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Technical Report

TARGET IMAGES IN THE SONAR OF BATS

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Echolocating bats (Eptesicus fuscus) perceive complex sonar targets as consisting of individual reflecting elements separated by short distances. The target's nearest element, which returns the earliest component of the echo. is represented by the timing of neural discharges encoding echo delay. In simultaneous discrimination tests, the range of this part of the target relative to that of a comparison target varies with the amplitude of comparison echoes because echo amplitude influences neural response latency. The target's more distant elements are represented by the shape of the overall echo spectrum. Their relative range is insensitive to changes in the amplitude of comparison echoes because the shape of the echo spectrum is independent of amplitude. However, the bat uses echo spectral properties to estimate the equivalent underlying delay separations. In sequential discrimination tests, which require the bat to judge targets from remembered acoustic images, the apparent ranges of all the target's elements shift together as echo amplitude changes, so that they maintain their correct positions with respect to the nearest (OVER)

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element. These results indicate that the bat initially develops a mixed time/frequency representation of echoes but ultimately expresses the acoustic images of targets exclusively in the time domain, which corresponds directly to the natural spatial dimension along which the target is distributed. [illegible]

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Summary. 1. We conducted a series of experiments to identify the composition of the acoustic images of complex targets perceived by the echolocating bat, *Eptesicus fuscus*. A complex sonar target can be described as a series of discrete reflecting points, or *glints*, distributed along the dimension of target range. The target's range is conveyed by echo delay, and the range separation of the glints is conveyed in the temporal and spectral structure of the sonar echoes returned to the sonar receiver.

2. In Experiment I, bats were trained in a two-choice *sequential-presentation* task to discriminate between an electronically-simulated complex target consisting of 2 glints (separated by 17.2 mm or 100 μsec) and a simple target consisting of 1 glint. The range of the complex target was about 56 cm (3.275-msec echo delay), while the range of the simple target was varied around this value. The performance of the bats shows an increase in errors when the simple target coincides in apparent range with either glint in the complex target, providing an index of the perceived distance of the simple target with respect to the individual elements of the complex target.

3. In the first experimental condition, echoes for both glints in the complex target were presented together, and the bats made errors when the simple target coincided in simulated range with either glint of the complex target. Thus, the bats actually perceive the complex target as having a structure along the range axis. In the second condition, only echoes for the

first glint of the complex target were delivered, but they were filtered to recreate spectral notches ordinarily produced by overlap of echoes from the two glints. The bats perceived the filtered echoes as though the target contained two glints, indicating that the spectral composition of echoes conveys the glint structure of complex targets. In the third condition, echoes for the two glints of the complex target were presented alternately, from one sonar emission to the next (echo jitter procedure). The bats perceived the range of each glint separately, as before, but without spectral cues caused by overlap of echoes delivered together. The error peaks in the bats´ performance curves are similar in height and width in all three conditions, indicating that the range profile of the target rather than its intermediate representation by the spectrum of echoes ultimately is responsible for discrimination of the complex target.

4. The distance to the target´s leading edge, or nearest glint, must be represented by the time-of-occurrence of neural discharges encoding the delay of the first component of echoes. The perceived distance to a target is therefore susceptible to errors introduced by changes in echo amplitude, since stimulus amplitude influences neural response latency. Auditory evoked potentials (N_1 and N_4) recorded from anesthetized bats show a latency shift of 13-18 μsec for each decibel change in the amplitude of a frequency-modulated (FM) sweep. In contrast, interference notches in echo spectra do not move to new frequencies as echo amplitude changes. The amplitude-dependence

of response latencies and the amplitude-independence of spectral-notches were exploited in Experiment II to dissociate the image of the complex target into a delay-encoded first glint and a spectrally-encoded second glint.

5. In Experiment II, the bats again discriminated the simulated complex target from the simple target, but with *simultaneous presentation* as well as *sequential presentation* of the target echoes. The amplitude of echoes for the simple target was changed over a 15-dB range to elicit latency shifts that would change the apparent range of the target. For each decibel change in the amplitude of echoes in the simultaneous-presentation condition, the perceived range of the simple target relative to the *first glint* of the complex target changes by 2 to 3 mm, equal to a change in echo delay of approximately 13 to 17 µsec. However, the perceived distance of the simple target relative to the *second glint* of the complex target does not change with echo amplitude, as would be expected if the simultaneous presence of echoes from the simple target obscured spectral notches that represent the separation of the two glints in the complex target. In the sequential-presentation task, the perceived distance of the simple target relative to *both glints* in the complex target changes by about 2 mm for each decibel change in echo amplitude, indicating that the apparent range of the second glint in the image of the complex target is perceived with reference to the absolute range of the first glint.

6. Our data show that *Eptesicus* converts the spectral information about the second glint of the complex target into an

estimate of the equivalent delay or range separation of the glints, in the process referring the range of the second glint to an absolute range of the first glint that is assigned from the timing of neural discharges. Evidently the bat initially develops a mixed time-frequency auditory representation of echoes from a complex target but ultimately expresses the acoustic image of the target along a single axis which corresponds directly to the natural spatial dimension of range over which the target is distributed. The output of the bat's sonar receiver thus is displayed in the time domain, even though intermediate auditory representations partake of both the time and frequency domains. The neural basis for this transformation probably requires convergence of information between tonotopic displays of echo spectra and topographic displays of echo delay.

Introduction

Echolocating bats emit sonar sounds and perceive objects from the echoes of these sounds that return to their ears (Busnel and Fish, 1980; Griffin, 1958; Nachtigall, 1988). Echolocation is a biological acoustic-imaging process in which the capabilities of the auditory system for processing sounds are devoted to the task of creating spatial images. The formation of the images that bats perceive is of considerable interest because it illuminates aspects of auditory function as well as principles of spatial perception in general.

Bats that emit constant-frequency (CF) signals for echolocation use the dimension of echo frequency to create images of targets. These bats have evolved unusually sharply-tuned peripheral auditory filters which improve their resolution of the small frequency changes associated with Doppler-shifted echoes (Neuweiler, *et al.*, 1980). They take advantage of the rapid modulations in the frequency and amplitude of echoes returning from flying insects to identify targets in terms of wing-beat rates (Henson, *et al.*, 1987; Schnitzler, *et al.*, 1983; von der Emde and Menne, in press). Sharp peripheral filtering of echoes appears to be a crucial part of the process that renders these fluctuations in CF echoes perceptible to the bat.

Bats that emit frequency-modulated (FM) signals have equally effective means for identifying targets (Griffin, *et al.* 1965; Sum and Menne, 1988), but the specific nature of this process is not yet well understood. Although "FM" bats can discriminate differences in a variety of target and echo parameters (Schnitzler and Henson, 1980; Simmons and Grinnell, 1988; Suthers and Wenstrup, 1987), no specific dimension of echoes has yet been conclusively demonstrated to support, or be the basis for, the acoustic images these bats perceive. FM bats do not, for example, use especially sharply-tuned auditory filters to analyze echoes (Suga and Jen, 1977), so it is unlikely that the frequency composition of echoes by itself can play as dominant a role in FM echolocation as it does in CF echolocation. Several experiments have shown that FM bats can discriminate between targets that reflect echoes having different spectra (Bradbury, 1970; Habersetzer and Vogler, 1983; Schmidt, 1988; Simmons, *et al*., 1984). These experiments leave the impression that FM bats perceive the spectrum of echoes as the acoustic equivalent of target shape, but they do not specifically address the nature of the images actually perceived by bats. Although perception of target shape may involve the use of echo spectral information, this does not necessarily mean that FM bats perceive the echo spectrum *instead* of target shape. Do FM bats perceive targets that differ in shape merely as having "spectrally distinct" echoes, or do they perceive the spatial differences in target structure that are responsible for differences in echo spectra?

Experiments on the perception of very small differences in the delay of echoes by the big brown bat, *Eptesicus fuscus*, reveal a fine structure to the images of targets along the delay axis that corresponds to the crosscorrelation function between emissions and echoes (Simmons, 1979; Simmons and Altes, in preparation). This finding raises the possibility that *Eptesicus*, and perhaps other FM bats, perceive the structure of complex targets along the range axis (Simmons, 1979; 1980, 1987; Simmons and Stein, 1980). That is, the perceptual dimension of target range might support the creation of acoustic images in FM echolocation in a manner similar to the role of echo frequency and target velocity in CF echolocation. This possibility exists because targets that reflect echoes having different spectra would also reflect echoes having correspondingly different crosscorrelation functions. If the bat in fact perceives the crosscorrelation function as its image of a target, the target's shape would be represented along the range dimension as a series of discrete reflecting points, or *glints* (Altes, 1976) corresponding to side-peaks in the crosscorrelation function. The placement of these side-peaks would reflect the spectral composition of echoes. The spectrum of echoes would indeed be different depending upon the target's shape, and this spectrum would enter into the determination of the crosscorrelation function, but the bat would perceive the shape itself rather than just the spectrum. In this view, to the degree that the spectrum of echoes specifically conveys information about target shape, that spectrum would have to be converted back into a set of estimates of the locations of glints along the range axis prior to the final display of the image perceived by the bat. This paper describes a series of experiments that identify the composition of the acoustic images of complex targets perceived by *Eptesicus fuscus* and indicate how these images must be displayed in the bat´s sonar receiver. The results demonstrate that FM bats perceive the shape of a target in terms of the target´s range profile, and they show that bats convert depth-structure information from the spectrum of echoes back into a range-axis image of the target.

General Methods

Behavioral Experiments: We conducted a series of psychophysical experiments aimed at dissecting the structure of acoustic images perceived by bats. The animals used in these experiments were two big brown bats, *Eptesicus fuscus* (family Vespertilionidae), obtained from the attics of houses in Rhode Island and southeastern Massachussetts. The general procedures pertaining to all of the behavioral experiments are described first (see also Simmons *et al.*, 1988), and then the specifics of each particular stimulus condition are considered separately.

Each bat was trained in a two-alternative forced-choice procedure to discriminate between an electronically-simulated complex target containing two components at slightly different distances and a simulated simple target containing only one component. A simple sonar target consists of a single reflecting point, or glint, located at a discrete distance, or range, from the bat (Altes, 1976). It thus reflects a single filtered replica of the incident sound that arrives at a discrete delay after each emission. A complex target consists of two or more acoustic glints located at slightly different distances. It therefore reflects compound echoes composed of two or more filtered replicas of the incident sound separated by correspondingly small differences in delay. Each millimeter of distance to the glint adds approximately 5.8 µsec to the delay of its echo component.

If the sonar signal impinging on a complex, multiple-glint target is longer in duration than the time separation of the individual echo components within the compound echo, the echo components overlap. The resulting spectrum for the compound echo contains alternating peaks and notches or nulls created by interference between the overlapping echo components. These spectral peaks and notches are made available for perception by the bat if the time separation of the echo components is shorter than the integration-time of the sonar receiver (Beuter, 1980), which has been estimated to be about 350 µsec in *Eptesicus* (Simmons, *et al.*, in press). The frequencies at which these peaks and notches occur are related to the time separation of the echo components, and, hence, the range profile (depth-structure) of the target. The peaks occur at frequencies that are integer multiples of the reciprocal of the time separation, while the notches are interposed between the peaks. The frequency separation of either the peaks or the notches is equal to the reciprocal of the time separation. The peaks are broad and flat-topped, while the notches are sharp and well-defined (see below, especially Fig. 5). Consequently, the notches are likely to be a better index of the characteristics of the echo spectrum than the peaks (Schmidt, 1988; Simmons, *et al.*, 1974). From the periods or wavelengths of the frequencies at which these peaks or notches occur, one can determine the equivalent echo-delay or target-range differences that produced them.

Target simulation: Fig. 1 shows schematically the design of the experiment and the method used to present the bat with

INSERT FIG. 1 ABOUT HERE

electronically-reproduced echoes that simulate sonar targets at different distances. The bat was trained to sit on an elevated, Y-shaped platform and broadcast its sonar sounds to the front--somewhat to the left and the right--to discriminate a complex target (a_1 and a_2 in Fig. 1) from a simple target (*b*). The simple, *single-glint* target consisted of a single replica of each of the bat's sonar emissions, simulating an echo from a point target. The complex, *two-glint* target consisted of two replicas of each emitted sound delivered with a time separation of 100 μsec. It thus contained two reflecting elements. The apparent distance to the simple and complex targets was regulated by controlling the delay of the echoes electronically. The bat was rewarded with a piece of a mealworm offered in forceps for each correct response (arrow in Fig. 1), which consisted of crawling forward onto the left or right arm of the platform--whichever was in the direction of the complex (positive) stimulus for that particular trial. The bat's ability to determine which stimulus was the complex target varied according to the range of the simple target in a manner that revealed the apparent shape of the complex target in the data. The appearance of the complex stimulus on the left or right was determined by a pseudorandom schedule and set by a switch located beneath the platform. The experiment was set up in a 4.5 x 3.5 x 2.4 meter chamber whose walls, ceiling, and floor were lined with convoluted polyurethane foam (Perma Foam Corp., Irvington, NJ) that reduced the amplitude of ultrasonic reverberation by at least 20 to 30 dB compared with what would occur if the chamber had smooth, hard walls.

