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MECHANISMS OF TARGET DISCRIMINATION

BY THE ECHOLOCATING BAT,

VAMPYRUM SPECTRUM

A thesis submitted to the Faculty of The Rockefeller University

in partial fulfillment of the requirements

for the degree of Doctor of Philosophy

by
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Vampyrum spectrum

PREFACE

I wish to extend my appreciation to Dr. D. W. Bronk for the opportunity to study at The Rockefeller University. Much of my education in these last five years has been received from the simple daily contacts that make Rockefeller a unique institution, and to Dr. Bronk goes much of the credit. In addition, my thanks go out to all my friends, both students and faculty, at whose hands I have learned so much.

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Many other friends have contributed in large measure to the completion of this study. Several of the bats used in my experiments were provided solely through the courtesy of Mr. Robert Loregnard and members of the Trinidad Regional Virus Laboratory. Two others were provided, along with an enormous body of contributed assistance, by the New York Zoological Society, and I offer my thanks to Mr. W. G. Conway, Mr. B. House, and others of that organization.

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ABSTRACT

Five specimens of the neotropical false-vampire bat, Vampyrum spectrum, were studied in an attempt to decide whether they were capable of discriminating between targets of differing shapes and sizes using echolocation alone. The study commenced with the demonstration that the bats could capture live mice, items similar to their normal prey, without recourse to visual or olfactory cues. The subsequent use of dead mice in place of live ones indicated that target identification was much more difficult for the bats when the mice were not moving, but could still be effected by some of them.

Bats were then trained to discriminate between two inedible targets of differing shape or size, for which they received food as a reward. Initial discrimination problems began with targets which were very disparate, both in size and shape, and progressed to two targets which differed very little. Disparate targets, such as a 15 cm. diameter ball and a 2.5 X 10.5 cm. wooden "sausage", were easily discriminated by all the bats and clearly by echolocative cues alone. Discrimination scores for more similar targets, such as a 6 cm. diameter sphere and a 2.5 X 7.0 cm. sausage were not as high as the previous series, but considerably greater than chance.

Since the bats could clearly discriminate between rather similar targets using echolocation alone, an attempt was made to design targets which, if discriminated, would allow for some interpretations regarding the actual echo parameters used by the bats. In particular, the targets and flight paths were adjusted so as to discourage the use of overall intensity cues, but to encourage the use of the frequency dependent properties of the echoes.

Of the five bats begun on this problem, two learned the discrimination with an accuracy of 70% or better. Because the elimination of overall intensity differences was contingent upon the point at which

the bats selected a target and the angle at which they approached it, actual discrimination flights of the two best performers were submitted to extensive photographic analysis. This suggested that one of the bats selected the targets and approached them along a path that was consistent with the use of the frequency dependent properties of the target echoes, but not with the use of their overall intensities. The opposite was true of the second animal. Further proof of this point came from the discovery that the threads supporting the targets were contributing to the frequency dependence of the echoes, the amplitude of this frequency dependence being a direct function of the diameter of the thread. When threads of small diameter were used, (thereby reducing the frequency dependence of the echoes), the first bat was unable to discriminate above the chance level while the second animal's performance was quite high. When larger diameter threads were used, both animals were able to discriminate. This was thus taken as additional proof of the use of the frequency dependence of the echoes by the first bat, and of the use of other cues, presumably overall intensities, by the other.

Since echolocation is effected by the use of emitted pulses of sound, the structure of the pulses emitted during discrimination flights was examined in detail. From this examination it was possible to show that at different stages along each flight, differently structured pulses were emitted. In addition, the two bats which apparently were using different echo cues to discriminate produced pulses of different structure at the points of target selection. No obvious explanations for the use of any given type of pulse at any given point in a flight could be given, but some relevant speculations were presented.

In summary: it was shown 1) that these bats could discriminate between very similar targets using echolocation, 2) that at least one of the animals was probably using as a cue the frequency dependent properties of received echoes, and 3) that there may be some correlations between the kinds of pulses these bats emitted and the kinds of problems they encountered.

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INTRODUCTION

Of all the patterns of vertebrate locomotion, one of the most striking is flight in darkness by bats. Flight, in any form, requires rather extraordinary sensory equipment and coordination, and the rapid nocturnal flights of bats can only inspire a certain degree of wonder and respect. The experience is in fact so foreign to diurnal and ambulatory man, that for centuries bats have been the subjects of elaborate tales and folklore.

However remarkable these animals seem at first glance, they are only more so when examined in detail. The earliest investigators who studied the orientation skills of flying bats did so in the face of numerous existing myths. Yet, they reasoned that, as fellow mammals, bats should be amenable to classical physiological study. They therefore set about a program of successive sensory impairments. The results of these studies, notably by L. Spallanzani and C. Jurine, (Cf. Galambos, 1942), were the conclusions that bats did not need their eyes to navigate in darkness, but that they did require the use of their ears. However, neither investigator was able to identify the actual auditory cues used by their animals. In the face of this difficulty and the contemporary myths, their work was ignored for the following 140 years.

The solution to the problems of orientation by flying bats came with the development of high frequency microphones. These were first used by Pierce and Griffin (1938) to demonstrate that bats in flight emit "pulses" * of high frequency sound which are inaudible to the human ear. This discovery led to the pioneering studies of Griffin and Galambos in which the present explanation of obstacle avoidance by bats was first advanced

* The usage of the term "pulse" in this thesis will follow that of Griffin (1958); that is, any relatively short acoustic signal, regardless of frequency composition, rise times or modulations, will be called a "pulse".

(Griffin and Galambos, 1941; Galambos and Griffin, 1942). They repeated the experiments of Spallanzani and Jurine on two species of North American bats and confirmed the conclusions of the early workers: vision was not necessary, but audition was. Then using the recently developed microphones, they demonstrated that these animals were continually emitting high frequency sound pulses while in flight. When the mouths of the bats were covered, no pulses could be detected and the abilities of the bats to avoid obstacles were greatly reduced. They also noted that in normal flying bats, the rate of emission of the pulses showed a marked increase as the bats neared an obstacle. This clear-cut behavioral response convinced them that the bats were able to detect obstacles while still some distance from them. Griffin and Galambos reviewed all this data and concluded that the bats were using the echoes from emitted cries to indicate the presence of obstacles. Griffin (1944) subsequently called this process "echolocation".

Since this original work, a notable literature on bat echolocation has accumulated. Most of this work can be divided into two methodological camps: descriptive and analytical. The descriptive studies have resulted in the examination of over 65 species of bats in 13 of the 16 microchiropteran families, and all have been shown to produce high frequency pulses (Griffin and Novick, 1955; Novick, 1958, 1962, and 1963; Pye, 1967; Möhres, 1953 and 1967a). In each of these cases, variations in pulse repetition rate seem to follow the degree of obstacle proximity, and this is taken as evidence that the pulses are used in echolocation.

The analytical studies have been prompted by the obvious versatility of the echolocation system. Part of this versatility is evident in the apparent use of echolocation by so many species in so many different environmental contexts. It is most notably evidenced, however, by the fact that most bats use echolocation in the detection and capture of food items, as well as in obstacle avoidance. This was first demonstrated by

Griffin, (Cf. Griffin, 1953), in the genera Myotis and Eptesicus, and has since been shown to be the case for other species as well. As with obstacle avoidance, a hunting bat increases the rate of emission of sound pulses when the target is approached and this is taken as evidence that the echolocation system is being used in capture. The ways in which echoes are being used can be inferred from the rather complicated maneuvers which bats seem able to execute in capturing flying insects in the dark. To intercept a flying insect, a bat must be able to continually adjust its flight to changes in the flight of the prey. To do this, it must be able to ascertain the "azimuth and altitude" of the insect at each point in time. Secondly, since many bats use a series of special capture movements which must be begun prior to contact with the prey item, (Webster and Griffin, 1962), the bat must also be able to judge the distance to the prey, at least at close range. In view of visual and olfactory controls performed in conjunction with insect catching by bats, Griffin, Webster and Michael (1960) argued that bats seemed able to determine both range and location of a target using echolocation alone.

Analytical studies have also suggested that bats are able to extract some information about the "nature" of a target by listening to received echoes. Part of this evidence comes from suggestive field data, and part from laboratory experiments. The field data is based on the observation that many bats hunt specialized food items in the presence of numerous non-food items. For example, insectivorous species such as Plecotus are known to pluck insects from branches, leaves, and even from flowers (Poulton, 1929). Carnivorous forms such as Vampyrum spectrum (Goodwin and Greenhall, 1961) and Megaderma lyra (Mohres, 1967b) often feed on sleeping birds which they must capture amidst dense jungle foliage. Trachops cirrhosus apparently captures geckoes under similar conditions (Goodwin and Greenhall, 1961). Noctilio leporinus and Pizonyx vivesi hunt over rivers and coastal waters and seem able to capture small fish at the water's surface even in the presence of floating debris (Suthers, 1967).

In each of these cases, food items return only a small fraction of the total echo field received by the hunting bat. Without some means of discriminating between food items and non-food items, these bats would be expected to make frequent attacks on foliage or debris. Yet this is rarely observed (Poulton, 1929; Suthers, 1965). It thus seems likely that bats have evolved some means to discriminate between different components of the total echo field. The immediate question which arises is whether such discriminations can be made on the basis of echolocation alone or whether some other sensory modality is necessary.

Several recent studies have attempted to investigate this latter question. Since these studies were performed under laboratory conditions, one must be careful in using them to interpret habits in the wild. However, they do point out the potential use of skills under natural conditions.

The most notable of these studies is that of Griffin, Friend, and Webster (1965). These workers taught little brown bats, Myotis lucifugus, to capture insect larvae, (mealworms), which were tossed into the air by means of a catapult. When the bats had learned to capture over 90% of the mealworms offered, small discs were randomly substituted for the mealworms. At first, the bats captured as many discs as mealworms, but in several days they were rejecting 80% of the discs, and still taking 90% of the mealworms. To check for the use of visual cues, several bats were flown in darkness. To control for possible olfactory cues, discs were smeared with mealworm juices, and both kinds of targets were dusted with a vitamin powder. In all cases, the bats were still able to discriminate between discs and mealworms. It was thus clear that these bats could discriminate between two similar targets solely on the basis of echolocative cues.

Webster (1967) has used a similar method to teach Myotis to capture mealworms which were catapulted simultaneously with non-food items or adjacent to large non-food objects. Among the former experiments

were those in which small spheres and mealworms were both projected into the air, and Webster describes successful captures of mealworms under these conditions. Examples of the second kind of interference object included large static spheres or conifer branches. In these cases, the mealworms were catapulted against or adjacent to these backgrounds, and captures by the bats were found to be highly successful. These latter experiments are similar to what might be encountered in natural conditions and are thus valuable in showing that the inferences from field data can be verified in the laboratory. However, they need not infer any skills beyond what has been already described for target localization. This is a result of the fact that the target was moving and the background static. Given that a bat can accurately plot trajectories of different objects, it need only select the moving object to obtain food. The experiments with simultaneously catapulted targets, and those of Griffin, Friend, and Webster do infer an additional ability: that of detecting from echoes something about the shape, size or texture of targets.

Suthers (1965) taught fishing bats, Noctilio leporinus, to obtain a small piece of submerged fish impaled on a fine wire which protruded 5 mm. above the surface of a shallow pool. When the bats had learned this problem, he taught them to obtain this food at only one of two possible targets, one being the single wire as above, and the other being of two finer wires placed close together. To eliminate visual cues, Suthers blinded several of his bats, and to eliminate olfactory cues, he smeared fish on both targets. The bats learned the discrimination with 80% accuracy or better. It is thus clear that Noctilio can also select between targets of different shape solely on the basis of echolocation.

The force of the preceeding discussion is that localization, selection, and capture of food items requires much more of an echolocative system than simple all-or-none detection. In short, it requires that the bat "visualize" its surroundings acoustically, perhaps even ascribing a shape

or size to each component of the echo field, and placing each one accurately in space. How does the bat accomplish this?

The determination of target angle by echolocating bats has been studied in detail in at least two insectivorous species, Myotis lucifugus and Plecotus townsendii. In these studies, (Grinnell, 1963c and, Grinnell and Grinnell, 1965), a good case is presented for the determination of target angle by means of binaural comparisons of echo intensity. Using neurophysiological methods of monitoring evoked responses from the posterior colliculus, these workers showed that the head and external ear structures of bats confer a high degree of directionality on the echo-receiving organs. Shifts of only a few degrees in target position can produce detectable responses in the colliculi of these animals. This accuracy is probably not accomplished by using the difference in arrival times since a shift of one degree corresponds to a difference in arrival time of only one μ sec, a value well below the known powers of auditory resolution in bats. Detection of differences in the phase of arriving echoes between the two ears is also unlikely due to the high frequencies used by bats. However, bats can detect fine intensity differences, and this fact coupled with the directionality of the ears, suggests that by measuring the intensity of an echo at each ear for several of the component frequencies, the target can be accurately placed in space (Grinnell, 1963c).

The determination of target range is presently the subject of much debate, probably as a result of the use of different methods by different species. Some investigators (Pye, 1961; Kay, 1961) have suggested that bats use long duration pulses so as to provide overlap between the outgoing pulse and returning echo. If the pulse contains variations in frequency, the greater the distance to the target, the more out of step these variations will be in the region of overlap. This could provide a measure of distance. However, only a few bats seem to use long enough pulses to produce pulse-echo overlap. Many, such as vespertilionids,

seem to actively avoid overlap by shortening the duration of their pulses as they near a target (Griffin, 1958; Cahlander, et.al, 1964). In these species, it has been argued that the temporal delay between the emission of the pulse and the return of an echo is used to estimate the distance to the target (see below pp. 36-37).

The skill which seems to have received the least attention is the ability to distinguish between targets which differ in size or geometry. Part of this dearth of data stems from the complexity of most echoes. Until the recent development of radar and sonar, there was little theoretical interest in the relation between echoes and the shapes of the targets that generate them. Now, such a theoretical background does exist, but the treatment for any non-simple body is an immense task. However, one can make some general qualitative statements about echo-target interactions that can help in planning experiments and these follow.

The potential information about an object that can be extracted from an echo is quite large. In general, the more complicated the echo, the more information which can be extracted from it. However, echoes are rarely more complicated than the sounds which generate them; in most cases, as will be shown below, the generation of an echo involves some selective elimination of the components of the impinging sound, rather than the production of new ones. The nature of this selective elimination will be fixed by the shape, size, texture and composition of the target. For this reason, any echolocative system which can compare the received echo with the emitted signal should therefore be able to deduce at least some of these target properties. It will be even more effective if it can compensate for elimination of components which is not target-related, such as atmospheric attenuation. It will be most effective if it can vary the emitted sounds at will, and thereby receive a string of different pulse-echo pairs, each of which supplies a slightly different piece of information about the target.

Since the differences between the emitted signal and the echo provide the information for the bat, it will be helpful to provide a brief description of the kinds of pulses used by different species, and then to describe the kinds of interactions these pulses might have with various targets. The kinds of changes wrought during echo formation and transmission through the medium must then be ones which are physiologically detectable by the bat. These topics will each be discussed below.

The Structural Properties of the Emitted Pulses

A bat pulse can be considered as a delimited packet of sound energy. It has a finite duration in time and occupies a given amount of space along its axis of travel. The net energy in the pulse may be distributed over several component frequencies and the relative distribution may vary in time. The distribution may also vary in space: the distributions along the axis of travel will usually follow the distributions with time; the distributions to either side of the axis of travel will depend on the frequencies present and the nature of the bat's emitting organs. In comparing the pulses from different bats, or in comparing an echo with its generating pulse, it is helpful to divide these parameters into those which describe the overall energy of the pulse and those which define the internal distributions, or "fine structure" of the pulse (Griffin, 1967). The fine structure parameters can in turn be divided into those which describe the temporal distributions of energy and those which describe the spatial distributions. These are not exclusive categories and a change in one will usually change others. However, they allow an orderly comparison between pulse and echo which is illuminating when the mechanisms of sound scattering are considered.

The Overall Energy of the Pulse The total energy of a pulse is the product of the average intensity of the pulse and the pulse duration.

Both parameters are known to be different for different species, (Griffin and Novick, 1955; Novick, 1958; Pye, 1967; Mohres, 1967a), and different for the same individual at different times, (Griffin, 1958; Suthers, 1965; Schnitzler, 1967). In spite of these variations, one can usually determine for each species an "average intensity" and an "average duration", which have predictive value. When these values are compared for different species, it is seen that they may differ by as much as three orders of magnitude in intensity and two orders of magnitude in duration.

These wide variations are usually attributed to differences in the food habits of the different species. For reasons discussed above, bats which may use pulse-echo delay to determine target distance will tend to use short pulses; those which may use pulse-echo overlap tend to use longer pulses (Schnitzler, 1967; Suthers, 1967). The variations in intensity seem to correlate with the hunting environment of the animals. Griffin (1958) has pointed out that bats which feed on fruit or sleeping prey tend to use very faint pulses; bats which hunt in open spaces, such as most vespertilionids tend to use loud pulses. Consider also the fact that if a bat attempts to discriminate between the echoes from different objects, as the jungle species must, using soft pulses would have the advantage that only adjacent objects would return detectable echoes. Using loud intensities would return many echoes from various directions and analysis might be difficult. An insectivorous species, on the other hand, which must detect small insects in open air will do best to shout. Then any echo will probably imply food and pursuit maneuvers can be initiated earlier.

The Distribution of the Pulse Energy Over Time Every pulse consists of waves of sound, and waves are by definition time-variant functions. In those cases where the pulses of bats are relatively constant in amplitude and frequency, description of temporal parameters is fairly straightforward. However, most bats produce pulses which are not constant in amplitude or frequency, or which contain harmonics whose relative amplitudes may vary.

In these cases, the description of temporal parameters becomes more complicated.

Any purely sinusoidal signal which has infinite duration, (not switched "on" or "off"), can be completely described by specifying its amplitude, its frequency, and its phase relative to some temporal or spatial reference point. Whenever the signal waveform is non-sinusoidal, or whenever the signal has a finite duration, complete description of the signal will require other parameters to describe the shape of the waveform. It is possible however, to treat almost all signals as a linear sum of pure sinusoidal waves, each component being completely described by specifying a frequency, an amplitude, and a relative phase. This system has the great advantage that one can compare equivalent portions of complex signals in a rigorous way; if one had to describe different waves by including some textual comments on their shapes, it might be very difficult to compare the different changes wrought in different signals by a similar force.

As with any analytical tool, however, the breakdown of complex signals into a precise list of components has its limitations. These arise out of an acoustic counterpart of the Heisenberg "uncertainty principle", which was first demonstrated by Stewart (1931). In short, Stewart showed that the sinusoidal breakdown of any signal, (which is known as Fourier analysis), cannot simultaneously give the time of occurrence and the frequency of a given component exactly. In mathematical terms, the uncertainties in frequency determination, Δf , and the uncertainty in locating a given component in time, Δt , are related by

$$\Delta f \cdot \Delta t \cong 1 \qquad \text{(Stewart, 1931)}$$

When a pure sinusoid has an infinite duration, Δt is infinite, since there is no way to distinguish between successive cycles, and thus to determine when any one occurred. Since Δt is infinite, Δf goes to zero. This means that the single component frequency is known exactly

and the corresponding frequency spectrum, (a plot of amplitude vs. frequency), will consist of a single, infinitely thin line (Cf. Licklider, 1951).

Whenever an infinitely long signal has a periodic waveform, it can be broken down into a set of sinusoidal components whose frequencies are known exactly. This exactness of frequency analysis is possible because Δt is infinite. Although the signal may consist of an infinite number of components, these are not spaced randomly along the frequency scale. To produce a periodic signal, all components must be commensurable: that is, the ratio of any pair of component frequencies must be a rational number (Cf. Courant, 1962). For many periodic signals, the ratio of any component with the component of lowest frequency is an integer. When this occurs, the lowest component is called the "fundamental", and the others are "harmonics". The frequency spectrum for such a signal will show a set of infinitely thin lines spaced at equal intervals along the frequency axis (Cf. Licklider, 1951).

The Fourier analysis of an infinitely long periodic signal gives not only the frequency of each component, but also the amplitude and relative phase of each. Clearly, changing the relative amplitudes of the different components will change the waveform of their sum. The importance of phase is more subtle. This is because the relative phases of two different frequencies will shift with successive cycles. However, if the two are commensurable, the shifts in phase will be restricted to a certain repeating set. It is this repetitive recycling of a fixed set of phase relations which results in the periodicity of the resultant waveform (Cf. Courant, 1962). When a signal contains two non-commensurable frequencies, one must wait an infinite number of cycles before any one set of phase relations recurs. Non-periodic signals therefore must contain frequencies which are non-commensurable.

A single finite signal, (such as a bat's pulse), is effectively an aperiodic

signal. For that reason, it must contain frequency components which are non-commensurable. Where would these components lie in the frequency spectrum of such a pulse? We can consider the pulse as the result of turning on and off an infinitely long pure sinusoid. This signal now differs from the non-switched sinusoid in that there are two points, the turning on, and the turning off, which are unique events. One can thus reduce the uncertainties in determining the temporal occurrence of any given wave of the sinusoid to the set of points between the turning on and the turning off of the pulse. In other words, Δt is no longer infinite, but is finite and equal to the duration of the pulse. By Stewart's relation, Δf must therefore be greater than zero. This increase in the value of Δf corresponds to a spread of energy to frequencies on either side of the major component. Many of the new components are non-commensurable; in fact, the spread of energy is continuous over all adjacent frequencies, whether commensurable or incommensurable. This results in the formation of a "band" of frequencies centered about the major component, f , which is the only component in the unswitched sinusoid, (Cf. Barton, 1964).

As the pulse is increased in duration, the frequency spectrum of the signal should approach that of an infinitely long sinusoid; i. e., the width of the band should decrease and approach the infinitely thin line spectrum of the unswitched wave. This in fact follows from Stewart's equation:

$$\Delta f \cong 1/\Delta t$$

where here, Δf equals the bandwidth on either side of f , and Δt equals the pulse duration. The total bandwidth about f is equal to $2\Delta f$, or $2/\Delta t$.

Note that a finite signal can be divided into two parts: the two ends during which any small piece of the signal will not recur again in the wave, and the middle section, which may approach a pure sinusoid in waveform.

Because the ends are unique and distinct parts of the signal, one can talk about two durations: Δt , the duration of the whole pulse, and $\Delta t'$, the duration of the switching on or off. Again, using the version of Stewart's equation, above, one can calculate two bandwidths, $2\Delta f$, the bandwidth during the middle of the pulse, and $2\Delta f'$, the bandwidth at either end. The parameter $\Delta t'$ is known as the "rise-time" or "fall-off time" of the pulse and must of necessity be shorter than or equal to the duration of the pulse. For this reason, the bandwidth, $2\Delta f'$ at the ends is usually larger than the bandwidth during the middle, $2\Delta f$. However, in most cases, $2\Delta f'$ does not form a continuous band, but is itself composed of a set of bands: a large single band around f with a total bandwidth of $2\Delta f$ ($=2/\Delta t$), and a set of smaller bands, each with a bandwidth Δf ($=1/\Delta t$). The number of smaller bands will depend on how many can be fitted into the interval between the major band and the limits of one-half the total bandwidth, $\Delta f'$ ($=1/\Delta t'$) (Cf. Barton, 1964).

As an example, consider a pulse with temporal dimensions similar to those of many bats, say a duration, (Δt), of 1 msec., a rise-time, ($\Delta t'$), of 0.1 msec., and a frequency (f) of 100 kHz (Cf. Griffin, 1958). During the middle section of the pulse, the bandwidth ($2\Delta f$), around the major component will be 2 kHz, i. e., all detectable components will lie between 99 and 101 kHz. During the ends of the pulse, there will again be a major band between 99 and 101 kHz, but there will also be 9 additional bands, each with a 1 kHz bandwidth, (Δf), between 101 and 110 kHz, and another 9 between 99 and 90 kHz. It is helpful to recognize that during the middle section of this pulse, which accounts for 80% of the total pulse duration, all detectable components are within a few percent of the fundamental frequency f . In other words, to a first approximation, one can treat the middle section as if it were a pure sinusoid of infinite duration. This does not mean, however, that the ends are not important to bats. On the contrary, the large spectral range of the ends increases the amount of potential information that

might be carried in evoked echoes.

As with infinite signals, the complete Fourier analysis of finite signals results in specification of the amplitudes and phases of each component. The importance of amplitudes is again obvious. A case for the importance of phase when commensurable frequencies are present has already been presented. What about the phase relations between incommensurable components? If any two incommensurable frequencies are observed initially with one set of phase relations, successive cycles will never reproduce that set in a finite amount of time. Since, in general, the waveform resulting from the sum of these two frequencies will shift with the shifts in their phases, the initial waveform and each successive waveform will be unique. It therefore follows that to produce a given waveform from a set of incommensurable frequencies, only one set of initial phase relations can be used. The phases must therefore be specified in the analysis of any finite signal, whether there are periodic parts of the signal or not.

The previous discussion assumed that a bat's pulse could be considered as a pure sinusoid of infinite duration that was switched on and off, and that variations in amplitude, phase or frequency composition were due to the switching. Most bat pulses, however, contain frequency and amplitude modulations which are not due to switching, but are variations introduced by the bat in addition to turning the pulse on and off. The simplest of these is amplitude modulation. Consider first an infinitely long pure sinusoid of frequency f which is sinusoidally amplitude modulated with a frequency w . The Fourier breakdown of the resulting waveform will consist of three components having frequencies respectively of $f-w$, f , and $f+w$, (Cf. Littler, 1965). The greater the amplitude of the modulation, the greater the amplitudes of the side frequencies, $f-w$ and $f+w$, relative to the fundamental component f . The frequency spectrum for such a signal thus

consists of three infinitely thin lines, spaced apart by the interval w , and with relative heights which depend on the degree of modulation. Since the signal waveform is periodic, the phases of all components will be defined by the analysis.

When the amplitude modulation is non-sinusoidal, it can usually be broken down into sinusoidal components, w_1, w_2 , etc., and each of these will generate side frequencies to give $f \pm w_1, f \pm w_2$, etc. If the signal is finite in duration, as bat pulses are, there will be a spread of energy around each component, and the bandwidth of each band will depend on the duration of the pulse for the middle section, and on both the rise times and pulse duration for the ends (Cf. Barton, 1964).

Modulation of the frequency of an infinitely long sinusoid follows similar rules as for amplitude modulation. If the modulation is sinusoidal with a frequency w , side frequencies will occur at $f \pm w, f \pm 2w, f \pm 3w$, etc. The greater the variation in frequency relative to the fundamental f , the greater the amplitudes of the side frequencies (Cf. Littler, 1965). When the modulation is non-sinusoidal but periodic, the side frequencies increase in number and amplitude depending upon the decomposition of the modulating waveform. When the signal is finite in duration, the component frequencies will be found in bands rather than lines, and the bandwidths will depend on the duration and rise-times of the pulse. As with amplitude modulation, the phase relations of the separate components are defined by the analysis and no other set of phase relations can be used to give the same resultant waveform.

A third form of modulation is that of the phases of the components of complex signals. In general, this follows the same rules as the analysis for frequency modulation, producing side frequencies or bands at integral multiples of the modulation frequency (Hund, 1942).

Bat pulses very frequently contain modulations. The pulses of bats

like Rhynchiscus and Chilonycteris, for example, are characterized by having long durations of constant frequency, but with modulations of pulse amplitude (Griffin and Novick, 1955; Novick and Vaisnys, 1964). Such modulations certainly result in a spread of energy to adjacent frequencies. The pulses of both these species are further complicated by the presence of several harmonics in addition to the fundamental component. Amplitude modulations can be expected to generate side bands around each of the harmonics also.

Other bats such as Myotis, many of the phyllostomids, and megadermatids, produce pulses in which the frequency is swept from a higher to a lower value during the course of the pulse (Griffin, 1958; Pye, 1967). The rate of frequency modulation in bats is very high. The usual measure for modulation rate is the modulation index; this is correctly used only for sinusoidally modulated signals of infinite duration and equals the frequency range produced by the modulation divided by the modulation frequency w . One can calculate an approximate modulation index for a bat like Myotis by dividing the frequency range, (about 40 kHz), by the reciprocal of twice the pulse duration, (about 3 msec.). This gives an index of several hundred. The highest indices for which spectral composition is usually provided are several orders of magnitude smaller (Cf. Wever, 1949 or Littler, 1965). If one extrapolates from those values, the higher the index, the greater the spread to other frequencies. Thus at the rates of sweep used by bats, the spread of energy to side bands should be quite large.

To summarize the time dependent properties: each bat pulse will consist of a complex waveform which can be considered as a sum of many pure sinusoidal components. Since it is a finite signal, these components will be found in bands, the width of which is a function of the pulse duration and rise times. In some cases, pulse may contain frequency components which are harmonically related. This will result in periodicity of the waveform, at least during the middle part of the pulse. In other species,

the amplitude or frequency of the pulse may be modulated resulting in an increase in the frequency composition of the pulse. All parts of the pulse, onset, offset, and middle sections with their harmonics or modulations, will be the result of precise sets of phase relations; any change in these phase relations will result in a change in the waveform of the pulse. Similarly, any change in the relative amplitudes of the components will also alter the waveform of the pulse.

The Distribution of Pulse Energy in Space The spatial properties of the pulse will depend greatly on several of the previous properties. In the first place, the temporal duration of the pulse will determine its linear dimensions along the axis of travel. For example, in air, the beginning and ending of a 1 msec. pulse will be separated by about 34 cm. Longer duration pulses will of course have greater lengths.

Secondly, the distributions of pulse energy away from the axis of travel will depend partly on the frequency composition of the pulse and partly on the nature of the bat's emitting organs. When the component frequencies are high, most of the energy will be concentrated within a small solid angle (Griffin, 1958; Pye, 1967); when they are lower, the energy will tend to spread out over a greater solid angle. In those cases where the frequency is modulated, a spread of energy to greater solid angles will occur as the frequency is swept down.

