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THE RESISTANCE OF BATS TO JAMMING

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ABSTRACT

Obstacle-avoidance by echolocating long-eared bats (Plecotus townsendii) was tested while the bats were flying in random noise. Previous experiments had indicated that bats could achieve a surprising degree of success when dodging wires in a room filled with random noise in the band 20 to 50 kc, which covers the fundamental frequencies in the pulses of orientation sound used by Plecotus. The present experiments show that at a given noise power per cycle, the effectiveness of masking was far greater for a 10- to 90-kc noise than for one that merely covered the fundamental frequencies in the bat pulses, but that the bats can still echolocate when the noise power, per cycle of bandwidth, exceeds the energy in the echo. Further broadening of the noise spectrum, to an upper limit exceeding 120 kc, had no discernible effect.

The effect of coherent noise, originating in a single random-noise generator connected to all the loudspeakers, was compared with the effect of noncoherent noise, which originated in four noise generators, each of which supplied one-quarter of the loudspeakers. In the noncoherent noise field, a bat always received noise from at least two independent noise generators. Though the bats seemed to fly with more assurance in coherent than in noncoherent noise, obstacle avoidance in the coherent noise was only slightly and inconsistently better.

The signal-to-noise ratio at the moment of detection of the wires was estimated as follows. Detection was evidenced by a drop in time interval between pulses. From motion-picture films carrying sound tracks, the distance of detection was determined for the average of a few cases. The echo strength E', in $ergs/cm^2$, was calculated for this detection distance, using the scattering cross section of the wire and the energy spectrum of the bat's sound pulse. The noise level N'_0, in $ergs/cm^2$ (i.e., in $ergs/sec\ cm^2$ per cycle of bandwidth), was measured also. The ratio E'/N'_0 at the bat's ear at the moment of detection was about -5 db, in noncoherent noise.

Operation at such a low signal-to-noise ratio is possible because the bat has several ways of discriminating against the noise when it does not come from the same direction as the echo.

By itself, the directionality of the external ear seems to be hardly enough to account for the bat's success. However, neurophysiological studies have disclosed an interaction between the bat's two auditory channels, such as to enhance directional discrimination. There is also an interaction such that at the level of the posterior colliculus — a midbrain auditory center especially well developed in bats — a favorable signal-to-noise ratio at one ear (achieved by directional discrimination) results in suppression of the effects of noise received at the other ear. By flying in such a way as to exploit these means of discrimination based on direction, Plecotus can enhance the signal-to-noise contrast by 20 db or more. The resistance of bats to jamming has therefore been brought into consonance with the demands of the statistical signal-detection theory developed for electrical communications.

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THE RESISTANCE OF BATS TO JAMMING

I. INTRODUCTION

During the evolution of insectivorous bats, one of the critical factors in their survival has been the ability to locate flying insects precisely and rapidly in darkness. Although detection is sometimes based on sounds generated by the insect,[1,2] insects are commonly intercepted by echolocation.[3,4] Echoes from single small insects must be detected despite the presence of louder echoes from other objects at about the same distance such as twigs, leaves, the ground, and larger insects, and often in the presence of orientation sounds from other bats nearby. The nervous systems of these animals are doubtless highly adapted for the extraction of pertinent information from a complex and unpredictable background of other sounds. Bats thus face a problem exactly parallel to a basic problem of communications engineering: the recognition of meaningful change ("signal") in the presence of irrelevant change ("noise").

A preliminary experiment has shown that long-eared bats (Plecotus) can detect echoes from small wires despite the presence of intense ultrasonic noise.[5] That experiment was designed to ascertain the ratio of S, the power level of the detected echo, to N, the power level of random noise occupying — as nearly as was practicable — the same band of frequencies. In ordinary observations with oscilloscopes it is usually necessary for S/N to be one or higher before a signal can be detected reliably. It was therefore surprising to find that the more skillful bats consistently detected echoes for which S/N appeared to be about −35 db. When S/N is considerably less than one, detection is no simple matter, and the resistance of these bats to jamming therefore called for further study.

The problem of distinguishing signals from noise has evoked the concept of an "ideal detector"; this is, by definition, a device that processes optimally the complex of signal and noise that reaches its input.[6,7,8,9] For any detecting system to distinguish in difficult cases whether a given waveform is partially ordered (e.g., a signal) or entirely random (e.g., "white" noise), it is of advantage for T, the duration of the signal, to be long, so that the order may have time to make itself manifest. The frequency bandwidth W is also of importance; stated in general terms, the reason is that if W is larger the signal can have more characteristics by which it may be recognized. To take account of these considerations, it is now customary to consider the detectability of signals not in terms of S/N but of WTS/N or some equivalent ratio. A commonly used equivalent is E/N_o, where E is the signal energy, ST, and N_o is the noise power per unit bandwidth, N/W. According to well developed theory, E/N_o must considerably exceed unity if reliable detection is to be possible even under the most favorable circumstances, which include advance knowledge of the exact character of the signal and of the precise time when it will reach the ideal detector, if it arrives at all.

For the case of a _Plecotus_ dodging a 0.54-mm wire in a noise where S/N appeared to be −35 db, it is possible to estimate E/N_o, but the result is difficult to reconcile with the theory of signal detection. For a single pulse of sound emitted by this species, T may be taken as 10^{-3} sec. Although many pulses may be as long as 2 or 3 msec, the peak amplitude is maintained only for a fraction of this time, and the estimates of S/N were based on maximum amplitudes of emitted pulses and the assumption that this amplitude was maintained for one millisecond. The bandwidth of the fundamental frequencies is about 1.5×10^4 cps (40 to 25 kc in a typical instance). These figures lead to an estimate of −23 db for E/N_o in the echo from a single pulse. If more than one pulse is used to detect the wire, E/N_o may increase by as much as the sum of the individual pulse energies.[10] But only a very few pulses are emitted when the bat is as close to the wire as 10 cm, the distance for which S/N was estimated, so that a considerable discrepancy remains to be explained.

The experiments described below were therefore designed to explore this question more thoroughly, with particular reference to (1) the bandwidth W of the noise, and the uniformity of noise level throughout the frequency spectrum used by the bats and the flight space where the experiments were conducted; (2) the distance at which wires were actually detected (necessary to estimate S); (3) the quantitative relationship between noise intensity and the bats' success at dodging small wires.

Certain limitations of the earlier experiments required that improved facilities be employed. The principal improvement was in the noise field, in respect to its spatial uniformity and especially its frequency coverage. Originally 70 "Isophon" electrostatic loudspeakers had been used to generate jamming noise, and these were located in two arrays at the ends of a 4 × 4-m space containing four rows of vertical wires. The acoustic output of these speakers declined over the frequency range used by the bats, and despite the high-pass filter between noise generator and power amplifier the noise energy at 40 to 50 kc was distinctly lower than at 20 to 30 kc, while above 55 kc it fell off sharply. Although the fundamental frequencies in the pulses of _Plecotus_ sweep over about an octave located between 50 and 20 kc, the presence of higher frequency components is often indicated by subsidiary peaks on the graphic representation of the waveforms when they are displayed on the cathode ray oscillograph. Furthermore, auditory evoked potentials from the brains of anesthetized _Plecotus_ commonly show minimum auditory thresholds at 55 to 65 kc;[11] but between 65 and 100 kc the threshold rises by 60 to 80 db, and above 100 kc it was only rarely possible to obtain any evoked potentials at all. Thus it is plausible, on electrophysiological grounds, to assume that these bats have considerable auditory sensitivity one octave above the fundamental frequencies in their orientation sounds, although not much higher. It was therefore important to determine whether components above 50 kc in the echoes had escaped jamming in our earlier experiments with _Plecotus_. The new noise field permitted this to be done.

II. METHODS

A. Experimental Animals and Obstacle-Avoidance Tests

The bats used in these experiments were _Plecotus townsendii_ from caves in West Virginia; these bats are called _P. rafinesquii_ in our previous papers, but see Handley.[12] They were allowed to fly in the quiet or in noise almost every day. The success of bats at dodging small wires is variable, and we have been interested primarily in the more expert individuals that consistently

avoid wires day after day with considerable skill. When jamming noise is added to the experimental situation, the variability increases and a more stringent selection is necessary to obtain consistently good performance. In these experiments, a preliminary screening selected those bats that seemed adapted to life in captivity, in that they ate mealworms well, flew freely, and avoided wires reasonably well in the quiet when first tested in the flight room. Of the total number captured, about one fifth were chosen. About half of these were actually used in the experiments presented below; the other half consisted of animals whose health or performance deteriorated during the period of the experiments. The selected bats, roughly 10 percent of the total number caught initially, usually improved in obstacle-avoidance scores during the first few days of testing, and then remained at approximately their peak performance consistently for two or three weeks. All data presented below were obtained during such a period of peak performance that was maintained for at least 7 to 10 days.

Only after each bat had demonstrated the ability to dodge wires well in the quiet was it exposed to the noise. The first reaction to noise at high intensities was to land. In the high noise levels, it was often necessary to release a bat repeatedly in various parts of the flight space before an adequate number of flights through the rows of wires could be obtained. Flights in the quiet or in less disturbing noise were included before and after all tests in the highest noise levels, and tests in different kinds of noise were interspersed in a variety of sequences to balance out possible changes in general level of performance. No significant trends were observed during the periods over which these data were collected, and it was possible to include almost all flights during the period of peak performance.

