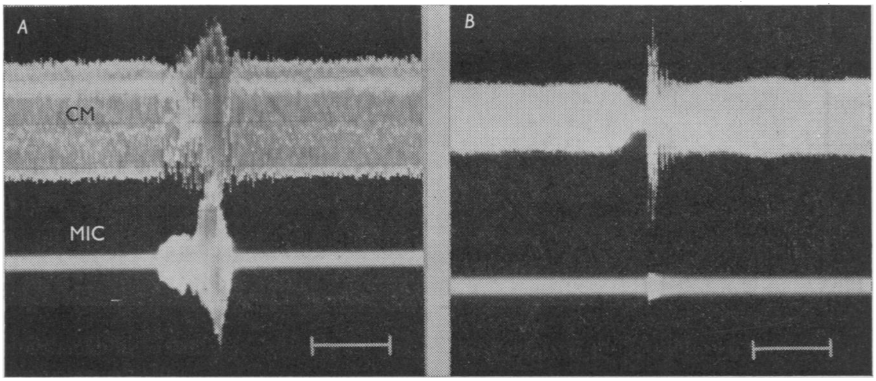

Fig. 2. Cochlear microphonic responses elicited by pure tone sound fields and orientation pulses (CM), and the cries as detected by a microphone (MIC). *A*. Response to 55 kc/sec tone with stapedius muscle removed, and *B* response to 10 kc/sec tone with stapedius muscle intact. Time bar represents 5 msec in *A* and 20 msec in *B*).

### *Attenuation of cochlear potentials*

From records similar to those shown in Fig. 3 it was possible to calculate the amount of attenuation provided by stapedius-muscle contractions before, during and after the emission of a pulse. This was done by measuring the amplitude (in microvolts) of the potentials at millisecond intervals and comparing the values with intensity function curves determined for the same bat. If, for example, a 30 kc/sec tone produced a 100 $\mu$V potential when the free-field sound pressure was 80 db, and a 10 $\mu$V response when the sound pressure was 60 db, a similar change in amplitude resulting from stapedius muscle contraction would be equivalent to 20 db of attenuation.