The organs used for emitting pulses vary with the species. In some bats, such as most vespertilionids, the pulses are emitted through the mouth resulting in a fairly broad spread of the sound energy (Griffin, 1946; Griffin, 1958). In other genera, such as Rhinolophus, or Megaderma, the pulses are emitted through specialized nasal appendages which serve to "beam" the sound energy in a forward direction (Mohres, 1953, 1967b). In addition to the basic principle of curved reflectors, some bats seem to have utilized the fact that two nares set up interference patterns in space. In Rhinolophus, the nares are set apart by $1/2$ the wavelength of the

principal frequency in their pulses, an arrangement which produces a highly directional beam of sound (Möhres, 1953).

This completes the discussion of the properties of bat pulses. Clearly, one limit on the amount of kinds of information which bats can obtain from echoes is set by the nature of the pulses they emit. To assess the importance of different properties of pulses in conveying target information, the processes of echo formation must be discussed. This will point out a second kind of limit: that set by the number of overlapping effects during echo formation and transmission through the medium. In many cases, different effects will alter the same property of the incident pulse, and this results in ambiguities in interpretation.

The Structural Properties of Echoes

In discussing the mechanisms of echo formation, it is helpful to follow the same procedure used for describing the emitted pulses; that is, to distinguish between the overall properties of the pulse and the fine structure properties, and within the latter category, to treat separately the temporal and spatial properties.

The Overall Energy of the Echo As before, the total energy content of the signal will depend on the average intensity and the duration. The average intensity of an echo will depend on many factors. First, the intensity of the echo-forming pulse will be of primary importance; all other properties being constant, the louder the emitted signal, the louder the echo.

Secondly, the greater the distance between bat and target, the fainter the echo. This attenuation of acoustic signal with distance is the result of two contributing effects. One is simply the loss of energy due to atmospheric viscosity and absorption which occurs during the passage of any perturbation through any physical medium. The second form of attenuation

is the result of geometrical expansion of the sound waves into space as they travel away from their source. The rate at which this expansion occurs will depend on the actual shape and distribution of the sound field, and this will be determined by properties of the source. A spherical source will produce sound waves with a spherical geometry and these will radiate unbounded into all dimensions. A cylindrical source, on the other hand, produces cylindrical waves, (at least over most of its surface), and these waves, being bounded in one dimension at the source's surface, radiate only into two dimensions. Since the cylindrical waves must spread into one less dimension than spherical waves, the attenuation losses due to geometrical expansion are lower in rate for a cylindrical source than for a spherical one. A source which produces waves which are bounded in two dimensions at the source can expand in only one dimension and thus do not attenuate geometrically at all. These are plane waves.

In general, these two sources of attenuation are combined into a single exponential equation relating an initial signal pressure to the pressure at a distance r . For plane waves, which are attenuated only by the atmospheric losses,

$$P = P_0 e^{-r/\alpha} \quad (\text{Beranek, 1949})$$

where P_0 is the initial signal pressure, r is the distance between the point where P_0 is measured and the point where P is measured, and α is an attenuation space constant with dimensions of distance. This constant combines the effects of molecular dispersion and absorption with those of heat and viscous losses. Its value will be a function of temperature, humidity, atmospheric composition, and the frequencies of the sound present in the signals. The proportional rate of attenuation of a plane wave (in pressure terms) with distance is

$$\Delta P/P = -1/\alpha \cdot \Delta r$$

For waves which are cylindrical in distribution, the peak pressure at a distance r from the source is

$$P = \frac{P_o e^{-r/\alpha}}{k \sqrt{r}} \quad (\text{Morse and Feshback, 1953})$$

and the proportional rate of attenuation will be

$$\Delta P/P = -(1/\alpha + 1/2r) \cdot \Delta r$$

For waves which are spherical in distribution, the peak pressure at a distance r from the source is

$$P = \frac{P_o e^{-r/\alpha}}{mr} \quad (\text{Morse and Feshback, 1953})$$

and the proportional rate of attenuation will be

$$\Delta P/P = -(1/\alpha + 1/r) \cdot \Delta r$$

These equations demonstrate the fact that the rate of attenuation of acoustic signals is greatest for spherical, next largest for cylindrical and least for planar waves ($1/\alpha + 1/r > 1/\alpha + 1/2r > 1/\alpha$). This means that the signals received at a distance r from cylindrical and spherical sources of comparable sizes will differ by a factor of \sqrt{r} in their pressures, the cylindrical source producing the louder signal.

In the previous discussion, the sources of these different waves were treated as if they were radiators of sound. The more realistic case from the bat's point of view is to consider them as scatterers of incident sound. In this case, there will be three attenuative steps between the emission of a signal and the reception of an echo. The first step will occur during the passage of signal from source to scatterer and the rate of attenuation will follow both the rules for atmospheric losses and those dictated by the geometries of the emitting source. For bats, the waves may be considered

as approximately spherical, although some of the more highly directional beams may attenuate geometrically at lower rates than predicted for spherical waves (Cf. Möhres, 1953). Secondly, at the surface of the scatterer, an echo will be generated, its pressure being a function of target size, a , and a complex function of target shape and incident frequency, F . The resulting echo signal will then be attenuated once again during its passage back to the source, both atmospheric and geometric losses contributing. Assuming the bat is producing spherical waves which are scattered by a spherical target, the peak pressure returned to the bat will follow the equation

$$P_{\text{echo}} = \frac{P_o \cdot a \cdot F \cdot e^{-2r/\alpha}}{\rho r^2}$$

The corresponding equation for a cylindrical target is

$$P_{\text{echo}} = \frac{P_o \cdot \sqrt{a} \cdot F \cdot e^{-2r/\alpha}}{\rho r^{3/2}}$$

Consider now two targets, one cylindrical in shape and the other spherical, and of such a size that in the vicinity of their surfaces, they produce equal intensity echoes. All a bat need do, (knowing beforehand that the echoes were equal in initial intensity), is to evaluate the intensity of the echoes produced at some point away from the surfaces of the targets and equidistant from the two of them. The larger intensity echo will correspond to the cylinder and the other to a sphere. To make such a judgement, the bat would require some prior knowledge of the relative sizes of the targets, and the abilities to make accurate range and intensity evaluations. Since the ratio between the echoes of the two targets will become more and more different from 1 as the target distance increases, the greater the bat's range, the easier the discrimination should be.

An alternative method for discriminating between two such targets would be to measure the rates of increase in echo intensity resulting from

a constant decrease in target range. At a given distance, the greater rate of increase would indicate a sphere echo, and the lesser a cylinder echo. This method would not require any prior knowledge about target sizes, but would still include two measurements made at equal distances. One possible complication to this method would seem to arise from the fact that at large values of r , the attenuation rates of both kinds of echoes converge to the rate for plane waves: $-2/\alpha$. One can calculate for a given value of α , at what distances the two rates are within any given degree of convergence to the plane wave rate of attenuation. For example, at a distance of 50 space constants, the rate of attenuation for a spherical wave will differ from the plane wave case by only 1%. At a distance of one space constant, the difference is on the order of 50%. As an example of a bat-like signal, a 100 kHz tone emitted under atmospheric conditions of 25° C. and 50% relative humidity will have a space constant of about 2.2 meters (Kneser, 1965). A hundred such space constants would be about 220 meters. Since discrimination studies have suggested that the apparent distances of target evaluation for bats are somewhat less than a meter, the use of attenuation rates by these animals could easily be within their capabilities (Cf. Griffin, Friend and Webster, 1965).

The third factor affecting echo intensity, (and one that has already been mentioned), is the apparent size of the target. This apparent size, usually called the "cross-section" of the target, is a complex function of the size and shape of the target, the orientation of the target relative to the incident sound field, and the wavelengths of the impinging sounds. Since this factor depends so highly on the temporal and spatial properties of the incident pulse, it will be discussed in the following sections on those properties.

The fourth factor which affects overall echo intensity is the location of the target relative to the bat. This is due to the fact that both the emitting organs and the receiving organs of the bat are directional

(Grinnell, 1963c; Grinnell and Grinnell, 1965). Whenever an echo arises from a point other than those within the directional optima of the bat's ears, it will be perceived as of lower intensity (Grinnell, 1963c). As with most of the other parameters, the degree of apparent attenuation will be frequency dependent.

The use of echo duration in target discrimination is only possible under a certain set of conditions. Since these depend on certain temporal and spatial properties, this will also be deferred until a later section.

The Distribution of Echo Energy Over Time The alterations in the temporal patterning of an incident pulse during the formation of an echo are by far the most complicated aspects of echo formation. Real targets will in general alter the incident pulse in several ways simultaneously. To separate out these different effects, it is easier to consider a series of ideal and extreme cases.

The first case is that of a totally rigid body. In acoustics, this means a body which absorbs only a trivial amount of the incident sound energy. Targets will be rigid bodies when their acoustical "impedance" differs greatly from the acoustical impedance of the medium in which they are immersed (Morse, 1948). Outside of the region immediately adjacent to a boundary, (where interactions between target and medium produce a complicated impedance pattern), the acoustical impedance of any material is approximately the product of its density and the velocity of sound in the material (Beranek, 1949). Thus a rigid body for a bat is one which has an acoustical impedance which is significantly different from that of air. For most liquids and solids, both the density and velocity of sound are much greater than for air, and, as a consequence, little sound energy is absorbed by these materials. However, hollow shells filled with air,

or some synthetic or living materials may have a better impedance match with air and may thus absorb non-trivial amounts of sound energy (Hickling, 1967). These will be considered later.

Given a rigid body in air, the nature of a reflected echo will depend first on the relative sizes of the object and the wavelengths of the impinging sounds. These are usually combined in the dimensionless parameter ka , where k is the wave number, (in waves per unit distance), and a is some appropriate dimension of the target, e.g., the radius for a sphere or cylinder, $1/2$ the interfocal distance for a prolate spheroid, etc. It is helpful to think of ka as 2π times the ratio of the target dimension, a , to the wavelength of the sound.

Acoustic theories predict that for rigid bodies, where $ka = 1$ or less, the echo intensity will follow the well-known laws of Rayleigh scattering (Morse, 1948). This means that the echo intensity for a sphere will be a function of the fourth power of the frequency of the incident sounds; or less familiarly, a function of the sixth power of a (Morse and Feshbach, 1953). When ka is equal to 1, the wavelength of the impinging sound is about 6 times the value of a ; for a frequency of 100 kHz, the value of a for $ka = 1$ is about 0.6 mm.

For values of ka greater than 1, but less than about 35, the echo properties are more complicated. This is due to the fact that part of the incident sound energy is reflected from the nearest surface, while the rest forms a "creeping wave" which circulates around the target and interacts with the reflected waves (Hickling, 1958; Uberall, 1966). This differs from Rayleigh conditions where due to the large size of the waves, relative to the target, most of sound energy flows around the target, and whatever energy is scattered is distributed in all directions.

The interactions between reflected and creeping waves, (usually called "diffraction effects"), are frequency dependent and generate an

echo "spectrum" that is characteristic of the shape and size of the target (Spence and Granger, 1951; Hickling, 1958; Uberall, 1966). For simple geometries such as spherical or elliptical solids, the frequency spectra are also simple, and in fact, closely resemble a single damped sinusoid (Hickling, 1958). The damping of the variations with increasing frequency (or ka) is a result of the fact that as a creeping wave circulates about an object, its amplitude is decreased by a continual tangential loss of energy (Uberall, 1966). Since it is only that energy which is radiated parallel to the reflected waves which contributes to the interactions, the degree of interaction will depend on the amount of energy remaining after each circuit of the target. The rate of energy loss will depend upon the number of cycles the sound waves go through per circuit. This will depend on the frequency, or k , and the circumference of the target, a function of a . The larger either k or a , the less energy which is available in the creeping waves for interactions. Frequency spectra for diffraction effects are thus usually plotted with ka as the independent variable and echo intensity as the dependent variable. The spectrum for a sphere shows that for a $ka = 10$, small changes in ka can produce up to 10% variations in echo intensity. At higher ka , these variations damp out for the reasons stated above, and the echo intensity becomes effectively frequency independent. The upper limit for diffraction is usually set around $ka = 35$, which for an incident frequency of 10 kHz, corresponds to a target dimension of about 21 mm.

The differences in frequency spectra for different target shapes arises out of the fact that the interactions between creeping and reflected waves consist of interference effects between two waves of the same frequency. Since the distance each travels to the point of convergence will determine their relative phases, the nature of the interference, destructive or constructive, will depend in large measure on the circumference and shape of the targets. If a target is symmetrical

in all directions, i. e., a sphere, there will be only one set of such dimensions and thus a single frequency spectrum. For other targets, which have more than one but less than an infinite number of axes of symmetry, the angle of incidence of the sounds will affect the distances creeping waves must travel, and thus each incident angle will generate a different echo spectrum (Spence and Granger, 1951).

A rigid body with a ka greater than 35 produces echoes which mimic optical shadow effects and this region is thus called the "optical region" (Morse, 1948). When this occurs, about half of the incident energy is reflected from the near side of the target, and the rest is deflected behind the target where it interferes with the unchanged sound field to produce a "shadow". For simple rigid targets with no abrupt discontinuities of curvature, the echo intensity is not a function of frequency in the optical region. However, if there are discontinuities, each acts as a separate reflector of sound, producing a set of sub-echoes (Freedman, 1962a; 1962b; 1963; 1964). Unless these discontinuities are all equidistant from the source of the sounds, the sub-echoes will be out of phase and can thus interfere. Again, the distances between reflectors and wavelengths of the impinging sounds will determine whether this interference will be constructive or destructive. Slight shifts in frequency will clearly produce echoes of different amplitude. An additional complication when many discontinuities are present is the possibility of successive scattering; that is, waves may be reflected sequentially from several points before being scattered back as an echo. The phase relations and frequency dependence of this effect will be very complicated.

In each case discussed above, it was assumed that the target was an absolutely rigid body. If, on the other hand, the target absorbs some of the incident energy, this energy can be reradiated after a time delay to produce interference effects with the directly reflected component

(Faran, 1951; Hickling, 1962, 1967; Hickling and Wang, 1966; Doolittle and Uberall, 1966; Diercks and Hickling, 1967). In general, the absorbed energy sets up vibrations within the target, and the nature of the interaction between these vibrations and the reflected waves will depend on ka , the environment of the target, and the target's composition.

If the target is free to move, e. g., is not attached to some immovable substrate, impinging sounds with a ka of 5 or less will set up whole body vibrations of the target (Hickling and Wang, 1966). These interfere with the scattered waves to produce a frequency dependence which is different from the diffraction effects. If the composition of the target is of a relatively rigid, incompressible material, these whole body vibrations disappear above a ka of 5 and the only frequency dependence will be due to diffraction or multiple scattering. If on the other hand, the material composing the target is relatively pliant, increasing ka only changes the nature of the vibrations set up within the target. The vibrations then become internal "shear waves" which can interfere also with the scattered components to produce frequency dependent echoes. Hickling (1962) has shown that for solid metallic spheres in water, the location of interference maxima and minima along the ka scale is highly dependent on the material composition of the target. While the degree of frequency dependence for the whole body vibrations, (low ka 's), seems to follow the ratio of target density to medium density, the elastic vibrations, (high ka 's), seem to be a function of the velocity of induced shear waves in the target. In general, the higher this velocity, the more widely spaced are the interference peaks along the ka axis. Diercks and Hickling (1967) examined the frequency dependence of echoes from hollow metallic spheres in water and found that decreasing the thickness of the wall increased the number of interference maxima in the ka range studied.

It should be clear that if a target falls in any of several categories, (a ka less than 35, a surface with discontinuities, or a composition which

results in absorption of incident sound energy), it will produce frequency dependent echoes. When the incident pulse of sound contains many frequencies, as we showed to be the case for most bat pulses, the distribution of energy among the component frequencies in the echo will differ from that in the emitted pulse. This will thus provide potential information to the bat about the target, since most of these effects are characteristic of the shape, surface texture, or composition of the target.

Information is also potentially present in another form when the incident pulse contains many frequencies. All of the interference mechanisms, (diffraction, multiple scattering, and vibrational interactions), produce phase shifts which are dependent on ka (Morse, 1948; Hickling, 1958; Hickling, 1962; Freedman, 1962a, 1962b). This means that in addition to altering the relative amplitudes of each frequency component, these mechanisms also alter the relative phases. Since the waveform of the echo will be the Fourier sum of these various components, any shifts in the relative phases of the components can drastically alter the echo waveform. If a bat could utilize either phase or echo envelope data, these effects could provide additional information about target parameters.

Finally, the duration of the echo is also potentially alterable by the various interference mechanisms. In the case of diffraction, each circuit of the creeping wave results in the release of sound energy parallel to the direction of travel of the reflected components. If an incident sound pulse has a spatial dimension equal to or smaller than the size of the target, the reflected component and the creeping wave components will be perceived as separate echoes (Uberall, 1966). As the incident pulse duration is increased, the time lag between reception of the separate components decreases, and eventually they begin to summate. Initially, overlap of the components produces a pulse with longer duration and amplitude modulations, the first amplitude peak being the "reflected" echo, and

subsequent peaks being creeping wave "echoes". When the duration is increased still more, part of the reflected wave component will overlap significantly with the creeping wave components and interference as described above will occur. The resulting echo will begin with pure reflected components, will have a middle section which is the result of interference effects, and will have a terminal section of pure creeping wave components. For such an echo, the increase in duration corresponds primarily to the time delay between the reflection of any part of the incident wave by the face of the target and the later radiation of creeping wave energy. Since for a given ka , this time is fixed, the percent increase in echo duration will diminish as the pulse duration is increased beyond the region of initial overlap.

Exactly the same effects on echo duration occur when the target has multiple scatterers due to surface irregularities (Freedman, 1962a; 1962b), or when the target absorbs energy and produces vibrational interactions (Hickling, 1962). For these targets also, the fractional change in echo duration decreases once the spatial dimensions of the pulse are larger than the target. For a bat producing a 1 msec. pulse, this critical size would be on the order of 1 foot. For bats using frequencies in the range of 20-100 kHz, this corresponds to a ka of between 120 and 600. This is far beyond the region where creeping wave components would make detectable contributions to the echo. For this reason, duration alterations due to diffraction are unlikely in bats. However, the effects of multiple scattering and vibrational interactions could still produce either amplitude modulated, longer echoes when the pulses were very short, or simply longer ones when pulses were longer.

To summarize the effects of echo formation on the temporal properties of echoes: most real targets will produce echoes which are to some degree frequency dependent. Many of these will also produce phase shifts, and some may produce echoes of longer duration than the initial pulses.

These changes will change the relative amplitudes of the various frequency components and produce an echo with a different waveform than the pulse which produced it. The greater the number of frequency components, the greater the amount of information which is potentially available. Temporal fine structure properties are therefore of potential value in determining target size, shape and composition.

An ambiguity which can arise in the evaluation of frequency dependent echoes follows from the frequency dependence of atmospheric losses. In a previous section, it was noted that the atmospheric attenuation space constant, α , is a function of the temperature, humidity, density, and viscosity of the medium, and also of the frequency of the sound. As a rule, the higher the frequency, the greater the attenuation. Unfortunately, this relationship is rarely a simple function and must be computed for each set of parameters. In any case, it is clear that some frequencies will be attenuated more rapidly than others during the passage of the pulse and echo through the air. Since the relative amplitudes of the component frequencies in the echo will thus be changed, so will the echo waveform. A bat could learn to compensate for these effects if he had an independent measure for target range. As mentioned above, this may be achieved by the use of the delay between pulse emission and target reception. Such compensations would of course not be simple; a bat which flies from a cool dry environment into a warm and humid cave would have to make different compensations in the two conditions.

The Distribution of Echo Energy in Space The spatial distributions of scattered sound energy depend in large measure on the mechanisms of echo formation. When no sound energy is absorbed, and Rayleigh conditions apply, the distribution of sound energy scattered from the target is about equal in all "backward" directions (Morse, 1948). When ka is larger and diffraction effects occur, the distributions of backscattered energy are more complicated. The same interference

patterns which produce the frequency dependence of the diffracted echo also produce an unequal distribution of back-scattered energy. These distributions are usually depicted as polar plots about the target, where a single contour line connects all points which share some arbitrary level of sound intensity. In the diffraction region, polar plots for simple targets show a series of "lobes" whose position in space is characteristic of ka , the target's shape, and its orientation (Morse, 1948; Spence and Granger, 1951). As a rule, increasing ka results in an increase in the number of lobes. Similar lobing occurs with vibrational interference effects (Diercks and Hickling, 1967) and presumably also with multiple scattering.

Since these polar distributions are characteristic of target parameters such as shape, they are potentially sources of information to the bat. However, for a bat to utilize this information, certain conditions will have to apply. The polar patterns around any target, and particularly, the number and location of lobes, will depend on the orientation of the target relative to the direction of travel of the incident sounds. Since a sphere has the same shape when viewed from any angle, the distribution of lobes around spheres is symmetrical about the axis of travel of the incident waves, (Morse, 1948). For an elliptical solid, each angular position of the target relative to the incident sound waves will produce a different pattern of lobing (Spence and Granger, 1951). There are two ways a bat might use this information to make target discriminations, one requiring a qualitative judgement, the other requiring a quantitative plotting of the polar pattern.

For the first case, suppose the bat knows that he must choose between two targets, and that one target will produce lobing that is symmetrical about the axis of incidence, while the other will produce an asymmetrical pattern. An example of the former would be a sphere, and of the latter, a prolate spheroid, lying on its side and with one end tipped towards the bat. The sphere will produce a symmetrical pattern of

lobing at any angle of approach, and as a consequence the echo levels perceived by the bat's two ears will be the same. However, at many angles of approach, the prolate spheroid will produce assymmetrical lobing, and the two ears will receive echoes of different intensities. By simply varying the angle of approach, and measuring binaurally the intensity of the perceived echoes, the bat could fairly easily choose between these two targets.

However, few targets will consistently give the same degree of pattern symmetry for all angles of approach. Most in fact will give one pattern at one angle, and another pattern at another angle. Unless the bat has some independent measure of the target orientations, qualitative judgements of pattern symmetry will not suffice for discriminations. To use polar information, the bat must attempt to reconstruct at least part of the polar patterns for each target. How might this be done?

One usually generates a polar plot by specifying the distance, r , which gives some standard level of intensity for each angle, θ , relative to the axis of the incident sound waves. A bat however cannot specify what intensity he wishes to receive, and consequently must use the alternative method of specifying the intensity for a given value of r for each value of θ . If the ears of bats were located on the axis of travel of the emitted pulses, it would be very difficult for the bat to measure the polar field for any other angle than $\theta = 0$. In fact, however, the ears are usually displaced off of the axis by a distance d . This results in a sampling angle, θ , which is equal to $\arctan d/r$. To reconstruct a polar plot, the bat must attempt to sample the field for several values of θ . To do this, he can either vary d , or vary r .

The anatomical component of d is relatively fixed. However, the bat could get around this limitation by emitting a pulse and then dodging quickly to one side a distance d' during the interval it takes for the pulse

to travel to the target and for the echo to return. The value of θ is now equal to $\arctan (d + d')/r$. By dodging different amounts and in different directions, the bat might be able to plot a reasonable amount of the polar field. It is unlikely however that in those cases where discriminations have been studied, this mechanism can account for the demonstrated skills of bats. In the study by Griffin et al. , (1956), noted earlier, the bats were discriminating the targets at distances of 50-60 cm. Even if the bats were able to translate their full forward velocity, (measured at about 1.2 m/sec.), into a lateral dodge, the intervals between pulses would only allow for increases in θ of about 1° .

Alternatively, the bats might attempt to vary r . This they do as a matter of course during the approach to a target. Under these conditions, decreasing values of r result in increasing values of θ . Since each echo represents a different value of θ , it also represents a new part of the echo field. This means that as the bat approaches a target which has a lobate polar field, the intensity of the perceived echoes should vary up and down as the ear passes successively through lobes and interlobes. These variations will be superimposed on the gradual rise in echo intensity which results from decreasing geometrical and atmospheric losses. The resulting pattern of echo intensity as a function of the distance r will clearly be a function of target shape, ka , and target orientation. If the latter two parameters are held constant, the bat should be able to discriminate targets of different shape.

There are several limitations on the use of this method. To obtain a characteristic pattern, the bat must be at such a distance that it passes through detectable changes. If for example, the distance were very great, or the polar pattern had few lobes per unit angle, changes in r would not produce very marked differences in intensity. For a given pattern, there will thus be an optimal distance at which the bat will pass through regions

of great enough variation to characterize the field. In the discriminations described by Griffin et al. (1965), it is questionable whether the bats were making their choices in such an optimal region. In these experiments, the appropriate values of d and r were 1 cm. and 50 cm. respectively. This corresponds to a value of θ of about $1-2^\circ$. Unless the polar patterns were very finely lobate, it would seem that the bats would have had difficulty in characterizing the echo fields. While the targets used should give highly lobate patterns with constant frequencies, the FM pulses used by these bats tend to smear and simplify the polar patterns, an effect predicted by Morse (1948) on theoretical grounds and verified by Griffin et al. (1965) in the course of calibrating their targets. This fact further reduces the probability that polar patterns were used by these bats. A final limitation arises from the fact that the targets in these experiments were tumbling in space. As a consequence, successive echoes would not necessarily provide new points in any given polar plot, but different points of different plots corresponding to the different angles of target orientation. The resulting ambiguities would seem to make the method of little use under these conditions.

A rather different method of target discrimination might be achieved by using the spatial properties of the emitted beam of sound. Since the emitting organs of most bats produce frequency dependent beams of sound (Griffin, 1958), a pulse which sweeps downwards in frequency will also produce a beam of increasing solid angle. When a target is either large enough or close enough to completely fill that beam, the width of which is determined by the frequency, the bat will receive a maximum echo. At lower frequencies, and greater beam widths, not all of the emitted energy will be reflected and a softer echo will be returned. For a given distance, the frequency at which the echo intensity begins to decrease will be a function of the effective cross section of the target. For example, if the beam itself has a circular cross section, and intercepts a circular target, the drop-off in intensity when the beam

is wider than the target will be fairly sharp. However, an elliptical target with the same cross-sectional area will show a decrease in echo intensity at a higher frequency than the corresponding sphere, but will drop off less sharply. Such a mechanism would work much like simple optics at large ka , but would become more complicated with diffraction or vibrational interactions.

To summarize the spatial properties of echoes: most targets will produce unequal distributions of backscattered energy. Under certain conditions, (such as when there are differences in the symmetry of the patterns, when the orientations of the targets relative to the bat are constant, or when it is possible to make the discriminations at close distances), the bats may be able to measure and utilize these echo fields. In addition, the use of narrow beams and FM pulses could supply some information about the sizes and shapes of targets if the beam widths and targets are of comparable size.

Physiological Limits on the Use of Echo Properties

The previous discussion has suggested several ways by which a bat might extract information about a target from echoes. It is now timely to ask which of these methods are within the known physiological capacities of the animals. Fortunately, just enough is known about the workings of bat audition to comment on these limitations.

The "potential" ability of bats to distinguish between sounds of different intensity has been established by several workers. Grinnell (1963a), recording in the posterior colliculus of Myotis licifugus, obtained neurophysiological responses to changes in overall intensity of 0.1 to 0.2 dB. This corresponds to a change in sound pressure of 1-2%, which is quite small. For a simple target like a sphere and for a ka in the optical region, the amplitude of the echo at any given distance is proportional to the radius of the sphere (Morse, 1948). If the behavioral

limits of resolution are the same as the observed neurophysiological ones, (which they are not necessarily), a Myotis should be able to distinguish between two spheres which differ in diameter by only a few percent.

There are several reasons however for believing that the behavioral limits of resolution are not the same as the neurophysiological ones. In the first place, most bats hunt on the wing, and the distances between them and successive targets will rarely be the same. Thus, as the bat moves slightly, a change in echo intensity could mean either a differently sized target, or a change in the distance between bat and target. To sort out these two effects, the bat must have some independent means of measuring one of them. The most likely solution is that the bat can ascertain distance by using the time interval between pulse emission and echo reception.

In most mammals, the ability to distinguish separately two successive pulses of sound is limited by their separation in time and by their relative intensities. The longer the interval, the greater the amount of recovery which the auditory system can complete following the first pulse, and thus the greater its response to the second. The fainter the first pulse relative to the second, the less the recovery that is needed to resensitize the system (Cf. Wever, 1949).

In bats, the recovery times of some medullary neurons are very high, (on the order of a few msec.), and this allows for rather fine temporal resolution (Grinnell, 1963b). The recovery times are further reduced by contractions of the middle ear muscles during pulse emission, thereby decreasing the perceived intensity of the first sound (Henson, 1967). Finally, there seem to be special cells in some bat colliculi which are actually sensitized by the first of two sounds, thus making them more sensitive to the echo than to the outgoing pulse (Grinnell, 1963b).

All of these mechanisms increase the ability of bats to distinguish between two very closely successive sounds. Grinnell (1966) has examined this ability in several species of bats and has concluded that for at least two species, (Myotis lucifugus and Plecotus townsendii), the most parsimonious explanation of range detection is by use of pulse-echo delay. This provides an independent measure of target range and can thus be used to reduce the ambiguities in measuring target size by echo intensity.

Another source of ambiguity in the use of echo intensity as a measure of target size is generated by the directional properties of bat emitting and receiving organs. Echoes received from angles outside the major field of sensitivity will be perceived as fainter echoes. This could also complicate the evaluation of target size unless the bat had some independent measure of target angle. Again, Grinnell has investigated this problem and has concluded that bats can use binaural comparisons of echo intensity to localize a target within several degrees of arc (Grinnell, 1963c; Grinnell and Grinnell, 1965).

It thus seems physiologically possible for a bat to use overall echo intensity levels as measures of target size. While this is probably a necessary condition for target discrimination, it is hardly sufficient. For example, in the mealworm vs. disc discriminations described by Griffin et al. , (1965), the targets were tumbling in space and thus provided rapidly changing cross sections. Griffin and his colleagues examined the echoes from such targets and concluded that neither the "average" values of echo intensity, nor the variations in overall echo, differed enough between the two targets to explain the success of discrimination demonstrated by these bats. The use of differential attenuations would also not explain this success, since the nature of the target shape, and thus the nature of the waves, would also vary as the targets tumbled.

Under such conditions, it would be impossible to measure attenuation rate, since this would be different for each target orientation. Similarly, measuring the results of attenuation by comparing echo intensity could not be separated from the effects of varying cross section. Clearly, the bats must have used some parameters other than overall echo intensity.