The ability to avoid wire obstacles was measured by means of the scoring methods described elsewhere.[5] The wires were vertical, spaced about 45 cm apart, in rows that formed obstacle planes, and the chance score for bats approaching such wires in a direction normal to the plane of the wires was about 40 percent misses. The scoring unit was a "trial," defined as a flight through a plane of wires.

B. The Flight Chamber and Obstacles

Ideally, bats should have ample room to maneuver when they are tested for ability to avoid small obstacles, but it was necessary in the present experiments to fill the flight space with high-frequency noise, and since the available loudspeakers were highly directional, many were necessary to generate a reasonably uniform noise field even in a small flight space. The compromise necessitated by these two conflicting requirements was the 5 × 2-m flight space shown in Fig. 1. The height was 2.4 m and the ceiling and floor were of hard material — plywood and linoleum respectively — which reflected sound almost totally. The walls were made of nylon mosquito netting, which allowed observation as well as affording almost total transmission of sounds. Beyond the netting were hard cinder block walls of the laboratory room; these were, respectively, one and three meters from the sides of the flight space, and one and four meters from its ends.

The vertical wires serving as test obstacles were attached, by stretched rubber bands at both ends, to the sliders of standard traverse rods designed for holding window drapes. The wires were arranged in rows one meter apart across the flight space, and for each row the sliders were connected to a cord that passed over pulleys so arranged that a single movement of the cord shifted all wires horizontally without altering appreciably the 45-cm spacing between
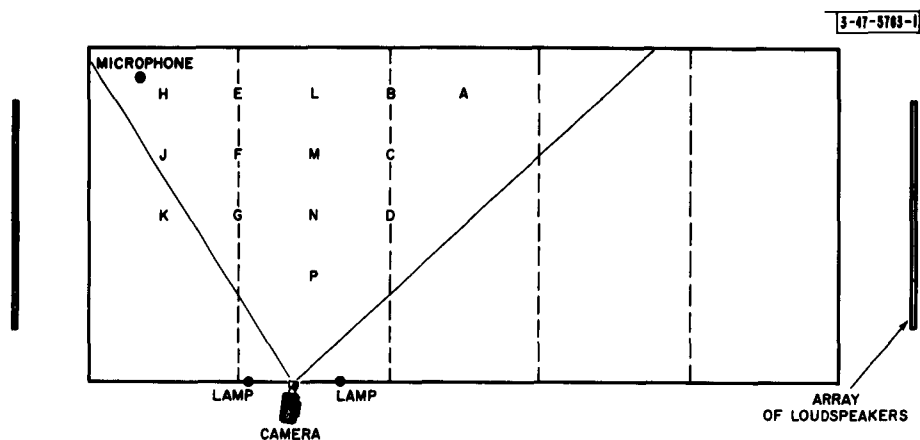
Fig. 1. Plan of the flight space. The enclosure represents a wall of gauze hung from floor to ceiling, so that it was 2.4 m high. The broken lines mark the normal positions of the obstacle planes. The drawing is to scale, and the separation of these planes is 1 m. The letters mark places at which the noise was measured; some of the measured values appear in Table I. Light solid lines delineate the field of view of the camera. The microphone was connected to an amplifier and rectifier, and thence to the sound track of the camera.

them. The ends of the wires and their attachments were covered by boards placed on edge so that all supporting fixtures were screened.

In all experiments reported below, the wires were shifted frequently and irregularly in position within each of the four wire planes shown in Fig. 1. It was thus impossible for the bats to learn the positions of the open spaces between the wires; each flight required careful dodging maneuvers if collisions with the wires were to be avoided. When a bat passed through the plane of the wires by flying within about 15 cm of the boards framing each row of wires the flight was not counted, because of possible variations in the noise field close to the boards.

C. The Noise-Generating Apparatus

The loudspeakers were arranged in two rectangular arrays about two meters square and 50 cm from the ends of the flight chamber, as shown in Fig. 1. There were 26 speakers in each array and all were directed towards the flight space and parallel to its long axis. The loudspeakers were built on the principle described by Kuhl, Schodder, and Schröder.[15] The design resembles that of an ordinary condenser microphone, except that the diaphragm is a metal film on a Mylar (polyethylene terephthalate) foil that is stretched in contact with a grooved rear electrode. The electrodes are much more closely spaced than they are in a microphone for use at audio frequencies, and the Mylar film prevents them from coming into electrical contact.

In the experiments designated here as Series II, III, and IV, some of the speakers had domed backplates and others had plane ones, but for Series V and VI, all the speakers had domed backplates such that the diaphragm formed a 20°-wide portion of a sphere. The doming gave each speaker a broader radiation pattern than that from a plane diaphragm with the same area and therefore the same power-handling ability.

The jamming noise originated in one or four random-noise generators, General Radio Type 1390-A. Each generator was followed by a step attenuator and a bandpass filter. The speakers were powered by a battery of 16 special amplifiers, each of which was capable of supplying

300 volts peak-to-peak to a capacitive load of 6000 μμf. The frequency range of the amplifiers was 20 to 300 kc.[13,14] The raw output of the noise generator was far from Gaussian in its amplitude distribution. After the bandpass filtering, however, the noise was approximately Gaussian; the power amplifiers, operated in a region of good linearity, did not appreciably distort the amplitude distribution.

The noise field designated below as "coherent" was generated by connecting one random-noise generator to all 16 amplifier inputs, and thence to all 52 loudspeakers. A "noncoherent" field was generated in most of the later experiments by connecting four of the amplifier inputs to each of four random-noise generators, so that there were four sets of loudspeakers in each array, each set being driven by a statistically independent waveform. The sets were interspersed so that each point in the noise field was irradiated significantly by speakers from at least two different sets.

The characteristics of the noise field were determined with the help of the microphones described below and an ultrasonic analyzer (Model SB-7bZ, Panoramic Radio Products, Inc., with an additional integrating capacitor in the vertical deflection circuit). The waveform at the speaker inputs had a power spectrum that was uniform within ±1 db from 20 to 200 kc. Variations in the spectrum of the noncoherent sound field arose primarily from the frequency response of the loudspeakers, and secondarily from absorption by the air.

When the field was coherent, interference produced sharp spectral variations in the sound level at any one point in the field. Since the maxima and minima caused by interference were presumably narrow compared with the voltage-response curve of our analyzer, which at the time in question had an equivalent rectangular bandwidth of 2300 cps, we cannot estimate the magnitude of these fluctuations; on the spectrograms, the dips and rises attributed to interference depart from a smoothed curve by amounts as large as 10 db. A noncoherent field is far easier to measure and to draw conclusions from because there is no permanent pattern of interference. The coherent field was used originally because only one random-noise generator was available; after the procurement of more generators, the coherent field was used in certain experiments in order to observe whether the bats could exploit the coherence.

To calculate the noise power per cycle from the noise level indicated by the sonic analyzer, one must know the noise bandwidth of the analyzer. This was found by photographing the resonance-like curve displayed by the analyzer when the input to the analyzer was a sine wave from an oscillator, squaring the ordinates to convert from voltage to power, and replotting. This power-response curve has the same area as a rectangle whose height is that of the curve's maximum, and whose width is 1.1 kc. The measurement to determine this figure was made at several frequencies, and the result is independent of frequency, because the filter circuit and detector do not change as the analyzer scrutinizes successive parts of the spectrum. The noise power indicated by the analyzer is higher by a factor 1100, which is 30.5 db, than the indication that the analyzer would give if its passband were a rectangle with a bandwidth of 1 cycle.

When the loudspeakers were excited noncoherently, the noise at a typical spot in the flight room had a power spectrum that was smooth and slowly rising in the interval from 20 to 120 kc, unless the frequencies at the upper end of this spectrum were suppressed by filtering at the amplifier inputs; it appears that from 120 to 150 kc, the intensity certainly did not fall off very rapidly, and may even have been rising, but lack of any microphone calibration prevents us from making a quantitative statement. When the filters were set for passing the band 10 to 200 kc, the

sound level rose about 6 db between 20 and 30 kc, and another 6 db between 30 and 100 kc. Limiting the band by low-pass filtering caused no change in the level of the low-frequency part of the spectrum. Spatially, the sound field varied little except near the walls of the flight space, where the intensity diminished because the width of the speaker array was less than that of the flight space. The sound level at 30 kc, for some of the places marked in Fig. 1, is listed in Table I. The probable error in these measurements is estimated as 2 db. The levels at the other places marked in Fig. 1 were closely similar to those in the table.

Table I Noise power per cycle per square centimeter in the neighborhood of 30 kc, in db re $(0.0002$ microbar$)^2$ per cycle, for locations marked by the same capital letters in Fig. 1. For dependence of noise level on frequency, see p. 5. These levels apply to what is designated as the maximum available noise. They were measured with a Western Electric 640-AA microphone facing the nearer array of speakers, with the axis of the microphone along a normal to the array. The heights are measured from the floor.

Height (cm)	C	E	F	G	L	M	N
170	26	26	29	29	24	29	28
140	23	23	24	24	25	24	26
100	22	21	22	22	24	21	21
70						20	28

Though the ceiling, floor, and room walls were acoustically hard, absorption in the air limited reverberation. At the center of the room, the sound flux was chiefly longitudinal, and near either end of the room, the sound came predominantly from the nearer array of speakers. (In the experiments designated as Series II below, auxiliary loudspeakers were employed, and this statement does not apply.)