The electronic system for simulating sonar targets was built around the bat's observing position on the Y-shaped platform. Two Bruel & Kjaer Model 4138 condenser microphones (*m* in Fig. 2) were mounted at the ends of the arms of the platform to pick up the bat's echolocation sounds. The electrical signal from each microphone was amplified, filtered to a 20 to 100 kHz band with a Rockland Model 442 band-pass filter, delayed by a controlled amount, and then returned to the bat from an RCA electrostatic loudspeaker (Part No. 112343; *s* in Fig. 2) that was mounted next to the microphone. During representative trials, echolocation sounds recorded from the bats were stored on analog magnetic tape with a Racal Store-4 tape recorder and subsequently reproduced for digital signal analysis in an IBM PC-AT computer operating with ILS programs from Signal Technology, Inc. Spectrograms of the sounds were made with a Unigon digital sound spectrograph. Both the microphones and the loudspeakers were located 20 cm from bat's observing position at the center of the platform, so that together they provided a propagation delay of 1.16 msec for any sound emitted by the bat and returning to the bat's ears after passing through the simulator. The angle separating the two sets of microphones and speakers was approximately 40°.

The bats were tested six days a week, and on the test-days each bat was run on a number of trials that was determined by its current body weight and the quantity of mealworms consumed after correct trials. Each day's run constituted a block of trials for one of the experimental conditions (various combinations of echo-presentation regimes for echoes a_1 and a_2, and various delay and amplitude settings for echo *b*), and the stimuli were set to a new condition on the following day. The bats typically worked through 35 to 60 trials in each block. If the number of trials achieved on a single day was less than this, the same stimulus conditions were repeated the next day to accumulate more trials. The data take the form of percentages of errors made over all trials at any particular stimulus condition and delay setting, and the primary mode of presentation of the data is a graph of percentage errors as a function of the delay of echo *b*. The data were not arbitrarily divided into above- and below "threshold" states because our concern is with the form of the images perceived by the bat as revealed by the shape of the entire curve for each condition (Simmons, 1973; 1979), rather than with reduction of the data to a single, artificial estimate of discriminability.

During individual experimental trials, which lasted for several seconds, each bat emitted FM echolocation sounds with durations of about 1.5 to 2.5 msec at rates of 5 to 15 sounds per second (see section on sounds, below). Each sound was received at both microphones, with an amplitude at each microphone that depended on the aim of the bat´s head during head-scanning movements as the bat searched for the simulated targets (Simmons and Vernon, 1971). The amplified and filtered signal representing each of the bat´s sonar sounds was delayed electronically by a digital delay system (*delay* in Fig. 1) designed and built by the Science Services Shops at the University of Oregon (Simmons, *et al.*, 1988). The signal was digitized with 12-bit accuracy at a rate of 730 kHz, stored in a circulating buffer memory, and then read out and reconstituted as an analog signal after a preset delay. The total gain of the analog circuitry feeding into the delay lines was about 80 dB to bring the peak-to-peak amplitude of the majority of signals to a level just below the 12-bit limit of the digitizer for maximum signal-to-noise ratio. The magnitude of the electronic delay was chosen so that, when added to the 1.16-msec propagation delay from the bat to the microphone and from the loudspeaker to the bat, it created a total delay corresponding to the desired simulated target range. Each microphone-loudspeaker channel was equipped with a dual-delay system, so the bat could be presented with multiple simulated glints that appeared on the bat´s right and on its left from the observing position on the platform.

Acoustic calibration: The target simulator is an acoustic recording and reproducing system whose performance can be summarized by a frequency-response curve or transfer function.

The frequency response of the left and right channels of the simulator is shown in Fig 2. These curves refer to the ratio of

INSERT FIG. 2 ABOUT HERE

the acoustic output of the system measured at the bat´s observing position relative to the acoustic input delivered to a point 20 cm in front of the bat--that is, at the location of the microphone. The attenuators internal to the simulator (placed just prior to the mixer in each channel which sums the echo components after they are delayed) were set to zero (maximum system gain) for these frequency-response measurements. At a setting of zero on the attenuators, the absolute acoustic gain of the simulator system at 40 kHz in Fig. 2 was about -10 dB. In the experiments themselves, the electronic attenuation of echoes was set to produce a lower gain (see below). Calibration was accomplished by replacing the bat with a loudspeaker-microphone assembly. An uncovered Bruel & Kjaer Model 4135 condenser microphone was set at the bat´s location, and test signals were put into the simulator by broadcasting 1-msec FM sounds (10 to 100 kHz) from a specially-built electrostatic loudspeaker (Simmons, *et al*., 1979). The system´s overall performance was monitored daily by an automatic calibration system built into the target simulator to detect any malfunction of the simulator´s acoustic or electronic components. Over a one-year period, the unadjusted gain of the system drifted downward by about 3 dB.

The simulator was adjusted daily to maintain its absolute acoustic gain within a 1 to 2 dB span for all experimental trials.

The amplitudes of the echoes delivered to the bat were set to fixed levels with respect to an estimate of the bat´s threshold for detecting a single-glint test target (at the location of a_1) presented in isolation. To determine the threshold for each bat prior to the beginning of the experiments, the amplitude of test echoes was reduced from about 80 dB SPL peak-to-peak in steps of 5, 2, or 1 dB on successive blocks of trials to determine the level at which the bat´s performance in the two-choice detection task fell to about 50% correct responses. The threshold was found by plotting percent correct responses against echo sound pressure level in dB, and the echo level corresponding to 75% correct responses was arbitrarily defined as threshold. In all experimental conditions, the amplitude of echoes representing target glints a_1 and a_2 was set at 15 dB above this detection threshold; the amplitude of echoes representing target b varied across conditions, as described below.

Experiment I

In the first series of experiments, each bat performed a *sequential discrimination* task in which the simple target (negative stimulus) and the complex target (positive stimulus) were presented one-at-a-time in the following manner: The bat emitted sonar sounds while at its observing position on the platform (Fig. 1), and a voltage comparator determined whether the left or right microphone picked up the stronger signal (i.e. the side towards which the bat's head was aimed). Only the channel on that particular side was activated. Thus, the bat received echoes from either the left or the right loudspeaker---never both at once. The bat learned to scan on the left and the right to sample echoes from both simulator channels. Since only the left or the right channel could be activated at any one time, the bat's scanning determined the sequential presentation of the simple and complex targets through the two channels. This paradigm forced the bat to rely upon remembered images of the targets to select the side on which the complex target was presented.

Condition A

The bat was trained in the sequential-presentation task to select a complex target that reflected two echoes delivered together and separated by a 100 μsec delay. The complex target (a_1-a_2 in Fig. 1) was presented through either the left or the right channel with a propagation delay of 1.16 msec added to electronic delays of 2.115 (glint a_1) and 2.215 (glint a_2) msec to create overall echo delays of 3.275 and 3.375 msec. (These are nominal delays that varied somewhat in practice with the movement of the bat's head during trials. The 100-μsec separation of the echo components remains invariant, however.) These delays simulate the first and second glints of a depth-structured target with glints at ranges of 56.47 and 58.19 cm, respectively. The 100-μsec delay separation between the two glints corresponds to a spatial separation of 17.2 mm, which is a realistic distance for insect-sized targets that FM bats are capable of identifying (Simmons and Chen, in press). Since the sonar sounds of *Eptesicus* in this experiment are approximately 2 msec in duration (see below), the electronically-reproduced echoes of the first and second glints of the complex target are largely ovelapping, creating peaks and notches across frequencies in the composite spectrum at 10 kHz intervals. The delay separation of 100 μsec was chosen because it is shorter than the approximately 350-μsec integration-time for echo reception by *Eptesicus* (Simmons, *et al.*, in press), and because earlier range discrimination data show that *Eptesicus* can distinguish between two glints separated by this delay, even if the perceived range of the individual sonar targets is smeared by head movements (Simmons and Grinnell, 1988: see Simmons, 1973). When bats are trained to discriminate between two single-glint targets at different simulated ranges (echo delays), the bat's error curve shows a peak that is less than 100 μsec wide. Fig. 3 shows the results of an echo-delay discrimination experiment for two single-glint targets (Simmons, 1973) to serve as a reference for reading the graphs presented below.

INSERT FIG. 3 ABOUT HERE

In Experiment I, the simple target (*b*) consisted of electronically reproduced echoes of the bat's sonar emissions arriving at a single delay. The echo delay for the simple target was constant on any given test day but varied from day-to-day over a range from 50 µsec before the first glint (a_1) of the complex target to 150 µsec after a_1. The total echo delay of the simple target thus varied between 3.225 and 3.425 msec (target ranges between about 55.6 and 59.1 cm). The bat's performance at choosing the complex target thus was assessed as a function of the delay of echo *b*. Echoes representing a_1, a_2, and *b* were all presented at a level 15 dB above the detection threshold measured for a_1 alone.

Results

Figure 4A shows the performance curves of two bats trained to discriminate the complex two-glint target (a_1-a_2) from the simple one-glint target (*b*), with varying delays for the echoes of the simple target. The two curves plot the individual data for each bat, showing percent errors for nine different echo delays of the simple target. The delay plotted on the abscissa is that of the simple target with respect to the first glint of the complex target. Thus, an echo delay of zero µsec represents the condition in which the first glint of the complex target

INSERT FIG. 4 ABOUT HERE

coincides in range with the only glint of the simple target (at an actual delay of 3.275 msec). Around this delay, both bats show an increase in errors compared to neighboring delays. At an echo delay of 100 μsec in Fig. 4A, the second glint of the complex target coincides in simulated range with the simple target. At this delay the bats´ errors increase again. (These peaks only reach about 25% errors because two glints are present to identify the correct target. Only one of these can be masked by the single-glint target, leaving the other to be recognized by the bat. As Fig. 3 shows, when only one glint is present in the positive stimulus, the bat´s performance reaches 50% errors. The factors responsible for the reduced height of the peaks in Fig. 4 compared to Fig. 3 are examined below in Condition C of this experiment.)

In spite of the fact that the separation of the echo components for the complex target is only 100 μsec, *Eptesicus* still can perceive the presence of two glints in the target at their correct ranges. Some acoustic feature of the overlapping echo components enables the bat to discern that the target contains two reflecting points rather than only one. The small size of the separation of the echo components in relation to the integration-time for echo reception makes the spectrum of the compound echo the most likely cue for the bat to use.

Condition B

If the bat indeed perceives the 100-μsec delay separation of a_1 and a_2 in the complex target from the spectrum of the compound echo, an appropriately filtered *single* echo for a_1 alone should be perceived by the bat as a complex target with two glints separated by 100 μsec. We tested this possibility by electronically filtering echo a_1 with six parallel, voltage-tunable band-pass filters (Voltage Variable Systems, Model 330A) to mimic the spectral peaks at 30, 40, 50, 60, 70 and 80 kHz and the intervening spectral notches at 25, 35, 45, 55, 65, 75 and 85 kHz that are ordinarily created by mixing a_1 and a_2 into a compound echo. Fig. 5 shows the frequency response of the components creating this filtered echo in comparison with the frequency response associated with two overlapping glints separated by 100 μsec. These measurements were obtained by passing a 1.0-msec FM calibration signal (100 to 10 kHz sweep) through one channel of the target simulator and determining the transfer function at the point in the circuit where the filters were introduced. The curves in Fig. 5 show the interference peaks and notches created by overlap of two echo components (dashed line) and these same notches simulated by placing filter resonances at frequencies corresponding to the interference peaks (solid line). The filtered version of the complex echo is not a

INSERT FIG. 5 ABOUT HERE

perfect replica of the interference effect, particularly with respect to the depth of the notches, but it is good enough to cause two distinct time delays to appear in the compound echo. Fig. 6 shows the impulse response for the filters in comparison with the impulse response created by two separate echo components

INSERT FIG. 6 ABOUT HERE

being added together. Both impulse waveforms contain two discrete clusters of peaks separated by about 100 μsec. These clusters represent the two glints created by spectral notches originating either from interference or from filtering. The relatively shallower notches in the filtered echo result in a smaller amplitude for the second set of peaks relative to the first set of peaks, but the two glints are clearly present in both cases.

In Condition B of the experiment, only echo *b* and the filtered echo a_1 were presented to the bats, whose task still was to select the complex target (filtered echo a_1). Echo *b* was moved to different locations to determine whether the bat perceived the complex spectral structure of echo a_1 as if the simulated target contained two glints. The delay of echo a_1 was always 3.275 msec, the same as that in Condition A. The delay of echo *b* varied between 3.225 and 3.450 msec--that is, from 50 μsec before to 175 μsec after echo a_1. In Condition A, the delay of *b* was changed in steps of 25 μsec, and this same step size was used in condition B with the exception of two values that had a step size of only 12.5 μsec. These intermediately-spaced delays of *b* were at 12.5 μsec and 112.5 μsec relative to the delay of a_1. They were used because the filters which created the notches in the spectrum of a_1 also retarded the phase of the signal by an average of about 90° across much of the frequency range used by the bat. The resulting echo delay was thus about half of the 25-μsec step size later than in condition A. The two half-step points were inserted to avoid missing the true delay of the echoes while collecting the data. The amplitude of the filtered echo a_1 was adjusted to match that of echo a_1/a_2 in Condition A, and echo *b* again was 15 dB above each bat´s detection threshold for a_1 alone.