Consider also that under natural conditions, a hunting bat would continually receive echoes from a variety of objects. A jungle species for example would find it advantageous to be able to distinguish between a potential food item and foliage with the same apparent "cross section". While the use of overall echo intensity may be useful in some contexts, it cannot by itself supply information about target shape or composition without ambiguities. An echo may be loud or soft depending on shape, on size and on orientation. Clearly different combinations for different targets could produce echoes of the same intensity. Thus hunting bats must have to use several parameter systems such as intensity vs. distance, intensity vs. time, intensity vs. angle, etc. Such two parameter systems reduce the ambiguities since a given combination of size, shape and orientation parameters usually results in a unique relation between such properties as intensity and frequency, or frequency and angle. In general, these two-parameter methods of analysis depend on the fine structural properties of the echoes.

In the preceeding sections, it was argued that there are many ways in which targets can impose a characteristic signature upon the fine structure of an echo: diffraction, multiple scattering, elastic and vibrational interactions, and interactions with structured pulse beams. These effects can alter the relative amplitudes and phases of various frequency components, can produce complicated spatial distributions of backscattered energy, and can sometimes change the duration of the echo. Which of these effects are physiologically detectable by bats?

One two-parameter system which bats might use is the frequency spectrum

generated by a given target. Bats which produce pulses with many component frequencies, either as harmonics, or as part of an FM sweep, would have particularly easy access to this information. The main requirement would be an ability to quickly and accurately determine the frequency and amplitude of any given component in the echo. In FM bats, the quickness will be of particular importance since no 10 kHz band of frequencies lasts longer than several hundred microseconds (Griffin, 1958).

Grinnell (1963a; 1963b) and Suga (1964) have investigated this in several species of bats and have concluded that the speed and accuracy of frequency determination is quite high. In Phyllostomus, a tropical species which uses FM pulses, the accuracy of frequency determination is on the order of several percent. In these same animals, there are "tuned" collicular units which can respond after only 2-3 cycles of the sound stimulus. Many of these same units code for both frequency and amplitude, (Grinnell, 1963a; Henson, 1967), and may thus be the most likely cells to analyze the frequency spectrum of an echo. It would thus seem that the physiological abilities to analyze echo spectra are present in at least some bats.

Another two-parameter system would be the relationship between phase and frequency in the echo. Analysis of this information, which will depend on the size, shape and orientation of the target, could be accomplished in either of two ways. One is by actual determination of the phase of each frequency component separately. The other is by the presence in the cochlea of some region or regions which respond to the unaltered original waveform of an incoming signal. A case for both mechanisms has been advanced for humans, but only under specific conditions.

In general, a vertebrate cochlea is thought to act as a "Fourier analyzer" of incoming sound waves, thereby breaking up complex waveforms

into a series of pure sinusoidal components, and assigning an amplitude to each (Cf. Littler, 1965). The classical studies by Bekesy, (Cf. Bekesy and Rosenblith, 1951), showed that this is accomplished by setting up a series of travelling waves in the fluids and basilar membrane of the cochlea, one for each frequency component. The separation of the components is achieved by the fact that each travelling wave reaches a maximum displacement at a different point along the cochlea. In all mammals studied to date, the higher frequencies generate maxima near the basal or "input" end of the cochlea, and lower frequencies at the apical end (Cf. Bekesy and Rosenblith, 1951). Increased separation is presumably then achieved through inhibitory interactions, (both in the ear and in higher centers), resulting in a fairly accurate determination of frequency (Galambos and Davis, 1944; Suga, 1965a; 1965b).

If separate frequency components are effectively analyzed in different regions of the cochlea, comparisons of phase must be made after analysis, e.g. at the nervous level. There are several ways this may be done. Higher centers could compare the time of onset of firing from different frequency regions of the cochlea and thereby evaluate their relative phase differences. Clearly, the higher the frequencies to be compared, the shorter the possible differences in onset times will be. At the low range of bat echolocation frequencies, about 20 kHz, the maximum differences in onset time will be on the order of 50 microseconds or less. This time is somewhat shorter than the lower limits of detection which have been described for bats (Grinnell, 1967).

An alternative method has been suggested by Wever (1949). In this model, the cochlear nerve fibers reproduce the frequencies of incoming sounds in their firing rates. If this nerve discharge were synchronous with the sounds, the detection of phase would be possible. Again, the use of high frequencies by bats makes this model inappropriate. The highest rates of firing which are possible invertebrate sensory axons are an order

of magnitude lower than what they would have to be to fire synchronously with sound waves at bat frequencies: thousands/second for the axons vs. tens of thousands/second for the sound waves (Wever, 1949).

Wever (1949) has tackled this objection by suggesting that each nerve fiber in a bundle fires at some sub-multiple of the incoming sound frequency. If several fibers in such a bundle fire out of phase with each other, the "bundle" frequency will be greater than that of any one fiber and may even duplicate the sound frequency. While the model is intriguing, such synchronous firing has not yet been observed in bat auditory systems.

The second major method for phase detection would be possible if there were regions in the cochlea where frequency separation was incomplete. Whenever this occurred without distortion of the original phase relations, the underlying portion of the cochlea would be stimulated with a signal approaching the unanalyzed original in waveform.

In humans, there seem to be two times when this can occur. The first occurs whenever two frequencies are fairly close together. This can happen anywhere along the cochlea, but is more likely in the upper range of frequencies which tends to be more compressed anatomically than the lower end. In any region where two travelling waves produce significant overlap, (significant being determined presumably by the degree of sharpening which is possible through neural interactions), the underlying cochlear membrane will respond to their summed waveform. Since the latter will depend in part on the relative phases of the two components, any shift in that phasing which alters the waveform will be detectable. This appears to be the case when humans hear beats (Wever, 1949). As the relative phases of the two waves shift with successive cycles, they can add and subtract to produce the impression of a single frequency which is amplitude modulated.

It will be remembered that there is only one set of phase relations

which will produce amplitude modulation when two frequencies are mixed. Another set of initial phases will produce a different waveform which one cannot produce from the first set, no matter how many cycles one waits. Consider now the mixture of three similar frequencies, the larger and the smaller being equidistant from the center component. Suppose one varies the phase of one component relative to the others. When all three components are in phase, we can produce a wave with an apparent frequency which is equal to that of the middle component and an amplitude modulation which occurs at a rate equal to the spacing between components. If the phase of the central component relative to the others is advanced or retarded 90° , we obtain a wave which is constant in amplitude, but is frequency modulated. Other phase relations will produce mixtures of the two kinds of modulation (Hund, 1942). The relative amplitudes of the components are not irrelevant here; to obtain pure frequency modulation from pure amplitude modulation would require careful selection of the degree of amplitude modulation which one started with (Hund, 1942). However, even if the amplitudes are ignored, unequal shifts in phase of the components can alter the nature and degree of either kind of modulation.

Mathes and Miller (1947) have made just such mixtures of three equally spaced frequencies. When the frequencies are similar and in phase, a human observer perceives the combination as an amplitude modulated wave; when the middle component is advanced in phase, the same components produce the impression of a frequency warble. When the three components are not close together in frequency, a human observer hears them as three separate tones. These experiments seem explicable if we assume that closely spaced frequencies produce regions of detectable overlap in the cochlea. When there is no overlap, as might occur for disparate frequencies, each component will be detected separately.

Since the pulses of bats contain numerous side bands, as discussed

previously, there will be regions in the cochlea where many components will be clustered in a small region. If they are close enough to produce overlap, as in the human example, the bat might be able to monitor their sum, rather than the components alone. This would allow for qualitative judgements such as whether a given part of the echo was amplitude or frequency modulated. Since many of the mechanisms of echo formation produce phase shifts which differ for different frequencies, it is conceivable that a section of emitted pulse which was frequency modulated, might return in the echo apparently amplitude modulated. This is probably an extreme and rare case however. More likely is the possibility that the portion of the cochlea monitoring the region of overlap could code for the variations in echo envelope instead of reducing this to its components. Phase information could therefore be used in characterizing the echoes from different targets.

There is a second kind of condition which may produce component overlap in the cochlea. The travelling waves recorded by Bekesy in vertebrate cochleas were assymmetrical in shape (Bekesy and Rosenblith, 1951). That is, the fall-off in travelling wave amplitude on the apical side of the maximum was less gradual than on the basal side. For this reason, the waveform of the travelling wave at any point along the cochlea is more likely to contain contaminants from the "basal tails" of low frequency components than from the "apical tails" of high frequency ones. If the original signal has a wide range of component frequencies, the movements induced in the basal regions of the basilar membrane will include both high and low frequency components; the movements in the apical region will contain only low frequency components (Cf. Littler, 1965). In addition, Bekesy (Cf. Bekesy and Rosenblith, 1951) showed that phase distortions were least in the basal region of the cochlea and increased with decreasing frequency. It is thus clear that a complex signal with many frequency components will be least decomposed in the basal end of the cochlea where all components are

present and where phase relations are least altered.

The importance of overlap in the high frequency region of a bat cochlea arises with the consideration of phase relations between harmonics. Since two low frequencies will usually produce travelling wave maxima at some distance from each other, overlap of maxima is unlikely. However, in the high frequency range, where harmonics will be found, the increase in overlap may allow for the detection of phase shifts in the echo just as above. For example, the harmonic content of the pulses from a bat like Chilonycteris results in a periodic waveform that is determined by the relative phases of the components. Slight shifts in the relative phases of these components will alter the waveform of the signal. Clearly, in regions of overlap, this might provide cues about target properties.

The physiological limits on the use of spatial properties of echoes have been touched upon in previous sections. To recapitulate, each of the possible methods for using this information requires accuracy in evaluating echo intensity, in some cases monaurally, (as in the reconstruction of polar fields by dodging, or by the use of structured beams of emitted sound, etc.), or binaurally (such as in the detection of polar field asymmetries). In some of these methods, accurate determination of range is also necessary and this has also been discussed (pp. 36-37). Finally, many of the methods also require accurate frequency determination.

In conclusion, the discrimination of different targets by bats requires rather few types of measurements; for most mechanisms, determination of intensities, frequencies, and target range (through pulse-echo delay) will suffice. However, use of any one of these measurements alone does not seem sufficient in the face of possible ambiguities to explain the demonstrated skills of bats. It thus seems reasonable that bats must have recourse to the use of several-parameter methods of measurement. The examples of such systems which

provide fairly unambiguous characterization of target properties are comparisons of amplitude vs. frequency, phase vs. frequency, and amplitude vs. distance, all of which may be done in several ways with the same basic sensory machinery.

The purpose of the following research was to examine the discriminative abilities of one species of bat in as great detail as possible. Once the discriminative skills had been clearly defined, it was hoped that reduction of the possible cues would allow for some judgements as to which mechanisms this species used for these problems. Granted that such judgements were possible, it would then be relevant to examine the kinds of pulses used by these bats to see if the information they should provide is compatible with the mechanisms proposed.

METHODS

The experimental design of this study depended in large measure on the species of bat selected. As will be argued below, the form chosen, Vampyrum spectrum, seemed a likely candidate for an animal which would need some form of object discrimination to successfully capture its food. However, the selection of the animal was in part due to the fact that several specimens of this rare and little-studied form were available. This resulted in some lucky and unexpected advantages, but also in certain disadvantages. To understand some aspects of the final experimental design, a description of the known natural history of these animals is necessary.

Food and Habits of Vampyrum Spectrum

Vampyrum spectrum, the neotropical false-vampire, is the largest member of the suborder Microchiroptera, reaching a wingspan of 70-90 cm., and a weight of 140-180 grams. It is armed with a full complement of teeth, including four very large canines, and these, in conjunction with its large masseter muscles, can inflict a wicked bite. In spite of their size and armament, the six animals used in this study proved to be quite tame and easily handled, although leather gloves were used at all times.

The food habits and hunting methods of Vampyrum spectrum have been subjects of considerable debate during the last two centuries. Early explorers to the American tropics attributed blood-sucking habits to this species, and to most other species of tropical bats as well. These stories account for the common generic name which Leach applied to these bats: Vampyrus. In point of fact, the stories of "vampire bats" were not totally erroneous, for bats of the genera Desmodus, Diaemus, and Diphylla do feed on the blood of mammals

and birds. However, these latter forms are shy and were rarely seen by early explorers. It was thus easy to mix the evil habits of one species with the bizarre appearance of bats like Vampyrum. One visitor to the American tropics described how these large bats fanned their victims to sleep with their wings (Kirke, 1898). Another speculated that the nasal appendages, common in the family of bats of which Vampyrum is a member, were used as suction cups to extract the blood from the victim (Herndon and Gibbon, 1854).

Later Bates (1864) dispelled this misconception of blood-letting by Vampyrum, but apparently by means of a mix-up in the identification of the bats he encountered. Bates' descriptions of bats of the Amazon valley included the following comments:

"Nothing in animal physiognomy can be more hideous than the countenance of this creature when viewed from the front, -- the large leathery ears standing out from the sides and top of the head, the erect spear shaped appendage on the top of the nose, the grin, and the glistening black eye, -- all combining to make up a figure that reminds one of some mocking imp of fable. No wonder that some imaginative people have inferred diabolical instincts on the part of so ugly an animal. The vampire is, however, the most harmless of all bats, and its inoffensive character is well known to residents of the Amazon. I found two distinct species of it, one having the fur of a blackish color, (Vampyrus auritus), the other of a ruddy hue, (Vampyrus spectrum), and ascertained that both fed chiefly on fruits."

It seems clear from Bates' subsequent accounts that he may have had some difficulty with the taxonomy of these bats. One of the species which he describes in a later section is clearly a member of the genus Artibeus or its kin, yet Bates ascribes it to the genus Phyllostomus. Similarly, his descriptions of the habits of Vampyrum spectrum and Chrotopterus (= Vampyrus) auritus do not jibe with more recent reports. For example, Bates comments that these two bats were very common and observed them each evening "trooping out in scores, twittering," to feed on fruits. Neither Vampyrum nor Chrotopterus are

are considered common in their ranges, and Trinidad populations of the former seem widely dispersed (Acosta y Lara, 1951; Goodwin and Greenhall, 1961). Species of the genus Phyllostomus however, are common throughout their ranges, do roost in large groups, and have been observed feeding on fruit in flocks (Goodwin and Greenhall, 1961). I suspect therefore that Bates incorrectly identified species of Phyllostomus as Vampyrum spectrum and Chrotopterus auritus.

At present, the evidence, (excluding Bates' report), suggests that Vampyrum and Chrotopterus are primarily carnivores. Mammalian dentition is usually a good guide to dietary specializations, and the teeth of these two genera are rather distinctive. Miller (1907) has examined the teeth of most of the genera of bats and concludes that the two genera, Vampyrum and Chrotopterus, with their enormous canines and blade-like molars, are most like the old world Megadermatidae, which are known to be carnivorous. Some insectivorous species also share this dentition, but certainly no frugivorous species.

Other evidence is in keeping with this conclusion. Acosta y Lara (1951) has reported the consumption of small bats by captive Chrotopterus and Ditmars (1935; 1936) reports that Vampyrum can be kept in good health solely on a diet of young chickens. In the field, the stomachs of Trinidad Vampyrum have been examined and found to contain solely animal material. Examinations of the roosts of these Trinidad specimens also disclosed the partially eaten remains of rodents, small birds and other species of bats (Wehekind, 1956). In spite of this evidence, it of course remains possible that either some populations, or any population occasionally, may feed on fruit as Bates maintained. This is certainly the case for the related Phyllostomus hastatus which is known to eat fruit, insects, and other species of bats as the occasion permits (Dunn, 1933). However, this latter species does not have the specialized dentition peculiar to Vampyrum, Chrotopterus, the Megadermatidae, and a few insectivores, a fact which argues against omnivorous habits for Vampyrum.

While it seems certain that Trinidad populations of Vampyrum are carnivorous, there are no available field data on their hunting tactics. Their roosts are generally found deep in forested areas, and it is likely that they also feed there. There seem to have been no field studies on when they feed or whether they hunt singly or in groups. The time of hunting would be of particular interest since if they capture the diurnal birds whose remains have been found at roosts during the dark part of the night, they must be able to accomplish some acute means of discrimination. To capture a sleeping bird in the midst of dense foliage is certainly no simple task, either by olfactory or echolocative means.

In view of the uncertainties in the exact diet and hunting tactics of Vampyrum spectrum, some simple hunting experiments by the bats were clearly called for. Initially this consisted of allowing the bats to hunt live mice in a large flight cage and observing their success with infra-red viewing gear. Since the primary aim in this study was to try to examine target discrimination and the mechanisms by which it can be accomplished, successive experiments involved the hunting of live mice in cluttered environments, of dead mice in cluttered environments, and finally the discrimination of non-organic artificial targets in controlled double choice experiments. Periodically throughout the series, infra-red movies and high frequency tape recordings were used during periods of successful discrimination. These were then subjected to analysis as described later. The force of the experiments, therefore, was to obtain a series of discriminations ranging from minimally controlled, but more nearly natural conditions, to some highly controlled, but very unnatural conditions. Between the two, it was hoped that some arguments about normal tactics could be made, and at the same time some information concerning possible mechanisms of discrimination could also be obtained.

Care of the Animals

The experience gained by the New York Zoological Society in keeping these bats plus our own acquired during the summer of 1966 in Trinidad made it clear that Vampyrum adapted well to captivity and could be maintained for many years in good health. Captive specimens eagerly ate laboratory mice, which could be fed living, freshly killed, or frozen and subsequently thawed. To prevent any dietary deficiencies, a small amount of a liquid vitamin supplement, Vi-Penta, was added to the drinking water (1/2 cc. vitamins per quart of water). Assuming the bats received some flight exercise every day, a dole of one 30 gram mouse per day resulted in fairly constant weights.

The bats were housed in pairs in wooden cages with horizontally grooved walls. This facilitated their clinging and moving about the walls. These roosts were each 12" X 12" X 18" inside dimensions and opened on one side by a screen door. The doors for all the roosts opened into the large 20' X 8' X 8' flight room which was used for both hunting and discrimination experiments. Both the flight room and the roosts were enclosed in an opaque black plastic which made the whole facility light-tight. During discrimination or recording sessions, an acoustically insulated wooden panel could be placed over the screen doors of all the roost cages, thus preventing interference or microphone pickup from the bats not being tested.

Early in the study, low humidities during the winter led to dryness and bleeding from the bats' nares. The humidity and temperature of the rooms were then raised to tropical levels (70-80% and 78° F. respectively), and these symptoms disappeared. No further health problems were encountered except in the case of two post-partum females. Both pregnancies which occurred during the study were unsuccessful, and in one case, a premature aborting of the fetus resulted in an infection and death of one female. The second female also lost her young, apparently by dropping it

to the floor, and during the post-parturitive period regained her weight very slowly. However, she has since regained health and vigor.

Training Procedures

The prerequisite to all training periods was to produce hungry animals. This was accomplished by partial starvation, most often by halving the daily food intake for 2-3 days. When the weight of the animals had been reduced by 5-10%, they were usually quite eager to hunt or perform discrimination flights.

Early in the study it became apparent that a constant food intake did not guarantee a constant body weight. In fact it proved very difficult to avoid day-to-day oscillations of weight and unfortunately, eagerness. Some of these variations were reduced when the heat and humidity controls were introduced. However, there was no way to predict or control the metabolic expenditures associated with a day's discrimination flights; on some days, a successful bat might obtain his daily quota with a minimal expenditure of energy; on others with greater effort or enthusiasm, he might use up more. Other factors which seemed to contribute to weight variations were changes in the flight room, changes in the nature of the discriminations, external noises, excessive disturbance to the bats prior to the discriminations, presence of a sexually active female, variations in the condition of the mice fed, and the recency of previous discrimination testing. I could find no systematic way to control for all these variables, but could only try to compensate for large changes by starving or by changing the amount of daily exercise. Daily weight records were kept throughout the whole study, allowing for selection of "test days" on the basis of the bats weighing less than some set criterion. The value of this criterion had to be decided by trial and error for each bat.

During the studies on hunting of whole mice, the food item and the target were identical, allowing for only one trial and reward sequence per day per bat. During the later studies, artificial targets were used and

the bats were rewarded for correct choices with a small portion of mouse. The latter was presented to the bat on a long pair of forceps by the experimenter. This meant that after each flight by the bat, the lights were turned on, the experimenter walked from the roost end of the flight room to the landing ring, and the food was presented to the bat. On the average, the delay between completion of a flight by the bat and delivery of the reward was 10-20 seconds. Finally, a single day's quota of mouse could be divided into 20-30 pieces, allowing for as many trials per day per bat.

The hunting experiments required no active training by the experimenter. The bats were simply removed from their cages, in some cases singly, and in other jointly, and the flight room darkened. Depending on the state of "hunger" and the time of day, the bats would soon begin flying and hunting on their own. The hunting of dead mice was not attempted until the bats were skilled in capturing live ones. Then they were allowed to spend several full nights free in the flight cage with dead mice placed in random positions until they had learned to locate and capture these items. Subsequently, they were released at a given time such evening and observed with infra-red equipment until they had fed.

For the experiments with artificial targets, the bats had to be taught to fly to the targets and some simple landing site. The latter had to be as small and anechoic as possible to prevent interactions with the target echoes, yet strong enough to support the animals. The landing site selected consisted of 3" diameter ring of 1/8" brass rod. This was suspended from the ceiling by three 3" lengths of the same size rod. The targets were then suspended on threads attached to the ceiling so that the targets hung directly below the landing rings, (See Insert, Figure 1). Small hooks were used to connect and disconnect the target threads from their supports so that target location could be rotated among the different landing rings.

Four such landing rings were placed in the flight room. Their disposition relative to the overall size and shape of the room can be seen in Figure 1. Two were placed symmetrically about the long axis of the room at a distance of 15 feet from the roost, the latter serving as the starting point for all flights. These landing rings will be subsequently called the "near" target positions. The second pair of landing rings were placed directly behind the first pair, but at a distance of $17 \frac{1}{3}$ feet from the roosts. These are the "far" target positions. Since the cage was oriented north and south, the landing rings on the left of the bat as he approached them are called the "west" target positions, and those on his right, the "east" target positions.

To teach the bats to land on these landing rings, several animals were placed on one ring, and another was prompted to fly from the roost. Usually after several such flights, the flier would attempt to join his fellows on the brass landing ring. This was repeated for each bat for over a week until five of the animals would land on the landing rings whether other bats were roosting there or not.

When the bats had learned to fly to the landing rings, a single target, always the one which would result in reward if chosen, was hung from one ring using the threads and hooks. Then each bat was flown as many trials as possible per day and rewarded with a small piece of food when the ring selected was the one with the target. When the bat seemed to be responding to the location of the target, the latter was moved randomly from ring to ring. Initially, this proved one of the most difficult steps in the training procedure. As discussed in the next chapter, these animals have a strong predilection towards position habits and consequently tend to fly to the same landing ring or sometimes the same side regardless of whether the target is there or not. However, by using stringent food schedules, all five animals eventually learned to follow the target.

Training with two targets followed essentially the same patterns.

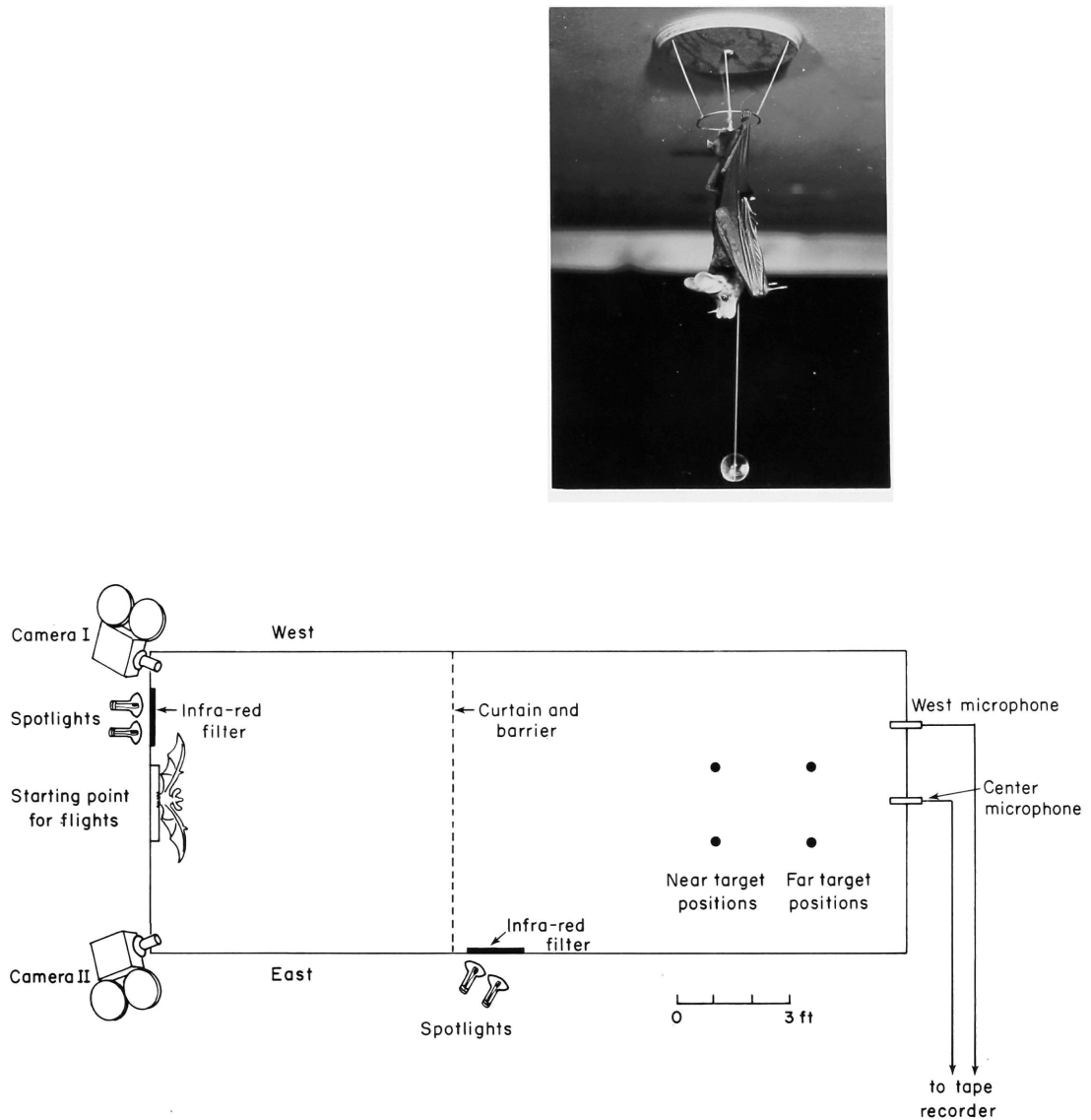


Figure 1. Top view of the experimental flight room. The roosts are located behind the wall which served as the starting point for all flights. The insert is a photograph of a bat on a landing ring from which the lucite sphere target is suspended by a thread.

Early stages in the learning would be typified by strong position habits, which would eventually disappear as the discrimination scores improved. When no further increase in average scores was apparent, training was ended and testing commenced according to the schedules outlined in the next section.

Testing and Scoring Procedures

During testing periods with the artificial targets, the positions of the targets among the four landing rings were varied approximately randomly. The "approximately" enters here in two ways. First, only two equidistant locations were used in any one flight; that means that for a given flight, either the near or the far pair of landing rings was used. The actual procedure, therefore, was to randomize the location of one target among the four positions and then to place the other target at the appropriate equidistant landing ring.

The second modification of the randomization was to eliminate all runs of 4 or more at the same platform from the sequencing. These long runs only served to encourage the formation of position habits, which especially in the hard discriminations, were always a major problem.

All moving of the targets was performed with a black curtain between the bat at the starting point and the landing rings. This was to prevent the bat from seeing the targets, since a small light was used in the room at this time. During flights, all lights were extinguished, with the exception of infra-red equipment, to prevent the use of visual cues. The curtain was also impervious to the echolocation sounds of the bat, preventing examinations of the targets before the recording and filming apparatus could be started. After moving the targets to new locations, any swinging of the targets on their strings was damped out, as the pendular motions would be different for the two targets. On several occasions,

olfactory controls were introduced by washing the targets after moving them, by replacing a "used target" with a clean one, or by replacing both strings and targets. When the targets had been moved, cleaned, made motionless and all lights had been extinguished, the curtain was opened and the bat either allowed to fly spontaneously or prompted gently with a gloved hand. Prompting was done in as consistent way as possible to prevent some cue from being passed between experimenter and animal. In general, a slight touch with the glove was sufficient to make the bat fly.

Training and testing were all performed during the hours of 3-9 P. M. Attempts to interest the bats in hunting or discriminating earlier than this were unsuccessful. Attempts to interest the experimenter in hours after this were also unsuccessful. The necessity for prompting in some of the experiments is certainly due in part to the fact that the bats would have preferred to fly later or in their own good time. It is also due to the fact that they were less willing to fly in the presence of the experimenter than in his absence. This latter point was clear during the hunting experiments, when the bats were simply left free in the flight room to hunt when they wished. In general, hunting began as soon as the experimenter went outside the room. The bats which began first were always those which did not need prompting in the discrimination flights; the others usually waited until at least 8 P. M.

During hunting experiments, bats were scored by noting how many passes of the target preceeded an attack, and how many false attacks, (any landing at a site other than the roost, whether an object was "bitten" or not), preceeded a successful capture. Control flights were performed by observing hunting when no mice were present.

During double choice experiments with artificial targets, every flight to a target was considered as a "trial". Only one chance to pick a target was allowed in any one trial, and if the bats circled or made several passes

before landing, the trial was discounted. All flights to landing rings with no targets were also discounted. By the time testing had begun, bats never flew to target-less landing rings or circled targets. Occasionally a bat attempted to land on a target instead of the landing ring above it. These cases were treated as if the bat had landed on the landing ring. All of these criteria for counting or discounting trials were determined by observing the trials with a Varo Detectirscope and infra-red light, or by making movies with infra-red film and light.

