Audible and Ultrasonic Sounds of Bats[1]

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The problem of obstacle avoidance by flying bats—the sensory basis upon which obstacles are perceived in darkness—was solved almost simultaneously in Europe and in the United States during the years 1940–3. This sort of coincidence of scientific discoveries is not uncommon, and presumably it occurs when the times have become ripe for a certain advance, perhaps because the necessary preliminary steps have been taken and the opportunity is recognized at approximately the same time in two or more widely separated laboratories. The American work received its impetus from the discovery that bats produced intense ultrasonic sounds of approximately 50,000 cycles per second (PIERCE and GRIFFIN[3]). This provided experimental support for the earlier speculation of HARTRIDGE[4] that bats guide their flight through darkness by means of sounds above the frequency range of human hearing. Our studies established the fact that to avoid obstacles with any skill and success bats must be able to produce and detect high frequency sounds (GRIFFIN and GALAMBOS[5], GALAMBOS and GRIFFIN[6]). Bats collided even with large and conspicuous obstacles when we covered either the ears or the mouth. The ultrasonic sound is produced in short bursts or pulses, each of which is accompanied by a faint *audible* click, so faint that even in a quiet room we could ordinarily hear it only at a meter or less.

A short time later the problem was approached in quite a different way by DIJKGRAAF[7]. Listening in quiet surroundings he was able to hear audible sounds made by flying bats; these were described as "*Ticklaute*" (resembling the individual clicks from the winding of a lady's wrist watch), or when repeated rapidly as a "*Ratterlaut*". In a quiet room these ticking sounds were sometimes audible at a distance of several meters. DIJKGRAAF also demonstrated that a bat could only avoid obstacles when its mouth and ears were free to emit and to hear these pulses of sound.

The question then arises, were the faint audible clicks which we found to accompany the ultrasonic sounds of bats identical with the "*Ticklaute*" described by DIJKGRAAF? Conversely, can we conclude that the European bats which he studied emitted ultrasonic sounds to accompany each "*Ticklaut*"? Most of the bats employed in both investigations belong to the family *Vespertilionidae*, in our study *Myotis l. lucifugus* and *Eptesicus f. fuscus*, in DIJKGRAAF's observations, *Myotis emarginatus*, *Myotis daubentonii*, *Myotis nattereri*, *Myotis dasycneme*, *Eptesicus serotinus*, *Pipistrellus pipistrellus*, *Nyctalus noctula*, and *Plecotus auritus*. These bats are all very much alike in general morphology except for *Plecotus* which has extremely large ears. *Rhinolophus ferrum-equinum* and *Rhinolophus hipposideros* belong to a different family and may, as DIJKGRAAF suggests, employ the nasal apparatus rather than the mouth for sound emission[1]. Thanks to the cooperation of HL. DE VRIES, several live *Myotis l. lucifugus* were recently carried to DIJKGRAAF's laboratory for direct comparison with the European species of this genus. DIJKGRAAF has advised me by correspondence that in listening to the "*Ticklaute*" he "could not find any marked difference between this species and *Myotis emarginatus*".

It is also of considerable interest to determine what correlation there is between the faint audible click and ultrasonic sounds. Do they represent two entirely different types of sound, each requiring a separate mechanism for its production as HARTRIDGE[2] has insisted? Or are the two sounds to be considered merely as two different components of the same bundle of waves, one low in frequency and the other higher? Clearly, an answer to these questions can come only from detailed acoustical analysis of sounds produced by bats, an analysis adequate to reveal the presence of any component which might explain either the audible click or the instrumentally detected ultrasonic emission.

Such analyses have been made, and some aspects of the results have been reported previously (GRIFFIN[3]). The primary purpose was to measure the acoustic dimensions of the ultrasonic sounds emitted by bats. but by slight modification of the apparatus, it was also possible to study the low frequency components. Such a comparison of low and high frequency components presents a difficult problem unless the apparatus is accurately calibrated. It was clear both from DIJKGRAAF's report and our own listening to the audible

[1] These investigations were made possible by financial support from the Elisabeth Thompson Science Fund and from a research contract between the Office of Naval Research and Cornell University.
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[3] G. W. PIERCE and D. R. GRIFFIN, J. Mammalogy *19*, 454 (1938).
[4] H. HARTRIDGE, J. Physiol. *54*, 54 (1920).
[5] D. R. GRIFFIN and R. GALAMBOS, J. Exp. Zool. *86*, 481 (1941).
[6] R. GALAMBOS and D. R. GRIFFIN, J. Exp. Zool. *89*, 475 (1942).
[7] S. DIJKGRAAF, Verslagen Ned. Akad. Wetensch. Afd. Natuurkunde *52*, 622 (1943); Exper. *2*, 438 (1946).