Results

Both of the trained bats made the transition from discrimination of the two-glint simulated target in Condition A to discrimination of the filtered echoes in condition B. Their performance did not suffer as the switch was made, suggesting that the bats regarded the tasks as similar. Figure 4B shows the performance curves of two bats trained to discriminate the filtered echo a_1 from echo *b*. Each curve plots the percentage of errors made by one bat for the different delays of echo *b* with reference to the delay of the filtered a_1. Again, a delay of zero μsec on the abscissa marks the time at which echo *b* is presented with the same delay as echo a_1. As in Condition A, the bats both show an increase in errors for echo delays close to zero and 100 μsec. The actual peaks of the error curves are at 12.5 and 112.5 μsec, the two points interposed to account for the phase lag of the filtered echoes. The peaks in Fig. 4B thus are shifted slightly to the right in comparison with the peaks in Fig. 4A.

Eptesicus perceives the filtered echo a_1, with its resonance-created peaks and notches, as though it consists of two discrete components separated by 100 μsec. Somehow the bat interprets the presence of notches in the echo spectrum to signify the existence of more than one glint in the target, so that a point corresponding to a_2 is inserted into the image. It converts the shape of the echo spectrum into an estimate of the equivalent underlying time separation of summing-and-interfering echo components and then uses this estimated time separation to perceive the range profile of the target.

Condition C

The combined results of Conditions A and B suggest that the bat uses the spectrum of echoes to perceive the structure of the target. However, this does not necessarily imply that the bat perceives the spectrum entirely as the *equivalent* of target depth-structure. Although the echo spectrum is used to determine the separation of a_1 and a_2, there may be aspects of the spectrum that the bat perceives without specifically using them to perceive the second glint. That is, the echo spectrum could contribute to discrimination of the complex target without this contribution being manifested in the appearance of the second glint in the image. This point is related to the observation that the error peaks in Figs. 4A and 4B only rise to about 25% errors, rather than the 50% that occurs when only a single glint is present in both of the simulated targets (see Fig. 3). Some feature of the two-glint target makes it more discriminable than a one-glint target in what is essentially a target-range discrimination task. Condition C was intended to determine whether the echo spectrum contributes any information beyond what is used to estimate the separation of the two glints. In this condition, the bats were tested with a complex target that returned two echo components without the spectral information created by presenting two overlapping echo components together.

The complex target again contained two glints, a_1 and a_2, at delays of 3.275 and 3.375 msec. However, in Condition C, the echoes of a_1 and of a_2 were returned to the bat *in alternation.* That is, the glints of the complex target were presented as though they really were a single glint that jittered back and forth in range between 56.47 and 58.19 cm from one echo to the next. Following each of the bat's sonar emissions, either a_1 or a_2 returned, but not both together--the two glints of the complex target were never presented in tandem for the same sonar emission. A digital circuit was added to each channel of the target simulator that counted the bat's sonar sounds and alternated the state of a flip-flop to gate a_1 and a_2 on and off in alternation (Simmons, 1979; Simmons and Altes, in preparation). Thus, the bat was presented with two glints separated by 100 usec (or 17.2 mm) without the spectral consequences of the direct mixing of their echoes. To the degree that each glint somehow activates neural mechanisms that represent its separate range, this continues to happen, but the spectral notches that ordinarily signify the presence of the second glint are removed. The simple target, containing only glint *b*, was presented at different delays from 50 µsec before a_1 to 175 µsec after a_1. As in Conditions A and B, all of the echoes were presented at 15 dB above the detection threshold for a_1 alone.

Results

Both bats smoothly transferred from Condition B to Condition C without showing any initial decrement in performance, again suggesting that they considered these tasks to be very much alike. Figure 4C shows the individual performance curves of two bats trained to discriminate the complex target that jittered between glints a_1 and a_2 from the simple target *b*. As before, the percentage of errors is plotted against the delay of the single glint *b* with reference to the delay of a_1. The results show an increase in errors when target *b* is presented at the same delay as either the first glint (zero µsec delay) or the second glint (100 µsec delay) of the complex target, even though the spectral cues present in Conditions A and B were removed by precluding overlap of echo components. By itself, the presence of glints alternating between two ranges is enough to create a "complex target" in terms of the bat´s ability to discriminate one target from another. Most significantly, the peaks in the error curves in the region of zero and 100 µsec delays closely resemble each other in height and width for all three experimental conditions. To the bats, the two-glint complex target is equally discriminable from the simple target whether the two glints are presented in compound echoes, simulated in a filtered echo, or presented in alternation.

Echolocation Sounds: During selected trials from conditions A, B, and C, the echolocation sounds used by the bats for discriminating the complex target from the simple target were tape-recorded and then reproduced for analysis to determine their properties. Both of the bats used essentially the same signals in all three conditions, with variations primarily in the overall duration of the signals from about 1.5 to 2.5 msec. Fig. 7 shows spectrograms of representative sonar sounds emitted by the two bats during trials of Condition C. In Experiment II (below), the bats also used sounds that were the same. The signals are frequency modulated, with three harmonics that together cover the frequency range from 23 to about 100 kHz. These sounds are similar to signals used by *Eptesicus* during other laboratory discrimination experiments (Simmons, *et al*., 1988, for example) and during the approach or tracking stage of interception of prey

INSERT FIG. 7 ABOUT HERE

(Griffin, 1958; Simmons, 1987). The frequency response of the target simulator (Fig. 2), shows that the echoes returned to the bat contained predominantly the first two harmonics of these sounds, and that the the small segment of the third harmonic around 90 kHz probably played little part in either bat´s performance.

Discussion

In all three experimental conditions of Experiment I, the bats explicitly perceive the location along the range axis of two glints in the complex target. Whether the second glint in the complex target is actually represented by its echo component or only represented by artificially created spectral notches seems not to matter; *Eptesicus* treats the three stimulus regimes as perceptually alike. The bats evidently derive their ability to perceive the complex target as being complex because it contains two glints located at different ranges. That is, the peaks in Fig. 4 only rise to about 25% errors instead of 50% errors as in Fig. 3 because the complex target´s range profile makes it appear different from the simple target. The bats perceive two glints in one target and only one glint in the other, so that, even when the simple target is at the same range as either of the glints in the complex target, the bats can still perceive the other glint to identify the correct stimulus. Each bat´s performance declines when the single glint coincides in range with one of the double glints, but the decline is not total (that is, to 50%

errors) because the other glint is still perceived and contributes to the discrimination.

The principal conclusion from Experiment I concerns the role of the spectrum of echoes in perception of complex targets. Under ordinary acoustic conditions--when the presence and range of the second glint in a complex target is represented by interference notches in the spectrum of the compound echo--*Eptesicus* perceives this spectral information as though it signifies the existence of an "event" along the range axis rather than simply events along the frequency axis. This is also true when the spectral notches are created artificially with filter resonances. The location and spacing of the notches along the frequency axis is sufficient to evoke an event at a reciprocally-related echo-delay or target-range separation. That is, the bat perceives the shape of a complex target from the spectrum of echoes, but it *perceives this shape directly in terms of the underlying delay or range separations required to produce spectral notches at specific frequencies*. The shape of the spectrum is converted by the bat into an image that expresses this spectral information in the domain of time rather than frequency, as would be expected if the bat used a crosscorrelation-like sonar receiver (Simmons, 1979; 1980; Simmons and Stein, 1980). Systematically-arranged spectral notches would appear in the crosscorrelation function of echoes as a discrete side-peak in delay or range, and this corresponds to what the bat actually perceives.

Not only does *Eptesicus* use the echo spectrum to perceive complex sonar targets in terms of their range profile, but the echo spectrum is *entirely* transformed into a time-domain representation. In Experiment I, the bat derives no capacity to discriminate complex targets from their spectra beyond what is used to estimate range profile. The range of the second glint may be specified from the individually-presented delay of separate, alternating echo components (Fig. 4C) or more naturally from the spectral consequences of mixing the two echo components together (Fig. 4A) without effecting the bat´s performance. *Eptesicus* perceives the spectrally estimated range profile of the complex target with the same level of performance as the two glints presented in alternation, with no available spectral cues. The spectrum thus does not contribute to the discriminability of the complex target beyond what is used to estimate the underlying delay separation implied by the presence of notches at particular frequencies.

The auditory system of *Eptesicus* must establish a physiological representation of echoes that separately incorporates information about the arrival-time and the spectrum of echoes, presumably using physiological axes of echo delay and echo frequency to display echo parameters in neural terms (Sullivan, 1982; Suga, 1988; Wong and Shannon, 1988). A hybrid representation of this sort previously has been proposed from considerations of peripheral auditory coding of echoes and the performance of bats in target-range discrimination experiments (Simmons, 1973). These two neural displays must coexist alongside one another, since the acoustic parameters they represent are distinct in their manifestations at early stages of the auditory pathways (Bodenhamer and Pollak, 1981; Simmons and Kick, 1984; Suga, 1988). The process of "reading" the two displays entails conversion of the terms of one (the spectral display) into the terms of the other (the delay display). The quite distinct peripheral physiological manifestations of delay and spectral information (time-of-occurrence of nerve discharges *versus* tuned frequency of neural "channels") provide a means for confirming experimentally that these two representations indeed are independent of each other prior to the convergence of their outputs onto the image-display perceived by the bat.

Experiment II

The results of Experiment I provide evidence that the auditory representation of a depth-structured target in *Eptesicus* involves a hybrid of frequency-domain and time-domain processing of echoes. Experiment II seeks to dissociate the components of the image of a complex target that have their origin in a time-domain representation from components that have their origin in a frequency-domain representation. The perceived distance to the first reflecting element of a complex target (or to a single-glint, simple target) is represented by the delay of echoes after emissions, which most likely is initially encoded by the time-of-occurrence of neural discharges marking the different frequencies in the FM sweep of emissions followed by similar discharges for echoes (Bodenhamer and Pollak, 1981; Pollak, *et al.*, 1977; Simmons and Kick, 1984). The resulting array of neural discharges for the emission or the echo resembles a spectrogram, with each point in the representation having both time-domain and frequency-domain information (Altes, 1980, 1981; Simmons & Kick, 1984). The time that elapses between neural discharges evoked by echoes and discharges evoked by their previous emissions ultimately is displayed in the bat´s auditory cortex (Sullivan, 1982; Suga, 1988; Wong and Shannon, 1988), but the neural representation of this time separation remains experimentally vulnerable to any factor which can perturb the faithful neural registration of the time at which echoes occur until the range display is actualy computed. The most obvious candidate for perturbing the timing of neural discharges to echoes is the relation between stimulus amplitude and neural response latency. As echoes are increased in strength, the latency of the discharges they evoke becomes shorter (Bodenhamer & Pollak, 1981; Bodenhamer *et al.*, 1979; Pollak *et al.*, 1977; Suga, 1970). It should be possible to shift the apparent range of the first glint in a complex target just by changing the amplitude of its echoes.

Fig. 4 shows that the perceived distance of the second element in a complex target is represented by the compound echo spectrum. This spectrum consists of notches placed in the echo from the first glint in the target by interference between the echoes from the two glints when they add together. The notches specify only the range separation of the two glints, with the absolute range of the second glint necessarily being referred to the absolute range of the first glint. *Eptesicus* perceives both glints at their correct ranges, indicating that the range separation somehow is expressed in terms of absolute range. The locations of the notches in the spectrum initially are represented physiologically by the amount of neural activity evoked in neural channels tuned to different frequencies across the frequency range of the FM sweep of echoes. The individual frequencies in the sweeps are registered as "excitatory frequencies" (Bodenhamer and Pollak, 1981) in neural response profiles that are not much influenced by the amplitude of echoes. *Only the latency of the neural discharges in any particular frequency channel changes with stimulus amplitude, not the frequency that evokes the discharges in that channel.* In other words, the time-domain part of the spectrogram representation of echoes is very sensitive to echo amplitude, but the frequency-domain part is not. If two echoes overlap and interfere with each other so as to create spectral notches, these notches remain at the same frequencies even though one echo changes in amplitude relative to the other. Only the depth of the notches changes with the relative amplitude of the echoes. The difference between the behavior of neural response latencies and the neural representation of spectral notches is exploited in Experiment II to distinguish between the images of the first and second glints in a complex target.

Auditory Evoked Potentials

We measured latency changes for neural responses to FM sounds at biologically appropriate stimulus levels (Kick and Simmons, 1984) in five *Eptesicus*. Bats were anaesthetized by intramuscular injection of a ketamine-rompun mixture (50 mg/kg), supplemented with metofane inhalation. The skull was exposed over the midbrain, and a small hole was made in the skull to insert a tungsten wire electrode onto the dorsal surface of the inferior colliculus to record auditory evoked potentials from the auditory nerve (N_1) and nucleus of the lateral lemniscus (N_4). FM sounds, 1.0 ms in duration and sweeping from 110 down to 20 kHz, were broadcast through a specially-built electrostatic loudspeaker (Simmons, *et al.*, 1979) located 10 cm from the bat's ear. These acoustic stimuli were presented over a range of amplitudes from 20 to 90 dB SPL peak-to-peak. The neural responses to these sounds were amplified with a WPI Model DAM-5A physiological amplifier and digitized at 100 kHz (12 bit accuracy). Sets of 256 responses for each amplitude were stored and averaged (RC Electronics Model ISC-16 data-acquisition system). We defined neural response thresholds to be the lowest sound pressure that still produced recognizable averaged auditory evoked potentials. Our methods are otherwise similar to those used earlier with *Eptesicus* (Feng et al., 1978), and our observed thresholds are within 10 dB of previously-obtained behavioral or physiological thresholds when the frequency response of our acoustic system is taken into account (Dalland, 1965; Gardner & Garvey, 1974; Kick, 1980).