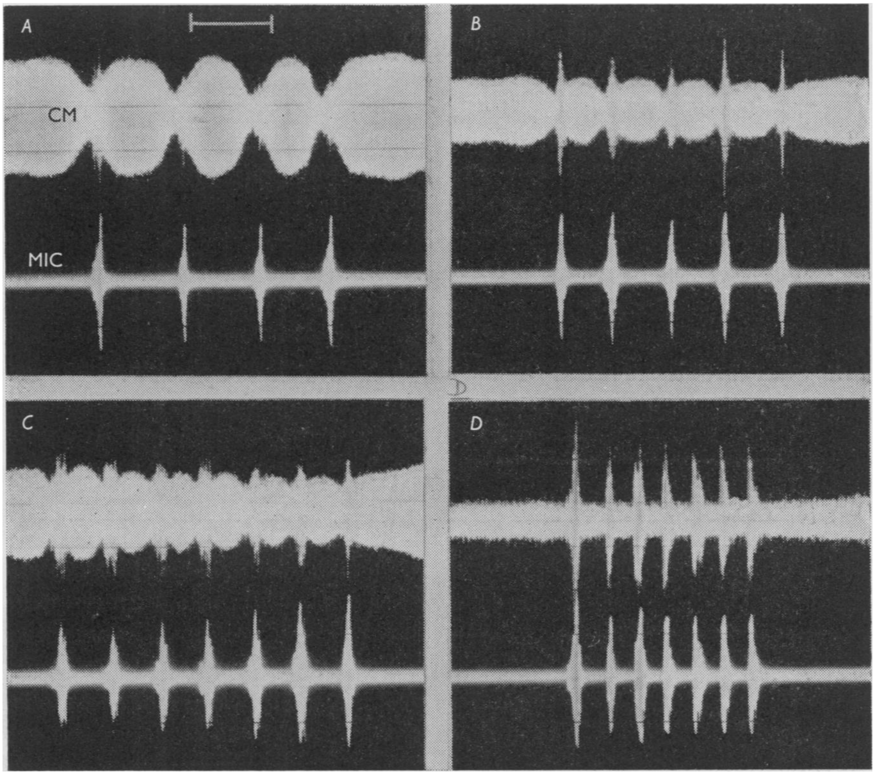

Fig. 3. Cochlear microphonic potentials elicited by pure tone sound fields and by the emitted cries (CM) at various pulse repetition rates; *A*, 25 kc/sec tone with a pulse repetition rate of approximately 60/sec; *B*, 15 kc/sec tone with a pulse repetition rate of approximately 80/sec; *C*, 40 kc/sec tone with a pulse repetition rate of 100/sec; and *D*, 15 kc/sec tone with a pulse repetition rate of 140/sec. Time bar in *A* represents 20 msec; *B*, *C* and *D* on same scale.

The data shown in Fig. 4 were obtained from records taken from the only bat which consistently emitted pulses at repetition rates ranging from a few to 140/sec. The values shown represent the average attenuation which occurred over millisecond intervals of three pulses in a given series. Three other bats from which similar measurements were made did not emit pulses at rates above 80/sec; nevertheless, the time and rate of amplitude change of the cochlear potentials were similar to those shown in Fig. 4 when similar pulse repetition rates were compared. The maximum amount of attenuation, however, varied from 12 to 22 db, with an average of 18 db, for forty-three different records where the pulse repetition rate was 50/sec or less.

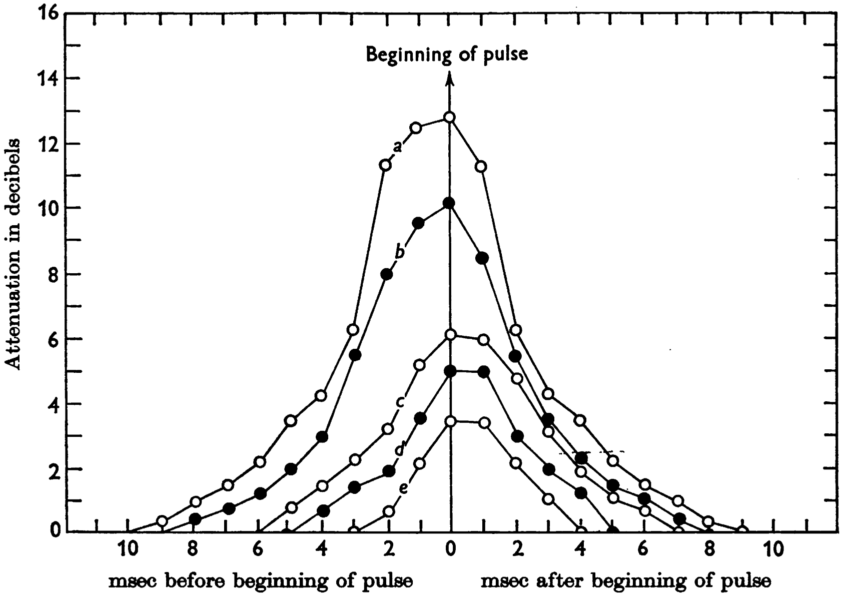

Fig. 4. Attenuation of cochlear potentials in association with pulse emission. Values shown are the average attenuations for three pulses in a given series at various pulse repetition rates. Curve *a* 50 pulses/sec; *b* 63/sec; *c* 83/sec; *d* 100/sec; and *e* 140/sec.

### *Cochlear potentials elicited by cries and echoes*

In *Tadarida* the cochlear microphonic responses evoked by the cries of another bat had the same general characteristics (frequency, duration, and shape) as the pulses detected by a microphone placed nearby. In these cases it could be shown that the middle-ear muscles did not contract until a few milliseconds after each cry was completed. On the other hand, when the microphonic responses elicited by a bat's own cries and echoes were recorded, the potentials were quite different owing to middle-ear muscle modification of cochlear input and microphonic output. As shown in Fig. 5 the first part of the microphonic response to each cry was attenuated in comparison with the output of the microphone. The responses shown in Fig. 5 were recorded from bats scurrying about on a table top. The high-amplitude portion of each response appeared to be evoked by strong echoes which returned to the bat's ear from the nearest vertical obstacles (an array of electronic equipment). When the bats faced the echo source the terminal high-amplitude portion of the response was very prominent

(Fig. 5*A* and *B*) but when they faced other directions the echo response was relatively faint (Fig. 5*B*) or absent.