The sound levels in Table I were determined by means of a Western Electric 640-AA microphone that had been calibrated throughout the range 1 to 100 kc at the Acoustics Laboratory of the Pennsylvania State University. All the tape recording employed a plastic-diaphragm microphone[15] in order not to discriminate against harmonics in the bat's orientation sounds. The plastic microphone was calibrated through comparison with the Western Electric microphone, by tape recording their outputs when first one and then the other was at a fixed spot in the noise field, and then displaying the responses as functions of frequency by means of the Panoramic analyzer. The plastic microphone was nearly uniform in its response from 30 kc to at least 120 kc; it was more sensitive than the 640-AA for frequencies above 35 kc.

The steadiness of the noise field over a period of months gives evidence that the plastic transducers have good stability. However, the tape records for calibrating the plastic microphone were made during the trials in Series VI, so that it is not necessary to assume temporal stability of the calibration for the plastic microphone. Moreover, the noise measurements in Series VI and all but one of the bat-pulse measurements were made with the same microphone, and in the calculation of E/N_o, any error in the calibration of the microphone will cancel out.

In what follows, the noise levels will be stated by reference to the field charted in Table I, which will be designated as "0 db."

III. EXPERIMENTS

A. Kinds of Experiments

Several levels and frequency bands of jamming noise were tested for their effects on the ability of <u>Plecotus</u> to dodge small wires. Over 10,000 trials registered by the 17 most skillful bats (selected as explained above) were grouped into six series, numbered chronologically. In Series I, reported previously,[5] only Isophon loudspeakers were available, but in all subsequent series we used the Kuhl-type loudspeakers described above. Series II (September 1959) and III (February 1960) were designed primarily to study the effects of different frequency bands of coherent noise. Series IV (February 1960) and V (April 1960) compared coherent and noncoherent noise at a range of intensity levels, and Series VI was a detailed analysis of the distances at which one particularly skillful and cooperative <u>Plecotus</u> from Series V detected wires in the widest band of noncoherent noise.

B. Bandwidth of the Noise

In preliminary experiments designated Series II, performed immediately after the array of Kuhl-type loudspeakers was available, noise was radiated not only from these loudspeakers, located as shown in Fig. 1 at the ends of the 2 × 5-m flight chamber, but also from the same 70 Isophon loudspeakers that had been used in Series I, now relocated at the sides of the flight space just outside the netting walls in an attempt to discourage flights back and forth across the flight chamber. This arrangement produced a noise field that was difficult to measure, and since the Isophon speakers did not appreciably discourage oblique approach to the wires, they were not used in Series III-VI. Series II comprised all trials of the three most skillful <u>Plecotus</u> available at the time, throughout their 20-day period of peak performance. In the quiet they averaged 96 percent misses of both 1.07- and 0.65-mm wires. In 20- to 60-kc noise at the highest intensity available (Table I) the average score for 841 flights with 1.07-mm wires was 67 percent misses. When the bandwidth of the noise was increased to 20 to 120 kc the average of 842 trials was only 54 percent misses. With 0.65-mm wires, 254 trials in 20- to 60-kc noise averaged 49 percent misses, whereas in the 20- to 120-kc noise the same bats refused to fly through the wires often enough to provide any meaningful scores at all. The results of Series II thus indicated that frequencies above 60 kc (and hence above the 45- to 25-kc fundamentals of the orientation sounds) can indeed contribute to the detection of wires in a noise that is jamming only the lower frequencies.

To explore more thoroughly the importance of various parts of the noise spectrum, Series III tested the effects of three bands of noise, 10 to 50 kc, 10 to 90 kc, and 10 to 120 kc. A close scrutiny of many records of <u>Plecotus</u> pulses has not revealed fundamentals above 45 or occasionally 50 kc, and at 45 kc the amplitude has not yet risen to anywhere near its peak value even when the pulse begins at 50 kc. It therefore is safe to assume that the 10- to 50-kc band covered the fundamental frequencies of echoes from the wires, and that the 10- to 90-kc band effectively covered both fundamentals and second harmonics.

The results of Series III are shown in Table II, where each of the five most skillful bats is listed separately, since they differed in the maximum noise level at which they would fly repeatedly in the wide-band noise. For example, No. 23 would not fly at all in the maximum intensity, although Nos. 26 and 30 flew willingly and performed distinctly better than chance in this noise. All tests included in Table II represent conditions under which the wide-band noise severely taxed the individual bat concerned. Hence the averages of all tests in Series III (last line of Table II)

			Avoidance Scores Using Various Bandwidths of Noise					
Bat No.	Wire Diameter	Over-all Noise Level	10 to 50 kc N	M	10 to 90 kc N	M	10 to 120 kc N	M
26	1.07 mm	0 db	58	81%	51	55%	46	59%
30	1.07 mm	0 db	50	86%	51	67%	31	45%
26	0.54 mm	−10 db	44	82%	33	27%	41	49%
30	0.54 mm	−10 db	29	86%	48	46%	43	42%
23	1.07 mm	−20 db	21	72%	21	67%	37	65%
28	1.07 mm	−10 db	33	73%	21	81%	41	81%
24	0.54 mm	−10 db	22	91%	20	30%	20	30%
Average of all bats in all tests of Series III	−	−	257	80%	245	51%	259	53%

Table II Results of Series III jamming experiments with Plecotus in coherent noise. N stands for number of trials, M for percent misses; noise levels are specified for the wide band, and the reference level is that of Table I. For the wide band, the noise extends well above 120 kc, though at diminishing intensity. All tests of these individual bats at high noise levels are included throughout the period of their peak performance.

are significant measures of the relative effectiveness of the three bands of noise. It is clear from Table II that increasing the upper frequency limit of the noise from 50 to 90 kc caused a marked drop in obstacle-avoidance scores. On the other hand the added effect of the band from 90 to 120 kc was insignificant in comparison to the marked drop from 80 to 51 percent misses when the noise band was widened from 10 to 50 to 10 to 90 kc.

A further reason for believing that the 10- to 90-kc band included all frequencies used effectively by Plecotus when taxed by severe noise is the fact that sensitivity of hearing, as indicated by auditory evoked potentials from the brain, is much reduced at 90 kc. The threshold there is about 60 db higher than it is at 60 kc.[11] Typically, the threshold there is 80 to 100 db above 0.0002 d/cm^2, or 2 to 20 microbars (μbar). Measurements and calculations like those discussed later show that even if all the energy of the pulse were concentrated at 90 kc — which is very far from being true — then the echo amplitude would be less than the 2 μbar threshold even when the bat was only 4 cm from the wire. On the assumption that the threshold for the evoked potential is the threshold of hearing, we may therefore conclude that Plecotus is too insensitive to 90-kc signals for them to be useful in finding the wires. In addition, it is most unlikely that the auditory system of a bat's brain is capable of its best discrimination between two classes of signals (echoes and noise) at the extreme spectral limits of its range of sensitivity.

Within a few days of the experiments of Series III, three of the same bats were tested briefly in 60- to 120-, 10- to 120-, and 10- to 50-kc noise. The other conditions were constant for all tests with each bat, but varied among the three animals in such a way that all were taxed about as severely as in Series III. Their scores averaged 76 percent misses at 10 to 50 kc, 66 percent at 10 to 120 kc and 79 percent in 60- to 120-kc noise. Since there were only 115, 150 and 82 trials,

respectively, in the three bands of noise, the differences in scores are of questionable significance, but the 60- to 120-kc noise reduced the scores appreciably below the level of performance in the quiet (96 percent misses for the bats of Series II). Clearly both fundamental and second harmonic frequencies are important to _Plecotus_ when detecting wires in these noise fields.

C. Effects of Intensity and Coherence of the Noise Field

The effects of varying the noise intensity were examined in Series IV and V. The former employed Nos. 26 and 30, the two most skillful bats of Series III; the twelve animals used for Series V included four that were approximately as skillful as 26 and 30, together with eight others that were distinctly less proficient, though these were vigorous fliers, seemingly in good health. Tables III and IV show the obstacle-avoidance scores of these bats when dodging two sizes of wires over a 30-db range of noise intensities. The lowest intensity employed had only a slight jamming effect with the 0.54-mm wires, and with the 1.07-mm wires some of the bats performed almost as well as in the quiet. But the maximum intensity caused severe jamming of all bats tested, and the less skillful could not be induced to fly through the wires at all. The improved noise field thus caused considerably greater jamming than the noise used in Series I.[5] Since adequate facilities for measuring the noise field were not available during Series I, it is not practicable to make quantitative comparisons between Series I and Series II to VI.

Coherent and noncoherent noise, as defined in Sec. II, were also compared in Series IV and V. In Series IV, which included a larger number of trials and employed the smaller size of wires, the obstacle-avoidance scores were slightly lower in the noncoherent noise (Table III). In Series V, half of the bats were tested for several days in each type of noise, and then the conditions were reversed; some bats performed more poorly in the changed type of noise, but others improved, and it made no discernible difference whether the change was from coherent to noncoherent or vice versa. The two groups had been matched in general proficiency before the comparison began, and there was no significant difference between the average scores in the two types of noise. Therefore, in Table IV the results obtained in Series V with coherent and noncoherent noise have been combined.