Results

As sound pressure level increases, the latency of auditory evoked responses in *Eptesicus* to brief FM sounds becomes shorter. Fig. 8 shows representative data for two individual bats. The latency of the N_1 evoked potential is plotted as a function of sound pressure level relative to threshold. For both animals, the evoked-potential latency shortens by approximately 0.55 msec as stimulus amplitude increases from near threshold to 40 dB above threshold. The inset of Fig. 8 shows the entire waveform of averaged evoked potentials from one bat for a series of amplitudes above threshold to illustrate how the latency of the whole ensemble of the response systematically shortens as the FM sounds become stronger. At a level 15 dB above threshold, the slope of the N_1 latency function is approximately -13 µsec/dB and the slope of the N_4 function is nearer -18 µsec/dB. If the bat uses the timing of neural discharges making up such evoked responses to FM sonar echoes to determine target range, an increase in echo amplitude in this region should shorten the target´s apparent range by about 2 to 3 mm/dB.

INSERT FIG. 8 ABOUT HERE

Behavioral Experiments

To determine which parts of the image of a complex sonar target are susceptible to changes in apparent distance due to amplitude-induced latency shifts, we again studied the bat's performance at discriminating between an electronically-simulated complex target containing two components separated by 100 µsec and a simulated simple target containing only one component (Fig. 1). We presented echoes of each component of the complex target (a_1 and a_2) at a fixed strength 15 dB above behavioral detection threshold, while we presented echoes of the single-component simple target (*b*) at several different strengths ranging from 9 to 24 dB above threshold in two separate tasks. Our intention was to use changes in the latency of neural discharges to the echoes of *b* to identify whether it is the timing of these discharges or the spectral consequences of mixing *b* with a_1 and a_2 that determines the delay at which the bat perceives *b* to be aligned with either a_1 or a_2.

Two different stimulus-presentation regimes were used in Experiment II to control the mixing of *b* with a_1 and a_2 and thus to create spectral cues between a_1 or a_2 and *b* that could mask the spectral cues used by the bat to perceive the separation of a_1 and a_2 from each other. The first was a two-choice *simultaneous* discrimination task in which both the left and the right channels of the target simulator were activated together by each sonar emission. (The electronic comparator that determined which way the bat aimed its sonar sounds was simply switched off.) In this condition, the complex and simple targets always were presented together. For each sonar emission, all three echoes--a_1, a_2, and b--were delivered at their appropriate delays to the bat's ears. Since the bat receives overlapping echoes from both the simple and complex targets each time it emits a sonar sound, echoes impinging on the bat's ears from both targets can interfere with each other and create spectral interference patterns. In particular, even as a_2 interferes with a_1 to create spectral notches signifying the separation of a_1 and a_2, so, too, can b interfere with a_1 and create competing spectral notches according to its own delay separation from a_1. If the absolute range of a_2 is represented by spectral notches in the compound echo of a_1 and a_2, then alignment of b with a_2 should obscure these notches, and the bat should make discrimination errors because it perceives b and a_2 to be at the same distance. Changing the amplitude of the echoes for b should have no effect on the bat's perception of the alignment of b with a_2 because the spectral notches associated with b will not change in their frequencies. The a_2 peak in an error performance curve of the type shown in Fig. 4 should thus not move left or right on the graph as the amplitude of b changes. When b is aligned with a_1, the bat also should make errors. If the absolute ranges of a_1 relative to b are represented by the timing of neural discharges evoked by each echo, a change in the amplitude of the echoes for b should shift its apparent range relative to a_1. For example, in the case of a decrease in the amplitude of the echoes for b, which should retard its corresponding neural discharges, these echoes would have to be moved earlier to coincide with a_1 in the bat's perception. The a_1 peak in an error performance curve of the type shown in Fig. 4 should thus move to the left on the graph as the amplitude of b decreases.

The second stimulus-presentation regime in Experiment II was a two-choice *sequential* discrimination task, as described above in the methods for Experiment I. In the sequential discrimination task, a voltage comparator determined whether the left or right microphone received the greater signal according to the aim of the bat's head, and echoes were returned to the bat from only that side. Since just one target is presented to the bat for each sonar emission, echoes from the complex and simple targets no longer can impinge on the bat's ears together. The bat has to remember the targets to compare them. Under this condition, any errors in discrimination made by the bat must depend upon interference between the *images* of the simple and complex targets rather than interference between the echoes themselves. In particular, echoes for b no longer mix with echoes for a_1 and a_2, so no competing spectral notches would be created. In this sequential condition (which is identical to Condition A of Experiment I except that the echoes for b are changed in amplitude), the distance from a_1 to a_2 can only be known from spectral cues created when a_1 and a_2 mix together. The bat's perception of the absolute range of a_2 thus depends upon perception of the delay-determined absolute range of a_1 because the spectral cues for a_2 are referred to a_1 when they are converted into images. Changing the amplitude of echoes for *b* thus should shift the error peaks for both a_1 and a_2 together (in a graph such as is shown in Fig. 4) in the sequential condition, rather than shift only the peak for a_1 as in the simultaneous condition. This should occur because the entire, remembered image of the complex target has a perceived absolute range that should depend on the latency of neural discharges to a_1.

In both the simultaneous and sequential tasks, the complex target contained two glints, a_1 and a_2, whose echoes arrived after delays of 3.275 and 3.375 msec, respectively. The delay of echoes from the simple target, *b*, varied in steps of 25 μsec from 150 μsec before the first glint of the complex target to 175 μsec afterwards. The peformance of the bats was measured for each delay of echoes from the simple target, and at amplitudes of echo *b* from -6 to +9 dB relative to echoes from the individual components of the complex target, which again were 15 dB above detection threshold.

Results

Simultaneous Discrimination: As in Experiment I, the data take the form of percentage errors recorded for each bat while discriminating the simulated two-glint target from the simulated one-glint target as the one-glint target appeared at a succession of different distances around the distance of the two-glint target. Fig. 9 shows the results of the simultaneous discrimination condition for two amplitudes of the echoes for *b* relative to echoes for a_1 and a_2. When echoes for the single-glint (*b*) target are equal in strength to echoes of each of the glints (a_1, a_2) in the complex target (0 dB condition, upper panel of Fig. 9), both glints in the complex target appear as peaks in the error curves at their correct, or objective, echo delays. This result is similar to that shown in Fig. 4A, even though the simple and complex targets were presented simultaneously in this condition. However, when the echoes for the single-glint target are 6 dB weaker than echoes for each of the glints in the complex target (-6 dB condition, lower panel), the error peak corresponding to the first glint in the complex target shifts to the left by about 75 to 100 µsec. That is, the bats perceive the single glint (*b*) to be at the objective range of the first glint (a_1) of the complex target when its echoes are presented about 75 to 100 µsec *earlier* than the objective delay for echoes of that first glint. In contrast, the error peak corresponding to alignment of the single glint (*b*) with the second glint (a_2) still appears at the objective range for the second glint. The leftward shift of the error peak for the first glint by 75 to 100 µsec with a 6-dB amplitude change in echoes for *b* is consistent with a -13 to -17 µsec/dB trading relationship between the amplitude of echoes and the latency of neural discharges to those echoes.

INSERT FIG. 9 ABOUT HERE

Figure 10 shows in more detail the shift in the apparent range of the single target (*b*) with respect to the first glint (a_1) of the complex target for one of the bats. The bat's

INSERT FIG. 10 ABOUT HERE

performance is shown on a contour graph of percentage errors for a wider range of amplitudes of the single-glint echoes than are shown in Fig. 9. In Fig. 10, the first glint appears as a ridge sloping upward to the right, and the second glint appears as a ridge aligned vertically. As the amplitude of the echoes simulating the single target is increased from -6 to +9 dB relative to the individual echo components of the complex target, the bat perceives the single target as aligning with the first glint at progressively greater ranges. In contrast, the delay of echoes from the single target aligns with the objective delay of echoes from the second glint at all amplitudes tested. The 15-dB variation in echo amplitude forces the apparent delay of echoes from the single target to shift over a span of about 200 µsec, which corresponds to 3.4 cm. The sloping contour ridge even appears to invert the complex target when the single glint must, paradoxically, appear further away than the second glint to align with the first glint. (This illusion is a consequence of manipulating the amplitude of echoes for *b* rather than for a_1 or a_2.)

Sequential Discrimination: When the bat has to rely on memory of acoustic images to discriminate the complex and simple targets, the effects of echo amplitude are different. Figure 11 shows the results of the two-glint *versus* one-glint sequential

INSERT FIG. 11 ABOUT HERE

discrimination experiment with two *Eptesicus*. When the echoes of the single-glint target have the same amplitude as echoes from either glint in the complex target (0 dB condition, upper panel in Fig. 11), the error peaks corresponding to the two glints again fall at their objective ranges. (These curves are the same as in Fig. 4A because this is Condition A from Experiment I.) However, when the echoes for the single-glint target are reduced in amplitude by 6 dB, the apparent range of the single glint shifts with respect to the range of *both* of the glints in the complex target (-6 dB condition, lower panel in Fig. 11). The size of the shift is in the range of 50 to 75 or 100 μsec. The two glints of the complex target are locked together relative to the single glint in the sequential-presentation task, where the image of the complex target must be retained to perform the discrimination. Figure 12 shows in more detail the performance of one bat for a wider range of amplitudes of the single-glint

INSERT FIG. 12 ABOUT HERE

echoes than are shown in Fig. 11. Here, the contour ridges associated with both glints in the complex target slant upward to the right. The apparent range of the target as a whole follows the shift that, in the simultaneous-presentation task, only affects the relation between the single-glint target and the first glint of the complex target. The size of the shift for the two peaks together is consistent with an amplitude-latency trading relationship of about -13 μsec/dB.

Discussion

In Experiment II, the dissociation of the first and second glints in the complex target from each other relative to the single glint in the simple target confirms the result of Experiment I--that different mechanisms encode their positions along the range axis. Starting at a level 15 dB above the bat's threshold, the latency of N_1 responses in *Eptesicus* are lengthened by about 78 μsec when FM stimuli decrease in amplitude by 6 dB (Fig. 5). The latency of N_4 responses is lengthened by about 108 μsec. To compensate for a greater neural response latency, the weaker echoes from the single-glint target in the "-6 dB" condition of Fig. 9 would have to be presented 78 to 108 μsec earlier (to the left along the delay axis) if their neural responses are to coincide with those representing echoes of the *first* glint of the complex target. The bats suffer this shift in the delay of the single-glint echoes, indicating that the delay of echoes of both the single glint and the first of the double glints probably is represented by the timing of neural discharges in response to the FM sweep (Bodenhamer & Pollak, 1981; Bodenhamer *et al.*, 1979; Pollak *et al.*, 1977; Suga, 1970; Kick & Simmons, 1984). In contrast, the single-glint echoes still appear to the bat to be aligned with the objective delay of the echoes from the *second* glint in the complex target even when they are made 6 dB weaker. Thus, it is not likely that the bat represents the range of the second glint relative to the first by the timing of neural discharges. It is more likely that the bat uses notches in the overall spectrum of the composite echo from the complex target to represent the separation of the two echo components. The arrival of the single-glint echoes on top of the echoes from the second glint of the complex target would obscure these spectral notches in a manner independent of amplitude changes as small as those which produce dramatic shifts in the apparent range of the single glint relative to the first glint in the complex target.

Experiment II confirms another result obtained in Experiment I. The tandem movement of the error peaks corresponding to the double glints in Figs. 11 and 12 demonstrates that, notwithstanding their differing physiological representations early in the auditory processing of echoes, the eventual neural representation of the complex target is positioned in absolute range at a point determined by the delay of echoes from the nearer of the two glints. The spectral information initially used to represent the range of the second glint relative to the first eventually is expressed in terms of absolute target range as this is registered by the timing of the discharges evoked by the first echo component. Evidently the bat converts the spectral information about the second glint to an estimate of its spatial separation from the first glint, using the time-based estimate of the range of the first glint to support construction of the image of the target as a whole. The output of the sonar receiver of *Eptesicus* thus is displayed in the natural spatial domain of the distance along which the target is distributed.

General Discussion

There already is a great deal of evidence that echo spectral information may be used by FM bats for perception of target shape (Beuter, 1980; Bradbury, 1970; Griffin, 1967; Habersetzer & Vogler, 1983; Schmidt, 1988; Simmons et al., 1974; Simmons & Lavender, 1976), but the crucial step taken in the experiments described here is to identify specifically how echo spectral information is incorporated into acoustic images of targets. It is widely assumed that spectral cues are used by FM bats, and FM bats certainly can distinguish between targets reflecting echoes that differ in their spectra, but none of this addresses what bats actually perceive when presented with complex targets. We have found that they perceive images which are organized along a psychological target-range axis. This result reconciles the extraordinarily fine acuity of less than 1 μsec for echo delay in the time-domain (Moss & Schnitzler, in press; Simmons, 1979) with the possible representation of the spectrum of echoes in the frequency-domain (Simmons & Grinnell, 1988).