In many records (see Fig. 5*B* and *C*), the echoes detected by the microphone appeared to be more intense than the emitted pulses. This varied, however, and was due to the fact that the microphone was usually more

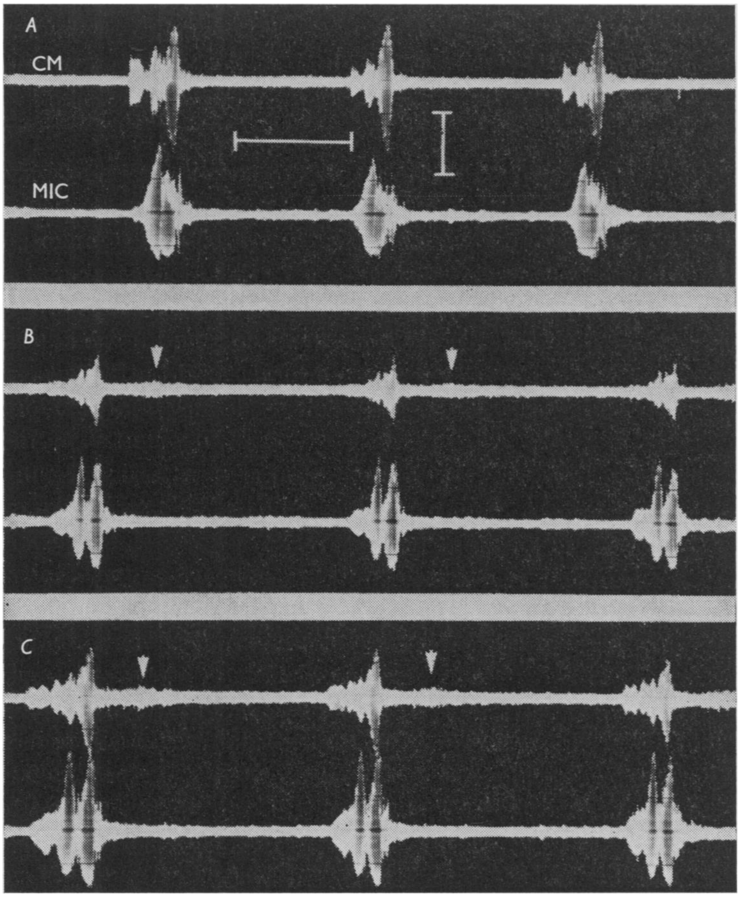

Fig. 5. Cochlear microphonic responses elicited by a bat's own cries and the returning echoes (CM) and the cries and echoes as detected by a microphone (MIC). In Fig. 5*A*, the microphone was not favourably oriented to detect the echoes, but in Figs. 5*B* and 5*C* it was more favourably oriented to detect the echoes than the pulses. In all the CM responses shown the first part of each record is that elicited by the outgoing cry and the high amplitude terminal portion is the echo response. *B* and *C* are continuous records; note that the CM response to echoes increases as the bat apparently turns toward the echo source. Vertical bar in *A* represents 50 $\mu$V and horizontal bar represents 10 msec. Faint echoes from a distant source are marked with arrows in *B* and *C*.

favourably oriented for detection of echoes than emitted cries. Nevertheless, the echoes returning to the bats under the experimental conditions were ordinarily quite loud since they returned to the ears within 1 or 2 msec. The closest wall of the room was about 2 m from the bats and in many cases echoes from this wall appeared to evoke small, but distinct microphonic responses (Fig. 5*B* and *C*).

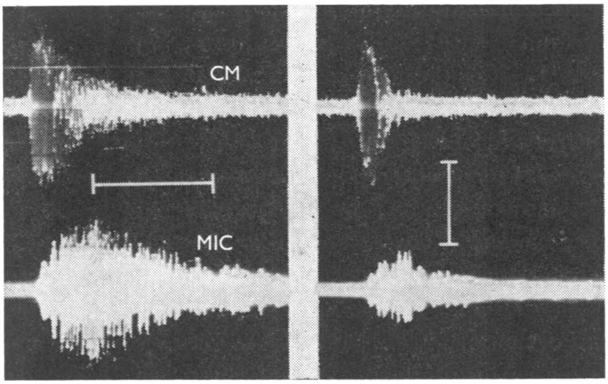

Fig. 6. Microphonic responses elicited by a bat's own cries (CM) and the cries as detected by a microphone (MIC). Recorded from a bat emitting pulses in a small closed chamber where the echoes overlapped the emitted pulses. Horizontal bar represents 10 msec and vertical bar 40 $\mu$V.