The chance avoidance score for a bat flying without attempting to avoid the wires was considered in Series I to be 40 percent misses, and on this basis, one might conclude that even the most skillful _Plecotus_ in Series IV and V were completely unable to detect the wires in noncoherent noise of the maximum intensity. However, the estimate of 40 percent as the chance score was based on the assumption that the bat was flying perpendicularly to the plane of the wires, as was usually the case in the quiet, in Series I, or in the low noise levels in the improved noise field of Series II-V. But in the higher noise intensities in Series II-V, the bats often flew back and forth parallel to the planes of the wires, and when they did fly through the planes, they did so at such oblique angles that the chance score must have been almost zero, a conclusion supported by the fact that when severely taxed the bats would indeed strike the wires in almost 100 percent of the few trials that it was possible to obtain. It is therefore likely that wires were detected at least some of the time in the maximum noise in Series II-V, even though the avoidance scores were as low as 40 percent.

We often had the impression when watching these bats that some attempt had been made to dodge a wire even when the bat touched the obstacle with its wing and the trial was therefore scored as a hit. Detection may have been too late, or directional localization not sufficiently

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| Table III | Results of Series IV, the effects of noise intensity and coherence on the obstacle-avoidance scores of two skillful Plecotus (Nos. 26 and 30). The noise frequency band was 10 to 120 kc, wire diameter 0.54 mm; abbreviations as in Table II. |

Noise Level re Levels Listed in Table I	Coherent Noise		Noncoherent Noise	
	N	M	N	M
−30 db	381	83%	288	76%
−20 db	873	68%	646	63%
−10 db	401	55%	316	50%
0 db	328	44%	249	40%

| Table IV | Results of Series V, the effects of intensity of 10- to 120-kc noise on two groups of Plecotus differing in general level of ability. Results with coherent and noncoherent noise are combined, since in Series V there was no significant difference between the two; abbreviations as in Table II. The wires were 1.07 mm in diameter. Obstacle-avoidance scores are averaged, followed in parentheses by minimum and maximum scores of individual bats. No. 43 employed in Series VI was a typical member of the more proficient group. |

Noise Level re Levels Listed in Table I	Four Very Skillful Plecotus		Eight Moderately Skillful Plecotus	
	N	Avoidance Scores	N	Avoidance Scores
Quiet	391	89% (81 to 95)	613	92% (84 to 95)
−31 db	175	86% (79 to 89)	214	84% (73 to 91)
−21 db	370	77% (71 to 81)	696	67% (50 to 85)
−11 db	310	71% (57 to 81)	178	61% (0 to 82)
−1 db	97	40% (37 to 46)	−	−

accurate, or motivation too low, to form the basis for a completely successful dodging maneuver. Objective evidence to this effect appeared in Series VI, described below; hits occurred even when a prior vocal reaction showed that the wires had been detected. This effect offsets, to some degree, the chance misses. At the highest levels of noise intensity in Series II-V, where misses by chance must have been almost nonexistent owing to oblique approaches to the wires, the percentage of detections was almost certainly higher than the percentage of misses.

D. Distance of Detection of Wires

Adequate estimates of signal-to-noise ratio or of E/N_o necessarily involve the distance at which the wires were detected, since the echo intensity varies inversely as the cube of this distance. A conservative approach would be to assume that detection occurred only when a dodging maneuver could be observed, and this was often at roughly 10 to 15 cm. Yet in the quiet bats detect wires, as shown most clearly by an increase in pulse repetition rate, at much greater distances than one would realize if only flight behavior was studied.[5] In Series VI, applying the same method used previously for bats flying in the quiet, we estimated the distance at which Plecotus first reacted vocally to 0.54- and 1.07-mm wires in our noise field. An Auricon 16-mm sound camera photographed the bat from one side of the flight chamber, and the bat's acoustic pulses were registered on the sound track of the same film. Since the sound track could record only audio frequencies, the bat signals picked up by the microphone were rectified, and thereby turned into click-like impulses, before being fed to the camera.

In our maximum noise intensity, Plecotus pulses were very difficult to detect unequivocally when the bat was at a sufficient distance from the microphone. In order to discriminate against noise, we used a microphone sharply tuned to 32 kc, approximately the frequency at which the Plecotus echolocation pulses have maximum amplitude. The microphone, made by the Massa Division, Cohu Corporation, has a peak sensitivity of −60 db re 1 volt/μbar, and a noise bandwidth of 190 cycles; the sensitive element is a disc of ferroelectric ceramic. A further measure of relief from masking by the noise was obtained by using in Series VI a noise level 20 db below the maximum intensity available. The benefit obtained by lowering the noise level was less than might have been expected, because when the noise was moderated, the bat's cries were less intense. However, the modest intensity of the noise had the additional advantage of increasing the distance of detection, so that inaccuracy of measurements of the bat's position from the film amounted to a smaller fraction of the distance of detection.

Series VI employed only one row of wires, about one meter from the end of the flight space. The camera was located just outside the netting, in the position shown in Fig. 1. For each frame of film that showed the bat approaching the wires, the bat's position was determined from its apparent location against the opposite wall of the flight chamber, together with parallax corrections based on notes of its direction of flight and its distance from the camera. The accuracy of each position so determined was about ±5 cm, and errors would be expected to vary randomly in direction and magnitude, so that the average of many experimental flights is the best available measure of the distance from the wires at which the bat typically increased its pulse repetition rate.

The bat was always released at the opposite end of the flight space headed towards the single row of wires. Between flights, it ordinarily remained at a favorite landing place in one corner of the flight space between the wires and the loudspeakers until it was picked up and carried,
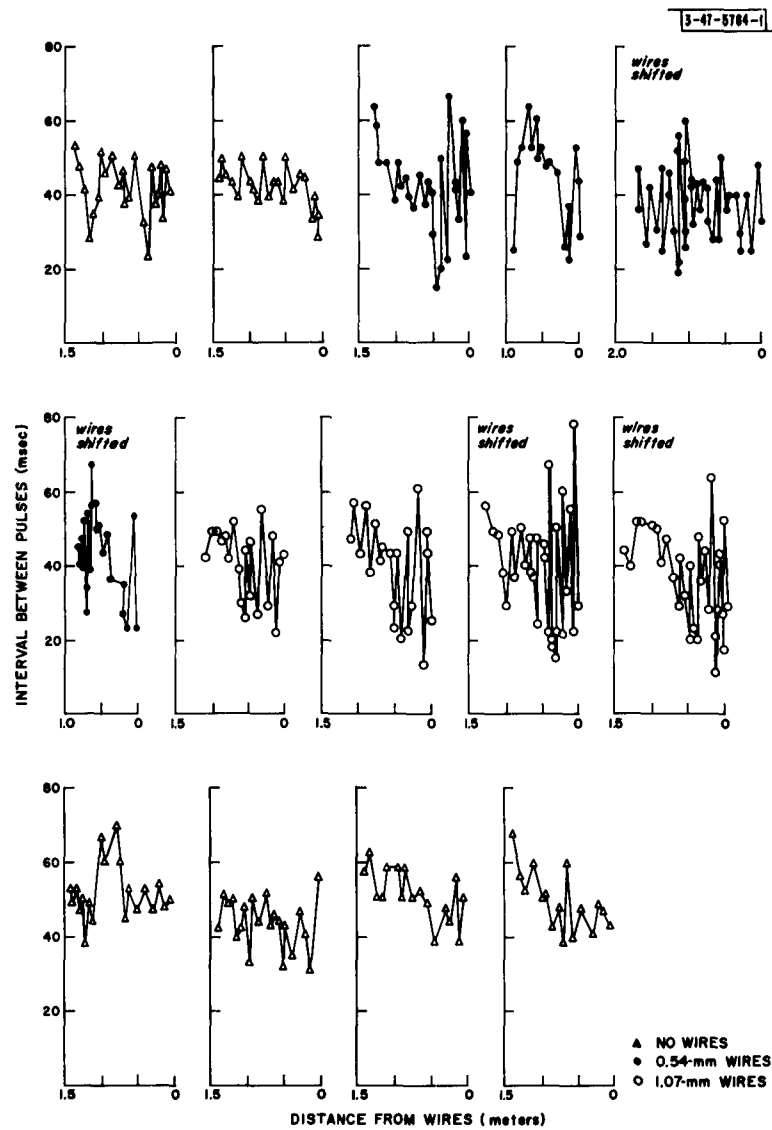
Fig. 2. Interpulse interval vs distance of bat from obstacle plane, for several flights with and without wire obstacles. The abscissae represent distance from the obstacle plane; for the "no wires" cases, the obstacle plane was taken to be the plane that most recently contained wires.

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inside a net or the closed hand, back to the starting point. It was given no opportunity to observe the positions of the wires when they were first put in place after control flights or after they had been shifted in position. Only one of the Plecotus used in Series V (No. 43) was still in its period of peak performance at the date of Series VI, and it was photographed during 102 flights — almost all the flights that it made in the noise during the three days devoted to this series. Thirty-eight control flights without wires were irregularly interspersed among 33 with 0.54-mm and 31 with 1.07-mm wires. To prevent the bat from learning the positions of the wires, these were shifted at least once in every four trials — usually across the flight chamber but occasionally 20 or 40 cm along its long axis.

Plecotus No. 43 performed approximately as well in the −20-db noise of Series VI as the skillful bats of Tables III and IV, registering 55 percent misses with 0.54-mm and 77 percent with 1.07-mm wires. Trials immediately after shifting the wires yielded scores that were not significantly different from those with unshifted wires (7 misses out of 15 trials with 0.54-mm and 10 misses out of 12 trials with 1.07-mm wires). A graph was prepared for each photographed flight, showing the interval i between pulses as a function of the distance d from the wires. A distinct drop of i on approach to the wires was present in 87 percent of the trials with 1.07-mm, and in 61 percent with 0.54-mm wires. In the control flights without wires there was a similar — though usually smaller — drop in this interval in 21 percent of the trials, but this occurred only very close to the plane of the wires and probably represented reaction to the loudspeakers, the end wall of the flight chamber, or the tripod holding the microphone.