The present experiments demonstrate how spectral information is integrated with temporal information to express spectrally-encoded target shape as the range profile of the target. To perceive the small range separations between glints in biologically realistic targets (Simmons and Chen, in press), the bat would have to register the absolute range of the target with considerable accuracy-- certainly greater accuracy than the 1 to 2 cm needed to intercept insect prey (Trappe, 1982; Webster and Griffin, 1962). For example, if the bat perceives a change of less than a millimeter in the range separation of two glints in a target, as *Eptesicus* has been shown to do (Simmons, *et al.*, 1974), the axis of range must be perceived in increments at least as small as a fraction of a millimeter to support such perception (Simmons and Stein, 1980).

In contrast to the prevailing view of echolocation by FM bats, in which target ranging with delay cues and shape perception with spectral cues are treated as separate processes (Habersetzer and Vogler, 1983; Neuweiler, *et al.*, 1980; Schmidt, 1988; Suga, 1988), we find that perception of range and shape are integrated together through creation of a synthetic perceptual dimension of range that expresses both kinds of information. In principle, this mutual arrangement is to be expected in echolocation (Simmons, *et al.*, 1974) because the time and frequency domains are no more than different representations of the same information, and much disparate stimulus information must of necessity be combined to achieve the evident unity of perception. Furthermore, previous experiments implicate the time domain as the form taken by the output of the bat's sonar receiver (Simmons, 1979; Simmons and Stein, 1980). Any property of echoes that might be conveyed by the spectrum and initially encoded on the auditory system's tonotopic maps will naturally appear in the time domain as an "event" along the delay or range axis if the output indeed does take a time-domain form. The possibility that FM bats actually might do this (Simmons, 1980; Simmons and Stein, 1980) typically has been rejected because, although the anatomical basis for spectral coding (tonotopy) is well-known, the physiological basis for fine temporal acuity in the microsecond range is not so obvious (Schmidt, 1988). The failure of physiologically-based arguments to seriously consider this possibility illuminates a weakness in the neuroethological approach to behavior that will require a closer relationship with a psychological approach to overcome it.

The neural response-latency shifts that form the basis for Experiment II amount to about 13 to 18 μsec/dB, which is equivalent to a shift of about 2 to 3 mm/dB in target range. The behavioral experiments show that *Eptesicus* indeed does experience such shifts in the apparent range of targets, so their occurrence must be taken into consideration when thinking about echolocation under conditions where echo amplitudes can be expected to change. The size of the shift is insignificant with respect to the accuracy of 1 to 2 cm needed to capture prey if the change in echo amplitude is only a decibel or two. However, when a bat approaches a flying insect, echoes from that insect can be expected to grow in amplitude by 40 to 60 dB or more, depending upon how large a segment of the pursuit maneuver one looks at (Griffin, 1958; Kick and Simmons, 1984). For such large changes in echo amplitude, the target-ranging process would surely be greatly disrupted if latency shifts of up to nearly a millisecond were to occur in neural responses to a succession of echoes. Behavioral experiments have also shown that *Eptesicus* regulates its hearing sensitivity as targets become closer by raising its hearing thresholds for echoes at a rate of about 11 to 12 dB for each halving of range (Kick and Simmons, 1984). A substantial portion of this regulation may be accomplished by the degree to which the middle-ear muscles are partially contracted at delays up to 5 to 8 msec following each emission. Regulation of echo sensitivity by the middle ear would keep the amplitude of echoes stimulating the inner ear at a constant level throughout a large part of the approach to a target. Experiment II establishes the practical importance of some such mechanism for preventing latency shifts from distorting the perception of target range.

Neural mechanisms of image formation: Target range is determined from echo delay (Simmons, 1973) and is represented in the bat´s auditory cortex by neurons that selectively respond to pulse-echo pairs with particular echo delays (O´Neill & Suga, 1982; Suga, 1988; Suga & Horikawa, 1986; Suga & O´Neill, 1979; Sullivan, 1982; Wong and Shannon, 1988). The frequencies in the FM sweep of echoes are represented topographically by tonotopic maps that are repeated at every stage of the auditory system from the inner ear to the auditory cortex (Suga, 1988, for example). Our working hypothesis is that the formation of acoustic images of targets takes place as a result of the convergence of information from frequency maps, which represent the spectrum of echoes using coordinates of frequency and amplitude, with information from range maps, which represent the delay of echoes using coordinates of time and amplitude (Suga, 1988). We presume that the conversion of echo spectral information back into range information occurs because frequency maps can "talk to" range maps, most likely at the level of the auditory cortex.

The mustached bat, *Pteronotus parnellii*, is the species in which the neural representation of echoes has been most extensively studied. Only in this species is the topographical representation of echo delay on computed target range maps well described. In *Pteronotus*, the neural display of target range occurs in at least three distinct cortical zones that are thoroughly segregated from other cortical regions representing the frequency of echoes (Suga, 1988). *Pteronotus*, however, emits CF/FM echolocation sounds and invests heavily in the neural machinery for identification of prey by detecting rapid modulations of CF echoes caused by the wing-beats of insects (Henson, *et al*., 1987; see also Neuweiler, *et al*., 1980, and Schnitzler, *et al*., 1983). In contrast, *Eptesicus* and other FM bats are committed to using only FM signals to identify prey. This does not preclude the perception of wing-beats to determine whether targets are in fact insects (Sum and Menne, 1988), but the bat must process FM rather than CF echoes to do so. In the FM bat, *Myotis lucifugus*, the tonotopic and range maps are not completely segregated as they are in *Pteronotus*; instead, they are found to overlap one another in one region of the auditory cortex (Wong and Shannon, 1988). In addition, the range map appears to be less precisely defined in FM bats than in *Pteronotus*. Our very preliminary observations suggest that this is also the case in *Eptesicus*. The nature of the transformation of spectral cues into images has been specified well enough in the behavioral data presented above to raise the possibility that overlap of frequency and time maps may be an integral part of the process whereby spectral and temporal features of echoes are fused.

The range separation of glints in a complex target evidently is represented by the location and spacing of notches in the spectrum of echoes. However, the location and spacing of spectral notches is perceived as a spacing of delays between echo components along a time scale--that is, along a scale that is the reciprocal of frequency. It would be difficult for the spectral representation of the range profile of a target to smoothly and seamlessly be transformed into the range profile itself without taking into account this reciprocal relationship. What is the tonotopic axis of frequency like in *Eptesicus*? At present, published data exist only for the nucleus of the lateral lemniscus in our species (Covey and Casseday, 1986). Fig. 13 shows these data plotted on axes that are linear with period, or

INSERT FIG. 13 ABOUT HERE

the reciprocal of frequency (hyperbolic with frequency). The data-points for the tonotopic map fall along a straight line with a correlation coeficient of -0.99, which is highly significant. It appears as though *Eptesicus* indeed represents the frequency of echoes along a scale having equal intervals of time rather than frequency.

The process of image formation by *Eptesicus* is shown schematically in Fig. 14. This diagram is to be considered a cartoon of the process rather than a quantitative model in every

INSERT FIG. 14 ABOUT HERE

detail. The target in Fig. 14, which is a moth at range r, is simplified acoustically into two glints, A and B, separated by a range difference of Δr. To perceive the target´s location and shape, the bat emits FM sonar sounds with a spectrogram structure similar to what is shown in Fig. 7. The echoes arrive after some delay, t, and have two components separated by the time-interval, Δt. The size of this time interval is determined by the range separation of the two glints in the target. The bat´s auditory system initially encodes the emission and then the echo as spectrograms consisting of patterns of excitation in the Organ of Corti (shaded areas) and neural discharges (dots) marking the time-of-occurrence of each frequency in the FM sweep. The frequency scale for these spectrograms is presumed to be hyperbolic (Fig. 13). The delay of echoes is encoded by the spectrogram delay of the echo representation, which consists of the time, t_f, between responses to the emission and to the echo at each frequency, f (Simmons and Kick, 1984; Suga, 1988). The range separation, Δr, of the glints, A and B, or the time separation of their echo components, Δt, appears in the echo as a series of notches in the spectrum (*) separated by a frequency interval, Δf, which is the reciprocal of the time separation of the echo components. These spectral notches have a peculiar manifestation in the neural spectrogram as a consequence of the reduced echo amplitude at frequencies near the center of each notch, which creates longer response latencies at these frequencies compared to other frequencies in the echo. The neural spectrogram thus has a scalloped appearance, with the spectral notches being marked by longer latencies as well as weaker response strength.

The spectrogram delays at each frequency are eventually represented topographically on an echo-delay or target-range map in the auditory cortex (O'Neill and Suga, 1982; Suga, 1988; Suga and Horikawa, 1986; Suga and O'Neill, 1979; Sullivan, 1982; Wong and Shannon, 1988). The schematic range map in Fig. 14 is the "auditory display" for target range. Neurons in the range map respond selectively to a particular region of delay for a particular frequency or span of frequencies. They also selectively respond to a specific range of echo amplitudes. In effect, the cortical location of delay-tuned neurons represents particular values of t_f, the spectrogram delay. The separation of tuned delays from one neuron to the next, *dt*, along with the sharpness of delay tuning, must constitute the resolution or "grain" of the range display at the single-cell level. Estimates of the sharpness of delay tuning fall in the region of hundreds of microseconds to milliseconds, which is very large compared to the behavioral acuity in *Eptesicus* of at least 1 µsec. New experiments indicate that this behavioral acuity is less than 0.4 µsec (Moss and Schnitzler, in press) and may be as small as 10 to 12 nsec (Simmons and Altes, in preparation). The spacing of adjacent delay-tuned neurons is unknown in FM bats, but it has been estimated to be on the order of 50 to 100 µsec in the CF/FM bat, *Pteronotus parnellii* (O'Neill and Suga, 1982; Suga and O'Neill, 1979). Presumably, creation of the perceptual range-axis image of a single-glint target, *A* (shown schematically at the bottom of Fig. 14 as a shaded peak that is narrower than the summed neural activity on the map), involves integration of estimates of the spectrogram delay across frequencies in the FM sweep. The demonstrated sharpness of the image of *A* requires interpolation and possibly other processes to "read" the range map, too.

The presence of notches in the spectrum of echoes should have two effects on the neural activity evoked in the range map. First, in the frequency region of the notches less activity will occur, or activity will be confined to neurons that are tuned to lower amplitudes than at other frequencies. Second, estimates of the spectrogram delay for frequencies close to the notch will be displaced to greater delays as a consequence of the greater response latency at notch frequencies. That is, the scalloped appearance of the neural spectrogram of echoes will be carried over into the activity on the range map when the spectrogram delays are transposed onto a topographic representation. The spectral notches are also represented along tonotopic maps at other sites in the auditory system, including one that overlaps the range map in the auditory cortex. Our behavioral experiments show that the location and spacing of these spectral notches is used to create new events along the delay axis at time separations related to the periods of the frequencies where the notches occur. The hyperbolic or period scale of the frequency axis may facilitate this computation. In Fig. 14 this transformation is shown as a shaded arrow extending from the notch frequencies to the perceptual image of the second glint, *B*, in the target´s image. We are presently engaged in further behavioral and physiological experiments to identify the nature of this transformation in more detail.