Since the randomness of the target positioning had been somewhat altered by removing long runs at one position, the chance scores could not be assumed to be 50%. Accordingly, the chance scores were determined experimentally by conducting discrimination flights using identical targets. During these chance score flights, all other conditions such as darkness and olfactory controls were identical with those under which the two target flights were conducted. In all cases, the chance scores were just about 50%, indicating that modification of the randomization had not increased the bat's chances of making successful choices.

Scores from testing with two different targets were collected over testing periods that were the same for all bats under any given set of conditions. The number of successful flights relative to the total number of trials was then compared to the chance scores and the probability of the results arising due to chance was evaluated using the χ^2 test. Throughout the study, results with a probability of 0.01 or less were considered to be significantly different from chance. Results with probabilities greater than 0.01 were rejected as within the variations predicted by chance.

Flight Analysis

During the end of the study, movies or discrimination flights were taken using infra-red light and infra-red film. The infra-red light was supplied by using two pairs of 75 watt tungsten spotlights and two 12" X 12" Kodak No. 87 Wratten filters. The latter were mounted in the walls of the

flight cage and the lights arranged outside them so as to illuminate the whole interior (see Figure 1). The movies were taken using 16 mm. Kodak High Speed Infra-red Film. Two cameras were used, both Auricon sound cameras, and each was mounted at a height of 16" below the ceiling of the room (see Figure 1). Using the microphones described below, the pulses emitted by the bats were translated into audible signals and recorded on the sound tracks of the two cameras. Since the sequencing of pulses by the bats was unique for any flight and also different throughout the flight, it was fairly easy to match pulse patterns on the soundtracks of the two films and thereby synchronize them. The walls of the flight cage were marked off with black photographic tape to form a grid of lines; horizontal lines were separated by 12" intervals and vertical lines by 24". By synchronizing the two movies of any flight, it was possible to triangulate the actual location of the bat at any point in the flight and thus to reconstruct the flight path. In analyzing the films, two plots were made: using the vertical lines, a "top view" of the flight was generated; using the horizontal lines, a "side view", as might be seen from one of the long sides of the cage, was reconstructed. In addition, by noting the distance travelled between frames, the velocity at different points in the flight could be calculated. In this way, it was possible to identify the position of the bat during the emission of any pulse within 8-10 inches, the main source of error being the blurred image of the flying bat on the film. It should also be mentioned that because it was most convenient to use the English system of measurement in taking the films, this system appears on the axes of the graphs in Figures 4-8 and in the scale for Figure 12. However, to allow for comparisons with other experiments on discrimination by echolocating bats, the textual discussion of distances of discrimination have all been converted to Metric units.

Pulse Analysis

On several testing occasions, recordings were made of the pulses emitted

by the bats on discrimination flights. These were picked up and amplified by the "bat detector" type units described by McCue and Bertolini (1964) and constructed for Dr. D. R. Griffin by the Lincoln Laboratories of Massachusetts Institute of Technology. These units utilize a condenser microphone with a 1" diameter metallized mylar diaphragm. The signals generated by this transducer are passed through a cathode follower, amplified, and rectified to produce audible clicks. The latter were used to produce the sound tracks of the films. When the original signals emitted by the bats were to be studied, the amplified outputs of the bat detectors were filtered with a 20-200 kHz band pass filter and recorded at 37.5 inches per second on a Precision Instruments Type 6100 Tape Recorder. The response of this latter instrument is essentially flat up to a frequency of about 100 kHz.

Once recorded, the bat orientation sounds could be analyzed in several ways. Because the tape recorder provided a series of decade speeds, it was possible to replay the tape at 1/10 or even 1/100 the original speed and thus to facilitate the examination of individual pulses. Analysis took the form of either photographing the waveforms of these pulses on an oscilloscope screen, or by decomposing them into separate frequency components on a Kay Sound Spectrograph. All photography of waveforms was made using a Grass C-4 Kymograph Camera and Kodak Kind-1732 Linagraph Paper. By replaying the tapes at 1/10 recorded speed and using a camera film speed of 1000 mm/sec., a record with a time scale of 1 msec./cm. was produced. When it was important to know the temporal spacing of pulses, a slower film rate was used, giving a time scale of 100 msec./cm.

Spectrographs were made in two ways. Original recordings were replayed at 1/10 original speed, filtered through a band-pass of 2-15 kHz (24 dB/octave slope), and recorded on the spectrograph drum at its maximal speed of 0.8 sec/revolution. Spectrographs made at this drum speed provided good information about the frequency composition of the pulses. By

recording the pulses at the same drum speed, and by slowing the tape speed to 1/1000 of the original, the pulses were spread out in time, giving good temporal resolution, but reduced frequency information. Both kinds of analysis were used in this study.

To evaluate this information, calibrations were made of each microphone in place in the flight cage. The calibration signals were the same as those used to calibrate the target echo properties and will be described in that section. The sound source, (also described under the section on target calibration) was placed in different places in the flight room and the frequency and amplitude characteristics of the recorded signals were examined and compared. Since the sound source produced a signal with a frequency composition dependent upon the angle between source axis and microphone axis, the effects of the source directionality were made constant by aiming it at the microphone until the maximum signal was received.

Target Calibrations

In order to interpret the final series of target discriminations, it was necessary to measure the echo properties of the targets. This was done in two ways. The first was to produce a series of short, constant frequency pulses, each with a slightly lower frequency than the one preceeding, and to measure the amplitudes of the resulting echoes. In this way, an echo frequency spectrum for each target was obtained. Since the frequency spectra varied with the angle of incidence, spectra were measured at a wide variety of incident angles for each target.

Constant Frequency Pulse Calibrations The test pulses were generated by connecting the output of a Bruel and Kjaer Type 1013 Beat Frequency Oscillator to a Grason Stadler electronic switch. This latter unit had two parallel channels: when an external signal switched one channel open, it also switched the second channel closed, and vice-versa. The oscillator

output was connected to the switch channel which only passed a signal when an external signal was present. This latter triggering signal was a square wave which was produced by Tektronix Type 161 and 162 units. By varying the duration and repetition rates of the square waves, it was possible to regulate the duration and repetition rates of the test pulses. The electronic switch also provided for a variable rise and fall time on the switched channel. The equipment was thus adjusted to produce a 1 msec. pulse with a rise time of 0.2 msec. and at a repetition rate of 40 pulses/sec.

The pulses thus generated were filtered with a band-pass of 20-150 kHz (24 dB/octave slope) to eliminate small switching artifacts. They were then amplified using a Krohnkite DCA-50 power amplifier. The amplified signals were broadcast from a 2" diameter curved Kuhl speaker. The latter uses the same metallized mylar also used in the bat detector microphones and a basic design first described by Kuhl, Schodder and Shróder (1954). The speaker emission pattern was calibrated by mounting a bat detector at 70 cm. from the speaker and moving it away from the speaker axis until the frequency and amplitude characteristics of the received signal began to change detectably (± 1 dB). To eliminate contributions from microphone directionality, the latter was aimed in each position to give a maximum signal. These measurements indicated that within a 6 degree cone about the speaker axis, the frequency and amplitude characteristics of the signal were constant. Since the speaker had a maximum efficiency at 110 kHz, the frequency spectrum of the speaker at points within the total 6 degree angle showed a smooth increase in signal amplitude as the frequency dropped from 120 to 110 kHz, and then a smooth, almost exponential decrease in signal amplitude as the frequency decreased still further. At points more than 3° away from the speaker axis, the overall signal decreased, and the high frequency components decreased most rapidly. At 5° a signal of 100 kHz was decreased by 2 dB and a signal of 60 kHz by 1 dB. At 6° the former was down by 4 dB from the on-axis value, and the latter by 2 dB. Therefore,

targets smaller than the overall 6° cone would encounter a relatively homogeneous sound field, the appropriate linear dimension at 70 cm. being about 3.5 cm. to either side of the speaker axis. It should also be noted that 70 cm. is well into the "far-field" for a speaker with a diameter of 5 cm. The standard criterion for "far-field" is about 10 times the diameter of the source.

The targets to be measured were mounted, one at a time, on a horizontal thread of the same kind used in the discrimination flights. The latter was attached at each end to a wooden frame made by removing a 3 foot diameter hole from a large piece of $1/2$ " plywood. The frame was mounted vertically on a rotatable clamp and centered so that the axis of rotation of the clamp passed through the center of the circular hole. By placing the targets at the center of this circle, they could be rotated about their centers without altering their positions in the incident sound field by more than 1 mm. in any direction. The whole target holding apparatus was set so that the targets lay on the speaker axis at a distance of 70 cm.

The echoes generated by this apparatus were recorded using the same type of bat detector microphone and amplifier previously described. The microphone and speaker were placed as adjacent to each other as possible, since this was the configuration most similar to the emitting and receiving organs of the bat. The maximum angle formed by the tips of the ears, a target at 70 cm. and the bats emitting organs would be about 2° . With the calibration apparatus, the closest that this angle could be approached was 4° . Since this close proximity between speaker and microphone produced a large amplitude direct signal, a sandwich of velvet paper and cotton was placed between the two and protruding towards the target about 2 cm. This greatly reduced the leak and was found to introduce no changes in the echo spectra by distorting the sound fields. A second step was also taken to reduce the recording of the direct signals. This was to connect the amplified signals from the bat detector

to the second channel of the electronic switch. This prevented the reception of any signal from the second channel while the pulse was being emitted, but allowed for unaltered reception of the echo. The received echo signals were filtered between 20 and 150 kHz (24 dB/octave slope) and recorded automatically on the peak measuring circuits of a Bruel and Kjaer level recorder. This latter instrument measures on a logarithmic scale $1/2$ the peak to peak values of any short duration signal. It is not completely linear at these high frequencies, giving a value for 100 kHz signals which is 2 dB greater than that for an equal intensity 20 kHz signal. This distortion, however, is small, and a smooth function of frequency. It is also parallel in its effects to the frequency spectrum of the speaker, and thus does not generate a second peak in the frequency spectrum of the recording apparatus.

Measurements of echo spectra were made by allowing the oscillator to sweep slowly from a high to a low frequency. The rate of scanning for all measurements was about 70 kHz in 64 seconds. At a pulse repetition rate of 40 pulses/sec., this meant that each successive pulse differed from the previous one by about 200-300 Hz. During a single pulse, the change in frequency was less than 0.01%. The recording unit was set at critical damping so as to produce a single average curve from the series of pulses. During each scan, the record was simultaneously calibrated by marking each 10 kHz step with a margin mark. The records from this level recorder could be read to within 1 dB in intensity and about 2 kHz in frequency.

FM Pulse Calibrations The second method of calibrating the targets utilized the recorded pulses of the bats. Since it is possible that a series of constant frequency pulses is not equivalent to a single FM sweep, a series of pulses, recorded on actual discrimination flights, was rebroadcast using the DCA-50 power amplifier and the Kuhl speaker and the echoes recorded on the tape recorder using bat detector microphones. Echoes were recorded in this manner for both targets used in the discrimination flights and on another channel of the tape recorder, the effects of amplification and broadcast were

measured by recording the reproduced signals at a distance of 140 cm. from the speaker. This arrangement mimicked the distance echoes had to travel between speaker, target and microphone, and thus gave a measure of atmospheric effects.

Each of these signals, (original, rebroadcast, and target echoes) were then analyzed on a sound spectrograph. Since the relations between frequency and amplitude were particularly important in these calibrations, a third type of spectrographic plotting was used: one that makes contour maps of the signals, connecting all points within 6 dB of some given intensity level. To obtain better frequency resolution, a scale magnifier was also employed, resulting in the spreading of the signal over a large fraction of the spectrographic record. Temporal resolution was increased by re-playing the signals at 1/100 of the recorded speed and by using an extra large print-out drum on the spectrograph. The resulting records allowed direct comparisons to be made between the constant frequency measurements made on the target with the automatic equipment, and the rapidly swept FM pulses used by the bats.

RESULTS OF DISCRIMINATION STUDIES

Hunting Studies

Hunting of live mice These experiments were carried out under the visual and olfactory controls outlined in the previous chapter. To recapitulate, the former consisted of flying the bats in either total darkness or in infra-red light only; the latter involved placing a mouse beneath a small plastic box which had been drilled full of holes on all sides. This box served not only as an olfactory control, but also as a control for the use of sounds generated by the prey itself.

It was clear from the start that the bats were able and eager hunters. The usual time which elapsed between the release of the mice and bats from their respective cages and the final capture was about 15 minutes. Movies taken in infra-red light showed that hunting began with several low circles and passes over the table on which the mice were present. After four or five such "examination" flights, the bats usually commenced a three or four revolution spiral that steadily decreased in radius. The actual capture was usually made following such a circling, and involved a direct drop onto the prey, the wings being spread so as to contain the mouse beneath their membranes. The "thumbs" were then used to manipulate the mouse's head so that it could be dispatched with a quick bite on the neck or head. Then the bat seized it by the head and flew off to the roost to eat everything except the tail.

On those occasions when the plastic box was present with a mouse inside, the bats showed no interest in attacking or even investigating it. Similarly, when other non-food items such as sticks, leaves, rocks, and equipment clamps were placed alongside the mice on the table, the bats never showed any evidence of attacking any object

except a mouse. These facts are taken as evidence that the bats were able to discriminate between these targets, and to do so without recourse to olfactory and visual cues or by hearing sounds from the prey. As a final comment on these experiments, it should also be noted that bat detectors indicated the continual emission of high frequency pulses during the circling and hunting flights. In those cases where the bat detector microphones were optimally positioned, it was even possible to detect a rapid increase in pulse emission rate prior to and during an actual attack. Such an increase is often cited as evidence that insectivorous species are using echolocation to capture their food items. (Griffin, 1953).

Hunting of dead mice It was apparent from the previous series that the bats could accurately detect and locate living mice without the use of visual and olfactory cues. To reduce the number of available cues still further, motion and prey-induced sounds were eliminated as sources of information by using dead mice instead of live ones. While the bats attacked this problem as eagerly as before, they were not all as successful. For example, two of them typically performed the circling flights over the table and the mice, but instead of narrowing the circles and falling directly on the prey, they tended to drop almost anywhere on the table and commence investigating their immediate surroundings. This investigation included rapid wiggling of the ears and nose-leaf, and also the emission of ultrasonic pulses. However, olfactory cues may have played a role under these conditions. Increases in pulse emission rate were not detected once the bats had landed; this may have been because microphone placement was rarely optimum for these conditions. Two other bats tended to engage in prolonged circling of the table, often making as many as 40 or 50 passes before actually attacking. On some occasions, these attacks actually were erroneous and involved the capture of a stick or stone. However,

out of 20 days of observation, during which each bat was allowed one mouse/day, these two animals only erred 6 times. The plastic control box was never attacked under these conditions unless it was left in position for long periods, such as overnight. Then it was frequently found overturned and its former occupant, a dead mouse for this series, absent. These experiments thus showed a reduction in discriminative abilities when motion was eliminated as a cue. Perhaps in the wild, motion is an important component in the recognition of prey items. However, the apparent, though limited success of two animals suggested that more controlled experiments with inedible and motionless targets were justified.

Other Hunting Experiments Because of the dearth of information on hunting by this species, it is also relevant to record some observations made on these bats in Trinidad during the summer of 1966. Among other prey items which these animals were seen to capture were other species of bats, (both captor and prey being in flight), flying birds, and mice which were tossed into the air with a spring-loaded catapult. During these captures, it was observed that the bats changed from echolocative pulses which were long in duration and loud in amplitude, to another type which was short in duration and reduced in amplitude (see p.138 and Fig. 15). This shift in emitted pulse structure suggested that in future studies, particular attention be paid to the kinds of pulses used by the bats in different situations. If a case for the use of certain echo parameters in a discriminative situation could be made, it would be very interesting to examine the nature of the emitted pulses to see if they maximized the availability of these parameters. This subject will be discussed at some length below.

Artificial Targets - Series I

The discrimination studies with artificial targets were begun with two very dissimilar targets in the hope that the discrimination would prove fairly easy for the bats. The two targets selected were a 15 cm. diameter, hollow rubber ball and 10.5 cm. length of 2.5 cm. diameter broom handle which had been rounded at both ends. Each target was suspended by a 0.35 mm. cotton thread so as to hang just 2-3 cm. below the landing ring. This close proximity between target and landing ring probably resulted in various interactions between the echoes from the two objects. However, it was hoped that this would make it easy initially to train the bats to pay attention to the targets; up to this point, they had only been trained to land on the landing rings.

Scores and Interpretation of Controls Early in the training period, only the ball was used. This target was to become subsequently the rewarded object in the testing flights. When the bats had learned to select the landing ring from which the ball was suspended, training with both targets was begun. As noted in the previous chapter, only pairs of positions equidistant from the roost end of the flight room were used. After about a month of training, the five bats which had learned to land on the rings had all learned to discriminate between the two targets. An all day testing period was then initiated and the scores from these flights are summarized in Table I.

It is quite clear from this first series that once the discrimination had been learned, it was fairly easy for the bats. All five animals scored 80% correct or better consistently. The chance score was established by using two similar balls, randomly positioned as with the experimental targets, and found to be just 50%. These chance-

Table I. Summary of scores during 11 days of testing on 15 cm. rubber ball vs. 10.5 x 2.5 cm. wooden sausage.

<u>Bat</u>	<u>No. Trials</u>	<u>No. Correct</u>	<u>% Correct</u>	<u>Value of p</u>
E	82	66	80	<0.005
A	82	75	91	<0.005
H	84	69	82	<0.005
T	85	75	88	<0.005
C	<u>80</u>	<u>73</u>	<u>91</u>	<u><0.005</u>
Total	413	358	87	<0.005

score flights served as multiple controls. First, they demonstrated that the modified random sequencing (runs of four or more in a row being ~~deleted~~) did not result in chance scores very different from what might be expected from non-modified sequences. Secondly, it introduced some controls for olfactory cues. If the bats were able to mark a rewarded target with urine, feces, secretion, etc., it would enable subsequent discriminations to be made by odor. Since this option was as available on the control flights as on the experimental series, the attainment of only 50% success on the former argues against the successful use of olfactory cues. The use of visual cues was presumably prevented by making all flights in either total darkness or in the presence of infra-red light. In these early studies, most flights were made in darkness only. Finally, as noted in the previous chapter, several bats were prompted to fly by the experimenter, who, knowing the correct target might have inadvertently communicated some cue to the animal. In these flights, three of the bats (E, A, and H) were hand prompted and two, (T and C), were not. The latter always flew spontaneously as soon as the lights

had been turned out and the screen between bat and target raised. It is clear from the table that there was no significant difference in the success of the two groups of animals. This fact plus the attempt made to prompt in a constant and uniform fashion argue against the use of such cues by the bats. On all flights in this series, a bat detector microphone was mounted in the wall behind the targets. The output of clicks by this instrument indicated that the bats were emitting pulses on all flights and that the rate of pulse emission increased to a high rate as the bat approached the target and landed on the ring. All of these facts argue for the use of echolocative cues in the making of a choice between the targets.

Having obtained such consistent success with these rather dissimilar targets, a new series was begun with the same wooden "sausage" but with a smaller ball. This ball was similar in composition to the previous one, but was chosen to have the same approximate cross-sectional area as the sausage. The reason for this was as follows. In the range of frequencies used by most bats, targets as large as the 15 cm. diameter ball or the sausage are in the "optical region" of echo formation. In this region, the amplitudes of the resulting echoes are approximately proportional to the cross-sectional areas of the targets. By equating the cross-sectional areas of the two targets, I hoped that the overall amplitudes of the echoes from these targets would be similar. The appropriate ball for this series was one with a 6 cm. diameter, and luckily the toy store had just the desired item.

After a short training period, a 10 day testing period was begun, resulting in a total of 111 trials per bat. The results from this series are summarized in Table II.

Table II. Summary of scores during 10 days of testing on 6 cm. rubber ball vs. 10.5 x 2.5 cm. wooden sausage.

<u>Bat</u>	<u>No. Trials</u>	<u>No. Correct</u>	<u>% Correct</u>	<u>Value of p</u>
E	111	89	80	<0.005
A	111	88	79	<0.005
H	111	89	80	<0.005
T	111	83	75	<0.005
C	<u>111</u>	<u>83</u>	<u>75</u>	<u><0.005</u>
Total	555	432	78	<0.005

While the overall scores are slightly lower than for the larger ball, they are still much greater than chance. The same controls apply to this series as to the previous one, and again it seems most parsimonious to conclude that echolocation was used to effect the discriminations.

While equating the cross-sectional areas of the targets probably equated the echo amplitudes at their surfaces, this did not necessarily result in equal echoes at successive distances from the targets. Since the bats presumably had to make a decision before reaching the targets' outer surfaces, they must have evaluated the echoes while still some distance from the targets. As discussed in the Introduction, targets of differing geometries produce echoes which expand into space in different ways. The echoes from a sphere spread in all directions and thus attenuate more rapidly with distance than the echoes from a cylinder, which expand effectively into two dimensions. In the case of the ball and sausage, the former is presumably a sphere and the latter a combination of the characteristics of spheres and cylinders. One would therefore predict that as the distance from the

targets is increased, the echoes from the sphere would become smaller in overall amplitude than those from the sausage. The greater the distance at which the bat made its choice, the greater the difference in the amplitudes of the two echoes.

There are two ways to move the point of echo equality away from the surfaces and nearer the point of presumed choice. One way is to increase the size of the ball again; the other is to reduce the size of the sausage. The latter was chosen since it had a dual effect: not only was the echo at the surface of the reduced sausage smaller than the echo at the sphere surface, but also, by shortening the long axis of the sausage it becomes more like a sphere in shape and in the mode of expansion of its echoes. The targets thus selected were the 6 cm. diameter rubber ball and a new sausage, 7 cm. long and 2.5 cm. in diameter.

Using these targets, a training period of several days was followed by 5 days of testing. The scores from this series are summarized in Table III.

Table III. Summary of scores during 5 days of testing on 6 cm. rubber ball vs. 7 x 2.5 cm. wooden sausage.

<u>Bat</u>	<u>No. Trials</u>	<u>No. Correct</u>	<u>% Correct</u>	<u>Value of p</u>
E	75	65	87	<0.005
A	75	56	75	<0.005
H	75	66	88	<0.005
T	75	58	77	<0.005
C	<u>60</u>	<u>57</u>	<u>95</u>	<u><0.005</u>
Total	360	302	84	<0.005

All five animals scored 75% or better on these flights which for a chance score of 50% was highly significant ($p < 0.005$). As before, the controls argued for the use of echolocative information in the effecting of these discriminations.

The force of these experiments was that Vampyrum can apparently discriminate between motionless, artificial targets which are quite similar in size and shape. While this conclusion was new for this species of bat, it was in no way an advance beyond what Griffin, Friend and Webster (1965) had already shown for Myotis lucifugus: that bats can discriminate between two similar targets using echolocative cues alone. In the case of the Vampyrum experiments, there was no immediate way to choose between the many possible cues which the bats might have used: overall intensity differences, echo spectra, phase shifts, elastic effects (in the case of the rubber balls), scanning of the targets with narrow pulse beams, etc. The final series should have been some help in this direction, since in regions at some distance from the targets the overall intensities would be nearly equal. However, without some knowledge of where in its flight the bat made a choice, one could never exclude overall intensity comparisons. Clearly, to get at some of the possible mechanisms of discrimination, further experiments would need to provide information about flight paths, target spectra, and the pulses used.

Analysis of the Emitted Pulses A series of recordings was made of the pulses emitted by bats E and H on discrimination flights to the 6 cm. ball and the 7 x 2.5 cm. sausage. These pulses were later examined by photographing them on an oscilloscope and by submitting them to spectrographic analysis as detailed in the previous chapter. This provided some interesting data.

The most striking feature of the waveforms of the emitted pulses is the consistent presence of irregularity in the envelope. When

the pulses are displayed on compressed time scales, they appear to have horizontal linings, as if several pulses of different amplitudes, but similar shape, had been superimposed. Griffin and Novick (1955) have described such structures in the pulses of other species, and at the time suggested that those waveforms resulted from the presence of several component frequencies, perhaps harmonically related.

Spectrographic analysis of the recorded Vampyrum pulses indicated that indeed several components were present. The pulses were uniformly of the "FM" type -- that is, they consisted of a sweeping of the component frequency from a high to a low value during the course of the pulse. However, these pulses contained in many cases two such sweeps, one always containing higher frequencies than the other. In general, the total frequency composition of these pulses was contained in the range 65-115 kHz. This range was usually broken into the two component sweeps: the first beginning at about 110-115 kHz and sweeping down to 80-85 kHz; the second starting at around 95-100 kHz and terminating around 65 kHz.

In initial stages of discrimination flights, the duration of the emitted pulses was from 1-1.5 msec.; by the end of the flights, the durations had decreased to about 0.5 msec. or even less. This steady decrease in pulse duration as the targets were approached was characteristic of all flights by all the bats. Usually the shortening of pulse duration was accompanied by a reduction in the total frequency swept through, (e. g., 95 to 70 kHz in 0.5 msec. was not uncommon), and sometimes in the loss of one of the sweeps. Sample pulses from one flight can be seen in Figure 2.

Because of the indications that Vampyrum might use different kinds of pulses under different conditions, examination of the temporal patternings of the two sweeps during the course of single flights was made. The results of these studies indicated that there was considerable

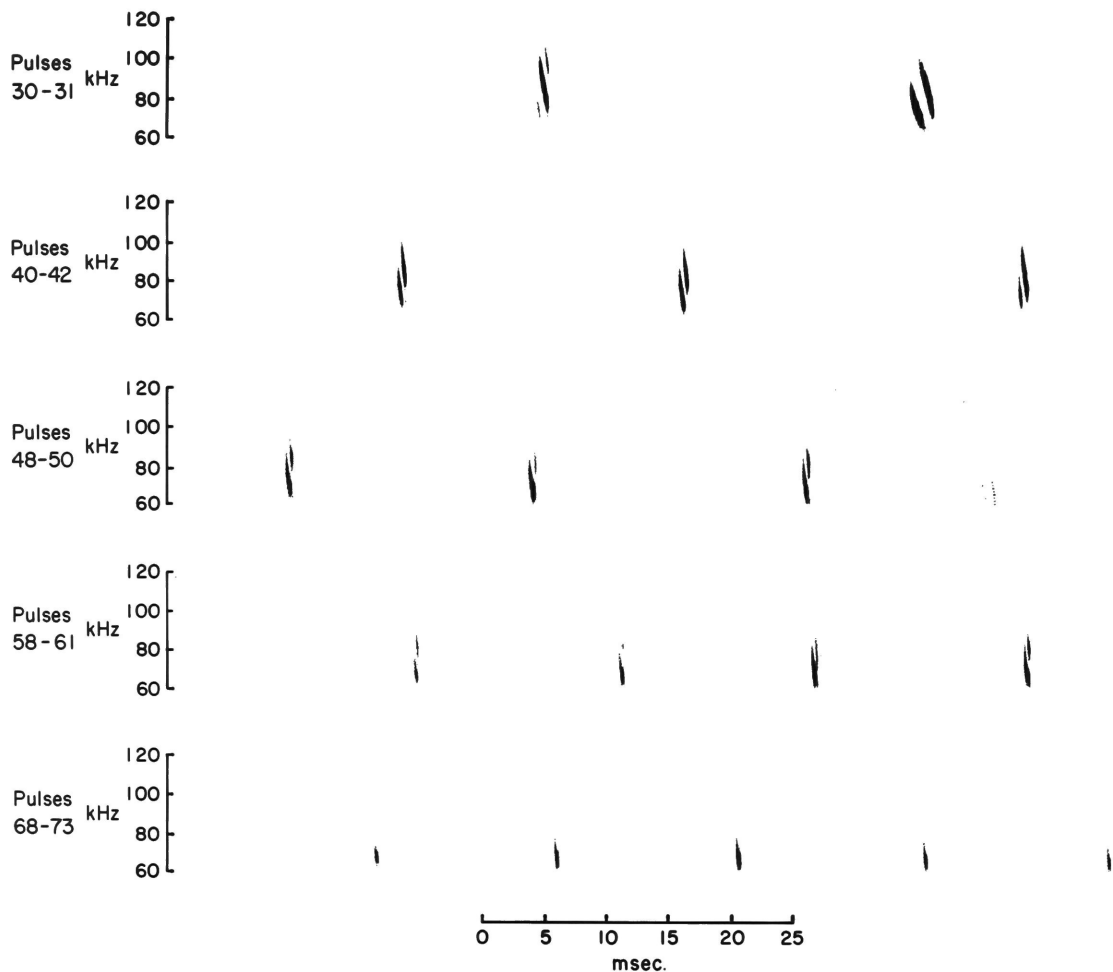


Figure 2. Sound spectrographs of pulses emitted by bat E on a flight to the 6 cm. ball vs. the 2.5 X 7 cm. sausage. Pulses in any one row are consecutive; pulses have been omitted between successive rows. The first two rows show pulses emitted during the first third of the flight; the second two rows pulses emitted during the second third; and the final row, pulses emitted during the final third. Pulse number 1, not shown, was the first pulse emitted after taking flight.

variation in the relative times of onset of the two sweeps: in some pulses, they began almost simultaneously and in apparent synchrony; in others, they barely overlapped temporally at all. It was possible in fact to divide all the emitted pulses into five general categories:

Type I pulses--Pulses with durations of 1.5 msec. or greater; several amplitude modulations; and two or more sweeps present, the degree of overlap being rather variable.

Type II pulses--Pulses with moderate durations (1.0-1.5 msec.); having a single amplitude modulation; and with only two component sweeps, the lower always preceding the upper, with at most about 1/2 overlap.

Type III pulses- Pulses with short durations (0.5-0.9 msec.); having a single amplitude modulation; and with two nearly simultaneous (total overlap) sweeps.

Type IV pulses- Pulses with fairly short durations (about 1.0 msec.); with two amplitude modulations, each having a single sweep only--this has been called the "double pulse".

Type V pulses --Pulses with very short durations, (about 0.5 msec.); a single amplitude modulation and a single sweep.

Examples of each of these waveforms and the accompanying spectrographs can be seen in Figure 3. While there are some pulses which are in a sense transitional or hybrids, most of the pulses emitted by bats E and H on discrimination flights can be placed in these five categories. A breakdown of the relative distributions of each type of pulse is given for two flights by each bat in Table IV.