[1] This has been recently confirmed experimentally by F. P. MOEHRES, Naturwiss. *22*, 526 (1950). (Note of the Editor.)
[2] H. HARTRIDGE, Nature *156*, 490 (1945).
[3] D. R. GRIFFIN, Anat. Rec. *96*, 519 (1946); Nature *158*, 46 (1946); J. Acoust. Soc. Amer. *22*, 247 (1950).

clicks that these were rather faint sounds, audible to a human listener only under favorable conditions, and even then only when produced close to the listener's ear.

A typical ultrasonic pulse of *Myotis l. lucifugus* on the other hand has a duration of 2·3 ms, a frequency that falls from an average of 78 kc at the start of the pulse to 39 kc at the end, and an average peak-to-peak sound pressure of 60 dynes/cm² at 10 to 20 cm from the bat's mouth. This intensity corresponds roughly to the sound level in the cabin of a very noisy combat airplane, so that it is clear that the ultrasonic sound is not by any means a faint one. If we ask what is the sound pressure of the audible click or "*Ticklaut*", we cannot immediately supply a simple answer. We can estimate the loudness of the audible click from experience with sound levels, or we can find some artificially produced ticking sound which seems to have approximately the same loudness. The former method suggests an intensity not more than 30 to 40 decibels above the threshold of human hearing; that is, roughly 0·01 dynes/cm². Hence, we are attempting to compare two sounds which may be excepted to differ in physical intensity by a factor of the order of 6000.

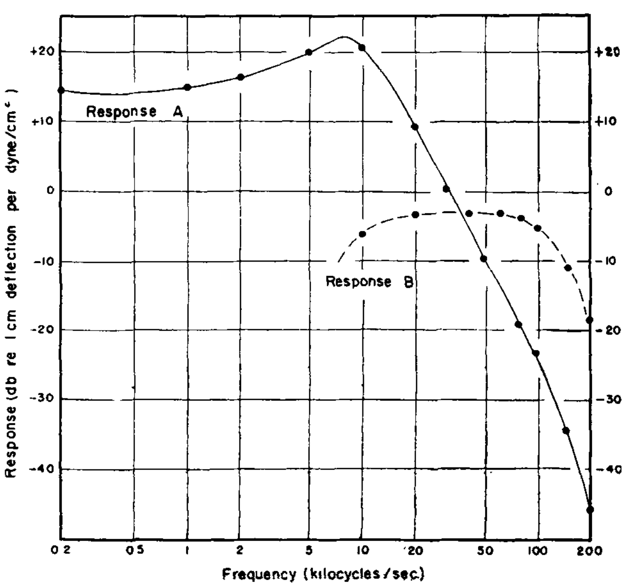

Fig. 1.—Frequency response of electro-acoustical system used to study the ultrasonic sounds of bats. When adjusted for response *A*, the electrical amplifiers were virtually uniform in amplification ratio from 0·2 to 10 kc. Response *B* was obtained with electrical filters to compensate for the declining sensitivity of the microphone and give a nearly uniform overall response from 10 to 100 kc.
(Taken from D. R. GRIFFIN, J. Acoust. Soc. Amer. *22*, 247 [1950]).

To understand the problems which arise in studying both the ultrasonic and audible sounds, we must consider briefly the nature of the apparatus used in our most recent and most precise measurements. A condenser microphone (Western Electric 640AA) picks up the sound energy and converts it to electrical waves which are in turn amplified and displayed on a cathode ray oscillograph. The wave form is then photographed and the resulting picture reveals the amplitude, the frequency, and duration of the sound. There is, however, a lower limit to the amplitude which can be recorded; it is set by the width of the cathode ray trace, and by the background noise level of the amplifiers. If the