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REFERENCES

Altes, RA (1976) Sonar for generalized target description and its similarity to animal echolocation systems. J Acoust Soc Am, 59: 97-105

Altes, RA (1980) Detection, estimation, and classification with spectrograms. J Acoust Soc Am, 67: 1232-1246

Altes, RA (1981) Echo phase perception in bat sonar? J Acoust Soc Am, 69: 1232-1246

Beuter, KJ (1980) A new concept of echo evaluation in the auditory system of bats. In R-G Busnel and JF Fish (eds) Animal sonar systems, Plenum Press, New York, pp 747-761

Bodenhamer RD, and Pollak, GD (1981) Time and frequency domain processing in the inferior colliculus of echolocating bats. Hearing Res, 5: 317-355

Bodenhamer, RD, Pollak, GD and Marsh, DS (1979) Coding of the fine frequency information by echoranging neurons in the inferior colliculus of the Mexican free-tailed bat, Brain Res, 171: 530-535

Bradbury, JW (1970) Target discrimination by the echolocating bat vampyrum spectrum. J Exp Zool, 173: 23-46

Busnel, R-G and Fish, JF (1980) Animal sonar systems. Plenum Press, New York

Covey, E and Casseday, JH (1986) Connectional basis for frequency representation in the nuclei of the lateral lemniscus of the bat Eptesicus fuscus. J Neurosci, 6: 2926-2940

Dalland, JI (1965) Hearing sensitivity in bats. Science, 150: 1185-1186

Feng, AS, Simmons, JA and Kick, SA (1979) Echo detection and target-ranging neurons in the auditory system of the bat Eptesicus fuscus. Science, 202: 645-648

Gardner, RE and Garvey, WT (1974) Directional sensitivity of the auditory system in bats producing FM signals. Honors thesis, Washington Univ., St. Louis

Griffin, DR (1958) Listening in the Dark. Yale Univ. Press, New Haven, CT (2nd ed., Cornell Univ. Press, Ithaca, NY, 1986)

Griffin, DR (1967) Discriminative echolocation by bats. In R-G Busnel (ed) Animal sonar systems: Biology and bionics, Laboratoire de physiologie acoustique, Jouy-en-Josas, France, pp 273-300

Griffin, DR, Friend, JH and Webster, FA (1965) Target discrimination by the echolocation of bats. J Exp Zool, 158: 155-168

Habersetzer, J and Vogler, B (1983) Discrimination of surface-structured targets by the echolocating bat <u>Myotis myotis</u> during flight. J Comp Physiol, 152: 275-282

Henson, OW, Jr, Bishop, AL, Keating, AW, Kobler, JB, Henson, MM, Wilson, BS and Hansen, RC (1987) Biosonar imaging of insects by <u>Pteronotus p. parnellii</u>, the mustached bat. National Geographic Res, 3: 82-101

Kick, SA (1980) Target detection and the operational range of sonar in the bat, <u>Eptesicus fuscus</u>. Doctoral thesis, Washington Univ., St. Louis

Kick, SA and Simmons (1984) Automatic gain control in the bat's sonar reciever and the neuroethology of echolocation. J Neurosci, 4: 2705-2737

Nachtigall, P (1988) Animal sonar: Processes and performance. Plenum press, New York

O'Neill WE and Suga, N (1982) Neural encoding of target range and its representation in the auditory cortex of the mustached bat. J Neurosci, 47: 225-255

Pollak, GD, Marsh, DS, Bodenhamer, R and Souther (1977) Characteristics of phasic on neurons in the inferior colliculus of unanesthetized bats with observations relating to mechanism for echo ranging. J Neurophys, 40: 926-941

Schmidt, S (1988) Evidence for a spectral basis of texture perception in bat sonar. Nature, 331: 617-619

Simmons, JA (1973) The resolution of target range by echolocating bats. J Acoust Soc Am, 54: 157-173

Simmons, JA (1979) Perception of echo phase information in bat sonar. Science, 207: 1336-1338.

Simmons, JA (1980) The processing of sonar echoes by bats. In R-G Busnell and JF Fish (eds) Animal sonar systems, Plenum Press, New York, pp 695-714

Simmons, JA (1987) Acoustic images of target range in the sonar of bats. Naval Res Rev, 39: 11-26

Simmons, JA and Chen, L (in press) The acoustic basis for target discrimination by FM echolocating bats. J Acoust Soc Am

Simmons, JA, Fenton, MB Ferguson, WR, Jutting, M, and Palin, J (1979) Apparatus for research on animal ultrasonic signals. Royal Ontario Museum Publications in Life Sciences, Toronto

Simmons, JA, Freedman, EG, Stevenson, SB, Chen, L and Wohlgenant, TJ (in press) Clutter interference and the integration time of echoes in the echolocating bat, Eptesicus fuscus. J Acoust Soc Am

Simmons, JA and Grinnell, AD (1988) The performance of echolocation: The acoustic images perceived by echolocating bats. In P Nachtigall (ed) Animal sonar: Processes and performance, New York, Plenum Press, in press

Simmons, JA and Kick, SA (1974) Physiological mechanisms for spatial filtering and image enhancement in the sonar of bats. Ann Rev Physiol, 46: 599-614

Simmons, JA and Lavender, WA (1976) Representation of target range in the sonar receivers of echolocating bats. J Acoust Soc Am suppl., 60: S5

Simmons, JA, Lavender, WA, Lavender, BA, Doroshow, DA, Kiefer, SW, Livingston, R, Scallet, AC and Crowley, DE (1974) Target structure and echo spectral discrimination by echolocating bats. Science, 186: 1130-1132

Simmons, JA, and Stein, RA (1980) Acoustic imaging in bat sonar: Echolocation signals and the evolution of echolocation. J Comp Physiol, 135: 61-81

Suga, N (1970) *Echo-ranging neurons in the inferior colliculus of* bats. Science, 170: 449-452

Suga, N (1988) Auditory neuroethology and speech processing: Complex-sound processing by combination-sensitive neurons. In GM Edelman, WE Gall and WM Cowan (eds) Auditory function, Wiley, New York, pp 679-720

Suga, N and Horikawa, J (1986) Multiple time axes for representation of echo delays in the auditory cortex of the mustached bat, J Neurophysiol, 55: 776-806

Suga, N and Jen, PH-S (1977) Further studies on the peripheral auditory system of "CF-FM" bats specialized for fine frequency analysis of Doppler-shifted echoes, J Exp Biol, 69: 207-232

Suga, N and O'Neill, WE (1979) Neural axis representing target range in the auditory cortex of the mustache bat. Science, 206: 351-353

Sullivan, WE (1982) Neural representation of target distance in auditory cortex of the echolocating bat Myotis lucifigus. J Neurophys, 48: 1011-1032

Sum, YW and Menne, D (1988) Discrimination of fluttering targets by the FM-Bat *Pipistrellus stenopterus*? J Comp Physiol A, 163: 349-354

Trappe, M (1982) Verhalten und Echoortung der Grossen Hufeisennasse (Rhinolophus ferrumequinum) beim Insektenfang. Ph.D. Thesis, Univ. Marburg

Webster, FA and Griffin, DR (1962) The role of the flight membrane in insect capture by bats. Animal Behav, 10: 332-340

Wong, D and Shannon, SL (1988) Functional zones in the auditory cortex of the echolocating bat, Myotis lucifigus. Brain Res, 453: 349-352

Figure Captions

Fig. 1. Diagram of the two-choice discrimination procedure for studying perception of complex targets. Bats chose between a two-component complex target (a_1 and a_2) with electronically-simulated echoes arriving 100 μsec apart (Δt) at fixed delays of 3.275 and 3.375 msec (simulated ranges of 56.47 and 58.19 cm, respectively) and a one-component simple target (*b*) whose echoes arrived at delays varying from 3.125 to 3.450 msec (ranges from 53.88 to 59.48 cm). The bat´s sonar sounds were picked up at microphones (*m*), digitally delayed, and then returned to the bat from loudspeakers (*s*) as echoes.

Fig. 2. A graph of the frequency response of the left and right channels of the target simulator shown in Fig. 1. The sonar signals of *Eptesicus* contain energy from about 23 to 100 kHz, and the simulator returned the entire first harmonic (60 to 23 kHz) as well as most of the second harmonic up to about 85 kHz.

Fig. 3. Echo delay discrimination data from *Eptesicus* for two single-glint simulated targets, replotted from Simmons (1973). The procedure is equivalent to discrimination of a_1 from *b* in Fig. 1. The shape of this curve is not changed as absolute delay or range changes. The zero point on the delay axis corresponds to the delay of echoes for a_1.

Fig. 4. Graphs from Experiment I showing percentage of errors produced by two bats (circles and triangles) in three different experimental conditions. (**A**) with two glints (a_1 and a_2) presented together as one complex target, (**B**) with the spectral effects of adding two glints created instead by filtering echoes of the first glint without presentation of the second glint at all, and (**C**) with separate, alternating presentation of the two glints from one emission to the next, using a jitter technique. Percentage errors is plotted as a function of the delay separation between the simple target (b) and the first glint (a_1) of the complex target. Zero indicates that the delay of echoes b and a_1 coincided.

Fig. 5. A graph showing the relative frequency response of the target simulator when two echo components are presented 100 µsec apart (glints--dashed line) compared with the frequency response created when parallel band-pass filters are used to impose peaks and notches in the spectrum of the echo from a single glint (filters--solid line).

Fig. 6. The impulse response of the target simulator when two echo components are presented (*glints*--upper curve) compared with the impulse response created by filtering the echo of a single glint (*filters*--lower curve).

Fig. 7. Spectrograms of representative echolocation sounds from each bat (triangle and circle data-points from Fig. 4) recorded during discrimination of echoes simulating two glints presented in alternation (Expt. I, Condition C). The sounds produced during trials in all conditions of both experiments are similar in all respects to these examples. The bats emit these sounds at rates up to 15 sounds per second prior to making their choice.

Fig. 8. A graph showing the dependence of the time-of-occurrence of neural responses on the amplitude of FM sounds in the auditory system of *Eptesicus fuscus*. (**A**) The N_1 (auditory nerve) evoked-potential latency for two bats (circles and triangles) shortens by 0.55 msec as stimulus amplitude increases from near threshold to 40 dB above threshold. (B) Averaged evoked potentials (inset) from one bat illustrate how the latency of the N_1 through N_4 (lateral lemniscus) responses systematically shortens as the FM sounds become stronger. At a level 15 dB above threshold, the slope of the N_1 latency function is about -13 μsec/dB and the slope of the N_4 function is nearer -18 μsec/dB.

Fig. 9. Results for two bats (circles & triangles) on *simultaneous* discrimination between the simple and complex targets (Experiment II). Percentage of errors is plotted as a function of the delay separation between the complex and simple targets. At zero on the abscissa echoes from the simple target

(*b*) coincide in delay with echoes from the first glint (a_1) of the complex target. Data are shown for conditions in which the simple target's echoes are equal in strength to echoes from each of the components of the complex target (*0 dB*, upper plot) and in which the simple target's echoes are half as strong (*-6 dB*, lower plot).

Fig. 10. More detailed data for one bat from Fig. 9 (circles) plotted as percentage-error contours over a 15-dB span of amplitude differences between echoes. Heavy sloping line shows the -13 μsec/dB latency shift of N_1 evoked responses (Fig. 5). Contour intervals based on a scale of 1-6 (shown as Scale C to the right of Fig. 9).

Fig. 11. Results for two bats (circles & triangles) on *sequential* discrimination between the simple and complex targets (Experiment II). Otherwise as described for Fig. 9.

Fig. 12. More detailed data for one bat from Fig. 11 (circles). Otherwise as described for Fig. 10. (Contours shown as Scale C to the right of Fig. 11).

Fig. 13. A graph showing the frequency map derived from experiments in the nucleus of the lateral lemniscus of *Eptesicus* (Covey and Casseday, 1986). The anatomical position of frequency-tuned cells across the ventral portion of the nucleus

is plotted on a scale that is linear with period (reciprocal of frequency--hyperbolic with frequency).

Fig. 14. A schematic diagram showing the process whereby acoustic images of complex targets are formed in the sonar receiver of *Eptesicus* (see text).