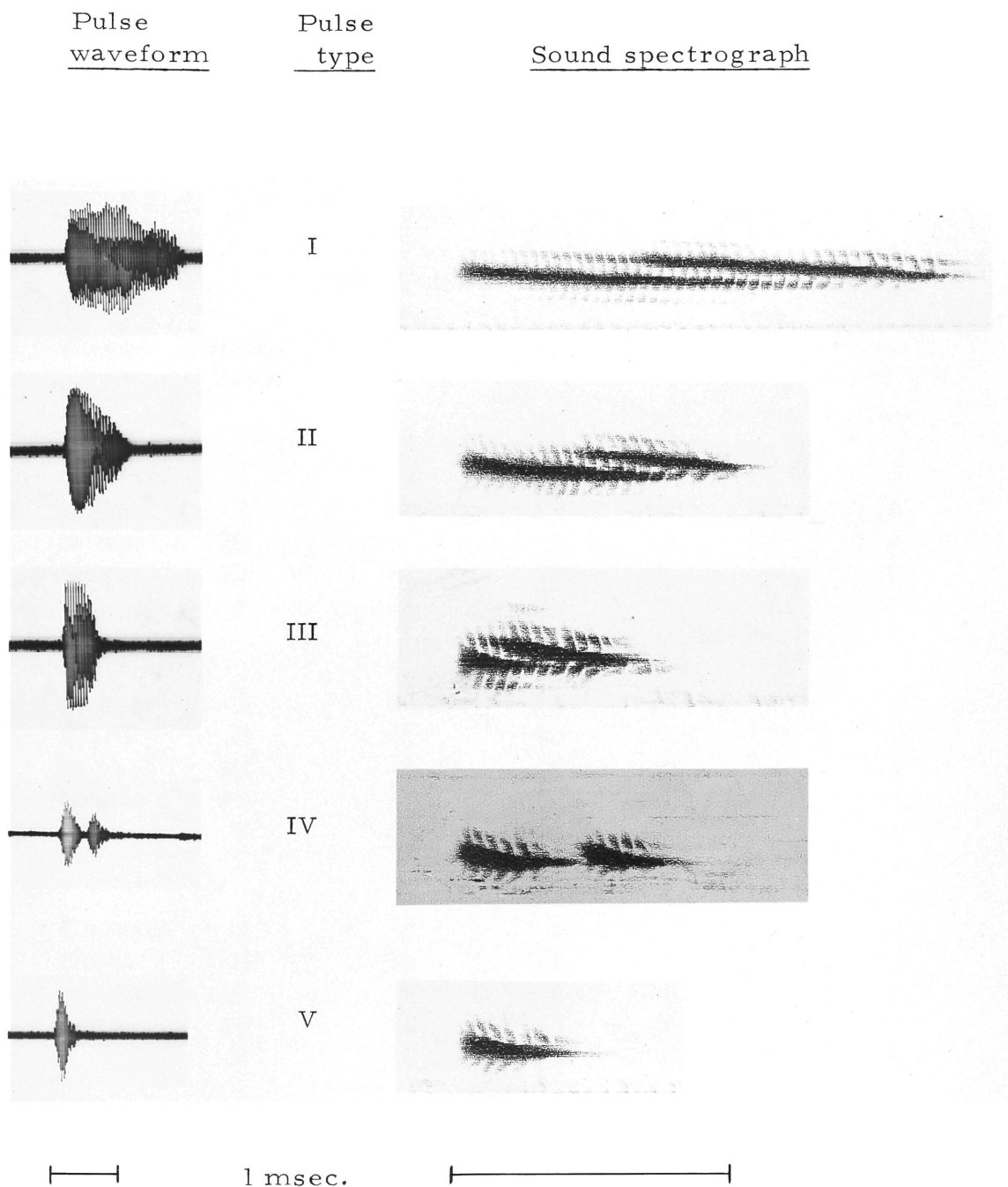


Figure 3. Examples of the waveforms and spectrographic composition of the five classes of pulse types. For both kinds of records, the time mark indicates 1 msec. The "rib-like" patterning on the spectrographs is apparently an artifact.

Table IV. Summary of pulse type distribution
for four flights by two bats to the 6 cm. ball
and the small sausage.

Bat	Flight	Pulse Type	No. Pulses in this type	%	No. Pulses in this type		
					First 1/3 of flight	Second 1/3 of flight	Final 1/3 of flight
E	Correct flight to west target	I	7	12	7	0	0
		II	17	29	13	4	0
		III	0	0	0	0	0
		IV	17	29	0	15	2
		V	18	30	0	1	17
E	Correct flight to east target	I	13	20	13	0	0
		II	14	21	9	5	0
		III	4	6	0	1	3
		IV	14	21	0	14	0
		V	20	31	0	2	18
H	Correct flight to west target	I	0	0	0	0	0
		II	30	62	16	13	1
		III	1	2	0	0	1
		IV	13	27	0	3	10
		V	4	8	0	0	4
H	Correct flight to east target	I	12	20	12	0	0
		II	35	58	8	17	10
		III	4	7	4	0	4
		IV	7	12	0	3	4
		V	2	3	0	0	2

Certain conclusions can be drawn from this table. For bat E, pulse types II, IV, and V were the most common with pulse Type I running a close second. Type III pulses are rare. In general, pulse type I begins the flight, pulse type II succeeds it and dominates during the first third (in time) of the flight. Type IV is most common during the middle third of the flight, and type V during the final third. Type III, when present, seems to be emitted during the terminal parts of the flight.

Bat H differs somewhat from this pattern. Again, types II and IV dominate, but type V is relatively uncommon. Type III is rare as for Bat E. The sequencing is similar: type I occurs first, is succeeded by type II, which instead of shifting to type IV, is predominant during the first and middle thirds of the flights. Type IV and V are present primarily in the final third of the flight. (The absence of type I pulses in the first of these two flights is due probably to a slow reaction time on the part of the experimenter. During the recordings, the beginning of a flight was noted by introducing a signal to one channel of the tape recorder. In this flight, the pulses preceding the marker are all of type I, indicating that type I pulses were emitted. In addition, the total number of recorded pulses in this run was about 20% lower than for the other three flights. This suggests a bit of slowness on the marker button.)

While it is impossible to generalize from as few as four flights, the temporal relationships between the components in these pulses seemed to follow some regular sequence. It is important to know whether this patterning was the result of some artifact of the recording environment or a result of the bat's own control over pulse composition. Unfortunately, without further information, one can only surmise about the importance of microphone directionality, location of the bats, effects of walls and roof, etc. Clearly, it would be very helpful to have flight

path information. It would also help to know the location of the bat during the emission of each pulse.

Artificial Targets - Series II

The previous experiments all pointed to a need for information on the flight paths of discriminating bats, including each bat's location in the flight room during the emission of given pulses. They also pointed to a need for greater control over the echo properties of the targets. The latter problem was tackled first.

Target Design and Initial Calibrations The hope in modifying targets was to reduce the number of available cues as much as possible by careful target design. This was not easy since it meant presupposing that the one cue left for the bats to use was one which they were capable of using. The use of overall intensity information seemed one that the bats could surely perform, but one which was least interesting and least useful in fine discriminations. Clearly, one of the more powerful skills would be the ability to utilize frequency spectra. This would open up to the bat all the information generated by diffractive, elastic and multiple scattering effects. In this regard it would suffice to demonstrate the use of frequency spectra in only one case; if a bat could use diffractive effects, it could presumably also use elastic or multiple scattering effects. Diffraction seemed the simplest method of generating a frequency dependent target, and was therefore selected. All other mechanisms would be hopefully eliminated by careful controls.

What were these other mechanisms? The most obvious was overall intensity. This was also the most difficult to eliminate. To produce two targets which differed in their diffractive spectra, one had to use two different shapes, and two different shapes automatically means two

different rates of geometrical attenuation in echo intensity. The approximate solution was to pick two targets which differed more in their frequency spectra than in the intensity differences at the ranges used by the bats, to adjust their relative sizes so that the point of equal echoes was reasonably near the points of decision, and to use target geometries which did not differ greatly in intensity with different angles of incidence.

The geometries selected were a sphere and a prolate spheroid with an axis ratio of 5:3. The latter is enough like a sphere to partly reduce the geometrical attenuation problem and the two should differ in their diffractive spectra. They also satisfy the criterion that if suspended along their major axes, any angle of approach in the horizontal plane should give echoes of equal intensity. However, variations in the vertical angle of approach would produce differences in echo intensity for the prolate spheroid: in fact any deviation from an approach perpendicular to its major axis should produce smaller intensity echoes. If this proved to be a problem, it would be necessary to restrict the flight paths of the bats by barriers.

Having selected shapes, it was then necessary to select a size for each target. It was known from the previous series of experiments that the bats were using frequencies in the range 50-110 kHz. This corresponded to a range of values of k of about 10-22 waves/cm. To keep the targets within the regions of diffraction, (values of ka between 1 and 35), the targets would have to have radii larger than 0.04 cm. and smaller than 3.5 cm. The choice of an actual value within this range was partly contingent on the training situation. It would be preferable to minimize the presence of other objects near the targets, thereby preventing interference and multiple scattering. It was impossible to use unattached targets and still insure a given orientation of the prolate spheroid. Thus the targets were fixed in space by suspending each from a thin thread as before. Since the thread and the target would both produce

echoes, it would be preferable to make the thread as small as possible relative to the target. A further argument for using targets in the upper range of ka 's was the increased likelihood that the bats would find the targets at all. A disadvantage of using large targets was the smaller degree of frequency dependence which would result. In an attempt to strike a middle ground here, a radius of 1.54 cm. was selected for the sphere.

Infra-red observations of previous experiments suggested that discriminations were effected rather late in the flights. The size of the prolate spheroid was thus chosen so as to produce approximately equal intensity echoes (as integrated over the whole frequency range of 50-110 kHz) at a distance of 70 cm. from the targets. Beyond this point, the echo from the prolate spheroid would become louder than that of the sphere; nearer than this point, the sphere echo would be louder. Using the target calibration methods outlined in the previous chapter, a prolate spheroid with an interfocal distance of 1.05 cm. was selected as satisfying these conditions.

These considerations reduced the chances that the bats could use overall intensity cues to make the discriminations. To prevent the use of elastic effects, the targets were made out of solid lucite. To prevent multiple scattering from the target surfaces, they were machined and polished until the surfaces were smooth and shiny. Since the target sizes were already fixed and since the size of the bats' pulse beams was unknown, the only control for beam scanning was actually to measure the beams using several microphones placed at different positions in the end of the flight room. Since it was impossible to control for phase variations, it was decided simply to record the discrimination pulses, replay them at the targets and examine the resulting waveforms which would include phase effects if appreciable.

When the targets had been constructed, they were calibrated as described in the previous chapter. At this stage, calibrations were made only at an incident angle of 0° . This later proved to have been a mistake, but given the time involved in making these calibrations it seemed most reasonable to begin the training as soon as possible and calibrate if and when the bats had learned the problem. The results of this calibration indicated that both the sphere and the prolate spheroid were quite frequency dependent, the former producing a series of 6 peaks in the range of frequencies 50-110 kHz, successive maxima and minima varying by as much as 8 dB. The prolate spheroid had fewer and broader peaks, and several of these maxima occurred at frequencies where the sphere had minima, and vice-versa. The difference in amplitude between successive maxima and minima for the prolate spheroid was also about 8 dB. The overall intensities at 70 cm. and 0° incident angle for the two targets differed by about 10%. All these calibrations were performed with the same 0.35 mm. diameter thread that was used to suspend the targets in the experimental flights.

Discrimination Scores for Flights Without Flight Path Restrictions

The calibrations were followed by a long and tedious training period. This problem was obviously of much greater difficulty for the animals than any of the previous ones and the attaining of a plateau was uncertain at best for several of the animals. It was not uncommon for an animal to score over 80% one day, drop to 60% success the next, and then climb again to the low 70's the third. Given this uncertainty in ascertaining when the learning was at a maximal level, records of test flights were kept for several days in succession and an arbitrary, but consistent, decision about how much of the record to accept as "test" data was made on the basis of examining the scores. The decision was always based on the observation that increased practice

in general led to higher scores and consequently the series of scores taken were always the last in the sequence. In Table V, two sets of scores are given: the first is the summary of all scores made during nine days of testing; the second is the summary of the scores made during the final three days of testing.

In general, scores increased during the nine day testing period. By the fourth day of testing, bats H and T were both scoring consistently 80% or better. Bats E and A both scored in the 50's and 60's until the final two days of testing when they both scored over 80% on both days. Bat C never scored over 80% in this series and overall scored an average of about 65%. The period of "plateau" testing was taken to be the final three days of the series. During these three days, Bat E scored 71% correct overall, Bat A scored 73%, Bat H scored 83%, Bat T scored 83%, and Bat C scored 60%. All but the scores of Bat C were significantly higher than the chance score of 50%, ($p < 0.005$ or smaller).

As before, chance score flights controlled in part for olfactory cues and established the base line against which to compare the experimental scores. All flights were conducted in total darkness or infra-red light and Bats T and C were able to fly without prompting by the experimenter. Since Bat T scored higher than all others except Bat H, it is apparent that prompting was not necessary for his discrimination abilities. It thus seems that at least four of the bats were able to discriminate between these two targets using echolocation.

This series should have set the scene for interpretations about discrimination mechanisms. Unfortunately, observation of discrimination flights with infra-red viewing gear had indicated that at least two of the bats, Bat T and Bat H, were not flying in a line perpendicular to the targets, but were dipping low in the middle of the flight and

Table Va. Summary of scores during nine days of testing on the lucite sphere vs. the lucite prolate spheroid. No flight path restrictions.

<u>Bat</u>	<u>No. Trials</u>	<u>No. Correct</u>	<u>% Correct</u>	<u>Value of p</u>
E	142	86	59	$0.05 < p < 0.10$
A	126	81	64	$0.01 < p < 0.03$
H	142	115	81	< 0.005
T	142	109	77	< 0.005
C	142	93	65	< 0.010

Table Vb. Summary of scores during the final three days of the nine day testing period on the lucite sphere vs. the lucite prolate spheroid. No flight path restrictions.

<u>Bat</u>	<u>No. Trials</u>	<u>No. Correct</u>	<u>% Correct</u>	<u>Value of p</u>
E	48	34	71	< 0.005
A	48	35	73	< 0.005
H	48	40	83	< 0.001
T	48	40	83	< 0.001
C	48	29	60	≈ 0.300

swooping up near the end to land. This maneuver immediately suggested that they were achieving the discrimination by means of the fact that the prolate spheroid, when approached from below, produced a less intense echo than the sphere. This violated one of the initial boundary conditions and prevented testing of the use of diffractive information.

To reduce deviations from horizontal approach, a horizontal bar with a suspended curtain was placed at a height such that only a 2' high space between bar and ceiling was left for the bat to fly through. This barrier was placed at a location which seemed to be the lowest point in the flights of the two animals: 8 feet from the roosts (see Figure 1). The curtain used to shield the targets from the bats prior to a flight was also situated at this position and arranged so that it opened from the middle of the room outwards. The training of the animals under these conditions was then commenced.

Discrimination Scores for Flights Made in Presence of Barrier

The scores of the bats with these changes proved to be even more variable than before. A large degree of this variability seemed to be a result of the disturbing effect of the barrier. This was demonstrated by the very low scores of all bats for several days immediately after the barrier was erected, even of those which had customarily flown paths that should not have been affected by the barrier. It was obvious from previous training periods that the bats could be easily disturbed by any major change in the geometry of the flight room. Microphone tripods, tables, observers at the edge of the room, etc. all had proved to be sources of major perturbations in the past. In the presence of such objects, a bat would often refuse to land on a ring, usually flying in rapid circles around the room and occasionally colliding with some familiar object. When the bat did land on a platform, it was usually a favored one, and not often the one with the

correct target. Even if it were the correct target, the bat would rarely take the proffered food, but would spit it out and fly back to the roost. Under such conditions, it was always difficult to prompt the bats to fly, and those that usually flew spontaneously would not do so. Promptings were usually rewarded with a hard bite on the glove.

The importance of familiarity under flight conditions is not a new finding in bats. On the contrary, it has been described in many species including Megaderma lyra, Myotis lucifugus, Eptesicus fuscus, etc., and Griffin (1958) gives a good discussion of this phenomenon. In the case of the barrier, the bats scored poorly for over a month after its erection. With time however, the bats began to improve, presumably as familiarity with the barrier increased.

The summary of the testing is listed in Table VI. As with the previous series, two sets of data are given. The first gives all scores recorded during 21 days of general testing. The second gives the scores for the last eight days of testing. Variations in the total number of trials are due to the facts that the number of trials per day was slowly increased over the experimental period, while the periods selected for training and testing differed for the different animals. For example, both Bat A and Bat C were not flown after the number of daily trials had increased to 25 as they were both pregnant at this time. Bat T was tested most often as he appeared to be trained earliest.

It is clear from these scores that only Bats E and T really learned to discriminate with any regularity. These are the only two animals whose overall scores exceeded 60% and whose scores for the final eight days exceeded 70%. Two of the other bats, A and H, were highly variable in their discriminating success, some days scoring as high as 81% (out of 16 trials) and 91% (out of 11 trials) respectively, but other

Table VIa. Summary of scores of 21 days of testing on lucite prolate spheroid with barrier.

<u>Bat</u>	<u>No. Trials</u>	<u>No. Correct</u>	<u>% Correct</u>	<u>Value of p</u>
E	372	228	61	<0.005
A	198	115	58	0.01<p<0.025
H	304	174	57	0.01<p<0.025
T	419	301	72	<0.005
C	218	116	53	0.250<p<0.500

Table VIb. Summary of scores on the last eight days of a 21 day testing period on lucite sphere vs. lucite prolate spheroid with barrier.

<u>Bat</u>	<u>No. Trials</u>	<u>No. Correct</u>	<u>% Correct</u>	<u>Value of p</u>
E	177	123	70	<0.001
A	122	78	64	<0.005
H	144	94	65	<0.001
T	200	156	78	<0.001
C	122	70	57	0.10<p<0.25

days scoring little better than chance. While both scored significantly better than chance during the final eight days, neither could be said to perform consistently or with great success. Bat C apparently never learned the discrimination.

Distributions of Errors on Flights in Presence of Barrier

In view of the apparent importance of familiarity of the room to these animals, it is interesting to ask whether errors were equally distributed between east and west target positions. The distributions of errors for the whole 21 day period of testing are summarized in Table VII.

Table VII. Summary of distribution of errors at east vs. west targets for 21 days of testing with lucite sphere and prolate spheroid. Barrier present.

<u>Bat</u>	<u>No. Errors</u>	<u>No. Errors at east target</u>	<u>% Errors at east target</u>	<u>Value of p</u>
E	114	114	79	<0.001
A	83	52	63	0.25 < p < 0.05
H	130	111	85	<0.001
T	118	35	30	<0.001
C	102	42	41	≅0.05

By chance, errors should be made equally at the two positions, east and west; this means a random distribution should give a score of about 50% errors at the east target. It is obvious from the table that for bats E, H, and T, the distribution is not random, bats E and H tending to fly erroneously to the east target more than chance ($p < 0.001$) and bat T tending to fly erroneously to the east target less than chance ($p < 0.001$). By our specified significance level, the

distributions of errors for bats A and C can be ascribed to chance.

This distribution of errors suggests two points. One simply reinforces the previous discussion concerning familiarity of the flight room. Whenever bats E, H, or T were disturbed, were not discriminating, or were simply chased out of the roost and forced to fly in the absence of targets, they invariably landed on a platform on a "favorite" side of the room. Under such circumstances, bats E and H flew to an easterly platform and bat T to a westerly one. This is precisely the bias of their respective error distributions. It thus seems to be the case that whenever these three animals could not or would not make a discrimination choice, they simply flew to their respective "favored" positions. Unfortunately, one cannot choose between the two possibilities of "could" or "would" for these bats.

In contrast, bats A and C did not seem to favor any positions, and when chased out of the roost were equally likely to land on any of the four rings. Similarly, their errors were distributed between the two sides of the room at about the chance level. The fact that these two animals never demonstrated consistent success in the final discriminations, plus the fact that they had no competing predilections for any particular side of the room, suggests that they were in fact unable, as opposed to unwilling, to effect the correct discrimination. It should be remembered that both performed moderately well on the ball and wooden sausage problems.

Analysis of Flights and Determination of the Distance at which Choice is Made

Having demonstrated that at least two of the animals could successfully discriminate between the two lucite targets in the presence of the barrier, it was next necessary to ascertain the point of apparent

choice. Consequently, infra-red movies and high frequency tape recordings were made of one day's discrimination flights (25 trials per bat) for each animal. The resulting films and tapes were then analyzed as described in the previous chapter and compared according to several criteria.

The first criterion examined was whether there were any consistent patterns in the distance at which the bats first turned towards the chosen targets. This was ascertained by constructing an envelope which contained all flights by a given bat to a particular target position. The envelopes for flights to each pair of equidistant target positions were then compared to see where the envelopes first began to diverge, and where divergence was complete. The first distance will be denoted D_1 and the second D_2 .

A second criterion was based upon the increase in emission of echolocative pulses which always accompanied the approach of the bat to the target. It seemed reasonable that as the bat prepared to make a choice, more information would be required and consequently, more pulses would be emitted by the bat. One way to evaluate whether any consistent behavioral changes in pulse emission rates had occurred, was to ask at what distance from the targets did the rate of pulse emission first exceed the mean for the whole flight. This distance was determined for all flights to a given target and the mean value computed. This mean distance will be denoted PR .

If the information required by the bat is a function of distance to the target, there are two ways in which the amount of information received at any given distance can be increased. The first is to increase the rate of emission as noted above. The second is to reduce the forward flight velocity so that the number of pulses emitted at any site can be increased without necessarily increasing the emission rate. To see whether any detectable changes in velocity occurred

during successive flights to a given target position, a parameter V was computed which gave the mean distance at which forward flight velocities first fell below the means for the flights.

Since in most cases, the bats both increased the emission rate of pulses and decreased the forward velocity, a combined parameter, PD , gave the mean distance at which the number of pulses emitted per meter of travel first exceeded the means for the flights. This parameter, (called pulse density by Schnitzler (1967) who used it to describe the behavioral changes demonstrated by bats in approaching barriers), is perhaps the best index of echolocative responses on the part of the bat. Since it combined both emission rate and velocity changes, it is also somewhat more dramatic in the range of values traversed between the commencement and completion of flights.

These five criteria, D_1 , D_2 , PR , V , and PD were to be computed for each bat on flights to each target position. If they proved to provide consistent patterns of behavioral responses to the targets, it would be possible to determine the approximate point of decision by the bats. If this point of decision was relatively close to the point at which the two targets gave echoes of equal overall intensity (70 cm.), a claim for the use of frequency spectra cues would be partly justified.

However, such a claim would only be possible if the second boundary condition was also satisfied: that the bat approached the targets without significant deviations from an horizontal angle. If the bat did not approach the targets in the apparent choice region in a horizontal fashion, no claim for the exclusion of intensity cues could be made.

Accordingly, all flights were also examined to see what sort of deviations from horizontal approach did occur. This was done by

constructing envelopes around side views of all flight paths to a given target and by comparing these with the known height of the targets. Several parameters were computed from these envelopes. The parameter θ_1 was the angle made by the midpoint of an envelope at the distance D_1 with the horizontal line passing through the center of the targets; the parameter θ_2 was the equivalent angle at the distance D_2 . The parameter θ_m was the maximum deviation the midpoint of an envelope made from the horizontal line passing through the targets in the region between D_1 and D_2 . The parameter D_m was the distance between bat and target where θ_m occurred. These parameters thus gave the approximate range of deviations encountered in the presumed region of choice and also the location and amplitude of the maximum deviation in this region.

Analysis of Flights by Bat T, November 7, 1967 On November 7, 1967, bat T was photographed and recorded while making 25 flights to the lucite targets, 22 of which proved to be correct choices by the bat. Of the total series, 20 flights proved to be sufficiently well recorded for analysis. Top view and side view envelopes, as well as pulse density plots are shown in Figures 4 and 5 which summarize flights to the near and far targets respectively.

It can be seen from these data that the value of D_1 , the point of initial divergence is about the same for flights to both pairs of target positions: about 125-150 cm. Similarly, the value of D_2 is consistent for the two pairs of target positions, being about 50-60 cm. The increase in pulse emission rate which is not shown in these figures was also consistently a function of the distance between the bat and the target. In general, early stages in the flights were characterized by pulse emission rates of 20-35 pulses/sec. Usually prior to passing over the barrier, this rate increased to about 35-40/sec. and then decreased to below 30 pulses/sec. again. At some point later in

the flight, the rate began a fairly monotonic increase and reached a peak of about 50-60 pulses/sec. The mean for all of the flights was about 30 pulses/sec., and using the criterion (PR), there would be two points of increase above the mean: one as the bat passed over the barrier, and the other somewhat closer to the targets. The second was taken as the appropriate value of PR. In Table VIII are listed the values of PR for bat T on this occasion for flights to each target position.

Table VIII. Summary of mean distances from targets at which bat T increased his pulse emission rate consistently over 30 pulses/sec.

<u>Target</u>	<u>No. of Flights</u>	<u>Mean Distance (PR)</u>	<u>Mean Variation of PR</u>
Near-east	4	183 cm.	\pm 51 cm.
Near-west	8	127 cm.	\pm 25 cm.
Far-east	5	132 cm.	\pm 25 cm.
Far-west	3	150 cm.	\pm 13 cm.

The velocity criterion for the flights by bat T on this occasion was satisfied only for flights to three of the target positions. On flights to the far-west position, the velocity never consistently dropped below the mean of the flight, and thus the criterion could not be satisfied. On flights to the other three positions, there was a consistent decrease in velocity towards the end of each flight, initial values being about 3 meters/sec., and final values, at about 30 cm. from the targets, being about 2 meters/sec. For the three sets of flights for which consistent decreases were noted, the values of V were between 90 and 100 cm. from the targets.

It can be seen from Figures 4 and 5 that the pulse density increased first in the vicinity of the barrier and again at some point between the barrier and the targets. The values of PD for these flights are summarized in Table IX.

Table IX. Summary of mean distances from targets at which bat T increased the pulse density consistently above the mean for all flights to a given target position.

<u>Target Location</u>	<u>No. of Flights</u>	<u>Mean Distance (PD)</u>	<u>Overall mean pulse density</u>
Near-east	4	122 cm.	13.2 pulses/m.
Near-west	8	91 cm.	14.1 pulses/m.
Far-east	5	102 cm.	13.2 pulses/m.
Far-west	3	71 cm.	13.2 pulses/m.

The side view data, which can also be seen in Figures 4 and 5, indicate that bat T tended to drop somewhat in height after passing the barrier, then flew horizontally, but below the targets until about 75-90 cm. from them, when it commenced its ascent. The values of θ_1 and θ_2 for flights to the near targets are 1° and 5° respectively, the deviation being below the targets' centers. The maximum deviation on flights to the near targets was 5° below the targets and at a target distance, D_m , equal to the end of the region of divergence, about 50 cm. Flights to the far targets indicated a 5° deviation below the targets at both D_1 and D_2 , and since this was equal to the maximum deviation in this region, no value can be ascribed to D_m for these flights.

To summarize the analysis of these flights by bat T: the earliest point of divergence of flight paths was at a distance of 125-150 cm.

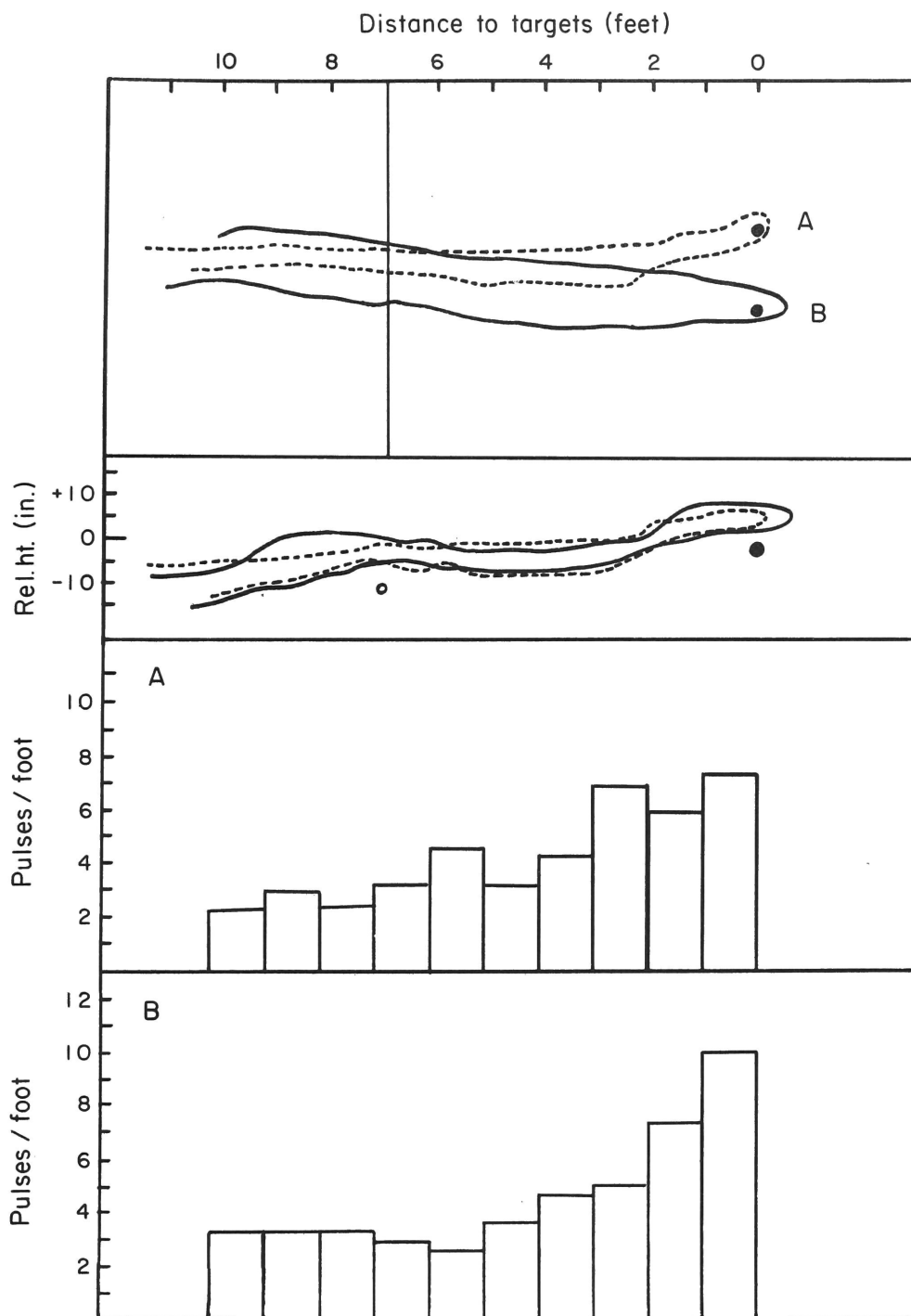


Figure 4. Summary of 12 discrimination flights by bat T on November 7, 1967 to the lucite targets at the near positions. The top figure illustrates top views of the flights, the dashed envelope indicating 8 flights to the west target position (A) and the solid envelope 4 flights to the east target position (B). The second figure shows the side view envelopes. In both figures the solid dots indicate the target positions, and the vertical line and the empty circle, the barrier. The lower two figures show the pulse density as a function of target distance for flights to the west target (A) and the east target (B).