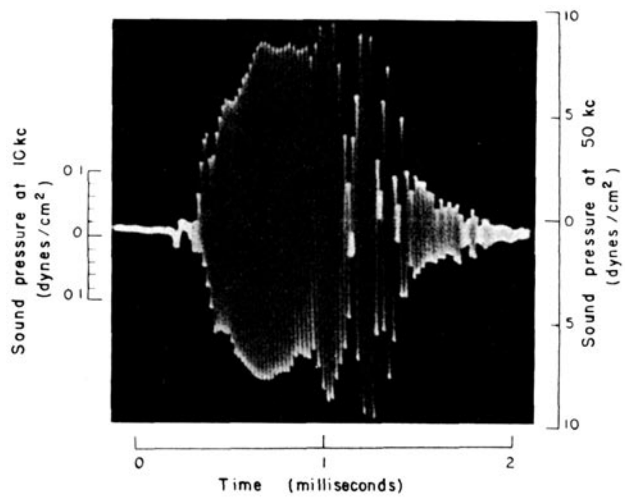

Fig. 2.—Oscillograph record of a pulse of sound from *Myotis l. lucifugus* obtained with frequency response *A*. The low frequency component at the beginning of the pulse is unusually strong for an adult bat.

apparatus is adjusted to render the 60 dyne/cm² of the ultrasonic pulses reasonably clear, then any components having sound pressure levels as low as 0·01 dyne/cm² will be quite invisible. It is therefore necessary to employ a detecting system which discriminates in favor of low frequency sounds relative to the intense ultrasonic waves. This is easily accomplished because the condenser microphone is much more sensitive to frequencies below 10 kc; ordinarily the amplifiers were provided with filters to compensate for this property of the microphone. These relationships can best be appreciated with reference to figure 1, which shows the frequency response of the system without filters (response *A*), and that obtained with the filters used to study ultrasonic sounds (response *B*). It can be seen that response *B* provides approximately equal sensitivity for all frequencies from 10 to 100 kc, while response *A* favors sounds of 1 to 10 kc, as compared with 50 kc, by a ratio of about 30:1.

When the system is used in a quiet room with response *A*, a bat's pulse of sound usually produces an oscillograph pattern intermediate between the types shown in figures 2 and 3. The range of variation in envelope form is considerable, but there is almost always some trace of a few low frequency waves just preceeding the pulse of ultrasonic sound. Generally there are only 2 to 4 clearly discernible waves with periods of approximately 0·1 ms (equivalent to a frequency of 10 kc). Even with frequency response *A*, these low frequency waves appear very much lower in amplitude than the ultrasonic waves; for instance in figure 2 they have about 1/10 of the peak-to-peak amplitude. Figure 2 has been provided with two scales for the ordinate, one for 10, and the other for 50 kc. As can be seen from figure 1, other frequencies would require different scales. Since the system was 34 times more sensitive at 8 kc, the true amplitude ratio of high and low frequency components in figure 2 is about 270:1. But figure 2 represents an unusually strong low frequency component; in figure 3 the corrected amplitude ratio is at least 1700:1, and ratios of 1000:1 or higher are common in the pulses of sound emitted by alert, active bats which show a high degree of skill at obstacle avoidance.

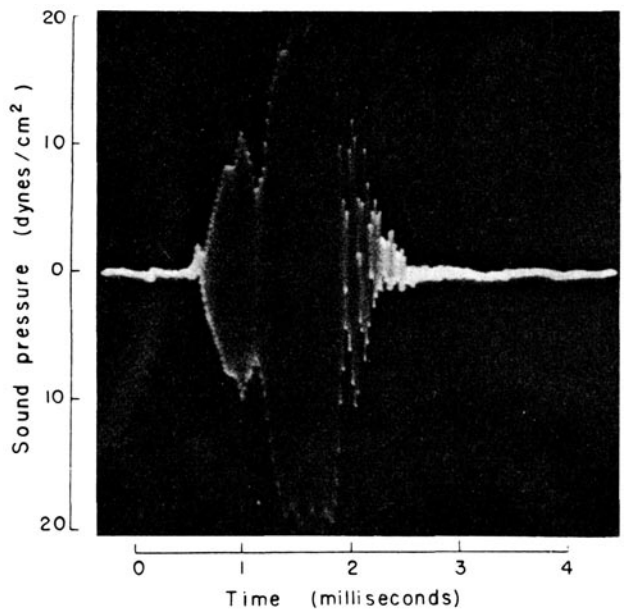

Fig. 3.—Sound pulse from *Myotis l. lucifugus* obtained with same settings of apparatus as figure 2; in this case the ratio of audible to high frequency sound was typical of adult bats in good physical condition, alert, active and capable of skillful flight. Sound pressure scale is for 50 kc.
(Taken from D. R. Griffin, J. Acoust. Soc. Amer. 22, 247 [1950]).