The behavior of Plecotus No. 43 can best be judged from Fig. 2, which shows i as a function of d for 14 successive flights of a typical sequence on the third day of Series VI. Here the row of wires was one meter from the end of the flight space; "shifting" moved the wires within that plane. On the first flight with wires in place, i dropped at about 50 cm, whereas in the preceding flight without wires there had been a smaller drop at a smaller distance from the obstacle plane. Much the same pattern continued through several flights with 0.54- and 1.07-mm wires, but when the wires were removed there was an immediate return to the type of curve characteristic of the control flights without wires. Had the bat been lowering the interval between pulses because of a simple expectation that the wires would confront it, there was every reason to have done so when the wires were absent. In the only other case where the change was made directly from no wires to 1.07-mm wires and vice versa, there was an equally clear and immediate change in the curves relating i and d. Most of the changes between wires and no wires in Series VI were made with 0.54-mm wires, and scrutiny of the several individual curves shows that only in about half the cases could a clear distinction be made between successive flights with and without 0.54-mm wires.

In Figs. 3 and 4 the average values of i are plotted against d for the whole of Series VI. Since there was no appreciable day-to-day variation in the data for flights without wires, the whole set of these control flights in Series VI is included in both Figs. 3 and 4. While the average curves fail to reflect the typical increase in fluctuation of i visible in Fig. 2 as the wires are approached, graphs of minimum interval (not shown here) diverge from control curves at approximately the same distances as in Fig. 2. A much more clear-cut indication of the distance at which i first falls consistently below control flights with no wires in place can be obtained from Figs. 3 and 4 than from the individual curves. As would be expected, the larger wires were detected at greater distances. It is clear from Figs. 3 and 4 that under both conditions there was
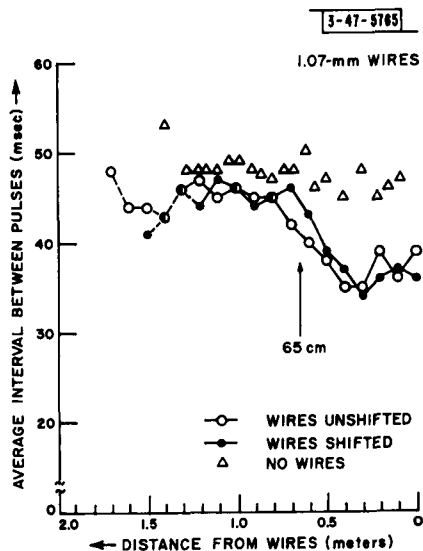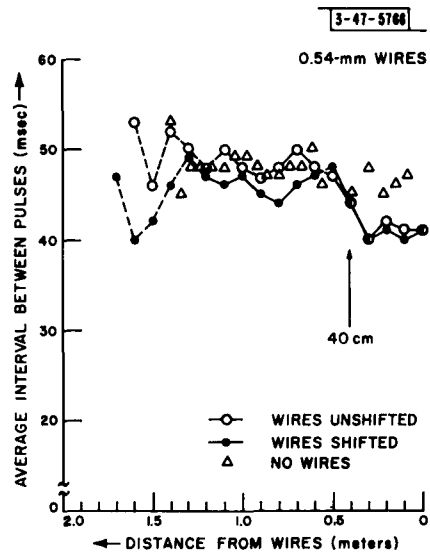
1.07-mm WIRES

Fig. 3. Average interpulse interval vs distance from obstacle plane containing no wires or 1.07-mm wires. "Shifted" designates the average for trials immediately after the positions of the wires had been changed. The dashed lines connect points for which data were available from fewer than 75 percent of the measured trials.

0.54-mm WIRES

Fig. 4. Average interpulse interval vs distance from obstacle plane containing no wires or 0.54-mm wires. "Shifted" designates the average for trials immediately after the positions of the wires had been changed. The dashed lines connect points for which data were available from fewer than 75 percent of the measured trials.

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a clear drop in i by 0.6 to 0.7 meter with 1.07-mm and by 0.4 meter with the 0.54-mm wires. These values thus appear to be conservative estimates of the distance of detection.

E. Estimation of E/N_0

The minimum detectable signal energy E was estimated by measuring the amplitude of the power spectrum of the bat's emitted signal in the forward direction at a known distance from the bat, finding a distance at which detection of a wire had occurred, and calculating the strength of the echo from the wire.

The bat's emitted level was measured in two ways. The first was the straightforward one of holding a bat in the noise field, at a measured distance from a calibrated microphone. However, an analysis of tape recordings from hand-held bats showed that very often more than half the energy in the pulse was carried by the harmonics. Recordings made while the bat was flying in noise showed that under these conditions the energy was predominantly carried by the fundamental. This difference makes us unwilling to assume that the pulses from the hand-held bat are emitted at the same acoustic level as those used when in flight. Nevertheless, the observations on hand-held bats were of use, because they confirmed our impression that the acoustic level of the bat's voice — at least when the bat is held — changes with the noise level.

Measurements on the pulses emitted by flying bats were limited by the fact that the bat was usually not on the axis of the microphone; the response of the microphone at other angles was determinable, but any practicable measurement of the angle between the axis and the line to the bat would have been subject to such uncertainty that we did not attempt it on any large scale. Instead, we have used two occasions when motion pictures showed that the bat was flying very close to the axis of the microphone, and headed toward it. In one such sequence, the noise level was "0 db" (i.e., maximum available) and the peak pressure of the bat's signal was 9.2 µbar at a Kuhl-type microphone 60 cm from its mouth. On another occasion, pulses were recorded when the bat was within 10° of the axis of the tuned microphone, in "−20 db" noise. The calibration for the response of the tuned microphone to a frequency-swept pulse was worked out by means of a frequency-modulated pulser (built by Lincoln Laboratory for electrophysiological experiments) that could simulate with accuracy the pulses emitted by the bat. The small correction of 1 db for the fact that the bat was not on the axis of the microphone was applied. The resulting pressure measurement was 0.28 µbar at 150 cm from the bat's mouth; this figure is a lower bound, because it is not certain that the bat was facing in the direction of its flight. Transposing these pressures to a standard distance of 1.00 m (using the inverse-square law for the power), we find values of 5.5 µbar for "0 db" noise and 0.42 µbar for "−20 db" noise. The first of these is the better measurement, physically speaking, but the best estimates of distance of detection were made in the "−20 db" noise (Series VI). On the basis of rather sketchy measurements on the variation of emitted signal level with noise level for hand-held bats, we conclude that for the "−20 db" noise, the peak pressure of the bat's emitted signal was probably not greater than 0.9 µbar at 100 cm from its mouth. We have therefore used this value in our calculations of the echo energy.

Since the diameter of the obstacle wire was much less than the wavelength of the bat's signal, the reflectivity of the wire increased strongly with frequency. It was therefore necessary to examine the harmonic content of the signals. This was done by re-recording the signals on a two-channel tape after passing them through a set of filters; one of these was 45 kc low-pass

and passed only the fundamental of the cry, whereas the other was 50 kc high-pass and passed only the harmonics. Ten kilocycles above or below 45 kc, the filter rejection was 25 db. The trains of pulses emitted in flight were examined by playing the re-recorded tape at reduced speed into a two-channel oscilloscope photographed with a moving-film camera, thereby procuring side by side a record of the fundamental frequencies and the higher ones in each pulse. The amplitude of the fundamental trace was nearly always greater than that of the combined harmonics by more than 10 db. The reflectivity of the 1.07-mm wire was nearly constant in the interval 50 to 110 kc, reaching a local maximum at 80 kc and then a local minimum at 150 kc. The nearly constant reflectivity of this wire for the second and third harmonics was 10 db greater than it was for 25 kc, the lowest frequency contributing significantly to the power in the pulse. Therefore, if a calculation of E, the energy in the echo, assumes that all the power was in the fundamental frequencies, the calculation is not an underestimate. Moreover, the noise power per cycle was higher for the harmonics than it was for the fundamental, by more than 3 db for the second harmonic and more than 6 db for the third. We have therefore calculated the echo level by assigning all the echo power to the fundamental frequencies.
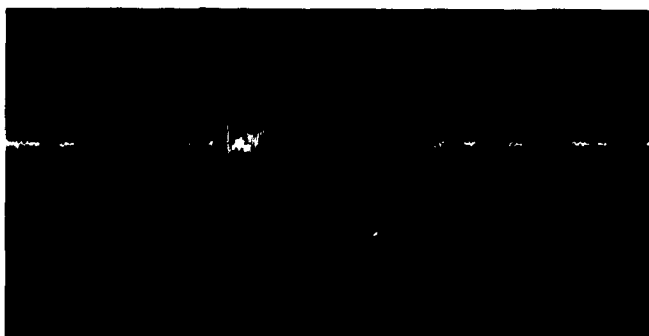

Fig. 5. A pulse emitted by Plecotus while flying in noise. The upper trace is the signal from the microphone. The lower trace presents the periodmeter output, which registers the time between successive positive-going zero-crossings in the acoustic signal. The horizontal divisions are milliseconds. For the periodmeter trace, each vertical division represents 10 μsec, with the zero on the lowermost line. The second line from the bottom therefore corresponds to a frequency of 100 kc, the next to 50 kc, the next 33.3 kc, and so on.