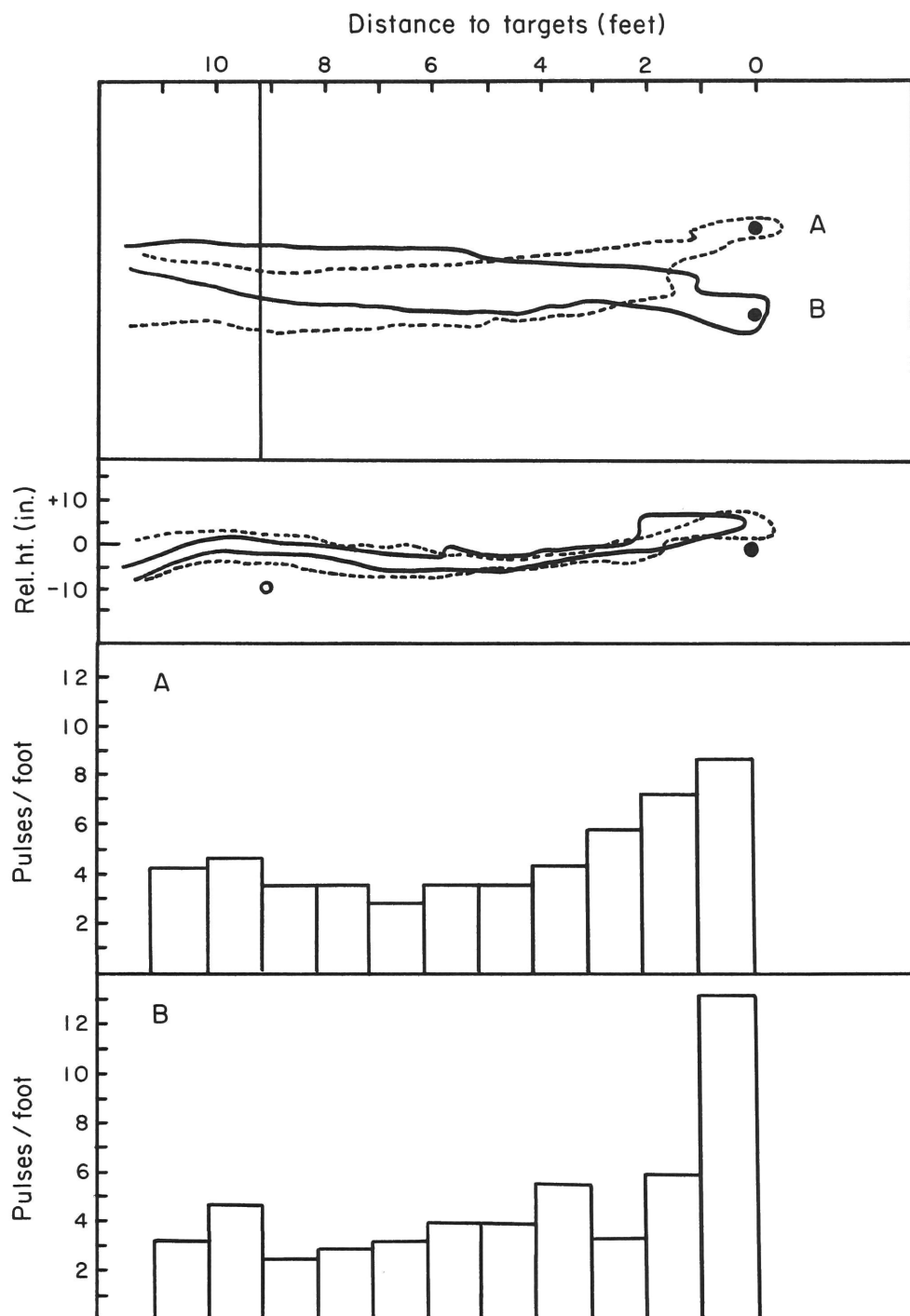


Figure 5. Summary of 8 discrimination flights by bat T on November 7, 1967 to the lucite targets at the far positions. The dashed envelopes indicate 3 flights to the west target position (A) and the solid envelopes 5 flights to the east target positions (B). Other conventions as in Figure 4.

from the targets. At this same point, the bat increased the emission rate of its echolocative pulses. At a target distance of between 70 and 120 cm., the pulse density increased above the mean for the flight, and around 90 cm. from the targets, the bat began to decrease its forward velocity. By the time the bat was 50-60 cm. from the targets, divergence was complete, and presumably choice had been effected. In the region between initial and complete divergence, the bat deviated from horizontal approach by about 5° , and that deviation was consistently below the targets.

Analysis of Flights by Bat E, November 9, 1967 On November 9, 1967, a similar series of flights by bat E was photographed and recorded. Of 25 flights, 21 involved correct choices and 20 were sufficiently well recorded to be submitted to analysis. In these flights by bat E, only the rear positions were used, 11 of the analyzed flights being made to the east position, and 9 to the west position. The top and side view envelopes and the pulse density plots are shown in Figure 6.

As with bat T, bat E showed initial divergence at a target distance of 125-150 cm. and complete divergence by around 70 cm. Pulse emission rates again averaged 25-30 pulses/sec. prior to passage of the barrier, and increased to a peak of 60-70 pulses/sec. just before landing. This rate is considerably higher than that noted for bat T and is further evidenced by the fact that bat E tended to produce more pulses during its flights than did bat T (about 60 pulses/flight for bat T vs. 80-90 pulses/flight for bat E). The average distances at which the pulse emission rate rose consistently above 30 pulses/sec. was 221 cm. \pm 13 cm. for 11 flights to the east target positions, and 229 cm. \pm 17 cm. for 9 flights to the west positions. These values are almost twice as large as the corresponding figures for bat T.

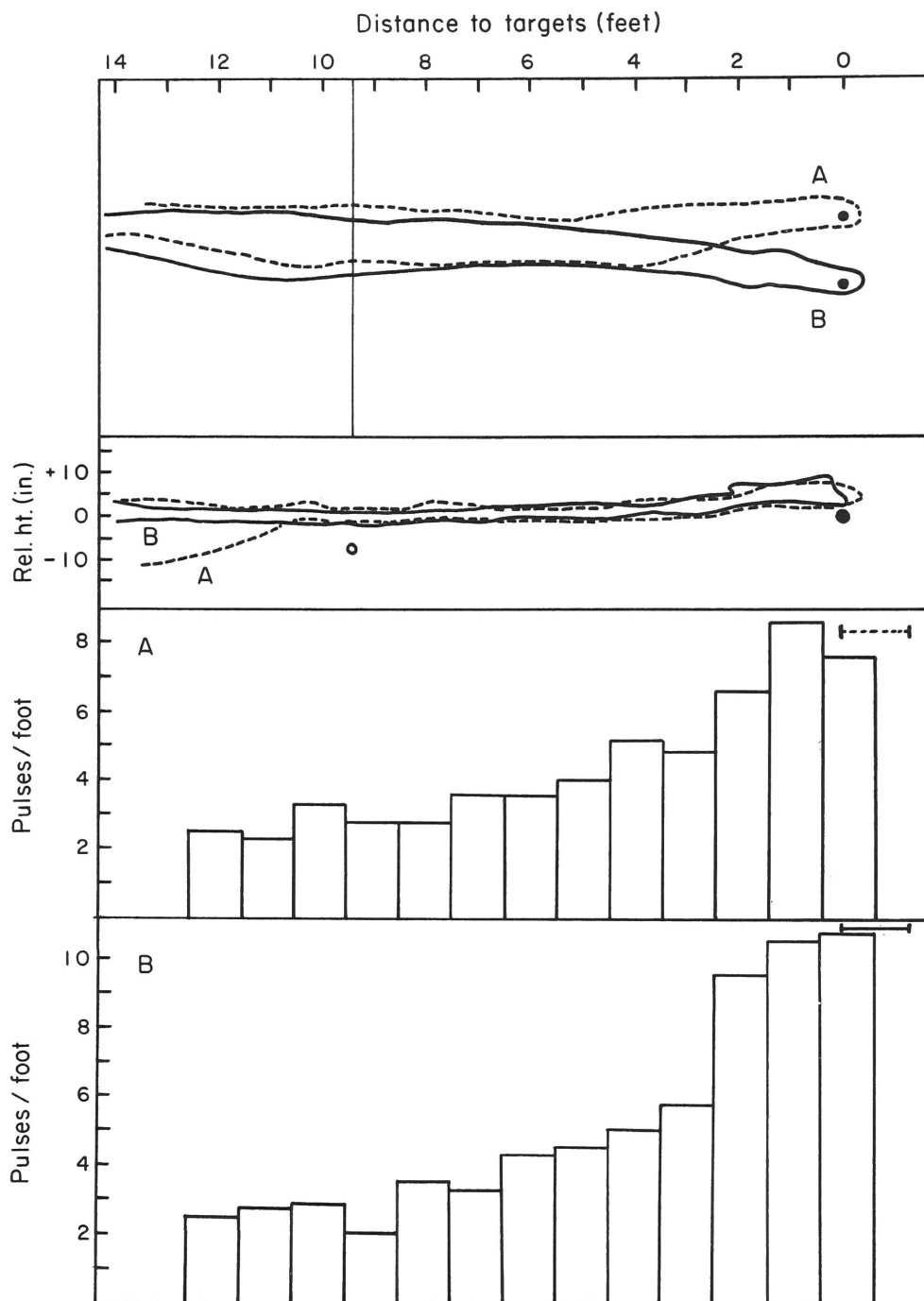


Figure 6. Summary of 20 discrimination flights by bat E on November 9, 1967 to the lucite targets at the far positions. The dashed envelopes indicate 9 flights to the west target position (A) and the solid envelope 11 flights to the east target position (B). Other conventions as in Figure 4.

Velocity data for this bat showed that the velocity remained very close to 2.7 meters/sec. for the major part of all flights. Then, at a target distance of about 100 cm., the velocity dropped suddenly to about 1.8 meters/sec. This was a consistent pattern in flights to both targets. The values of V were accordingly about 100 cm.

Pulse density plots are shown in Figure 6 for flights to each of the target positions. It can be seen that there are two phases of increase in pulse density, a gradual phase which begins about 200 cm. from the targets, and a rapid phase which begins at about 100 cm. Presumably these two phases correspond to the points of change in pulse emission rate and forward velocity respectively. The values of PD for flights by bat E are 132 cm. for flights to the east position, and 162 cm. for flights to the west target position.

Analysis of the side views of the flights indicates that bat E tended to fly higher and more horizontally than did bat T. The ascent usually began at a distance of 100 cm. from the targets and was rather gradual. The values of θ_1 for flights to both targets were 3° above the targets, and for θ_2 , 6° above the targets. Because the flights were smooth and the ascent was steady, the value of θ_m occurred at D_2 and was thus 6° above the targets.

To summarize the flights by bat E: divergence of top view envelopes began at a distance of 125-150 cm. and was complete by 70 cm. These values agree with those for bat T. The other criteria however were consistent for this animal, but differed from the corresponding values for bat T. The pulse emission rate for example, first exceeded the mean at around 220 cm. for bat E; the value for bat T was about 120-180 cm. The pulse density for bat E first

exceeded the mean at about 130 cm. from the targets, while for bat T the value was about 100 cm. Both bats were similar however in decelerating at a target distance of about 90-100 cm. Neither bat flew to the targets exactly along the line of horizontal approach, but bat E tended to fly a "flatter" flight than did bat T. The deviations for both bats were between $3-6^{\circ}$ in the region of choice, bat E tending to fly at an angle of about $3-4^{\circ}$ above the targets until it commenced ascent around 100 cm. from the targets.

The data presented above suggested that the earliest indication of choice by both bats occurred at a distance of about 150 cm. from the targets, and that choice had been made for both by about 50-60 cm. from the targets. All the other criteria, except pulse emission rates seem to provide choice distances somewhere between these two values. The fact that pulse emission rate increased prior to the region of choice might be interpreted as an initial step towards examination of the targets by the bat. In any case, it can be said that the point of equality between echoes from the two targets differed from the region of choice by a distance of 80 cm. or less. If one accepted the maximal difference, (80 cm.), the difference in echo intensities would be significant enough to warrant serious consideration of the use of intensity cues. If one accepts an intermediate value, say about 30 cm., the use of intensity cues becomes less likely. However, without direct calibrations of intensities in the choice region, this data could not exclude the use of intensity cues. Similarly, neither bat flew a completely horizontal flight path, and without calibrations of the targets at different angles of approach, it was impossible to exclude the use of intensity differences arising by these deviations. While these calibrations were being initiated, an attempt was made to add some minor improvements to the controls on the discrimination flights and to increase the size of the sampling. In the course of the latter several new results

suggested a completely different approach to the elucidation of the cues used by the bats in effecting the discriminations.

The Importance of the Supporting Thread The primary change in the conditions under which the discrimination flights were conducted was the use of a thread to support the targets which was somewhat smaller than the previously used one. Originally, a thread with a diameter of 0.35 mm. had been used to suspend the targets. Target calibrations now showed that at the frequencies used by the bats, the echo pressure from the target plus the thread was only about 4 dB greater than the echo from the thread alone. Under Rayleigh conditions ($ka < 1$), the pressure amplitude of sound scattered from a cylinder is proportional to the square of the cylinder radius. This means that utilizing the next smaller thread I had available, one with a diameter of 0.28 mm., would reduce its echo by about 4 dB. Accordingly, the targets were suspended on the smaller thread in the hope of further reducing any residual target-thread interactions.

Following this change in threads, the discrimination scores of bat E fell to the chance level, while those of bat T remained unchanged. In Table X, the scores for the two bats are given for the two days prior to the change, and the two days following the change.

Because bat E was clearly not discriminating, films and tapes were made only of the flights by bat T. These were then analyzed as above and compared with the earlier runs. In most respects, the new series, (made on November 28, 1967), confirmed the results of the previous ones. Top views of flights to the near positions indicated initial divergence at about 125 to 150 cm. from the targets, and complete divergence by about 50 cm. (See Figure 7). Flights to the rear target positions, (see Figure 8), showed somewhat later initial divergence,

Table X. Summary of scores for bats E and T for flights to the lucite targets suspended on two different diameter threads. The scores given for the 0.35 mm. thread were obtained on the two days prior to changing to the smaller size. The scores given for the 0.28 mm. thread were obtained on the two days after changing.

<u>Thread Diameter</u>	<u>Bat</u>	<u>No. Trials</u>	<u>No. Correct</u>	<u>% Correct</u>	<u>Value of p</u>
0.35 mm.	E	50	36	72	<0.005
0.35 mm.	T	50	38	76	<0.001
0.28 mm.	E	50	28	56	≈ 0.750
0.28 mm.	T	50	40	80	<0.001

($D_1 = 100$ cm.), but complete divergence was again obtained by 50 cm. Pulse emission rates first exceeded the base level of 30 pulses/sec. at distances of between 150 and 170 cm. for all target positions. On flights to the far targets, the pulse density increased above the mean at a distance of 100 cm., coinciding with a large decrease in velocity at this point. Flights to the near targets also showed a steady increase in pulse density, the means being exceeded at distances of 120 cm. and 70 cm. for flights to the east and west positions respectively. The velocity changes for these targets did not seem to be correlated with density changes.

By far the most striking change in the flights of this bat was the accentuation of the vertical dip made after passing the barrier. On flights to the near targets, the value of θ_1 was $6-8^\circ$ below the targets and θ_m was also equal to about 8° at a distance D_m of 80 to 100 cm. On flights to the far target positions, θ_1 was 11 degrees below the targets and was again equal to θ_m . These

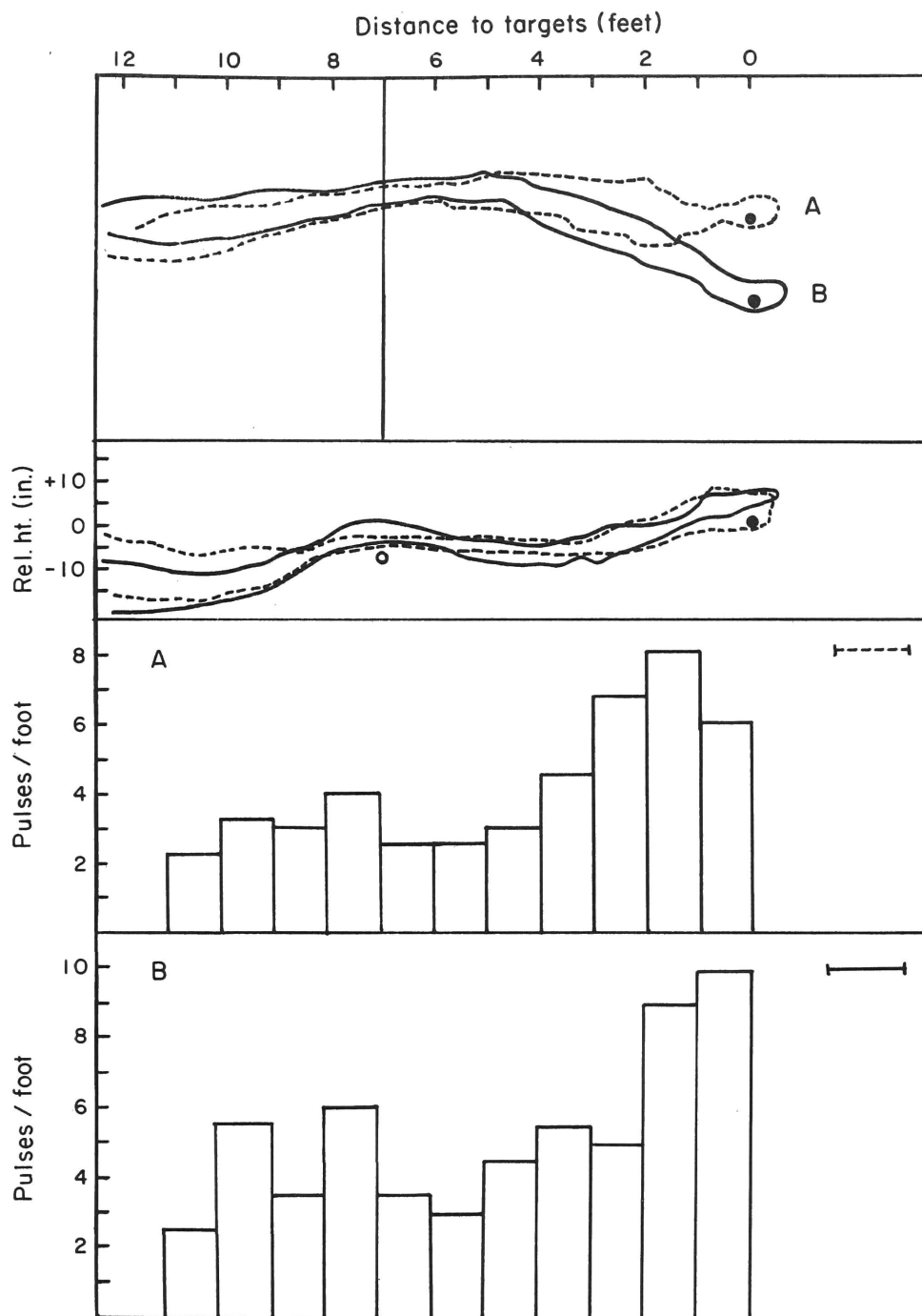


Figure 7. Summary of 9 discrimination flights by bat T on November 28, 1967 to the lucite targets at the near target positions. The dashed envelopes indicate 4 flights to the west target position (A) and the solid envelope 5 flights to the east target position (B). Other conventions as in Figure 4.

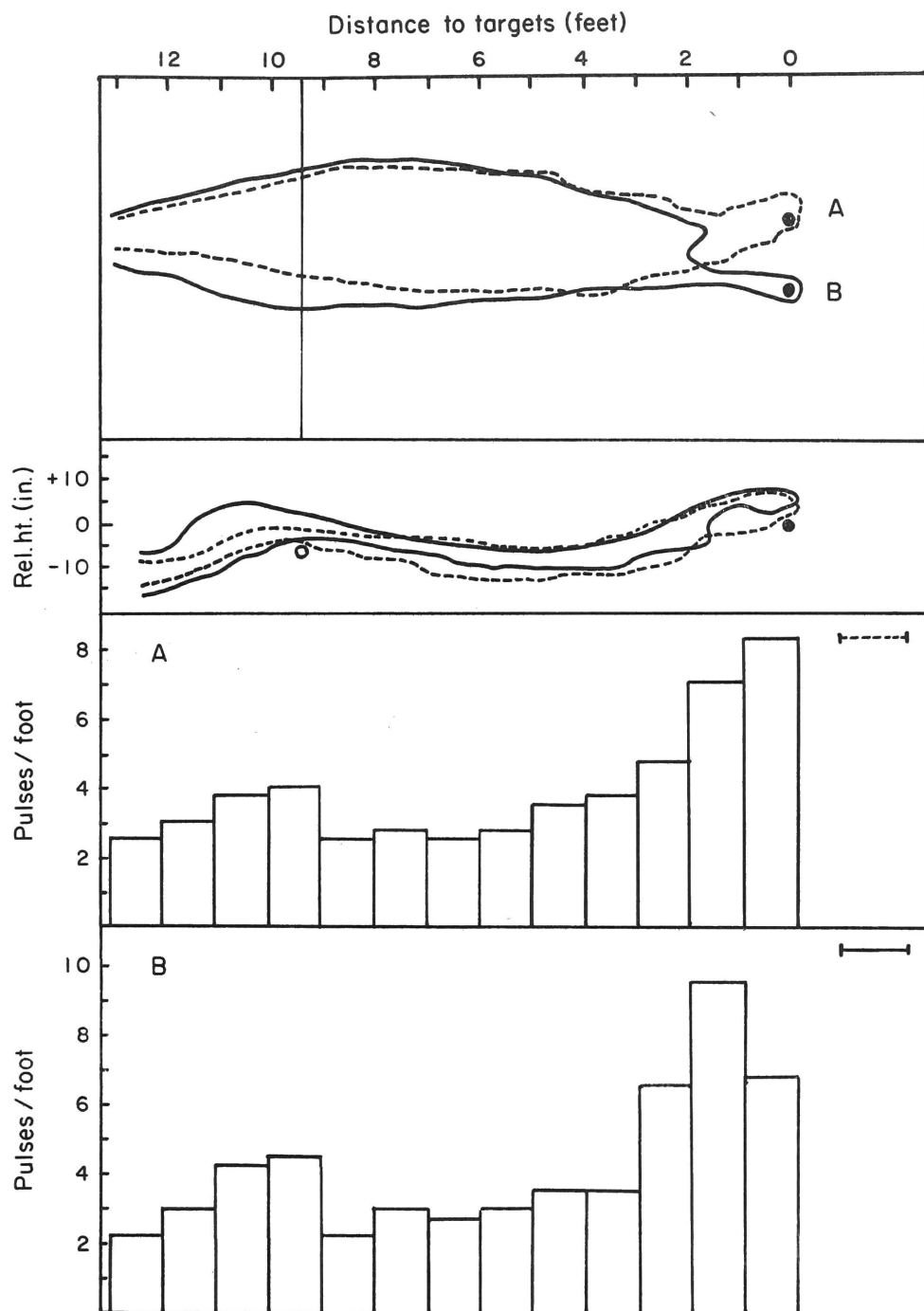


Figure 8. Summary of 15 discrimination flights by bat T on November 28, 1967 to the lucite targets at the far target positions. The dashed envelopes indicate 9 flights to the west target position (A) and the solid envelopes 6 flights to the east target position (B). Other conventions as in Figure 4.

deviations are almost twice the magnitude of the deviations in the previous flights by bat T, and again raise the need for target calibrations at incident angles other than 0° . In Tables XI and XII, the values of the various criterion parameters are tabulated for comparison.

Target Calibrations for Variable Angles of Incidence

Several questions had been raised by the preceding data that could not be answered without more extensive calibrations of the targets. Most pressing were whether the deviations from horizontal approach by either bat had resulted in large differences between the intensities of the echoes produced by the two targets. Equally puzzling was the apparent loss of discriminative powers by bat E when a smaller supporting thread was substituted for the larger one. To answer these questions, an extensive set of target calibrations was initiated utilizing the methods outlined in the previous chapter.

Target Calibrations Utilizing Constant Frequency Pulses The calibrations were begun by measuring the effects on echo spectrum of varying the angle of incidence of the emitted signals. From the outset, it was clear that the echo spectra could not be solely the result of diffractive interactions. For example, the diffractive patterns produced by a sphere are the same for all angles of incidence; the actual measurements, however, showed that at incident angles greater than 6° away from horizontal incidence, (that is, along the line perpendicular to the supporting thread and passing through the center of the sphere), no frequency dependence which could be attributed to the target was detectable. In fact, at all incident angles greater than 6° , the only frequency dependence apparent in the record was that attributable to the speaker characteristics.

Table XI. Summary of two days of analyzed flights by bat T and one day by bat E to the lucite targets. Given are the parameters, (see text for definitions), used in ascertaining the region of target discrimination. The first two days' trials involved the use of the 0.35 mm. thread; the last day's trials, the use of the 0.28 mm. thread.

<u>Bat</u>	<u>Date</u>	<u>Target Position</u>	<u>No. Flights</u>	<u>D₁</u> (all values in cm. from targets)	<u>PR</u>	<u>PD</u>	<u>V</u>	<u>D₂</u>
T	Nov. 7	Near-east	4	125-150	180	120	90	50-60
T	Nov. 7	Near-west	8	125-150	125	90	90	50-60
T	Nov. 7	Far-east	5	125-150	130	100	100	50-60
T	Nov. 7	Far-west	3	125-150	150	70	---	50-60
Average				138	146	95	93	55
E	Nov. 9	Far-east	11	125-150	218	130	100	70
E	Nov. 9	Far-west	9	125-150	225	160	100	70
Average				138	222	145	100	70
T	Nov. 28	Near-east	5	125-150	120	120	90	50
T	Nov. 28	Near-west	4	125-150	170	60	150	50
T	Nov. 28	Far-east	6	100	160	100	100	50
T	Nov. 28	Far-west	9	100	160	100	100	50
Average				119	160	95	110	50

Table XII. Summary of two days of analyzed flights by bat T and one day by bat E to the lucite targets. Given are the parameters evaluating deviations from a horizontal approach to the targets. (See text for definitions). The thread diameters are as noted in Table XI. A negative value of θ denotes a position below the centers of the targets; a positive value, one above their centers.

<u>Bat</u>	<u>Date</u>	<u>Target Position</u>	<u>No. Flights</u>	<u>θ_1</u>	<u>θ_2</u>	<u>θ_m</u>	<u>D_m (cm. from targets)</u>
T	Nov. 7	Near-east	4	-4°	-1°	-5°	120
T	Nov. 7	Near-west	8	-4°	-1°	-5°	120
T	Nov. 7	Far-east	5	-5°	-5°	-5°	50-150
T	Nov. 7	Far-west	3	-5°	-5°	-5°	50-150
E	Nov. 9	Far-east	11	$+3^\circ$	$+6^\circ$	$+6^\circ$	70
E	Nov. 9	Far-west	9	$+3^\circ$	$+6^\circ$	$+6^\circ$	70
T	Nov. 28	Near-east	5	-6°	-3°	-8°	90
T	Nov. 28	Near-west	4	-8°	$+3^\circ$	-8°	150
T	Nov. 28	Far-east	6	-11°	-3°	-11°	100
T	Nov. 28	Far-west	9	-11°	-3°	-11°	100

In addition, within the 6° range of a horizontal incident angle, small shifts in angle of only 1 or 2 degrees resulted in shifts in the location of maxima and minima along the frequency scale of as much as 10%. This again should not occur if the frequency patterns were truly diffractive effects. Examination of the prolate spheroid echoes indicated that small angular shifts resulted in changes in the location of inflections, and that outside of incident angles of about 6° no frequency dependence due to the targets was detectable. Examples of spectra for the targets on the two threads and for three angles are shown in Figure 9.

These measurements were all made with the targets placed on a length of the original 0.35 mm. diameter thread. When equivalent measurements were all made on the smaller, 0.28 mm. thread, only minimal frequency dependence was detectable at any angle of incidence. It will be remembered that the smaller thread produced echoes about 8 dB lower in pressure than did a target plus the small thread, while the comparable measurement for the larger thread was only 4 dB difference. It was also noted during measurements on the threads alone that maximal echoes were received from the threads when the latter were approximately perpendicular to the incident sound fields. At incident angles greater than $4-5^{\circ}$, no echoes were detectable from either diameter thread.

The most reasonable interpretation of these various pieces of evidence was that the thread and target echoes were not disparate enough to prevent interactions, and consequently the recorded echo spectra should be considered more as multiple scattering effects than as diffractive effects. This interpretation would account for both the loss of frequency dependence at angles oblique to the thread axis and the shifts in location of inflections when the incident angle was moved only a few degrees. It will also account for the much smaller degree of frequency dependence, (maximum to minimum variations in intensity of only 1-2 dB), observed with the 0.28 thread.