In the discussion of these relative amplitudes, no attention has yet been paid to the loudness of the audible click to a human ear. This also varies considerably from time to time with the same bat and from one individual bat to another. It is appropriate to consider next the correlation between the loudness of the audible click and the physical intensity of these low frequency waves.

In my experience, the loudest audible clicks have been found to occur either in bats which are not completely awakened from hibernation or "*Tagesschlaf-lethargie*". Whenever bats rest for any appreciable period of time the body temperature falls to about that of the environment; only after rather complete awakening does the body temperature reach the level characteristic of homoiothermic animals, and only at body temperatures of approximately 35°C or above are the bats capable of skillful flight and the emission of their characteristic pulses of ultrasonic sound. When not wide awake and fully "warmed up", they are very likely to make sounds which are clearly audible and which are intermediate between the well known audible cries and the ultrasonic pulses described previously (Griffin[1]).

A necessary first step in analyzing these relationship was to determine the loudness of the low frequency waves in the pulses from bats in good physical condition and capable of skillful flight. (Here "loudness" is used in the psychologists' meaning of subjective magnitude of the auditory sensation, as contrasted to the physically measured "intensity".) Loudness matches were made by two human listeners who compared a bat's audible click with artificially produced clicks that were reasonably similar in quality. The listener was then asked to adjust the electric voltage producing the artificial pulses until he judged their loudness to equal the average of the audible clicks made by a bat held approximately 6 inches from his ear. Since the bat's clicks varied considerably from one moment to the next, the loudness match could not be made with a precision better than $\pm$ 5 db. But in the most consistent set of loudness matches the clicks sounded equal when the peak-to-peak sound pressure of the artificial pulse was 48 db above the conventional reference level (0·0002 dyne/cm²). In three other trials the best match was 43, 39, and 35 db; the average of four loudness matches was thus 41 db peak-to-peak sound pressure re 0·0002 dyne/cm². During these experiments the wave form of artificial pulse and bat's ultrasonic sound were both recorded by means of the condenser microphone and amplifiers adjusted to yield overall frequency response A. In figure 4 are

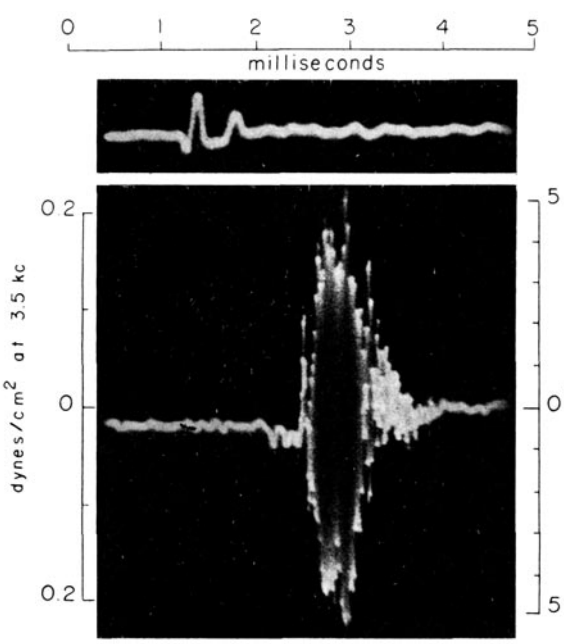

Fig. 4.—Oscillograph record of pulse from *Myotis l. lucifugus* together with artificially generated audible click judged by a human listener to be equal in loudness. Both were recorded with identical settings of the electro-acoustical system and with overall frequency response A.

[1] D. R. Griffin, J. Acoust. Soc. Amer. 22, 247 (1950).

shown oscillographic reproductions of a typical pulse emitted by one bat at a time when its audible clicks were judged equal in loudness to the artificial click shown at the top of figure 4. Clearly the low frequency waves at the beginning of the bat pulse are somewhat lower in amplitude than the artificial click. The difference, however, is not more than 50%, or 6 db. In view of the variability of the bat pulses, and in view of the considerable difference in quality between the two audible clicks, this discrepancy is not surprising.