The frequencies in the bat pulses were analyzed by a periodmeter circuit that plots, on an oscilloscope screen, the lapse of time since the preceding positive-going zero-crossing of the wave; the trace on the oscilloscope indicates the period of each cycle of the waveform. Except when harmonics complicate the pattern of the zero-crossings, the pattern for Plecotus pulses emitted in flight is usually rather close to a straight line, indicating that the instantaneous frequency varies approximately hyperbolically with time. Pulses from Plecotus No. 43 had maximum amplitude as the frequency swept through 30 kc; this parameter was notably constant. A typical pulse and its periodmeter analysis appear in Fig. 5. The frequency sweeps from 45 to 20 kc and the maximum amplitude is at about 30 kc.

At each frequency, the intensity scattered at 180° (reflected toward the bat) by the wire is S times the intensity incident on the wire, where

$$S = \frac{\lambda}{\pi^2 R} \sum_{m,n=0}^{\infty} \epsilon_m \epsilon_n \sin\gamma_m \sin\gamma_n \cos(\gamma_m - \gamma_n) \cos m\pi \cos n\pi \quad .$$

Here λ is the wavelength of the sound, R is the distance from the wire to the bat, $\epsilon_0 = 1$, $\epsilon_p = 2$ for $p > 0$, and the phase angles γ_p are tabulated functions of λ and the diameter of the wire;[16] it is assumed that the incident sound is a plane wave traveling horizontally, and that the wire is effectively infinite in length. The energy per unit area in the echo is

$$E' = \frac{1}{2\rho c} \int_0^T P^2 S \, dt \quad ,$$

where ρ is the density of air, c the velocity of sound in air, P the amplitude of the wave striking the wire (variable during the pulse) and T the duration of the pulse.

It is an adequate approximation to take T as 2.0 msec and to take P as rising linearly from 0 to a maximum value P_m in 1.0 msec, then falling linearly to 0 in another millisecond. The reflectivity S, which is expressed in the sum above as a function of frequency, can be evaluated as a function of time by inspection of the photographic records of the pulses. The product $P^2 S$, so estimated, was integrated graphically to get E'. For $P_m = 0.9 \mu\text{bar}$ and $R = 100$ cm, the result is $E' = 3 \times 10^{-10}$ erg/cm^2. Very nearly the same result was obtained from the simpler procedure of taking P^2 as having the fixed value $0.3 \, P_m^2$ during the entire pulse[5] and using the value of S that is appropriate for the peak amplitude at 30 kc.

This value of E' is the energy per unit area in the free field at 100 cm from the wire. The free-field noise power per cycle per unit area in the neighborhood where the bat detected the wire is available via Table I; the noise power per cycle in the "-20 db" noise, in the region photographed, was close to $+5$ db re 0.0002 μbar, so that

$$N_o' = (2\rho c)^{-1} (1.7 \times 0.0002 \, \mu\text{bar})^2 = 1.4 \times 10^{-9} \text{ erg/cm}^2 \quad .$$

The result is that $E'/N_o' = 1/4$ or -6 db, for 1.07-mm wires and an arbitrarily chosen distance of 100 cm. It is to be remembered that this result is an estimated upper bound, and that the primed quantities — energies per unit area — deal with fluxes whose directions are not identical. Figures 3 and 4 show that on the average, detection had occurred by the time the bat was between 60 and 70 cm from the plane of the wires. We may take 65 cm as the bat's average position at the time when it first emitted a pulse at a distinctly shortened interval since the last pulse. Detection had occurred prior to this time, and the most energetic echo on which it could have been based was the one from the preceding pulse. The bat was moving roughly 2 m/sec or about 10 cm during the typical predetection pulse-to-pulse interval of 45 msec. We conclude that the bat detected the wire by means of echoes from pulses emitted when he was at least 75 cm from the wire.* The value of E'/N_o' stated above must therefore be increased by a factor $(100/75)^3$, or 2.4, which gives $E'/N_o' = -3$ db for the 1.07-mm wires.

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* Although what has been said heretofore in the text does not guarantee that the bat was flying toward the wire, so that his travel in the interpulse period is a good approximation to the change in range during that time, it will appear below that in fact the bat usually was flying toward a wire (though not directly toward the plane of the wires) and that this wire nearly straight ahead of him was the one that he was most likely to detect. The 65 cm yielded by measurement of the movie film was a distance to the plane, and the distance to the wire was usually greater than the distance to the plane because the approach was quite oblique. The 75-cm range arrived at in the text is therefore a conservative estimate; the actual range may have been as much as 10 cm larger than that.

For the 0.54-mm wires, Fig. 4 indicates that the interpulse period had shortened by the time the bat was 40 cm from the plane of the wires, and that detection must therefore have occurred when the range to the wire was at least 50 cm. The reflectivity of these wires for the fundamental frequencies in the pulse was 11 db less than that of the 1.07-mm wires. For the second harmonic, the difference is 12 db. Combining this 11-db difference with the factor $(75/50)^3 = 3.4$, or 5 db, to take account of the difference in ranges of detection of the two kinds of wire, we find that for the 0.54-mm wires, $E'/N_o' = -8$ db. Here we have assumed that the level of the emitted bat pulse is the same for the 0.54-mm wires as it is for those 1.07 mm in diameter; on this point we have no evidence.

F. Neural Correlates of Resistance to Jamming

Electrophysiological studies of the auditory brains of bats have revealed neural mechanisms that relate to the discrimination of echoes from noise.[11,17] Plecotus were anesthetized and electrodes were placed in the cochlear nucleus (where impulses from nerve cells in the cochlea first enter the brain) or else in the posterior colliculus (a part of the midbrain auditory system prominent in bats). These electrodes recorded the electrical signs of nervous activity in response to constant-frequency pulses of sound lasting from 0.5 to 10 msec, at frequencies 10 to 150 kc. The sounds came from loudspeakers similar to those used for the noise field described above.

Two varieties of electrode were used. The gross ones, uninsulated platinum or silver wire roughly 100μ in diameter, recorded graded activity ("evoked potentials") from large populations of cells in response to the onset of the acoustic stimulus; the microelectrodes, which were electrolytically sharpened tungsten wires insulated to within 15μ of a 1- to 3-μ tip, sensed electrical changes in individual cells of the brain.[18]

There are several ways in which the bat's auditory system is equipped to discriminate signals from noise. In the first place, each of the two auditory channels includes certain selective mechanisms that can reduce response to unwanted inputs. Furthermore, the external ear is shaped so that its efficacy as a collector depends on the direction from which the sound comes, and in our experiments the noise and the echo were not usually from the same direction. In addition, the electrophysiological study has brought to light two forms of interaction between the two auditory channels. One of these sharpens the dependence of sensitivity on the angle from which a signal is received. It has effect even when there is no jamming. The other interaction is such that a favorable signal-to-noise ratio at one ear can suppress the effect of noise received at the other ear.

In the individual channels, i.e., in the channels activated by monaural inputs, the selective mechanisms known to us can be designated as tuning and pre-sensitization. Tuning is simply the restriction of sensitivity to a narrow range of frequency. A gross electrode picking up the evoked potential from a large population of auditory cells in Plecotus detects response to sufficiently energetic acoustic stimuli over a wide range of frequencies, from below 1 kc to above 100 kc. Microelectrodes show, however, that most of the individual cells contribute to the evoked potential only over a very restricted frequency range; a frequency change of 1 kc in the neighborhood of 50 kc can change the threshold of a cell by as much as 40 db. Pre-sensitization is a reduction of the threshold levels of certain cells after a pulse has been received, so that such a cell is more sensitive to a second pulse that has the same frequency. The lowering of the threshold amounts to 15 db or more; it begins about 2 msec after response to the first pulse, and

lasts typically for about 20 msec, or in some cases longer. Although the experiments have employed pulses of constant frequency, it seems likely that similar pre-sensitization can be effected by the bat's own frequency-modulated cries, so that an echo is favored over sounds of other frequency patterns. A population of narrowly tuned cells are presumably excited in a regular sequence, but no evidence is yet available to indicate the degree to which the detailed structure of the emitted pulse is coded into the sensory system.

The directional properties of the Plecotus ear were investigated through observation, with gross electrodes in the cochlear nucleus, of the earliest neural evoked potential (N_1, identified by a latency of less than 1 msec). The short latency is taken as a guarantee that the potential arises from a stimulus at the ipsilateral ear. The sharpest directional discrimination in Plecotus takes place at 50 kc and higher. Directional data were taken chiefly at the frequency for which the threshold of hearing was a minimum, usually between 50 and 60 kc. For these frequencies, the angle of greatest sensitivity, measured from the axis of the bat in what will be called "the horizontal plane" — a frontal plane passing through the two ears — is 15° to 30° ipsilateral to the ear; minimum sensitivity is at 90° contralateral. The average difference in these two sensitivities was 33 db, and the maximum, 38 db. At 30 kc, maximum sensitivity is at about 60° ipsilateral to the ear, and minimum sensitivity occurs at 90° contralateral; the average difference is approximately 20 db.