Two bats were placed in a small metal chamber (50 cm × 25 cm × 27 cm) such that the echoes would overlap the outgoing cries. Figure 6 shows typical microphonic responses recorded under these conditions as compared with overlapping cries and echoes as detected by a microphone placed near the top of the box. The responses recorded in the metal chamber differed from those recorded when the bats emitted cries in the open. The most notable difference was that the initial microphonic response to each cry had a high amplitude; in fact, the amplitude was equivalent to that obtained when the bat's ear was stimulated with sound pressures of 95 db or more. This high amplitude may be attributed to very short echo delay and high echo intensities reaching the ear. The cochlear potentials also had short durations compared to sounds as detected by the microphone. The microphone probably detected the pulse and all the reverberating echoes while the bat's ear was much more directional (due to the pinnae) and only the echoes reflected directly back into the ear elicited high amplitude microphonic potentials.

### *Pulse sound pressures reaching the bat's ear*

When pulses were recorded by a microphone placed several centimetres in front of a bat's mouth, the peak-to-peak sound pressures averaged 105 db. The maximum sound pressures were usually reached during the second millisecond of each 3–4 msec pulse, when the fundamental frequency was sweeping from approximately 40–30 kc/sec. In order to determine the intensity of the sounds reaching the ear the amplitude of the microphonic responses elicited by a bat's own cries was measured from records similar to those shown in Figs. 5 and 6. Only the 48 most intense pulses were measured; hence the sound pressures were probably well above 100 db. When pulses were emitted in the open, the peak amplitude of the potentials ranged from 30–60 $\mu$V with an average of 42 $\mu$V. These responses were equivalent in amplitude to those obtained when the bat's ear was stimulated with 30–40 kc/sec tones ranging in intensity from 65 to 75 db. On the other hand, when pulses were emitted in confined spaces, such that there was little or no significant echo delay, the amplitude of the potentials was equivalent to that normally obtained when the ear was stimulated with 30–40 kc/sec tones with free-field sound pressures of 95 db or more. Thus, it appears that a bat's own cries may not be loud to the ear unless the cries are reflected directly back into the ear.

## DISCUSSION

### *The function of the middle-ear muscles*

The results of this investigation generally support Hartridge's (1945) hypothesis that the middle-ear muscles of bats contract during the emission of each ultrasonic pulse and relax between pulses so that the ear is protected and maintained in a sensitive state for the perception of echoes. At pulse repetition rates employed by bats during the *search* and *approach* phases, the stapedius muscle seems well adapted to perform this function. By being strongly contracted before the emission of each pulse, the stapedius muscle can relax as the pulse begins and still provide protection when the peak sound pressures are emitted. Furthermore, since the muscle relaxes over the duration of each cry, the echo energy is more efficiently transferred across the middle ear than is the preceding pulse energy, provided, of course, that the echo returns before contractions preceding the next cry begin.

As mentioned previously, Hartridge's theory has not been widely accepted on grounds that it did not seem probable that the muscles could contract and relax at very rapid rates without attenuating the echoes (Griffin, 1958; Grinnell, 1963*b*). To be sure, the results show that as the pulse repetition rate rises above 50/sec, the time available for the stapedius muscle to contract before, and relax after, each pulse decreases until, at pulse repetition rates of about 140/sec, the muscle appears to remain tonically contracted while an entire series of pulses is emitted. At very fast pulse repetition rates (140 and above), stapedius muscle contractions would, therefore, attenuate both the outgoing cries and the returning echoes. It is only during the *terminal* phase, however, that pulses are normally emitted at these fast rates and since the echoes are relatively loud at this time the attenuation may not interfere with echo perception. In fact, some degree of stapedius muscle contraction may be beneficial for the analysis of echoes, especially during the terminal phase when sound pressures of echoes returning to the ear may well rise above 70 db. This is suggested by the fact that the stapedius muscle reflex threshold in *Tadarida* is normally exceeded when sound pressures of this magnitude stimulate the ear. Also, in cases of stapedius muscle paralysis in man, an irritability for normal sounds may develop if the sound pressures are 70 db or more; the spoken voice (as heard through a telephone) for instance, may become indistinct, uncomfortably loud, and annoying (Perlman, 1938). In this respect it is interesting to note that vampires, frugivorous and nectar feeding phyllostomatid bats and others which generally fly close to large obstacles characteristically emit faint pulses, and also, that loud bats reduce the intensity of their pulses during the terminal phase. This suggests that loud echoes are not desirable and that different mechanisms may be used to reduce echo intensity under certain conditions.