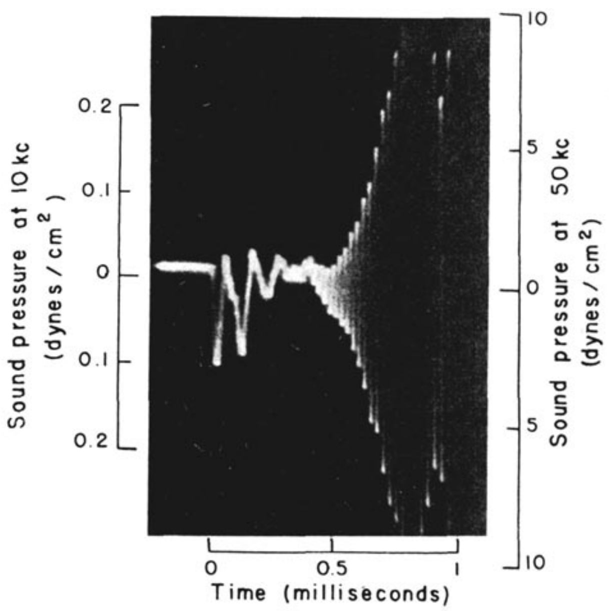

Fig. 5.—Oscillograph record of sound pulse from a half-grown *Myotis l. lucifugus* weighing 3·6 g, recorded with frequency response *A*.

It should be stressed that these loudness matches were probably made with pulses having somewhat louder audible components than those characteristic of normal bats in free flight. It was necessary to hold the bat in order to obtain a series of pulses at a constant distance from the listener's ear, and general experience with bats suggests that under these circumstances the audible clicks may be somewhat louder than in flight.

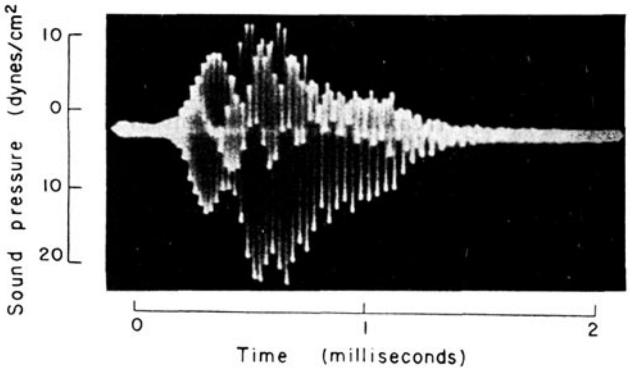

Fig. 6. Oscillograph record of a typical sound pulse from a halfgrown *Myotis l. lucifugus* (3·1 g) recorded with frequency response *B*. Note that while the low frequency components are no longer visible because of the electrical filter, the second harmonics are much more pronounced than in figure 2 to 4 obtained from adult bats.

Hence we should not be surprised at the range of variation in the level of the artificial pulses judged equal in loudness to the bat sounds. Indeed, we may be sure that under some conditions the audible clicks of bats are much louder than 48 db, and that at other times they are as faint as 30 db or even less.

Young bats produce pulses of sound with relatively loud audible components. In figures 5 and 6 are shown the oscillograph traces of pulses obtained from two half-grown *Myotis l. lucifugus*. The exact age of these bats was not known, but their weights were 3·6 and 3·1 g respectively, while a typical adult of this species weighs 7 to 8 g. Both of these bats were well enough developed to make attempts at flight, and the larger one was able to fly across a laboratory room. Figures 5 and 6 show that these half-grown bats had developed the same type of sound pulse emitted by the adults, but that the low frequency components and harmonics were relatively stronger.