At the posterior colliculus, the evoked potential (latency about 3.0 msec, indicating the intervention of three or four synapses between the cochlea and the colliculus) derives largely — but not exclusively — from the opposite ear. In a bat that has been rendered monaural by destruction of the ipsilateral cochlea, the results obtained from an electrode in the colliculus closely resemble those just summarized. In a bat whose auditory system is intact, the mixing of inputs from the two ears might be expected to reduce the directional sensitivity, but actually the bat's brain turns it to advantage. At the colliculus, the difference between thresholds for 50- to 60-kc signals at angles of greatest and least sensitivity averaged about 40 db, and in one case it was 68 db. Experiments with microelectrodes show that some of the individual neurons are even more sharply directional. Only a few experiments of this kind were made; in the extreme case, the threshold changed repeatably by 62 db for a 7° change in direction. This heightened directional discrimination is accomplished by mixing of inputs from the two ears, especially by inhibition of inputs ipsilateral to the colliculus by inputs to the contralateral ear.

The existence of binaural interaction has implications for the jamming experiments. In part, at least, these have been directly demonstrated, through experiments in which an anesthetized bat was stimulated with brief pulses of tone and simultaneously with steady noise. The tone source was placed at several positions in the horizontal plane through the bat's head, and for each of these, thresholds were determined when the noise-generating loudspeaker was stationed at various places in the same plane. The loudspeakers and the electrical noise generator were identical to those used in the jamming experiments; the minimum practicable angular separation between the two loudspeakers was about 5°. The noise was always set at a high enough level so that there was masking no matter what angle the noise came from.

The monaural directional discrimination, augmented by the binaural interaction described above, favors either the noise or the signal, if these arrive from different azimuths. The single-tone directional data taken at the colliculi of bats with both ears intact enable one to construct a curve to show the "expected" masking effect of the noise. For example, if the signal is at 30°

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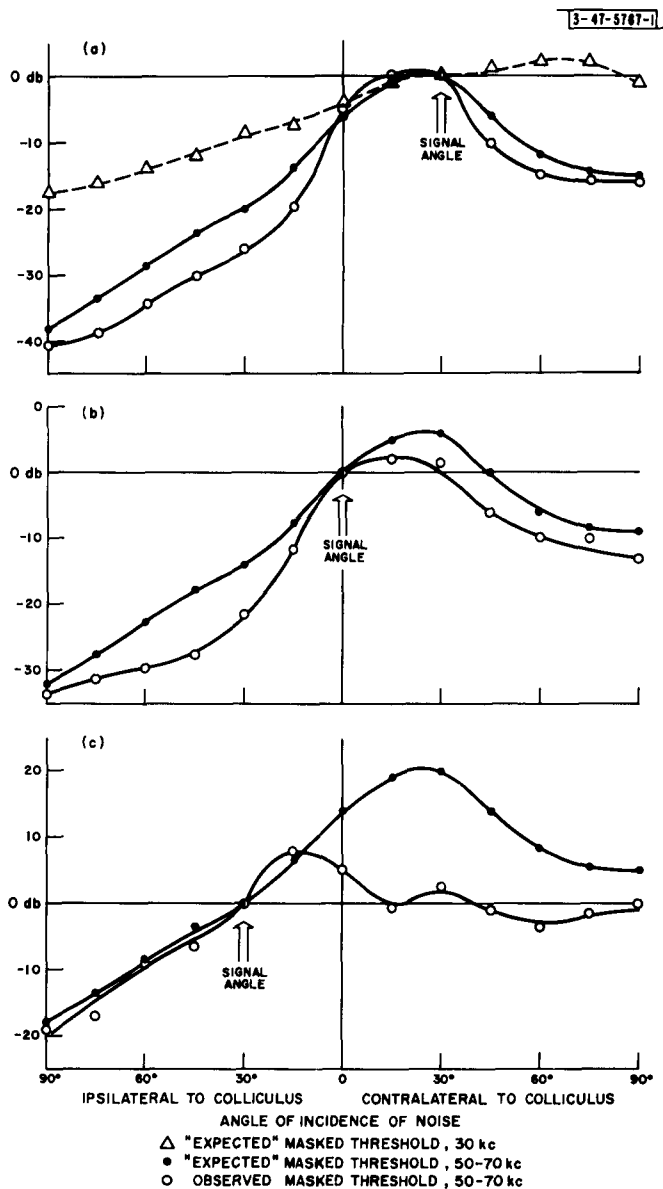
(a) "Expected" masked thresholds at 30 and 50-70 kc, and observed masked threshold at 50-70 kc, when the signal came from 30° contralateral to the colliculus.

(b) "Expected" and observed masked threshold at 50-70 kc, when the signal came from 0°.

(c) "Expected" and observed masked threshold when the signal came from 30° ipsilateral to the colliculus.

IPSILATERAL TO COLLICULUS   CONTRALATERAL TO COLLICULUS
ANGLE OF INCIDENCE OF NOISE
△ "EXPECTED" MASKED THRESHOLD , 30 kc
● "EXPECTED" MASKED THRESHOLD , 50-70 kc
O OBSERVED MASKED THRESHOLD , 50-70 kc

Fig. 6. Masking effect of broad-band noise on evoked potentials at the posterior colliculus. Each ordinate shows the threshold level for the signal when the noise came from the direction indicated by the abscissa. For each curve, the reference level (0 db) is the threshold observed when the noise came from the same direction as the signal.

The "expected" curve is derived from thresholds measured in the quiet for signals arriving from various directions. It is the same for all three cases, but it has been matched to each of the observed curves at the signal angle.

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contralateral to the colliculus in question – the direction of greatest sensitivity – then the directionality of collicular response to a tone can be expected to discriminate against noise coming from any other direction.

The data yielded by the masking experiments depart systematically from this "expected" masking curve, thereby indicating the existence of another kind of binaural interaction. For signals arriving from certain directions, the comparisons appearing in Figs. 6(a), 6(b) and 6(c) show that the noise had nearly the "expected" masking effect on signals that came from directions of high sensitivity, except when the noise was at 30° to 60° ipsilateral, where it was 5 to 10 db less effective than one might expect. However, Fig. 6(c) shows that when the signal is coming from an unfavorable direction and the noise from a favored one, the noise does not have anywhere near its "expected" masking effect.

The reduction in masking is not observed at the cochlear nucleus, nor does it occur at the colliculus when one ear is plugged. Moreover, experiment verified that when the tone and the noise came from the same direction, the threshold for the signal in noise was the same at all angles, as was assumed in the preparation of the "expected" curve. Hence the 10- to 20-db reduction in masking effectiveness must be assigned to our second binaural interaction. What appears to happen at successively higher levels in the brain is that the side whose directionality favors the signal, so that it "hears" the signal clearly, somehow influences the processing of the input from the other ear, in such a way that the noise is partially canceled out, or the signal selectively passed. Though the interaction cannot at present be explained in detail, its significance is evident. One ear gains in signal-to-noise ratio by virtue of its inherent directional sensitivity (equivalent to "antenna-pattern" discrimination in the radar analog). It is reasonable to assume (but not guaranteed) that even when noise is present, this directionality is augmented by the binaural interaction. The other ear suffers a corresponding loss in signal-to-noise ratio, but at the level of the colliculi, this loss is to a considerable extent canceled, and both colliculi may "hear" the signal clearly.

As an example of this discrimination, consider a 50- or 60-kc signal coming from 30° left, and a noise coming from 30° right. Reference to Fig. 6(a) shows that the right colliculus will be 26 db more sensitive to the signal than to the noise. Of this difference, the "expected" curve says that 20 db can be attributed to directionality. Were the second binaural interaction not present, the left colliculus would be 20 db more sensitive to the noise than to the signal. In fact, however, as Fig. 6(c) shows, the left colliculus is almost equally sensitive to the noise and to the signal.

The findings suggest that a bat should be able to reduce the masking effect of our noise by flying in such a way that the echo from a wire arrives from a direction of maximum sensitivity for one ear, while the noise arrives from a different direction. In the jamming experiments, the bats did indeed fly in this manner, routinely; they approached the wires very obliquely with respect to the long axis of the flight space, so that the echoes from wires were frequently coming from 0° to 30° on one side, and the noise predominantly from 60° to perhaps 30° on the other.

IV. DISCUSSION

The experiments in Series I established that some insect-eating bats are capable of successful echolocation in a very noisy environment, and made an effort to evaluate this success quantitatively. It was recognized that limitations of the noise field then available left open the possibility

that the bats might echolocate with the help of harmonics in their emitted pulses, since that part of the frequency spectrum was not strongly represented in the noise field.[5] Series II, undertaken when a better noise field could be provided, showed that the earlier noise field had actually not been masking all of the frequencies that <u>Plecotus</u> can exploit. Series III studied the effects of noise in three bands: 10 to 50, 10 to 90, and 10 to 120 kc. These experiments showed that at a given power per cycle, large enough to make finding the wires something of a problem for the bat, the effectiveness of masking was far greater for the 10- to 90-kc band than for the one that merely covered the fundamental frequencies in the bat pulses, but that a further increase in the bandwidth of the noise had no discernible effect (Table II).

Series IV was a preliminary, and Series V a more extensive, experiment on the effects of exciting the noise field coherently — i.e., from a single generator of random noise — with consequent destructive interference at certain frequencies for any given point in the noise field, these frequencies being dependent on position in the field. The results are not easy to interpret. In Series IV, it appeared that the bat's performance was definitely better in the coherent noise than in the noncoherent. In fact, we estimated at the time that to have an equal jamming effect, as measured by avoidance scores, the coherent noise had to be 5 db higher than the noncoherent. Moreover, in this series there was a noticeable difference in the style of flight in the two kinds of noise. In the noncoherent noise, when it was at levels high enough to affect markedly the bats' ability to find wires, their flight was often of a hovering, hesitant, sort. In coherent noise at the same level, the bats usually flew more confidently, as if they felt that the situation was under control.