Assuming that the magnitude and recovery time of evoked neural potentials (N4) are a measure of auditory sensitivity, it is possible to show how effective the stapedius-muscle contractions may be for maintaining the sensitivity of the ear. Grinnell (1963*b*) has shown that brief pure tone pulses (45 kc/sec) with sound pressures of 90 db (re-threshold) seriously affect the recovery of N4 potentials in *Myotis*. With a silent interval of 0·6 msec between two identical pulses, he found that the amplitude of the evoked response to the second stimulus was only 10% of that elicited by the first pulse alone. With silent intervals of 1·0, 2·0, and 4·0 msec, the recovery was 30, 45 and 60%, respectively. Similar experiments with intense frequency-modulated pulses have shown the same effect and indicate that the neural elements are not completely recovered until approximately 12 msec after each pulse (Grinnell & McCue, 1963). Since the cries of *Myotis* have peak-to-peak sound pressures of 109 db when measured by a microphone placed 10 cm in front of the bat's mouth, it would not appear that the auditory sensitivity would be sufficiently recovered to detect faint echoes within a few milliseconds after the completion of each cry. Griffin, Webster & Michael (1960), however, have calculated that *Myotis* can detect 15–30 db echoes from mosquitoes and fruit flies within 0–3 msec after the completion of each 2–3 msec pulse.

On physiological grounds, the ability of *Myotis* to detect echoes of this magnitude after short delays becomes more plausible if it is assumed that the stapedius muscle and other mechanisms function (as they do in *Tadarida*) to blank out the emitted cries. Indeed, Grinnell's results indicate that for every 10 db attenuation of pulse sound pressure (between 90 and 50 db; re-threshold) the sensitivity of the ear for a second stimulus may improve approximately 5 % after a 1 msec silent period, and 10 % after 2 and 4 msec silent periods. Thus, if middle-ear muscle contractions provide 20 db of attenuation the ear would appear to be about 20 % more sensitive after 2–3 msec than it would be if no muscle contractions occurred.

The recovery may be even greater, as the results presented here show that there is attenuation of pulse sound pressures reaching the ear in addition to that provided by middle-ear muscle contraction. This attenuation was evident from those records showing that the amplitude of the cochlear microphonic responses elicited by a bat's own cries (emitted in the open) was equivalent to that normally obtained when a 65–75 db tone was used to stimulate the ear. Since the emitted pulses probably had sound pressures over 100 db, and since the stapedius muscle contractions provided a maximum attenuation of 20db (usually less), the remaining attenuation of at least 5–15 db must be attributed to other mechanisms. This attenuation was also evident from records showing that the cochlear microphonic responses elicited by a bat's own cry (emitted in the open) were about 16 db less than those evoked by cries and echoes in a confined space where the echo delay was minimal. Under the experimental conditions there was always a surface beneath the bats which must have reflected a certain amount of pulse energy back into the ear. This would not normally be encountered in flight; hence the actual pulse sound pressures reaching the ear of a flying bat may be less than 65–75 db.