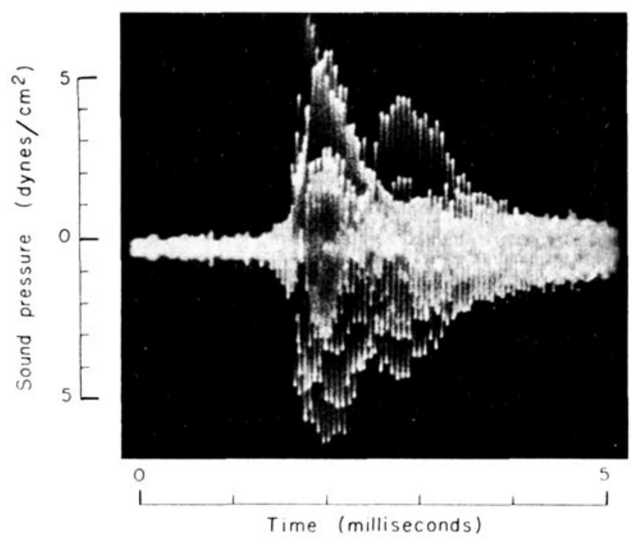

Fig. 7. Typical pulse of sound from a very young bat (less than one week old, weighing 1·4 g), obtained with frequency response *B*. The duration of the pulse is only slightly longer than in adult bats, but harmonics are present at extremely high amplitudes.

Still younger bats, however, emit sounds which are much more clearly audible and which show other differences from the adult pattern. A typical pulse from a bat less than a week old, weighing only 1·4 g, is shown in figure 7. The pulse duration is not appreciably greater than in the adult bats, but the envelope form is quite irregular and the peaks of successive waves are not of equal amplitude. In fact, this pulse resembles a short bundle consisting of 15 to 20 kc waves with the addition of harmonics whose amplitude equals or even exceeds the fundamental.

When we inquire what relation to obstacle avoidance these audible components might have, it is certainly striking to find that they are least prominent in those bats that are most skillful in avoiding obstacles. It is difficult to avoid concluding that the audible component is an incidental by-product of the ultrasonic pulse and that development of skill in using echoes for orientation involves a progressive decrease of the relative intensity of the low frequency waves. Whether these low frequency components are an unavoidable accompaniment of the ultrasonic pulses necessitated by the physiology of the larynx, we cannot say; certainly no bat pulse has yet been found to be entirely free from them. It is possible, however, that too strong a low frequency component would become audible to many animals besides the bat itself and thus diminish the advantage over predators and prey that is derived from an apparently silent flight.

It is also on interest to note that the frequency of these audible waves is approximately the same as that emitted by bats which have been deprived of the use of the crico-thyroid muscle, the principal mechanism for stretching the vocal membranes and "tuning" the larynx for very high frequencies (GRIFFIN[1]). When the motor nerves supplying the crico-thyroid muscles are cut bilaterally, the bat may continue to emit pulses of normal duration, but the frequency drops to 8 to 12 kc, and the pulses become clearly audible to a human listener. This suggests that the natural period of vibration of the unstretched membranes is approximately 0·1 ms, and that even in the most active and skillful bats a few low amplitude vibrations of this period cannot be avoided.

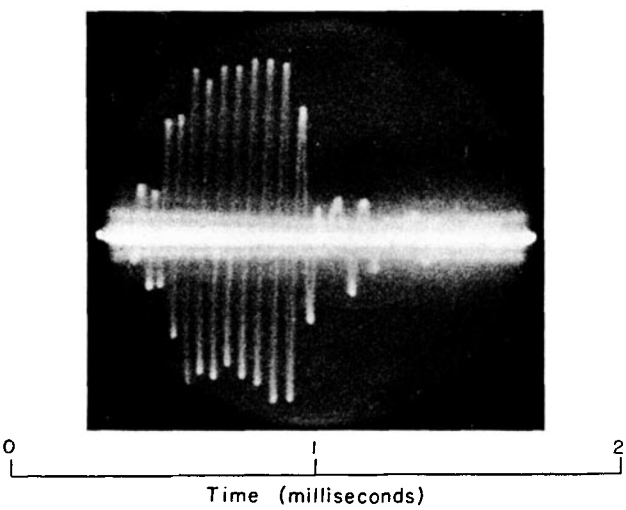

Fig. 8.—An unusual pulse of sound from *Myotis l. lucifugus* having a frequency of approximately 8 kc, obtained with an uncalibrated system having a frequency response intermediate between *A* and *B* of figure 1.

These detailed acoustical considerations make it clear, I believe, that the "*Ticklaute*" described by DIJKGRAAF and the ultrasonic sounds which PIERCE and I discovered in 1938 are one and the same. DIJKGRAAF, relying on his unaided ears, could hear only the faint audible component; we with our apparatus for detecting ultrasonic sounds were naturally concerned primarily with the high frequency component, both because of its considerably great intensity and because the audible click seemed to be a relatively unimportant by-product. The fact that a relatively high amplitude of the audible components is correlated with poor physical condition of the bat suggests that the low frequency waves are disadvantageous, and that an alert animal keeps them at a minimum. If this is a correct interpretation, we may consider that an important part of the ability to employ echoes for purposes of orientation is the power to emit relatively pure ultrasonic sounds of short duration.