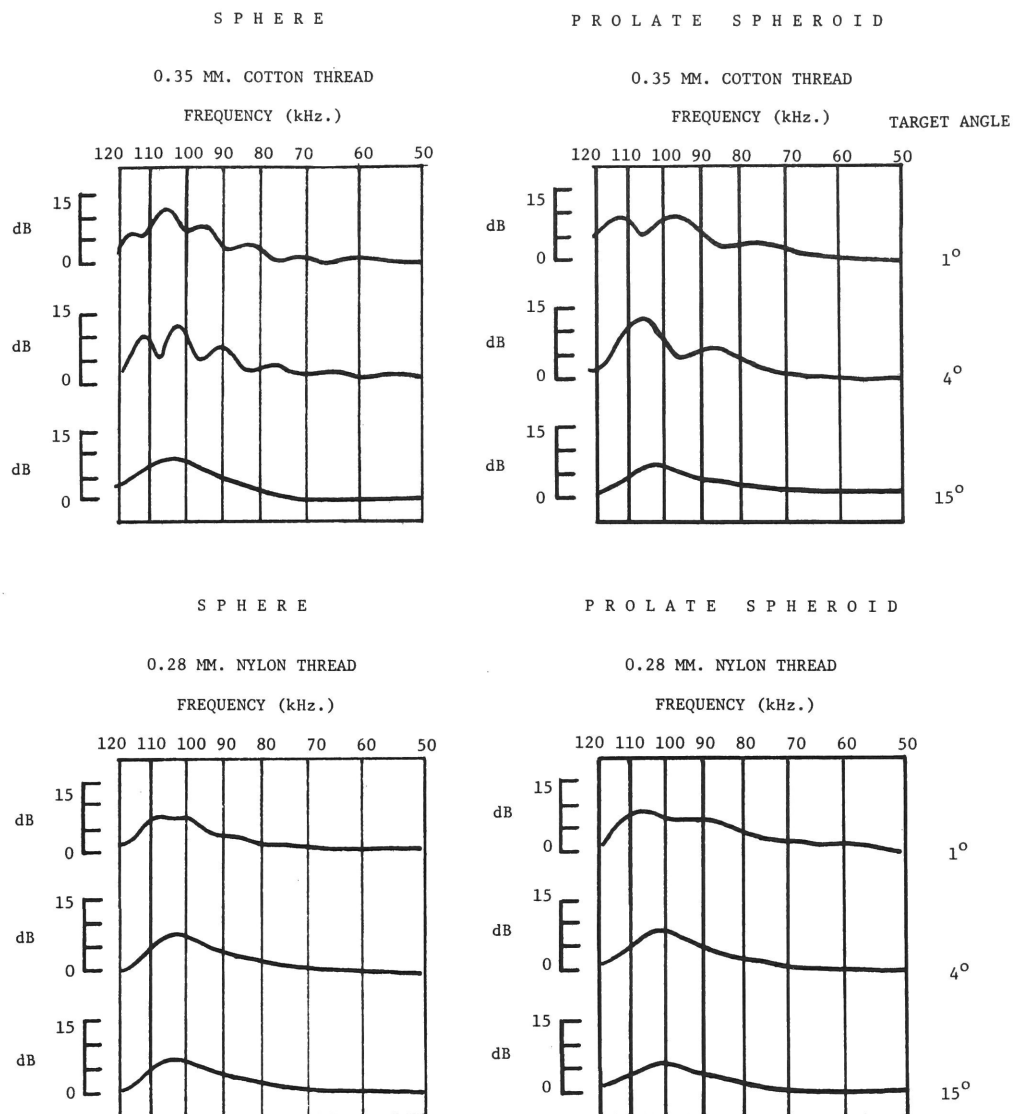


Figure 9. Frequency spectra of the echoes from the lucite targets on two diameters of thread and at three different incident angles. A target angle of 0° is one at which the axis of target and thread is perpendicular to the incident sound field.

(The corresponding values for the 0.35 mm. thread were 6-8 dB). The lack of any detectable frequency dependence at angles outside of those with thread interactions implies that any diffractive contributions due to the sphere alone were too small to be detected on the equipment. This was not totally unexpected on theoretical grounds.

Since the effects of thread echoes could not be avoided, some prior assumptions about calibration conditions became questionable. For example, in previous calibrations, the thread was stretched horizontally and the target strung upon it. This situation differed from the one encountered by the bats in that there were segments of thread on both sides of the target during calibrations, but on only one side for discriminations by the bats. Accordingly, comparisons were made of the frequency patterns generated by threads and targets with first, thread on both sides, and then secondly, thread on one side, and 0.15 mm. nichrome wire on the other. The latter had been examined alone and found to produce no detectable echoes at any angle with the present apparatus.

These measurements indicated that for a given angle of incidence, and for a given target, the location along the frequency scale of maxima and minima was independent of thread size. However, the amplitude of these inflections was directly related to the diameter of the threads. The presence of a large diameter thread on one side of the targets, but a smaller diameter one on the other did not affect the location of the inflections; however, at incident angles near 0° , it did reduce their amplitude by 2-3 dB. Thus the previous measurements using threads on both sides of the targets were good qualitative, though not perhaps good quantitative measures of the frequency dependent effects.

In spite of the nature of the frequency dependence of the echoes from the two targets, the original prediction that the sphere would

produce more maxima and minima in any given range of frequencies than the prolate spheroid was completely confirmed. In fact, the distance between successive maxima for the sphere was about 10-11 kHz, and for the prolate spheroid, about 20 kHz. Since this suggested that either the size or shapes of the targets might affect the spacing of inflections in the frequency spectra of the echoes, a series of measurements were made on four spheres of different sizes. These calibrations confirmed the previous results in regard to the importance of incident angle on the amplitude of the frequency dependence: only at angles of 6° or less was any target-specific frequency pattern detectable. The apparent effects of increasing target size were a decrease in the spacing between inflections and also a decrease in the amplitude of the inflections. The latter effect is similar to the reductions at oblique thread orientations: any change which reduces the amplitude of the thread echo or increases that of the target will reduce the interactions between them. The former effect is predictable, but does suggest that the smaller size of the prolate spheroid alone might have resulted in a greater spacing between inflections.

A final calibration must be noted. When it was clear that both thread and target echoes were important in producing the frequency dependent patterns, the loss of discriminative powers by bat E (the level flier), after changing to smaller threads assumed major importance. However, it was still necessary to know at what angles significant reductions in overall echo intensity from the prolate spheroid occurred. The appropriate measurements were made on both sizes of threads and the overall intensities computed by measuring the areas under the frequency spectra curves. These data indicated that the two targets produced echoes which were within 10-15% of each other for all angles between 0° and about 6° . At greater angles, the prolate spheroid echo was lower in overall intensity, the ratio of

the amplitudes of the two targets at an angle of 10° being about 2:1.

The critical angle was therefore about 6° relative to the mid-points of the targets: at approach angles greater than this, there was no detectable frequency dependence of the echoes, but the sphere echo was greater in overall intensity than the prolate spheroid echo. At smaller angles, the differences in overall intensity were small, both targets produced frequency dependent echoes, and the patterns of frequency dependence were different for the two targets.

Calibrations of Targets using FM Pulses A final consideration had to be made regarding the differences between the constant frequency pulses used in calibrating the targets and the FM pulses used by the bats. Perhaps the different waveform of the latter gives a different kind of echo spectrum -- what if, for example, the duration of any single frequency component in an FM sweep is too short for any detectable interference patterns to be established? To check this possibility, two flights were selected from those of bat E on November 9, 1967. These two flights were selected because they were almost identical in flight paths, in the structure of the pulses emitted, and in the fact that they were correct choices. The pulses from these flights were then broadcast at the targets, and the echoes recorded as outlined in the previous chapter. The echoes made by the first flight were made with the targets at an incident angle* of 4° relative to the sound field; those generated by the second flight were made with the targets at 15° to the incident sound field. The original pulses, the broadcast pulses, and the echoes from each target were then analyzed on the contour plotter equipment of a Kay sound spectrograph as described in the previous chapter.

* See page 106.

The results of these calibrations are shown in Figures 10 and 11. In the first two columns of each figure are shown the original pulses and the broadcast versions of them. It is clear that while there is a tendency for the lower frequencies to be somewhat reduced in intensity, there are no other major changes introduced by the process of recording, rebroadcasting, and transmission through the atmosphere. In Figure 10 the echoes from the two targets at an incident angle of 4° are displayed. One can see at the outset that the two sweeps composing the echo from the sphere tend to be "segmented" into several pieces. Presumably the center of each "segment" corresponds to one of the maxima in the frequency spectrum as measured by constant frequency pulses; in fact, the frequency interval between segments is just about that expected (10-11 kHz), and the location along the frequency axis of the segments is also about that expected on the basis of the earlier calibrations. The latter is somewhat harder to evaluate however, since the exact point in a segment of peak intensity may be due to either a maximum in the frequency dependent pattern of the echo, or to a maximum in the amplitude of the emitted pulse. However, the location of maxima is within 5% of the values expected from the constant frequency calibrations.

The corresponding echo patterns for the prolate spheroid are also as expected: there is less "segmentation", the spacing between segments is greater, and the approximate locations of maxima agree with the constant frequency calibrations.

The echoes from the targets at an incident angle of 15° again confirm the predictions: in this case the echoes from the two targets should not differ significantly from each other or from the emitted signals in the distribution of amplitude over frequency. This is indeed seen to be the case (see Figure 11).

Figures 10 and 11. Contour spectrograms of original pulses and the evoked echoes from the lucite targets on the 0.35 mm. diameter thread. In each spectrogram, time goes from left to right on the horizontal axis, the total duration represented in any one spectrogram being 1.8 msec. The vertical axis of each spectrogram represents frequency, the lower margin a frequency of 54 kHz., and the upper margin, 114 kHz. The contour lines represent 6 dB. steps in signal intensity. In each figure, the first column gives the original pulses as recorded from the bat in flight. The second column shows the pulses after having been rebroadcast and transmitted through 140 cm. of air. The third column shows the sphere echoes and the fourth column the prolate spheroid echoes. The echoes shown in Figure 10 were recorded with the targets and supporting strings at a 4° angle relative to the incident sound field; those in Figure 11 at an angle of 15° . In Figure 10, the first two pulses are type I pulses and were emitted prior to the region of choice. The third pulse, a type II pulse, was emitted just prior to the region of choice. The last three are all type III pulses emitted within the region of choice. In Figure 11, the first two pulses were type I pulses emitted prior to the choice region, the second two type III pulses emitted within that region, and the fifth a type V pulse emitted after the region of choice. In Figure 10, differences between echoes, or between echoes and generating pulses are indicated with arrows.

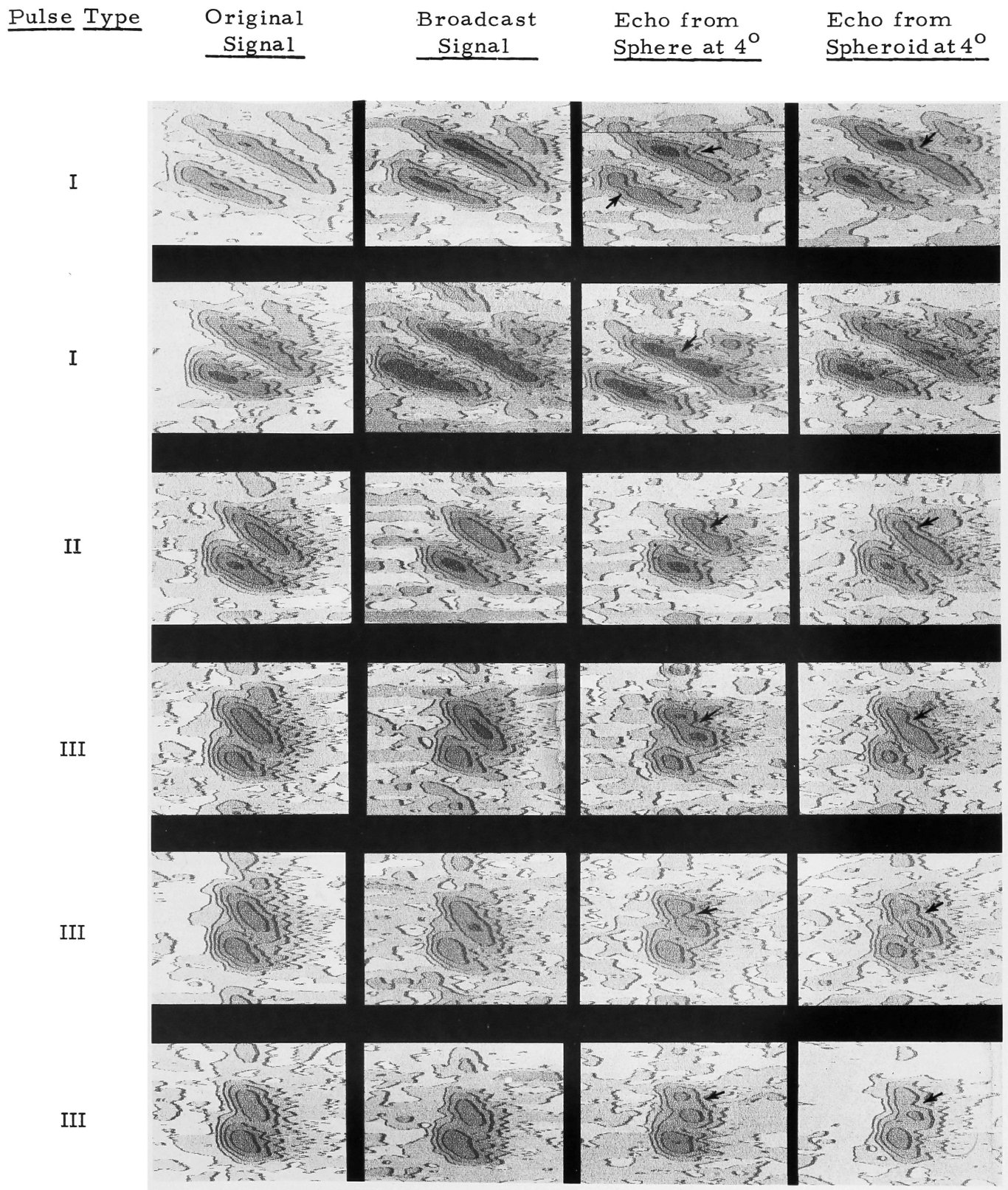


Figure 10

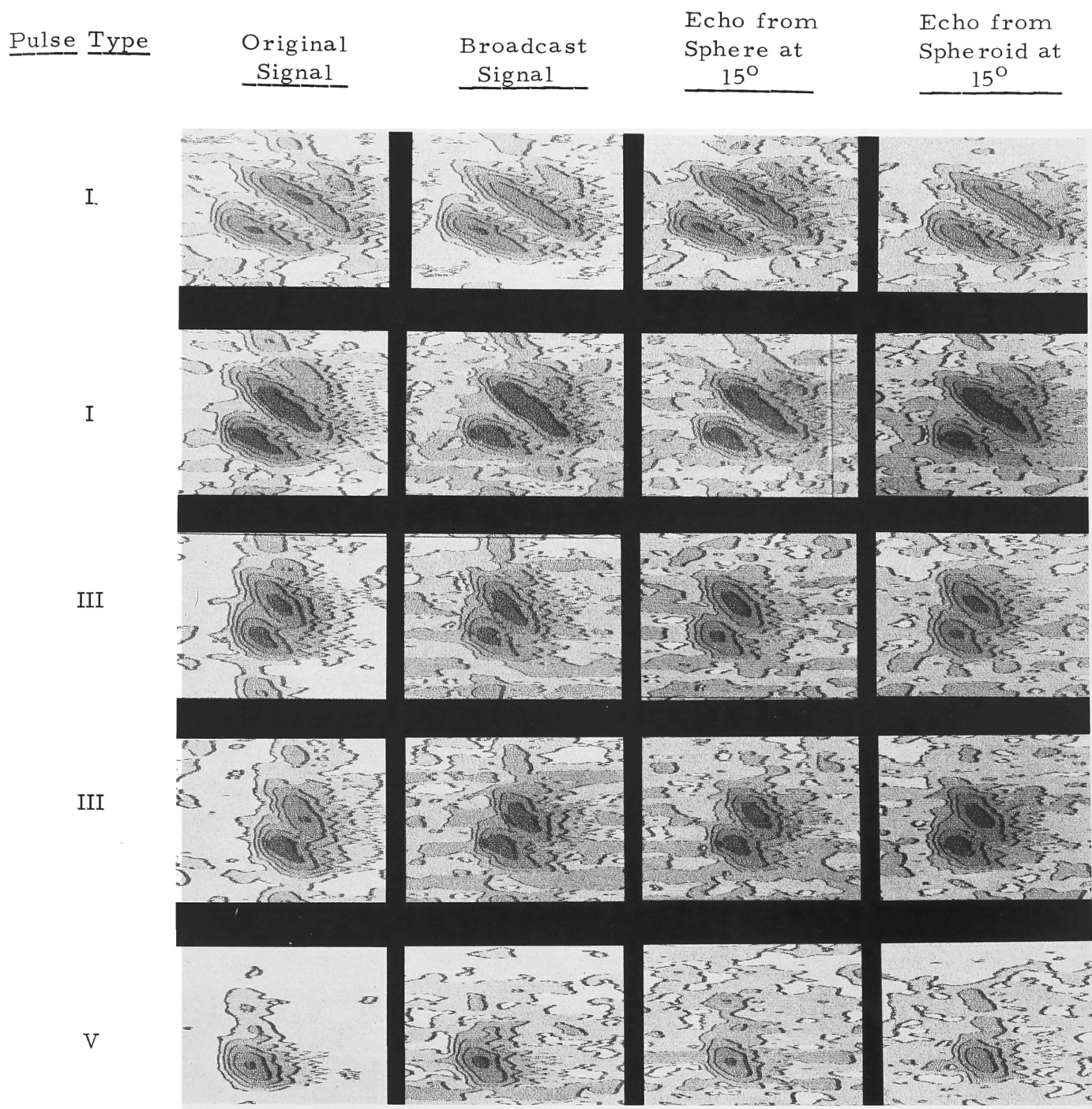


Figure 11

A Final Set of Discrimination Flights

The demonstration that the frequency dependence of the targets could be eliminated by either using smaller threads or by allowing the bats to use approach angles greater than 6° suggested that the loss of discriminative powers by the level-flying bat E might be restored by returning to the large threads. Accordingly, a series of flights was initiated in which the size of the supporting threads was changed every five flights. To increase the amplitude of the effect, the targets were suspended so that there were segments of thread on both sides of the targets. The calibrations had shown that this did not affect the number or placement of frequency pattern inflections, but did increase their amplitudes by 2-3 dB. The thread below the targets was tied to a weight and allowed to just brush the floor of the flight room. Other than the switching between the 0.35 mm. and the 0.28 mm. threads every five trials, all other controls were unchanged.

Three days flights by bat E on this schedule completely verified the predictions: of 53 flights to the targets on the 0.35 mm. threads, it scored 89% correct; out of 53 flights to the targets on the 0.28 mm. threads, it scored only 51%. Observations with infra-red viewing gear indicated that this series of flights was characterized by the same nearly horizontal angle of approach that was noted on the flights of previous series.

Conclusions Regarding the Mechanisms of Target Discrimination

The flight analyses for the discriminations by bats E and T could now be summarized as follows:

1. Both bats apparently detected and selected one of the two targets at a distance of between 150 and 50 cm. All the criteria, (divergence of

flight paths, changes in pulse emission rates, changes in pulse density, and changes in velocity), suggested this area as the region of choice.

2. Target calibrations showed that frequency dependent patterns depended upon characteristics of both the targets and the supporting threads; most importantly, the larger diameter thread and the targets produced echoes which were detectably frequency dependent, while the smaller thread and the targets did not. In addition, approach angles greater than 6° from the horizontal were found not to produce frequency independent echoes, but ones in which the prolate spheroid echo was much lower in amplitude than the sphere echo. Approach angles of less than 6° produced frequency dependent patterns that were characteristic of each target, but the overall intensities of the resulting echoes from the two targets did not differ by more than 10-15%.

3. Flight data showed that bat T approached the targets at angles as large as 11 degrees away from the "preferred" horizontal approach, and that his discriminative powers were not affected by using smaller diameter threads. Bat E on the other hand approached the targets at angles of 2-4 degrees in the region of choice and his discriminative success was contingent upon the use of the larger threads.

The most parsimonious interpretation of these results was that bat E had used the frequency dependence of the echoes to effect the discriminations, while bat T had used the overall intensity cues. As additional evidence it should be reiterated that alternative explanations had been made unlikely by the numerous controls. For example, the use of visual and olfactory cues was quite unlikely considering the success of discrimination in darkness and with cleaned targets. Similarly, since the ratio of dimensions between the pulses and the

targets was about 10:1, the use of cues such as prolongation of durations (see Introduction) was also improbable. However, several alternative mechanisms could have played a role in the discriminations, and these should be carefully considered. Without measurement of the emitted beams of sound it is impossible to exclude narrow beam scanning of target shapes. However, to be useful to the bat at these apparent distances of choice, the beam angle would have to be at most 2° . This is a very low figure (Cf. Möhres, 1953; Griffin, 1958). A second alternative is the use of phase information. As noted in the Introduction, all of the mechanisms which produce frequency dependent echo patterns also produce frequency dependent phase shifts. If the bat could utilize these cues, they would provide considerable information. However, without an actual demonstration of the use of phase information, its importance for discrimination cannot be ascertained. The final alternative which the bat might have used is the information provided by differential attenuation rates. Clearly, since decisions were sometimes made before the bat reached the point of target echo equality (about 70 cm.), the potential use of this information cannot be excluded. However, the fact that changing to smaller threads would not affect these rates, but did affect the performance of bat E suggests that he was not using this information. Similarly, the accentuated gymnastics executed by bat T in approaching the targets on the smaller threads should not have been necessary if the bat were using attenuation rate information. It therefore seems most reasonable to assume that the bats did not use either differential attenuation rates, or for that matter, the intensity differences generated by differential geometric attenuations.

THE STRUCTURE OF THE PULSES USED IN DISCRIMINATION FLIGHTS

The previous chapter indicated that bats of the species, Vampyrum spectrum, were capable of making discriminations between similar targets using echolocative parameters, and of effecting such discriminations at target distances of between 50 and 150 cm. In view of the early indications that different kinds of pulses might be used in different situations, and even that different kinds of pulses might be used at successive stages in a single flight, a detailed analysis of the pulses used by bats E and T on discrimination flights was undertaken. The methods utilized have been outlined in the second chapter and were previously applied in the analysis of pulses emitted on the first series of discriminations of artificial targets (see pp. 73 - 79). In all, every pulse emitted on five correct flights by bat E (the level flier) and four correct flights by bat T (the low-dipping flier), were photographed and analyzed spectrographically. From these data, several general patterns of pulse structure emerged.

Distributions of Pulse Types along Flight Paths

In general, the changes in pulse structure as the targets were approached were quite similar to those described for the earlier series: increasing proximity resulted in decreasing pulse duration and towards the end of the flight, a decreasing range of component frequencies. In addition, it is clear that the same general pulse structures, outlined on pages 73-79, can be used to classify the pulses used in these final discriminations. An advantage of the present data over the former series is the exact knowledge of

where in the flight each pulse was emitted. This immediately facilitates the characterization of those pulses emitted in the apparent region of choice and allows some evaluation of possible artifacts contributing to the variations in pulse structure. These variations were divided into five general categories in the previous chapter: type I pulses being long duration, amplitude modulated pulses with variable overlap between the two or sometimes three component sweeps; type II pulses were shorter, with a single amplitude peak, and with the lower sweep preceding the higher one by about $\frac{1}{2}$ the duration of the pulse; type III pulses were still shorter, and typified by complete temporal overlap of the two component sweeps; type IV pulses were composed of two single and successive sweeps; a type V pulse was simply a single short sweep. Examples of the waveforms and spectrograms of each type may be seen in Figure 3 , (p. 77).

The distributions of pulses among these types in the analyzed flights of bats E and T are summarized in Table XIII. This table gives the numbers and frequency of each type of pulse depending on whether they were emitted prior to entering the region of choice (a target distance of 150 cm. or greater), within the region of choice (150-50 cm.), or after leaving the region of choice (50 cm. or less). The figures given for each type are the total number of pulses emitted by a given bat in a given region.

For the five flights by bat E, (the level flier), which were analyzed, the most common type of pulse in the pre-choice region was type II, that in the choice region, type III, and in the final region, type V. In general, this bat seemed to produce "strings" of each type of pulse, so it was possible to ask at what distances each type shifted to the next. On all five flights, type I pulses began the flight and persisted until about 250 ± 15 cm. from the targets. Then the bat produced medium duration type II pulses

Table XIII. Summary of pulse type distributions for correct discrimination flights by bats E and T to the lucite targets in the presence of the barrier.

<u>Bat</u>	<u>No. Flights</u>	<u>Pulse Type</u>	Pre-choice region (up to 150 cm.)		Choice region (150-50 cm.)		Post-choice region (less than 50 cm.)	
			<u>Pulses</u>	<u>%</u>	<u>Pulses</u>	<u>%</u>	<u>Pulses</u>	<u>%</u>
E	5	I	22	29	0	0	0	0
		II	36	47	30	27	3	16
		III	18	24	53	48	2	11
		IV	0	0	0	0	0	0
		V	0	0	27	25	14	73
	Totals		76	100	110	100	19	100
T	4	I	29	66	0	0	0	0
		II	12	27	35	59	3	10
		III	3	7	9	15	5	17
		IV	0	0	7	12	2	6
		V	0	0	8	14	20	67
	Totals		44	100	59	100	30	100

until about 180 ± 10 cm. from the targets. At this point, a string of type III pulses invariably commenced and persisted until a target distance of 100 ± 8 cm. was attained. The pulses then shifted to pulses similar to type II pulses in structure, but much shorter in duration (about 0.5 msec.). At a distance of 80-90 cm., a run of type V pulses began and lasted until the end of the flight. An example of a single flight by this bat, indicating the structure of sample pulses and the points where they were emitted can be seen in Figure 12.

The distributions in pulse type were somewhat different for flights by the low-dipping bat T. Of the four flights analyzed, the most common type of pulse in the prechoice region was the type I pulse, in the choice region, the type II pulse, and in the post-choice region, the type V pulse. Type III pulses, which predominated in the choice region for bat E were rare and randomly distributed for bat T. (It will be remembered that type III pulses were also rare on the discrimination flights made by bat E to the rubber ball and the wooden sausage. See pp. 73-79). Since bat T showed no clear cut patterns of change in the region of choice, it is impossible to give distances for points of change in pulse structure. On the average however, this bat continued making type I pulses until considerably closer to the targets than did bat E: 180 ± 20 cm. vs. a mean of 250 cm. for the latter. This bat also produced a substantial number of type IV pulses in the region of choice, a type never seen in the flights by bat E. Both bats terminated their flights with type V pulses, bat T initiating this phase at a target distance of about 60 ± 20 cm. To summarize, while there were similarities in the pulse structures used by the two bats at the initial and terminal parts of the flights, there were distinct differences in which pulses were emitted in the region of choice. To these differences should be added the facts noted in the previous

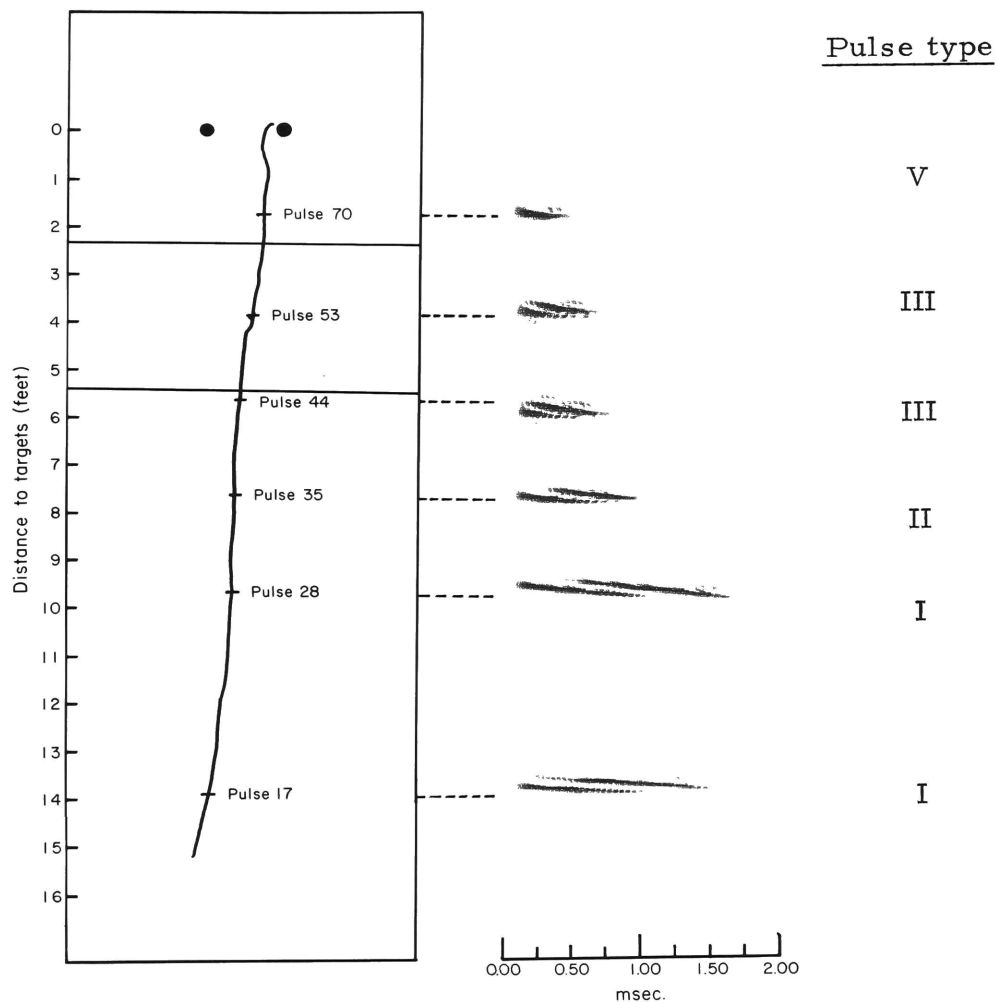


Figure 12. The spectrographic structure and point of emission of selected pulses emitted by bat E on a flight to the lucite targets at the far target positions. The two solid circles indicate the locations of the targets. Horizontal lines at 2.3 and 5.4 feet respectively from the targets contain within them the region of choice. The sample pulses shown are classified according to type. The definitions of the pulse types can be found on pages 73-76 and Figure 3, page 77 .

chapter: that in general, bat E approached the targets in a much more level manner than did bat T, that it increased its pulse emission rate sooner, that it produced pulse emission rates that were 20-30% higher than those of bat T, and consequently emitted about 30% more pulses on each flight than did bat T.