No studies were made to determine the mechanisms responsible for this constant attenuation. The most likely mechanisms, however, are forward beaming of the emitted pulses and the directional characteristics of the external ear (see Griffin, 1958; Grinnell, 1963*a*; Wever & Vernon, 1961). In any event, the attenuation provided by stapedius-muscle contraction and that by other mechanisms seems to amount to at least 30 db and perhaps more. This suggests that many of the auditory neurones in the bat's brain may be 75 % recovered after 2 msec when all attenuating mechanisms are considered. Obviously, the greater the attenuation, the greater the recovery of neural elements would seem to be. Indeed, if stimuli reaching the ear are less than 40 db and are of relatively high frequencies, Grinnell's studies indicate that there may be as much as a

20 db gain in sensitivity. While the peak sound pressures reaching the ear are not as low as this in *Tadarida*, the pulse sound pressures at the beginning of each pulse may be near this order of magnitude. It is interesting to note that the stapedius muscle exerts its greatest effect at the beginning of each pulse when the frequency is high, that high frequencies are beamed to a greater extent than low frequencies, and that the external ears are more directional to high than to low frequencies.

### *Distance determination by bats*

The effects on high frequencies described above could be of considerable importance if target distance is measured by echo delay, that is, from the beginning of the emitted pulse to the beginning of the echo. The idea that bats can detect or evaluate the beginning of an echo has not been widely accepted, especially in those cases where pulse-echo overlap occurs. Thus other theories have been advanced which advocate the perception of time-difference tones (Nordmark, 1960, 1961) or beat-notes (Pye, 1960, 1961*a*, *b*; Kay, 1961*a*, *b*, 1962). The results from *Tadarida*, however, indicate that under many conditions the echoes may sound louder to a bat than the emitted pulse and that these echoes can be perceived whether they overlap the pulse or not. Furthermore, Grinnell & McCue (1963) reported that the auditory neurones in a bat's brain can recover very rapidly if the preconditioning stimulus is a faint FM pulse. In fact they found instances where complete recovery occurred within 0·7 msec after the beginning of an FM pulse, even if the second stimulus (a pure tone with the same frequency as the beginning of the preconditioning FM pulse) overlapped the FM pulse. Thus, from their data and the results of this investigation it seems likely that bats can detect echoes which overlap the outgoing pulse, and possibly that they can measure distance by assessing the time delay between the beginning of the pulse and the beginning of the echo, or from the beginning of a given frequency in the cry and the return of that frequency in the echo. This method of determining target distance would seem to be much more accurate than that of measuring silent intervals, beat-notes or time-difference tones since variations in pulse duration and frequency sweep would be of no importance.

### *Stapedius-laryngeal muscle co-ordination*

There are several lines of evidence suggesting that contractions of the stapedius muscle are co-ordinated with contractions of the laryngeal muscles. In *Tadarida* the times of appearance and disappearance of stapedius-muscle action potentials is similar to the times of appearance and disappearance of laryngeal muscle action potentials recorded from *Myotis* and a number of other genera by Novick & Griffin (1961). The time and rate of stapedius-muscle relaxation in *Tadarida* correspond to that which would be expected of the cricothyroid muscle which is seemingly responsible for the frequency sweep of a bat's pulse. Furthermore, both the frequency and the frequency sweep diminish as the pulse-repetition rate increases, just as the amount of contraction and relaxation of the stapedius muscle diminishes as the pulse-repetition rate increases. If contractions of the muscles of the middle ear and larynx are synchronized during vocalization it would seem that the emission of frequency modulated pulses would be well suited for echolocative purposes since the stapedius muscle would relax over the duration of each pulse in the manner and with the results described above. The use of other types of pulses, especially those involving prolonged stapedius and laryngeal muscle activity would not seem to be as well suited as FM pulses. They could be effectively utilized, however, if the pulse characteristics, the associated middle-ear muscle contractions, the forward beaming of the emitted pulses and the directional characteristics of the ears were designed so that they did not effect the sensitivity of the ear for echoes. In this respect there are several possibilities: (1) the pulses could be of very high frequency so that the middle-ear muscles would not attenuate the sound energy; (2) the pulses could be of very short duration and/or of low intensity so that only minimum stapedius muscle contractions occur; or (3) the pulses could be very loud, highly beamed pure tones, so that the echoes would be loud enough to be perceived and evaluated even though the muscles were contracted throughout the pulse duration. In addition the external ears could be designed and oriented to favor echo rather than pulse perception. Indeed, these or a combination of these pulse characteristics are known to be used by various species of bats (Moehres, 1953; Griffin & Novick, 1955; Griffin, 1958; Novick, 1958, 1962, 1963*b*). Perhaps a bat's sensitivity for echoes is in part controlled by the relation between stapedius-laryngeal muscle contractions and the physical characteristics of the pulses. In some species, such as *Tadarida*, stapedius-muscle contractions may aid in the perception and analysis of echoes. In other species, such as *Rhinolophys*, *Chilonycteris* and 'whispering' bats middle-ear muscle contractions may either facilitate or perhaps not hinder the detection and evaluation of echoes.