Series V, which was designed to test the degree to which bats might be able to exploit the interference nulls in a coherently excited field, failed to show any difference between the effects of the two fields. In the most intense noise, Series V resulted in only 40 percent misses of 1.07-mm wires, whether the noise was coherent or not. Yet two bats of the earlier group used in Series III, when the excitation was coherent, achieved an over-all average score of 53 percent misses of 1.07-mm wires in the most intense noise. One possible explanation of this discrepancy is that these two bats in the February group were skillful enough to exploit the coherence, whereas those in the April 1960 group were not. Such a difference, if real, could perhaps be correlated with the hibernation cycle.

Series VI estimates, with as much accuracy as could be achieved with a reasonable amount of effort, the ratio of signal energy to noise-power-per-cycle when there is behavioral evidence that the signal has been detected. Two of the quantities that enter into this calculation are subject to considerable uncertainty; they are the acoustical level of the bat's emitted signal and the range at which the echo has been discerned. Undoubtedly these both vary from case to case, and there may be a systematic difference in the acoustical levels used by the bat when flying among wires of the two different sizes that were employed. Setting aside the possibility of such a difference, we find that detection is evidenced when E'/N'_o is about -6 db, or $1/4$. Here E' is the energy per unit area in the echo of a single pulse, and N'_o is the noise power per cycle per unit area.

A central concept in detection theory is that of "false alarm," a decision that a signal is present when in fact it is not. In the Neyman-Pearson strategy of detection the observer decides what false-alarm rate he is willing to tolerate, and then maximizes the probability of detecting a real target.

Though we watched for behavior suggestive of false alarms during the experiments reported here, we seldom saw anything that could be interpreted in this way. On rare occasions — perhaps four or five during all of the flights described here — we noticed dodgelike maneuvers when no obstacle lay ahead. In only 5 cases out of the 38 flights without wires in Series VI was there a drop in i as distinct as those that occurred when wires were present. During these 38 flights, there were about 750 interpulse periods that we timed, so the indicated probability of a false alarm on any one pulse was about 5/760 or about 1 percent. Since it is possible that some — or even all — of these alarms were true alarms incited by echoes from the microphone or other objects near the boundary of the flight space, the value 1 percent has to be taken as merely an upper-bound estimate of the fraction of the pulses on which there was a false alarm. The estimate is consistent with the impressions that we formed through watching flight behavior. To compare it with the customary measure of false-alarm rate, we need to divide it by the number of range intervals that an ideal receiver could search with a pulse waveform and a range like those of a bat. A conservative estimate of this number is 100, since a _Plecotus_ certainly can detect objects at distances up to at least 100 cm, and the pulse bandwidth of 15 kc permits a time resolution of $(15\,kc)^{-1}$, or 0.07 msec, which corresponds to a range resolution of 1 cm. We therefore arrive at 0.01 percent as an upper-limit estimate of the false-alarm rate, in the sense in which that term is used in statistical detection theory.

The conditions of the experiments were not well suited to the observation of false alarms; nevertheless, the rarity of behavior suggesting false alarms does tend to support the conclusion that whenever we could elicit enough flights to obtain obstacle-avoidance scores (Tables II-IV), the bats were operating with a high ratio of true alarms to false alarms.

For the very favorable case in which the observer knows exactly both the form and the time of occurrence of the signal (if any), but does not know its phase, a tabulation of detection probabilities for various false-alarm rates and signal-to-noise ratios is given by Helstrom.[9] For a false-alarm rate of 0.01 percent, a single-signal detection probability of 50 percent demands that the ratio E/N_0 be +10 db; when E/N_0 = 0 db, a single-signal detection probability of 50 percent can be achieved only at a false-alarm rate of about 20 percent. By contrast, we estimate that bats make detections rather successfully when E'/N_0' is about −5 db. However, single-pulse values of E'/N_0' do not tell the whole story.

To begin with, we have no assurance that the bat bases its detection decision on pulses treated singly. It is conceivable that the bat has a storage system for superimposing the energies of several received pulses before making a detection. When E'/N_0' is somewhat less than unity, but the angle between the directions of travel of E' and N_0' is sufficiently large, the directionality of the ears can raise E/N_0 at the input to the cochlea to some value exceeding unity; summation without regard to phases ("postdetection integration,"[10]) then becomes possible in principle. Apart from the phenomenon of pre-sensitization, we have no evidence that pulse-to-pulse summation actually occurs. With almost all of the cells for which it has been observed, pre-sensitization ceases to have any discernible effect when the time between pulses is as large as the 45-msec interval that was noted when the bats were searching for the wire obstacles. We therefore interpret pre-sensitization as a means of favoring sounds that are echoes of a recently emitted pulse, not as a mechanism for summing successive echoes. Though we do not rule out the possibility of echo-to-echo summation, there is no need to postulate that it exists, because directional selectivity for which there is definite evidence seems quite sufficient to account for the observed performance.

The maximum difference in direction that a bat in the jamming experiment could establish between the noise and an echo from a wire was about 60°. From the monaural experiments described above, one estimates that at 60 kc the most that a bat, in these circumstances, can gain through the directionality of a single ear is 20 db. Actually, this is certainly an overestimate, since it assumes that the noise is coming from a single direction, which was never true in the jamming experiment. The available monaural data at 30 kc are less extensive, but they indicate that 15 db is a generous estimate of the advantage that the directionality of a single ear could confer if the noise were coming from just one direction and the bat used optimum direction of flight.

The bats operated successfully with E'/N'_0 in the neighborhood of -5 db, with an emitted-energy spectrum that was maximum near 30 kc. To achieve a 50 percent detection probability with the estimated false alarm rate of 0.01 percent, an ideal detector needs to have E/N_0 equal to +10 db. Because the noise did not all come from the same direction, it is not possible to say that the 15-db discrepancy between the bat's E'/N'_0 of -5 db and the ideal detector's E/N_0 of +10 db can be accounted for by the directionality of the ear at 30 kc.

At 60 kc, the ear is more highly directional. Our knowledge of the harmonic content of the bat's pulses is very far from exact. The best indications are that for bat No. 43 in Series VI, the harmonics carried only a little less than 10 percent of the energy. The actual percentage certainly varied from pulse to pulse, and on some recorded occasions it exceeded this figure. Since the reflectivity of the wire obstacles was 9 db greater for the harmonics than for the fundamental component of the pulse, the energy in the echo was distributed somewhere near evenly between the fundamental frequencies (near 30 kc) and the harmonics (above 50 kc). The noise power per cycle was about 3 db higher for the second harmonic than for the fundamental, and not many decibels higher for the third harmonic. As a quite crude estimate, we can assess E'/N'_0 for the harmonics as -10 db. Since our data on the directionality of the ear at 60 kc indicate that this cannot (in the noise field in which the bats operated) have provided as much as 20 db of directional discrimination, the ear alone again fails to provide as much discrimination as we estimate to be needed.

The key to the bats' success in countering noise appears to be supplied by the binaural interactions. Figure 6 shows that if _Plecotus_ flies so that the echoes come from ahead or somewhat to one side, and the noise comes from about 45° on the other, preferential treatment of a 50- to 70-kc signal can amount to 30 db. The advantage obtainable at 30 kc is estimated from the masking experiments to be 10 to 20 db. Apart from the limitation that the noise did not all come from one direction, the bats actually did fly in this manner, as a matter of routine. If the noise did come from a single direction, the figures just mentioned would imply that the bat's ear-brain system could raise E'/N'_0 from -5 db for the components near 30 kc and -10 db for those near 60 kc to effective values of E/N_0 approximating +5 to +15 db for the fundamental and +20 db for the harmonic. Because of the high degree of noise rejection of which the _Plecotus_ ear-brain system is capable at frequencies above 50 kc, it appears likely that in the jamming experiment, these frequencies played a decisive part. Our information about the harmonic content of _Plecotus_ pulses emitted in flight during the jamming experiment is too crude to permit us to be at all insistent about our numerical estimates, but they tie in well with the fact, noted in connection with Series III, that 60- to 120-kc noise reduced the obstacle-avoidance scores to levels below those achieved in the quiet.

Even when allowance is made for the fact that the noise did not all come from the same direction, the last figures bring E/N_o up to a level at which an ideal detector could be expected to operate as successfully as the bats did. No estimate of this allowance need be made, because the curves in Fig. 6 are for evoked potentials, obtained with gross electrodes. As mentioned in Sec. III-F, the selectivity available at single neurons in the colliculus is certainly far greater (though for the monaural observations made in the cochlear nucleus, the evoked potentials are presumably representative of the single-neuron responses).

The over-all result of Series VI, therefore, is that the bats' successful echolocation in the presence of noise can be accounted for by the observed action of ear and brain; it appears that the ear and the lower auditory centers take advantage of directional differences to augment the signal-to-noise contrast, and that detection is then performed with an efficiency less than that of an ideal statistical detector. It appears further that the directionality of the ear alone is probably not sufficient to account for the bats' success, but that the brain introduces at least two kinds of interaction between nerve impulses from the two cochleas, and that these raise the signal-to-noise contrast to a level consonant with the observed behavior of the bats. The resistance of <u>Plecotus</u> to jamming is thus reconciled with signal-detection theory.

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