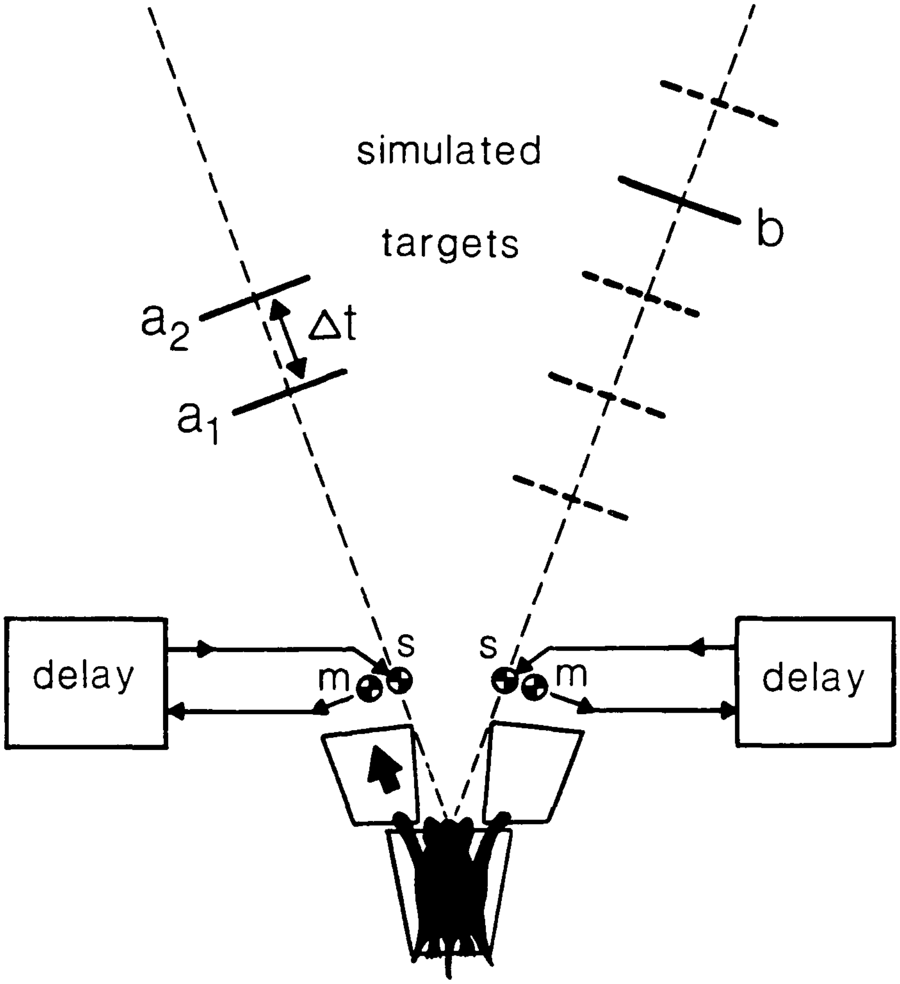


Figure 1

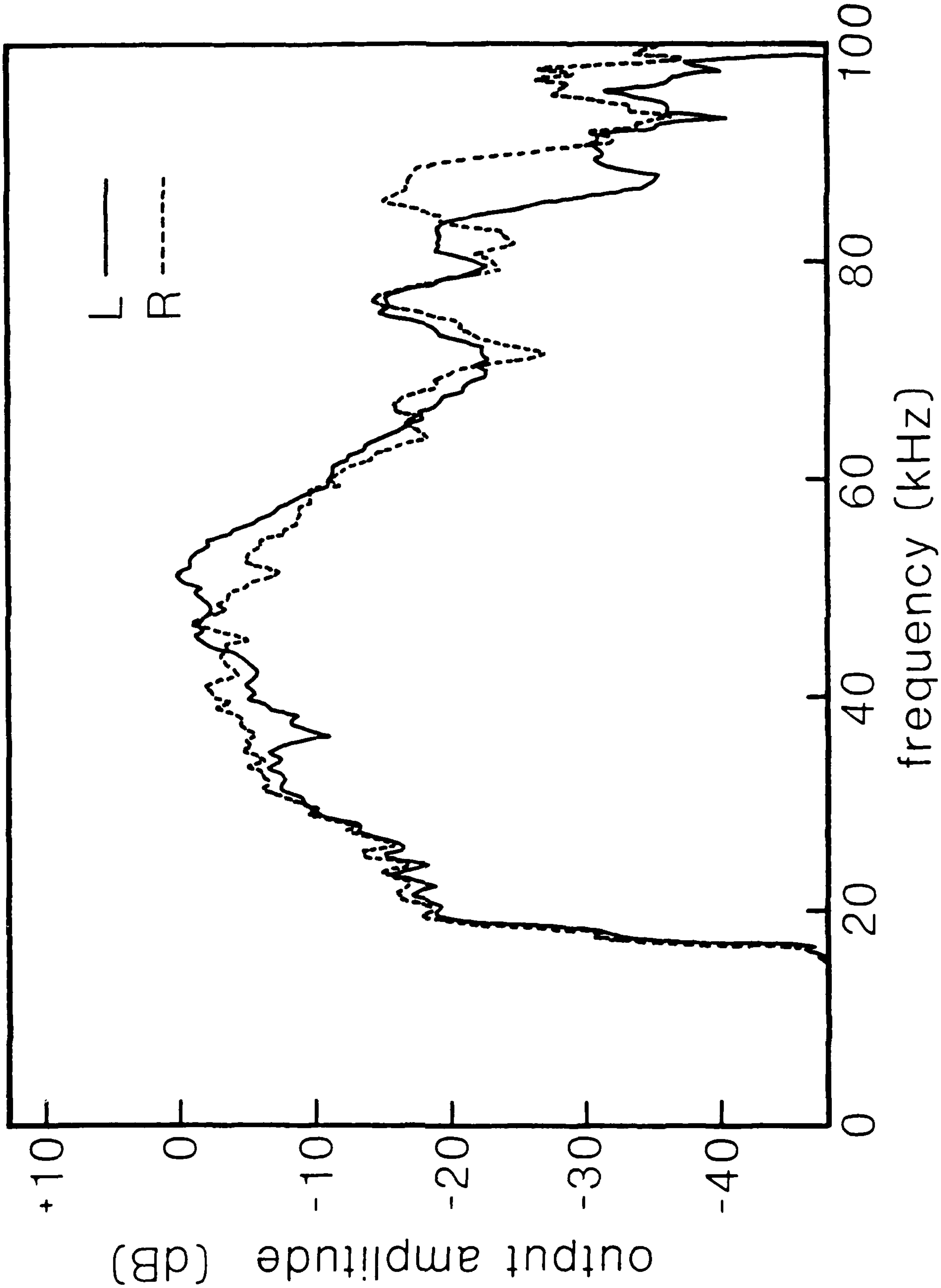

output amplitude (dB)
+10
0
-10
-20
-30
-40
frequency (kHz)
0
20
40
60
80
100
L
R

Figure 2

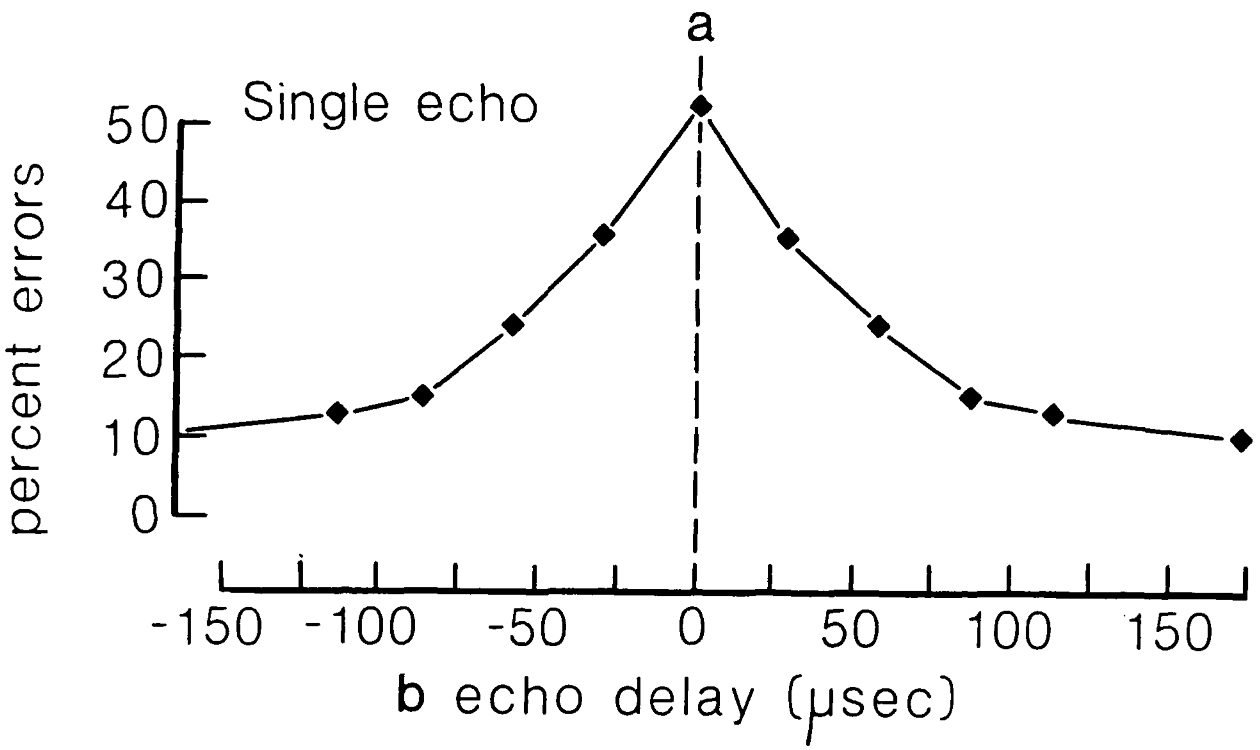

a
Single echo
50
40
30
20
10
0
percent errors
-150
-100
-50
0
50
100
150
b echo delay (μsec)

Figure 3

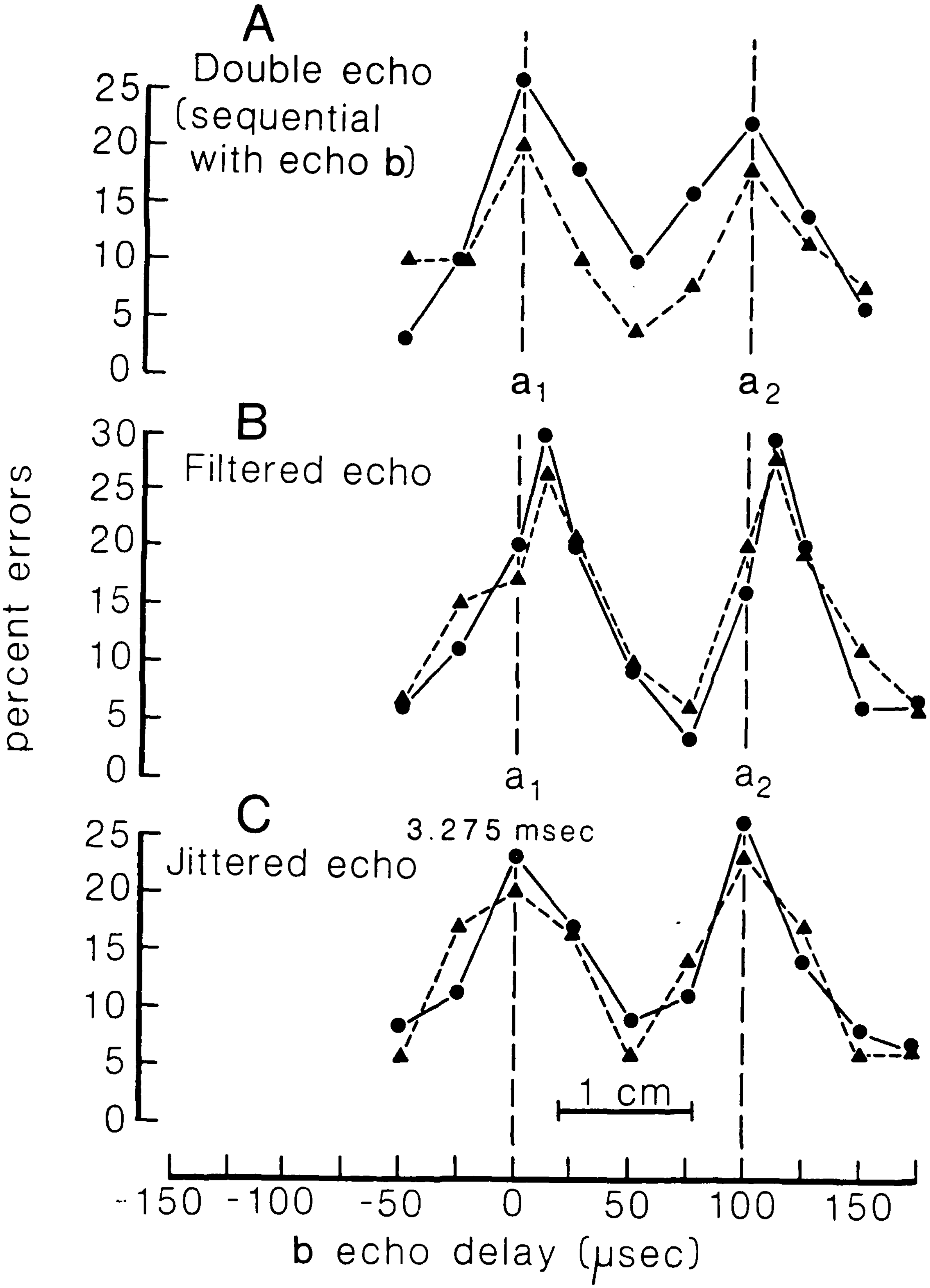

A
Double echo
(sequential
with echo b)
B
Filtered echo
C
Jittered echo
3.275 msec
percent errors
25
20
15
10
5
0
30
a1
a2
1 cm
-150
-100
-50
0
50
100
150
b echo delay (μsec)