## SUMMARY

1. Cochlear microphonic potentials and stapedius-muscle action potentials were recorded from bats (*Tadarida brasiliensis mexicana*) actively engaged in echo-location.

2. The stapedius muscle contracted before each vocalization. Muscle contractions usually began 4–10 msec before the emission of orientation pulses and a maximum state of contraction was achieved just before, or

at the time each pulse began. Stapedius-muscle relaxation began immediately and continued over the duration of each pulse. The muscle was completely relaxed (to its previous state) within 10 msec.

3. Since the stapedius muscle relaxed over the duration of each pulse, echo energy was more efficiently transferred across the middle ear than the preceding pulse energy. Thus, under many conditions the cochlear potentials elicited by echoes were greater in amplitude than those evoked by more intense outgoing cries.

4. Stapedius muscle contractions attenuated the pulse-sound pressures reaching the ear by 12–22 db when pulses were emitted at repetition rates of 50/sec or less. Smaller amounts of attenuation were provided at faster pulse repetition rates. At the fastest pulse repetition rates (140/sec), the stapedius muscle appeared to remain contracted while an entire series of pulses was emitted.

5. Other factors, probably forward beaming of the emitted pulses and the directional characteristics of the external ears, also appeared to attenuate the pulse-sound pressures reaching the ear.

6. The results of this investigation support Hartridge's (1945) hypothesis that the middle-ear muscles of bats contract during pulse emission and maintain the sensitivity of the ear for the perception of echoes. The tensor tympani muscle, however, does not seem to be involved in the attenuation of pulse-sound pressures.

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## REFERENCES

Cahlander, D. A., McCue, J. J. G. & Webster, F. A. (1964). The determination of distance by echolocating bats. *Nature, Lond.*, **201**, 544–546.

Galambos, R. (1942). Cochlear potentials elicited from bats by supersonic sounds. *J. acoust. Soc. Amer.* **14**, 41–49.

Griffin, D. R. (1958). *Listening in the Dark.* Yale: University Press.

Griffin, D. R. (1962). Comparative studies of the orientation sounds of bats. *Symp. zool. Soc. Lond.* no. 7, 61–72.

Griffin, D. R. & Novick, A. (1955). Acoustic orientation of neotropical bats. *J. exp. Zool.* **130**, 251–300.

Griffin, D. R., Webster, F. A. & Michael, C. E. (1960). The echolocation of flying insects by bats. *Anim. Behav.* **8**, 141–154.

Grinnell, A. D. (1963*a*). Neurophysiology of audition in bats: intensity and frequency parameters. *J. Physiol.* **167**, 38–66.

Grinnell, A. D. (1963*b*). Neurophysiology of audition in bats: temporal parameters. *J. Physiol.* **167**, 67–96.

Grinnell, A. D. & Griffin, D. R. (1958). The sensitivity of echolocation in bats. *Biol. Bull., Woods Hole,* **114**, 10–22.

GRINNELL, A. D. & MCCUE, J. J. G. (1963). Neurophysiological investigations of the bat, *Myotis lucifugus*, stimulated by frequency modulated acoustical pulse. *Nature, Lond.*, **198**, 453–455.

HARTRIDGE, H. (1945). Acoustical control in the flight of bats. *Nature, Lond.*, **156**, 490–494.

HENSON, O. W., JR. (1961). Some morphological and functional aspects of certain structures of the middle ear in bats and insectivores. *Univ. Kansas Sci. Bull.* **42**, 151–255.

KAY, L. (1961*a*). Perception of distance in animal echo-location. *Nature, Lond.*, **190**, 361.

KAY, L. (1961*b*). Orientation of bats and men by ultrasonic echo-location. *Br. Commun. Electron.* **8**, 582–586.

KAY, L. (1962). A plausible explanation of the bat's echo-location acuity. *Anim. Behav.* **10**, 34–41.