Possible Artifactual Contributions to Shifts in Pulse Structure

In the analysis of earlier discrimination flights, it had proved impossible to determine whether the observed changes in pulse structure might not be artifacts of the recording situation. The present situation, however, made it possible to eliminate most of the possible sources of artifact. In particular, there seemed to be three primary ways in which these artifacts might have occurred. Atmospheric attenuation of the emitted signals in a frequency dependent fashion could well have contributed by eliminating the higher frequencies from the records. A second type of artifact might occur if the bat flew outside of the directional optimum of the recording microphone. A third type of artifact might arise from the directional properties of the bat's emitting apparatus.

While it is very difficult to evaluate the possible contributions of these various artifacts, some comments are justified. The importance of atmospheric attenuation, for example, can be calculated from a knowledge of the conditions under which the flights were made and of the frequencies emitted by the bats. Using the data provided by Kneser (1965) and Pöhlmann (1959), a 100 kHz signal emitted under conditions of 60% relative humidity and an ambient temperature of 25.5°C. should attenuate at the rate of 2.5 dB/meter travelled. The equivalent figure for a 60 kHz signal is 1.3 dB/meter travelled. Atmospheric effects alone will of course not provide a

complete description of the attenuation imposed on these signals; as noted in previous discussions, the bat is probably a source of spherical waves and these will attenuate with increasing distance due to geometrical expansion of the waves. However, the geometrical attenuation will be equal for all frequencies.

Both of these sources of attenuation could have altered the apparent structure of the pulses. Clearly, if the atmospheric effects attenuated the higher frequencies more than the lower ones, the latter might arrive at the microphone at intensities too low to produce a mark on the spectrograms, while the former would still be recorded. This would give the impression of a later onset by the higher frequency sweep. Similarly, if the emitted signals initially contained a lower sweep of greater intensity than the upper one, an overall attenuation that was not frequency dependent, such as the geometrical effects, might reduce the amplitude of the upper sweep to a level below the minimum detectable by the instrument while still recording the lower sweep. This would again result in an apparent delay of onset of the higher frequency sweep.

Consider the distances at which bat E (the level flier), typically changed from one type of pulse to another. At a target distance of 250 cm., this bat usually switched from type I pulses to type II pulses. This particular shift was characterized by a decrease in pulse duration and a loss of multiple amplitude modulations. It is very unlikely that either atmospheric or geometric attenuations could account for this shift.

At a target distance of 180 cm., the bat ceased using the type II pulses and commenced type III pulses. This shift was characterized primarily by an earlier onset of the upper frequency sweep relative to the lower one, and consequently a greater degree of overlap. At a target distance of 250 cm. (and a microphone to bat

distance of 331 cm.), the losses due to geometrical expansion are 2.1 dB greater than if the same signal were emitted at a target distance of 180 cm. (a microphone distance of 261 cm.). In addition, the atmospheric attenuation for a 100 kHz signal emitted at a target distance of 250 cm. is 1.8 dB greater than when the same signal is emitted at a target distance of 180 cm.; the equivalent figure for a signal of 60 kHz is 0.9 dB. Therefore, the theoretical prediction for the total attenuation of a 100 kHz signal emitted at a target distance of 250 cm. is 3.9 dB more than the attenuation of the same signal emitted at a target distance of 180 cm.; the corresponding attenuation difference for a 60 kHz component is 3.0 dB.

It can be shown that these differences are small compared to the variations necessary to produce detectable changes on the spectrograms. For example, in preparing the spectrograms used in this study, the peak amplitudes of the input signals were adjusted to be within 2dB of each other. This adjustment was intended to compensate for the fact that pulses emitted at greater distances would be attenuated to a greater extent than would those emitted at nearer distances. As noted below, because the bat itself varied the amplitude of the emitted pulses, this adjustment was in most cases minimal. Under these conditions, it was found that all components within 6 dB of the peak amplitude would be faithfully recorded on the spectrograms without altering their apparent temporal patterning. Components which were more than 6 dB lower in amplitude were not always faithfully reproduced, and apparent shifts in patterning could result. Thus, since the overall amplitudes were adjusted to a constant level, the primary source of artifact was the frequency dependent attenuation of some components below the 6 dB threshold.

In the example just discussed, it was predicted that a 100 kHz

signal emitted near the point of initial emission of type II pulses would be 3.9 dB lower in amplitude than if emitted near the point of initial emission of type III pulses. The corresponding figure for a 60 kHz signal was 3.0 dB. The observed difference in amplitude between the two frequencies is only 0.9 dB, which is certainly less than the 6 dB threshold. This shift in pulse structure thus does not seem to be the result of differential attenuation of the pulses.

A similar consideration can be made concerning the shift between type III and the short duration type II pulses. A 100 kHz signal emitted at the point of initial type III pulse emission would be received at the microphone 5.2 dB lower in amplitude than if emitted at the point of commencement of short type II pulses. The value for a 60 kHz signal is 4.2 dB. The difference between the two is just 1.0 dB, a figure too small to account for the observed shifts in pulse structure. The final change to type V pulses occurred over such a short distance, that the possibilities of attenuative artifacts are even less likely than for the preceding cases.

Another factor which affected the generation of artifacts was the amplitude at which the pulses were emitted. On any flight, one expects the initial pulses to be lower in amplitude at the microphone than those emitted prior to landing. For example, the difference in amplitude between pulses emitted at a target distance of 250 cm., where type II pulses were begun, and those emitted at 90 cm., where type V pulses commenced, would be between 8 and 10 dB. The actual tape recordings showed, however, that the amplitudes of the recorded pulses were very constant throughout the flight, the maximum variations being only 3-4 dB and these being distributed rather randomly with respect to the distance between bat and microphone. This fact suggests that the bats were emitting louder pulses at the beginning of the flight and fainter ones later. Whatever value

this had for the bat, it resulted in a reduced probability that changes in pulse structure were artifacts generated by differences in overall signals at the microphone.

A final argument against attenuative artifacts as the agents producing the pulse structure shifts is the rapidity with which many of the shifts were made. In most cases, bat E switched from one type of pulse to the other with the emission of only 4 or 5 pulses. This corresponds to a time interval of about 50-100 msec., and a total distance travelled of 10-20 cm. This is a relatively minor change in position, and consequently the changes in attenuation are even less than those discussed above.

The possibility that the shifts in pulse structure were results of the bat being outside the directional optimum of the microphone was investigated by measuring angular dependence of the microphone amplitude and frequency response. The methods for these calibrations were described in the second chapter. In short, the calibrations indicated that for all positions within $10-12^{\circ}$ of the microphone axis, the fidelity of the recording was within 2-3 dB of the emitted signal. Outside of this angle, signals were received as if of lower amplitude, and the reductions were frequency dependent. Examination of the flights by bat E which had been analyzed indicated that up to the last 30 cm. of the flight, all pulses were emitted within the optimal range of the microphone. The observed changes did not therefore seem to be artifacts due to microphone directional patterns.

The final source of artifact, the directional properties of the bat's emitting organs, cannot be adequately evaluated without better measurements. During the flights when two microphones were used, there was an indication that some of the terminal pulses were received at one microphone and not the other. Whenever this occurred, it was

possible to compute the angles between each microphone and the apparent trajectory of the bat at those points. These measurements, though only involving two flights by one bat, indicated that a microphone located at an angle of 30° or more away from the apparent axis of the bat would probably not record the emitted pulses, or if it did, only those frequency components below 90 kHz. These measurements however were crude and could not be used as any quantitative measure of the bat's beam. In spite of these reservations, the similarity of both waveforms and spectrographs of pulses received at the two microphones, (at least through the region of choice), argues against the artifactual generation of shifts in pulse structure. For shifts after the region of choice, effects of the directionality of the bat's emitting organs cannot be excluded.

Relationships Between Spectrographic Analyses of Pulses and Actual Waveforms

In the previous discussions, attention has been focused primarily on the amplitude and frequency characteristics of the emitted signals. In principle, a third parameter, the phase relations between components, might play a very important role in the actual waveforms of the pulses. Since it is impossible to exclude the use of phase by the bats, a complete description of the pulses should include some comments on the importance of phase.

Examination of the waveforms of emitted pulses indicated that pulses of any given type were quite similar in their overall waveforms. In those pulses where the degree of overlap between the two sweeps was small, the waveforms tended to be rather "uniform" in appearance. This "uniformity" was generated by the fact that the individual peaks of the waves were fairly constant in height. In those regions of the pulse where both sweeps were present, successive peaks

were not constant in amplitude: in some cases there were two classes of peak heights, each occurring every other wave; in other cases there were as many as four different peak heights, repeating in regular, but complicated cycles during the course of the pulse. These multi-peak waveforms thus appeared as very "jagged" envelopes, and on compressed time scales, each peak height class formed an apparent horizontal "line" in the waveform (see Figures 3, 13, and 14 for examples). How much of this variation was due to the relative amplitudes of the two components and how much to phase variations?

To help answer this question, two pure sinusoids were mixed electrically and the resulting waveforms examined on an oscilloscope. To provide an approximate model of a bat's pulse, the sinusoids used had frequencies of 72 and 96 kHz respectively. The relative amplitudes of these two signals were adjusted to various ratios, and the overall result was then reduced to a constant value. Photographs were taken of short segments of each resulting waveform without any particular attention being paid to which segment. This was justifiable since in most cases, the resulting waveforms repeated after a given number of cycles, the repetition frequency usually being high enough to include a complete sampling in each photograph. The results of these mixtures are shown in Figure 13.

It is clear from this figure that the "jaggedness" of the resulting waveforms increases as the relative amplitudes of the two components are made more similar. Initially, when the components differed by 10-20 dB, the variations in amplitudes of successive peaks were not large; as the difference was decreased, the variations in peak amplitudes increased, and around a 2 dB difference, seemed to be maximal. In addition, at these low differences, shifting phase relations resulted in shifting classes of peak amplitudes, and thus in apparent diagonal lines which traversed the waveforms. It thus

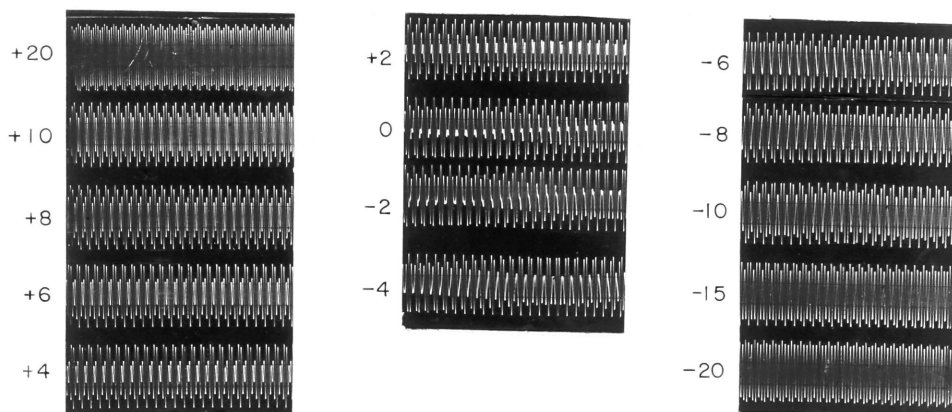


Figure 13. Oscilloscope records of signals produced by mixing a 72 kHz sinusoid and a 96 kHz sinusoid and varying their relative intensities. The figure adjacent to each record gives the amplitude in dB of the 96 kHz component relative to the amplitude of the 72 kHz component.

seemed apparent that while the actual temporal patterning of the peaks was determined by phase effects, more general descriptive features, such as "jaggedness" or "uniformity" depended primarily on the relative amplitudes of the components.

One limitation of this model was that it utilized components of constant frequency, while those composing the bat's pulses were being constantly swept to lower values during the course of the pulse. Accordingly, several pulses were examined to see just how much of the "regularity" of their waveforms could be explained on the basis of the relative amplitudes of their components. In Figure 14, a type I pulse emitted on a discrimination flight is displayed both oscillographically, (top trace), and spectrographically (lower trace). The former indicates the total waveform which will include intensity, frequency, and phase effects. The latter indicates only the intensity and frequency characteristics. That which cannot be explained in the former by recourse to the latter will be the result of phase effects.

In parts a and b of the pulse, only a single component is present, and that is clearly amplitude modulated to give two amplitude peaks. In accordance with the presence of only a single component, the waveform is otherwise rather "uniform". In the latter half of part c, the second sweep begins to make its appearance, and as it increases in intensity, the "jagged" appearance of the waveform also increases. This effect continues through part d of the pulse, and then, as the lower sweep dwindles in amplitude and disappears, the waveform reverts to more uniform patterns in parts e and f. Similar considerations can be made for the pulses shown in Figure 3 of the previous chapter.

It thus seems fair to claim that even in these FM pulses, the uniformity of the waveforms is largely dependent on the relative

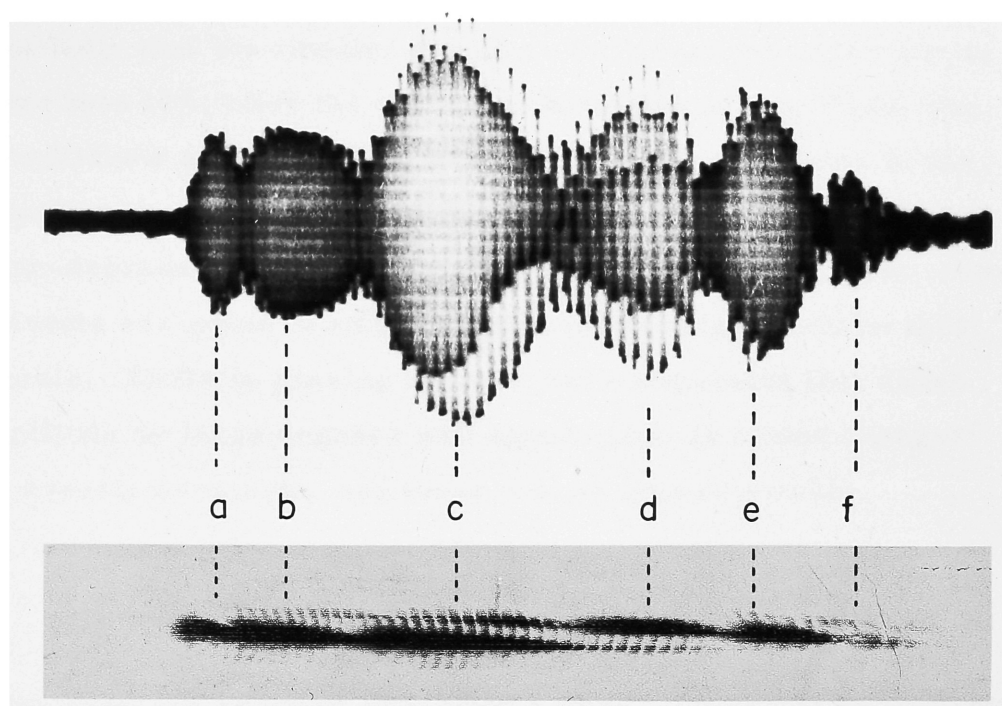


Figure 14. Comparison between the waveform and the spectrographic composition of a type I pulse to show the effects of variations in the relative intensities of the two sweeps on the waveform of the signal. See text for dicussion.

amplitudes of the components. Clearly, the importance of the phase relations between any two components will be directly a function of the degree to which each component contributes to the waveform. If two components differ in amplitude by as much as a factor of 10, it is unlikely that the smaller can alter the waveform of the larger by more than 10%; when the two are comparable in amplitude, the phase relations are maximally important. If as postulated in the Introduction the detection of phase means effectively the detection of a non-degraded waveform, it will be those parts of an echo where components are equal in amplitude that phase effects will be most noticeable. Shifts in phasing between two components that differ in amplitude by large degrees will appear only as minor changes in the overall waveform, and these will be less detectable.

Speculations on the Structure of the Emitted Pulses

The previous sections presented a case, though not an iron-clad one, against the artifactual generation of the changes in pulse structure observed as the bats neared the targets. If this conclusion is accepted, it seems pertinent to consider whether any reasons can be advanced for the production of type III pulses in the region of choice by bat E, (the level flier), and for their absence in equivalent flights by bat T, (the low-dipping flier).

One of the more obvious changes which occurred in the structures of the emitted pulses was a steady decrease in pulse duration as the bats neared the targets. Early in the flights, the durations averaged 1-2 msec; just prior to landing, the durations had been reduced to as little as 0.3-0.5 msec. This shortening of pulse duration must surely involve more than simply an attempt to reduce overlap between outgoing pulses and returning echoes. Griffin (1958) has suggested that prevention of overlap is a primary cause for the

reduced durations observed in other species. However, throughout the flights, the nearest sources of echoes would have returned signals to the bat after at least a 6 msec. delay. Since pulses lasted at most 2 msec., overlap between outgoing pulses and returning echoes would not therefore have been a problem for the bats. Overlap between different echoes however may have been a problem and could account for the reduction in pulse durations. This would have been especially true if the bat were interested in one echo among many. It should be noted however that for any given pair of objects, increasing target proximity results in increasing delay times between the reception of the two echoes. This would seem to argue against the necessity for shortening pulse durations. It is possible that as the bat nears the targets, it begins to receive extraneous echoes that were fainter or even undetectable at greater distances. This may account for the observed reductions in pulse intensity as the bat neared the targets. If this were so, the need to use short pulses in order to receive separate echoes would indeed increase as the bat neared the targets. Whatever the reason, however, it is clear that all the bats on all flights shortened the durations of emitted pulses as they approached the targets. As will be suggested, this shortening required other changes in the composition of the pulses.

A second factor which might affect pulse structure is the method of generation of the pulses. How, for example, might the two component sweeps be generated, and how might their temporal patterning be changed? Unfortunately, a clear decision on this point would require detailed physiological studies on the pulse generating organs of the bats. In spite of this, some speculations are warranted on the basis of the spectrographic data available.

In the previous chapter, (pp. 67), it was noted that these bats had on occasion produced a type of pulse which was longer in

duration and louder in amplitude than those used during discrimination or hunting flights. Spectrographs of these pulses indicated that they were composed of a relatively complete and constant harmonic series based on a fundamental of 20-30 kHz. In Figure 15 is a spectrograph of one of these pulses. In the same figure is an example of the shorter duration, two-sweep pulses which were so common in the discrimination flights studied. Of interest however is the fact that this particular example was emitted by the same bat which produced the long duration pulse, and only milliseconds afterwards. It is thus clear that Vampyrum can make at least two kinds of pulses: those with long duration, loud intensities, and a full harmonic composition; and those with short durations, reduced intensities, and only two rapidly swept components. One immediately wonders whether the latter are selectively filtered versions of the former.

One may decide whether two frequencies are harmonically related by examining their ratio to see 1) whether the ratio is constant from pulse to pulse; 2) whether the frequency interval between components bears any constant relation to the values of the frequencies; and 3) whether the slopes of component sweeps bear any relationship to the ratios of the frequencies at any instant. The reasons for these questions are as follows. Consider a fundamental frequency f and a second harmonic f' . If they are truly harmonically related, then $2f = f'$. Suppose the value of f is decreased from m to n . Simultaneously the value of f' should go from $2m$ to $2n$. During this decrease, the value of the interval, $f' - f$, will change; however, the quotient of f' and $(f' - f)$ at any instant of time will not change, but will in fact be some constant. Finally, if the time taken to make this sweep in frequency be denoted by t , the rate of sweep for the lower frequency component will be, $(m-n)/t$, and that for the upper component $(2m-2n)/t$, or

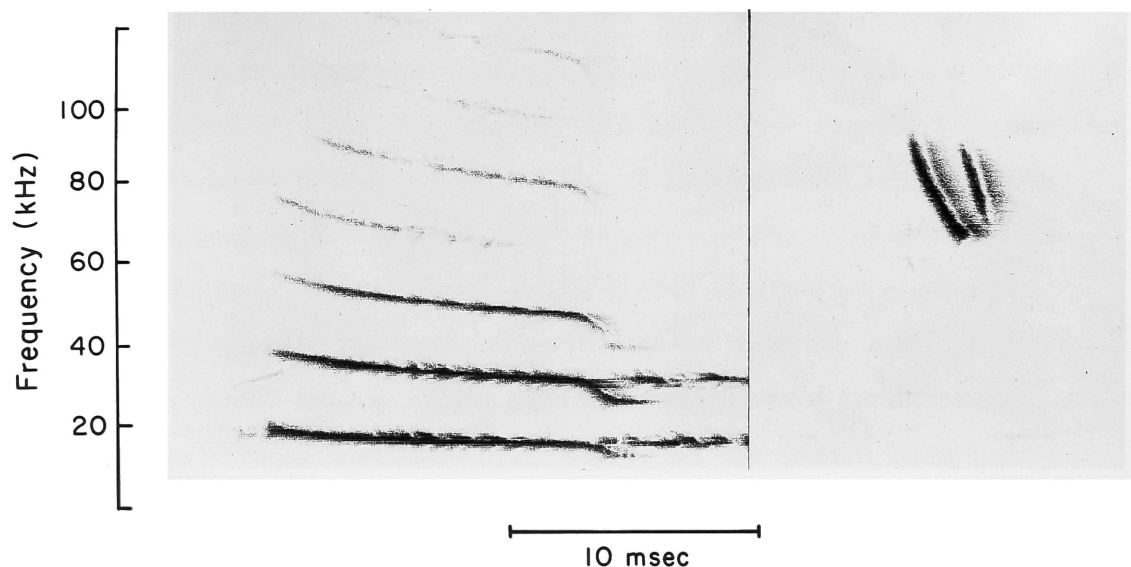


Figure 15. Two consecutive pulses emitted by a captive Vampyrus spectrum while in flight. The first is typified by a long duration, a high amplitude, and a complex harmonic composition. The second is similar to the pulses used by the bats in the discrimination studies, and is characterized by short duration, reduced amplitudes and only two components. Both pulses were recorded in a large flight cage in Trinidad.

$2(m-n)/t$. In other words, the ratio of the slopes is equal to the ratio of the frequencies at any point in time.

Using these criteria, pulses of all types were examined in detail. The data from four such pulses have been tabulated in Table XIV. It is apparent from this table that both within a given pulse and between different pulses, the ratio between the frequencies of the two sweeps is a constant: 1.3. It is also apparent that the ratio of the slopes of the sweeps is relatively constant and in fact equal to 1.3 also. These facts suggest that the two sweeps are indeed harmonically related. The values of $f/(f'-f)$ and $f'/(f'-f)$ identify the lower sweep as the third harmonic of a fundamental between 20-30 kHz, and the upper sweep as the fourth harmonic of the same fundamental. This is consistent with the harmonic series composing the long duration and loud amplitude pulses noted earlier.

The mechanism by which these two harmonics are selectively extracted could not be ascertained in the present study. It should be noted that Pye (1967) has compared the pulses of many species of bats and has proposed that the nasal and buccal cavities serve as resonant volumes, selectively filtering out certain components of initially complex harmonic series. This could well be the case for Vampyrum.

Consider now the assumption that bat E was truly utilizing the frequency spectra of evoked echoes to discriminate between targets. If this is true, it would be to the bat's advantage to maintain as broad a band of component frequencies as possible within the pulse. However, since the bat must apparently shorten the duration of the pulses as the targets are approached, it cannot simultaneously utilize the initial sweep rates and still produce the same range of component frequencies. The bat apparently solves this problem by

Table XIV. Values of the frequency in the two sweeps, f and f' , of selected pulses at three instants of time: t_1 is some point during the first $1/3$ of the pulse; t_2 a point in the second $1/3$; and t_3 a point in the final third of the pulse. Also given is the ratio of the slopes of the two components. All are pulses emitted by bat E on November 9, 1967. All frequencies are kHz.

<u>Pulse and Flight</u>	<u>Type</u>	<u>Sample</u>	<u>f</u>	<u>f'</u>	<u>f'/f</u>	<u>$\frac{f}{f'-f}$</u>	<u>$\frac{f'}{f'-f}$</u>	<u>Slope ratio</u>
# 17-Flight 7	I	t ₁	79	103	1.3	3.3	4.3	1.40
		t ₂	68	89	1.3	3.2	4.2	1.40
		t ₃	60	79	1.3	3.3	4.3	1.40
# 27-Flight 9	II	t ₁	75	101	1.3	2.9	3.9	1.25
		t ₂	70	91	1.3	3.3	4.3	1.25
		t ₃	65	84	1.3	3.1	4.0	1.25
# 35-Flight 7	II	t ₁	79	103	1.3	3.3	4.3	1.20
		t ₂	70	93	1.3	3.0	4.0	1.20
		t ₃	62	84	1.3	2.8	3.8	1.20
# 48-Flight 7	III	t ₁	74	100	1.4	2.8	3.8	1.50
		t ₂	71	92	1.3	3.4	4.4	1.50
		t ₃	67	82	1.2	4.5	5.5	1.50
Means					1.3	3.1	4.2	1.34
					+0.0	+0.3	+0.3	+0.11

increasing the rates of sweep. For example, pulses emitted at target distances of about 250 cm. had sweep rates of 25 kHz/msec. for the lower frequency component and about 32 kHz/msec. for the upper component; the corresponding figures for the pulses emitted near the end of the region of choice were 40 kHz/msec. for the lower component and 50 kHz/msec. for the upper one. The solution is of course not perfect: by the time the bat is producing pulses with 0.5 msec. durations, even these high rates cannot produce the same range of sweep as that of the longer pulses. Using the same examples, pulses emitted at a target distance of 250 cm. usually contained a lower frequency sweep of from 90-65 kHz and an upper sweep of from 110 to 72 kHz. The corresponding ranges for very short pulses emitted near the end of the region of choice are 80 to 65 kHz for the lower sweep and 98 to 77 kHz for the upper sweep.

If it is true that the bat must shorten pulse durations, must produce the two sweeps by selecting from a harmonic series, and must maintain a broad frequency range to effect the discrimination, it can be shown that an increase in sweep overlap (such as occurs in the type III pulse), is a straightforward result of satisfying all these conditions. Let the rate of sweep of the lower component be denoted by k . Let F be the initial frequency of the lower sweep and F' be the initial frequency of the upper sweep. In the pulse studied, the values of F and F' remained fairly constant from pulse to pulse up to the end of the region of choice. Perhaps this was done by gating the pulse at the proper moment; perhaps the upper sweep was gated by means of a filter which passed only frequencies less or equal to F' . In any case, let the pulse commence as the lower component begins to sweep downwards at the rate k . After a delay, d , the upper sweep starts. The frequency of the lower component at the onset of the upper sweep will be equal to $F - kd$. Since the two sweeps are harmonically related, the ratio of

their frequencies at any point will be equal to some constant, c . Therefore, at the moment of onset of the upper sweep

$$F'/(F-kd) = c \quad \text{or} \quad F - F'/c = kd .$$

Since F , F' , and c are all constants, this says that the product of the rate of sweep, k , and the delay of onset, d , is a constant. If the bat increases k , as it in fact does as the targets are approached, the value of d must decrease. This results in an increase in the apparent overlap, temporally, of the two sweeps. It in fact could account for the shift from type II to type III pulses.

One might ask why bat T, (the low-dipping flier), did not produce many type III pulses. The answer may lie in the fact that this bat did not reduce pulse durations as greatly as did bat E. On two flights to the rear targets by bat T, the mean duration of pulses emitted in the region of choice was 0.7 ± 0.2 msec.; the corresponding value for bat E on two equivalent flights was 0.4 ± 0.1 msec. Accordingly, the rates of sweep for pulses emitted in the region of choice remained similar to the rates just prior to this region. Why this bat did not or would not reduce its pulse duration as much as its fellow remains unclear. Also unclear is the reason for the production of the type IV pulses by bat T, but their omission from records of flights by bat E, (the level flier). Perhaps this reflects some differences in tactics between the two animals.

Conclusions on the Structure of the Emitted Pulses

While only a sampling of the flights was analyzed for each bat, several general points seem to emerge from this study:

1. The temporal structuring of the emitted pulses followed

a consistent pattern of changes as the bat neared the target. In bat E, (the level flier), the sequence began with the long duration type I pulses and then the shorter, 50% sweep overlap, type II pulses prior to the region of choice. In the region of choice, the predominant pulses emitted were type III, characterized by their short durations and nearly maximal temporal overlap of the two component sweeps. After the region of choice, single short sweeps (type V pulses) were most common. Bat T, (the low-dipping flier), differed from this pattern by prolonging the emission of type II pulses into the first half of the region of choice. There were no clearcut patterns for pulse emission in the balance of the region of choice, except for the emission of some type IV pulses, (two single short consecutive sweeps), never noted in flights by bat E. After the region of choice, bat T also produced primarily a type V pulse. The possible contributions of artifacts in the generation of these changes was found to be unlikely, at least up through the region of choice.

2. The variations in pulse waveform were shown to depend in large measure on the relative amplitudes of the component frequencies. Examination of both artificial signals and bat pulses indicated that phase effects are primarily detectable when component frequencies are equal in amplitude.

3. The frequency composition and modulation rates of emitted pulses were examined and found to support the claim that the two component sweeps of the pulses are harmonically related. This fact necessitates that as the bat shortens its pulse durations, it must either alter the temporal patterning of the component sweeps towards greater overlap, or must sacrifice the range of frequencies swept through in a pulse. It is suggested that since bat E, (the level flier), appeared to be using the frequency dependent

properties of the echoes, the second of the two choices might be detrimental to successful discrimination. This could explain the presence of type III pulses in the region of choice on flights by this bat.

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