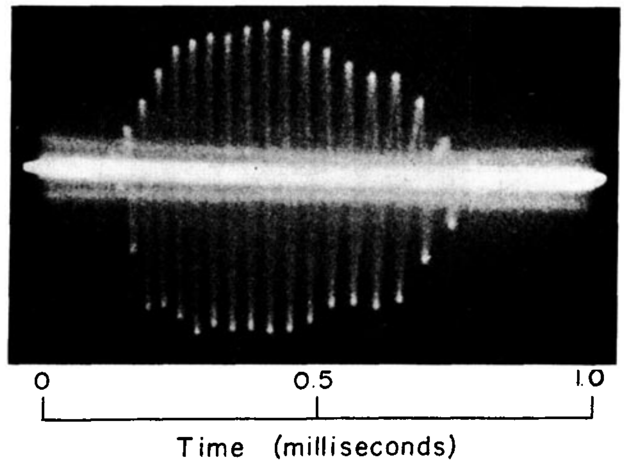

Fig. 9.—A pulse from *Eptesicus f. fuscus* having a frequency of 27 kc, obtained with an uncalibrated system having a frequency response intermediate between *A* and *B* of figure 1.

It is likewise important to stress that sounds intermediate between the typical ultrasonic pulse and the familiar audible cry are emitted even by bats that are in good physical condition. One type of intermediate sound from *Myotis l. lucifugus* is illustrated in figure 8. This pulse contains only 18 sound waves and has an average frequency of 8·2 kc. It occurred between several quite typical ultrasonic pulses. Another intermediate type of pulse is illustrated in figure 9; it was obtained from an *Eptesicus f. fuscus*, and the frequency is 27 kc. These atypical pulses are quite different from the audible cry which seems to contain a wide band of frequencies both audible and ultrasonic (GALAMBOS and GRIFFIN[1]).

Another important aspect of the bat's ultrasonic sounds is the frequency of repetition of individual pulses. Here too, there appears to be a slight discrepancy between the figures contained in our earlier papers and those reported by DIJKGRAAF[2]. We did not observe repetition frequencies above 50–60 per second, while DIJKGRAAF estimates that the number of "*Ticklaute*" per second in the "*Ratterlaut*" of some bats reaches 170 per second, immediately before landing. His estimate was based upon the apparent pitch of the audible rattling sound. Recent cathode ray oscillo-

[1] D. R. GRIFFIN, Anat. Rec. *96*, 519 (1946); Nature *158*, 46 (1946).

[1] R. GALAMBOS and D. R. GRIFFIN, J. Exp. Zool. *89*, 475 (1942).
[2] S. DIJKGRAAF, Exper. *2*, 438 (1946).

graph records show, however, that the ultrasonic pulses of *Myotis l. lucifugus* may be emitted at rates equal to those reported by DIJKGRAAF. A typical series is shown in figure 10. This figure was obtained by means of a slight modification of the apparatus whereby the photographic film was moved at a constant velocity while the sweep circuit of the oscillograph moved the electron beam horizontally with the usual saw-tooth