KUHL, W. C., SCHÖDDER, G. R. & SCHRÖDER, F. K. (1954). Condenser transmitters and microphones with solid dielectric for airborne ultrasonics. *Acustica*, **4**, 519–532.

LICKLIDER, J. C. R. (1951). Basic correlates of the auditory stimulus. In: *Handbook of Experimental Psychology*, ed. STEVENS, S. S. New York: Wiley and Sons.

MOEHRES, F. P. (1953). Über die Ultraschallorientierung der Hufeisennasen (Chiroptera-Rhinolophidae). *Z. vergl. Physiol.* **34**, 547–588.

NORDMARK, J. (1960). Perception of distance in animal echo-location. *Nature, Lond.*, **188** 1009–1010.

NORDMARK, J. (1961). Perception of distance in animal echo-location. *Nature, Lond.*, **190**, 363–364.

NOVICK, A. (1958). Orientation in paleotropical bats. I. Microchiroptera. *J. exp. Zool.* **138**, 81–154.

NOVICK, A. (1962). Orientation in neotropical bats. I. Natalidae and Emballonuridae. *J. Mammal.* **43**, 449–455.

NOVICK, A. (1963*a*). Pulse duration in the echolocation of insects by the bat, *Pteronotus*. *Ergebn. Biol.* **26**, 21–26.

NOVICK, A. (1963*b*). Orientation in neotropical bats. II. Phyllostomatidae and Desmodontidae. *J. Mammal.* **44**, 44–56.

NOVICK, A. & GRIFFIN, D. R. (1961). Laryngeal mechanisms in bats for the production of orientation sounds. *J. exp. Zool.* **148**, 125–146.

NOVICK, A. & VAISNYS, J. R. (1964). Echolocation of flying insects by the bat, *Chilonycteris parnelli*. *Biol. Bull., Woods Hole*, **127**, 478–488.

PEAKE, W. T. (1960). An analytical study of electric responses at the periphery of the auditory system. Tech. Report 365, M.I.T. Research Lab. of Electronics, Cambridge, Mass. (cited from GRINNELL, 1963*b*).

PERLMAN, H. B. (1938). Hyperacousis. *Ann. Otol.* **47**, 947–953.

PYE, J. D. (1960). A theory of echolocation by bats. *J. Laryng. Otol.* **74**, 718–729.

PYE, J. D. (1961*a*). Perception of distance in animal echolocation. *Nature, Lond.*, **190**, 362–363.

PYE, J. D. (1961*b*). Echolocation by bats. *Endeavour*, **20**, 101–111.

ROSENZWEIG, N. R. & AMON, A. H. (1955). Binaural interaction in the medulla of the cat. *Experientia*, **11**, 498–500.

ROSENZWEIG, N. R. & ROSENBLITH, W. A. (1950). Some electrophysiological correlates of the perception of successive clicks. *J. acoust. Soc. Amer.* **22**, 878–880.

ROSENZWEIG, N. R. & ROSENBLITH, W. A. (1953). Responses to auditory stimuli at the cochlea and at the auditory cortex. *Psychol. Monogr.* **67**, 1–26.

ROSENZWEIG, N. R. & SUTTON, D. (1958). Binaural interaction at the lateral lemniscus of cat. *J. Neurophysiol.* **21**, 17–23.

ROSENZWEIG, N. R. & WYERS, E. J. (1955). Binaural interaction at the inferior colliculi. *J. comp. Physiol. Psychol.* **48**, 426–431.

STANĚK, V. J. (1933). *Ktopografiké a srovnávací anatomi sluchoveho organu nasich chiropter.* Prague: Nakladem Ceské Akedemie ved a Umĕni.

STEVENS, S. S. & DAVIS, H. (1938). *Hearing.* New York: Wiley and Sons.

WEVER, E. G. & LAWRENCE, M. (1954). *Physiological Acoustics.* Princeton, N. J.: Princeton University Press.

WEVER, E. G. & VERNON, J. A. (1961). The protective mechanisms of the bat's ear. *Ann. Otol.* **70**, 1–13.

WIGAND, M. E. (1960). Hemmungserscheinungen an langsamen Rindenpotentialen beim Binauralhören der Katz. *Pflüg. Arch. ges. Physiol.* **271**, 296–315.