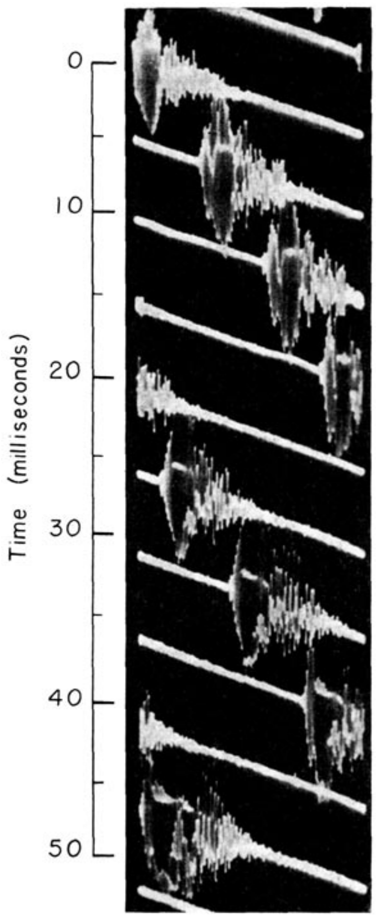

Fig. 10.—A rapid series of ultrasonic pulses emitted by *Myotis l. lucifugus*. In this photograph the film was moving continuously while the oscillograph sweep travelled horizontally, from left to right, at a uniform rate with an extremely rapid return (saw-tooth sweep generator). Each sweep occupied 5 ms so that this record reveals an instantaneous frequency of approximately 150 pulses per second. Such high pulse frequencies, however, never were observed to continue for more than a small fraction of a second.

wave form. Hence the rapid return trace is too faint to be photographed, and the visible trace is a sloping line drawn during the travel of the sweep at constant speed from left to right. In figure 10, the numbers of weeps per second was 200, so that the strip of film which has been reproduced covered a period of 50 ms. In that time 8 ultrasonic pulses occured at approximately equally spaced intervals. This corresponds to an instantaneous frequency of about 150 pulses per second. In none of my records, however, are such high repetition frequencies continued for more than a small fraction of a second.

Zusammenfassung

1. Neue akustische Messungen der Orientierungslaute der Fledermäuse haben die Verschiedenheiten zwischen GRIFFINS und GALAMBOS' Darstellungen (1941, 1942) einerseits und DIJKGRAAFS (1943, 1946) andererseits in Einklang gebracht. Bei den bisher erforschten Fledermausarten kommen der Ultratonstoß und der hörbare «Ticklaut» gleichzeitig vor. Der letztere ist eine tieffrequente und schwache Komponente, die dem hochfrequenten Tonstoß um den Bruchteil einer Millisekunde vorangeht.

2. Die Frequenz dieser tiefen Tonwellen bei *Myotis l. lucifugus* ist annähernd 8–10 kHz.

3. Die relative Amplitude der tief- und hochfrequenten Komponenten ist sehr verschieden und hängt vom Alter und Wohlergehen der Fledermäuse ab. Fledermäuse, die nicht völlig aus dem Winterschlaf oder der Tagesschlaflethargie erwacht sind, und junge Tiere senden häufig laute, hörbare Komponenten aus. Lebhafte, gut wache Fledermäuse, die geschickt herumfliegen, senden gewöhnlich Tonstöße aus, deren tieffrequente Komponenten, verglichen mit den hochfrequenten, sehr schwach sind; ihre Intensität beträgt häufig weniger als ein Tausendstel des Schalldruckes bei 50 kHz.

4. Versuche, in denen ein Zuhörer die Stärke künstlicher Ticklaute veränderte, bis sie subjektive Gleichheit mit den Ticklauten der Fledermäuse erreichten, zeigten, daß der Ticklaut von *Myotis l. lucifugus* etwa dieselbe Lautstärke hat ($\pm$ 5 db) wie eine kurze Serie von Schallwellen der Frequenz 3–5 kHz bei 35–50 db über 0,0002 dyne/cm^2. Eine normale, gut wache *Myotis l. lucifugus* sendet als Orientierungslaute Ultraschallwellen aus (50–60 kHz) von etwa 110 db und hörbare Tonwellen von etwa 40 db über 0,0002 dyne/cm^2.

5. Sehr junge Fledermäuse (noch keine Woche alt) senden Tonstöße aus, die vom Orientierungslaut der Erwachsenen deutlich verschieden sind, obwohl die Dauer des Stoßes nicht bedeutend länger ist. Die hauptsächlichsten Unterschiede sind eine außerordentliche Unregelmäßigkeit der Umhüllungskurve des Tonstoßes und sehr viel stärkere Obertöne (siehe Figur 7).

6. Mit einem zweckmäßigen Apparat kann man außer den typischen Ultraschallstößen und den bekannten, hörbaren Kreischlauten der Fledermäuse das Auftreten intermediärer Schalltypen feststellen.

7. Die Frequenz der Orientierungstonstöße erreicht bei *Myotis l. lucifugus* gelegentlich etwa 150 je Sekunde. Aber solch hohe Wiederholungsfrequenzen haben nie länger als 50 bis 100 ms gedauert. Diese Befunde bestätigen die Angaben DIJKGRAAFS.