Figure 4

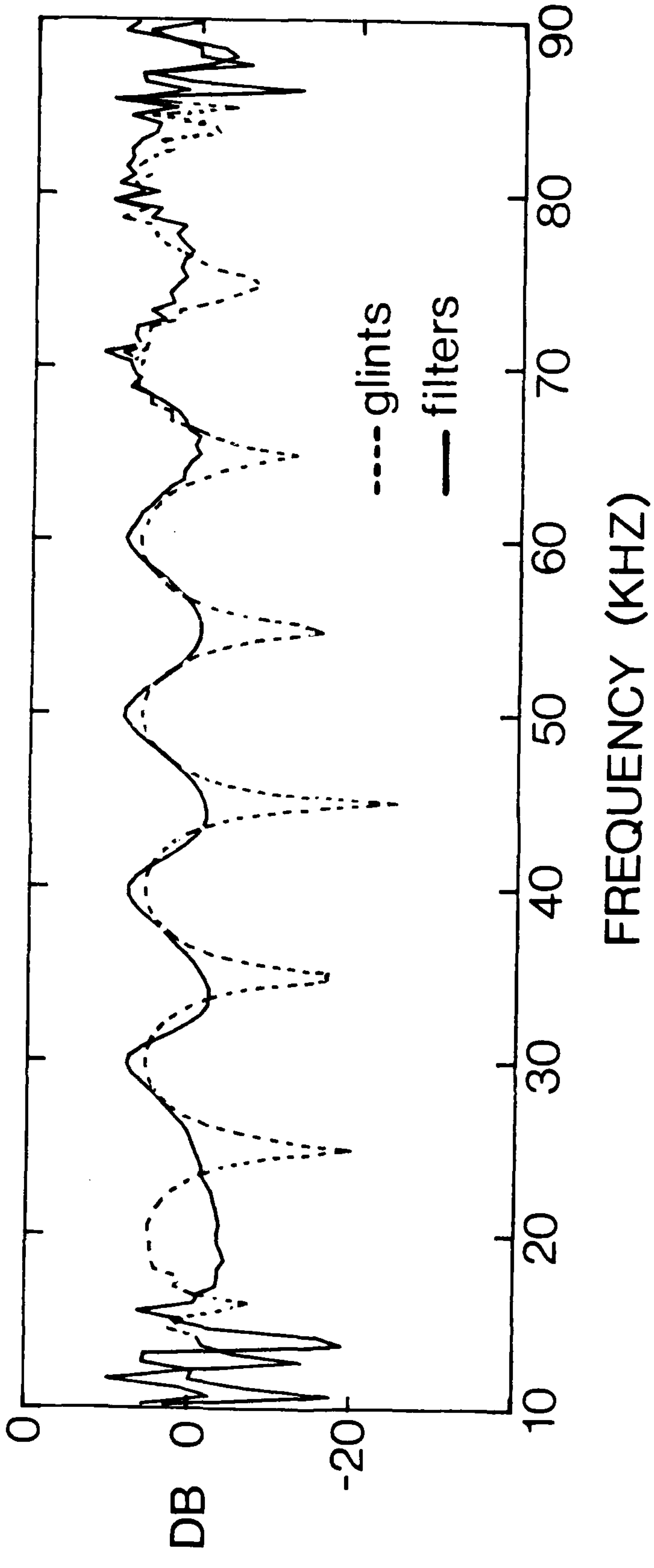


Figure 5

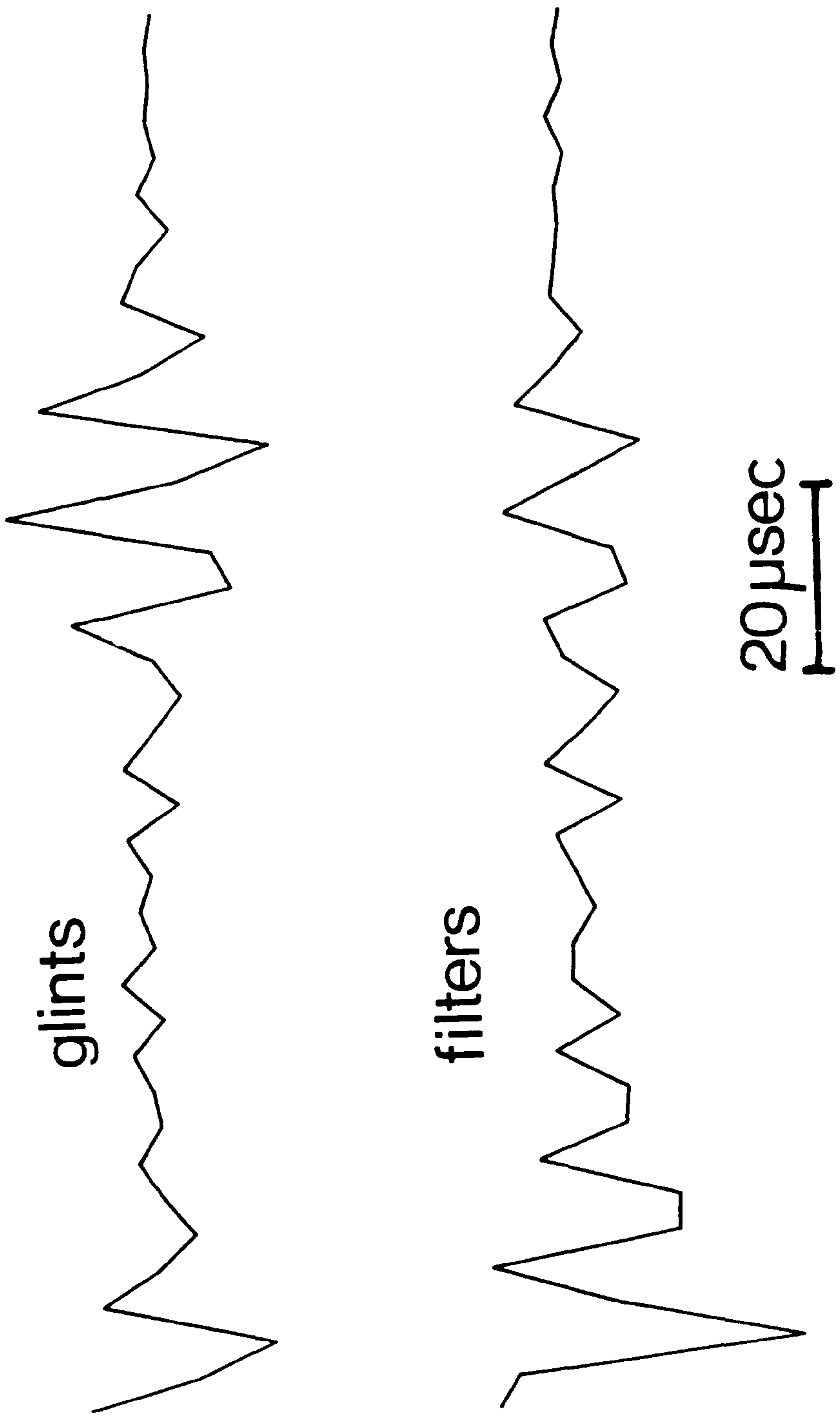


Figure 6

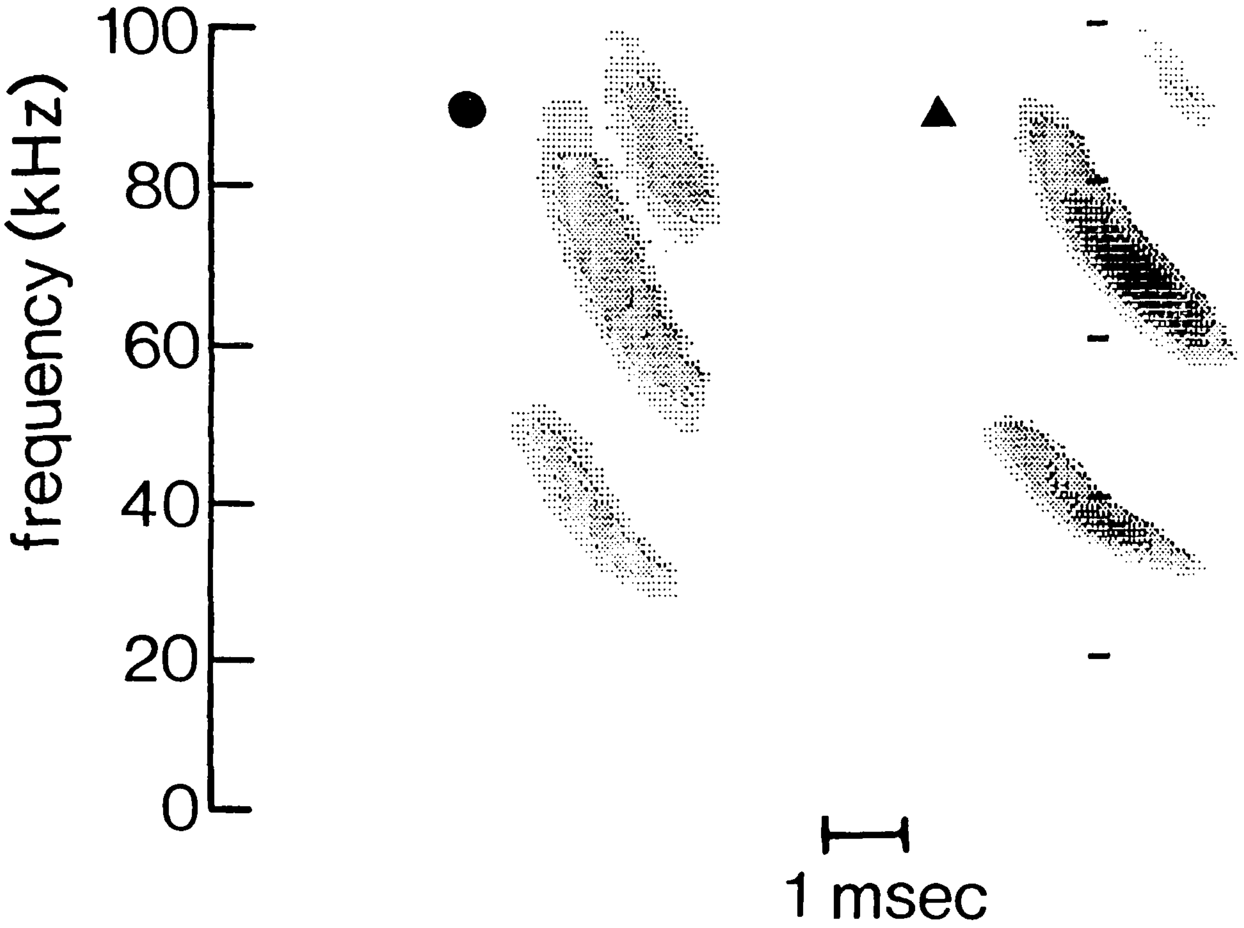


Figure 7

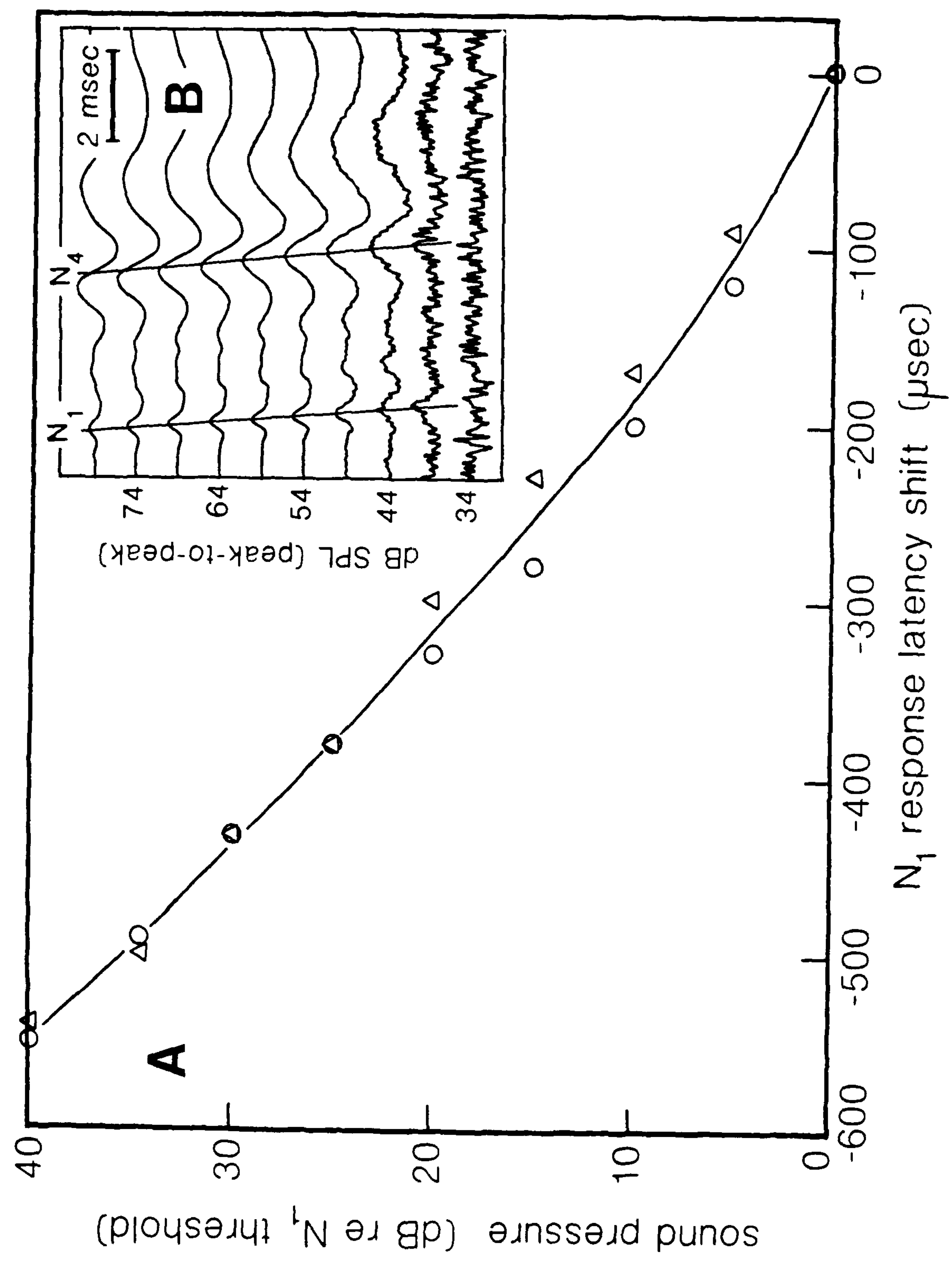

A
B
sound pressure (dB re N$_1$ threshold)
40
30
20
10
0
-600
-500
-400
-300
-200
-100
0
N$_1$ response latency shift (µsec)
dB SPL (peak-to-peak)
74
64
54
44
34
N$_1$
N$_4$
2 msec

Figure 8

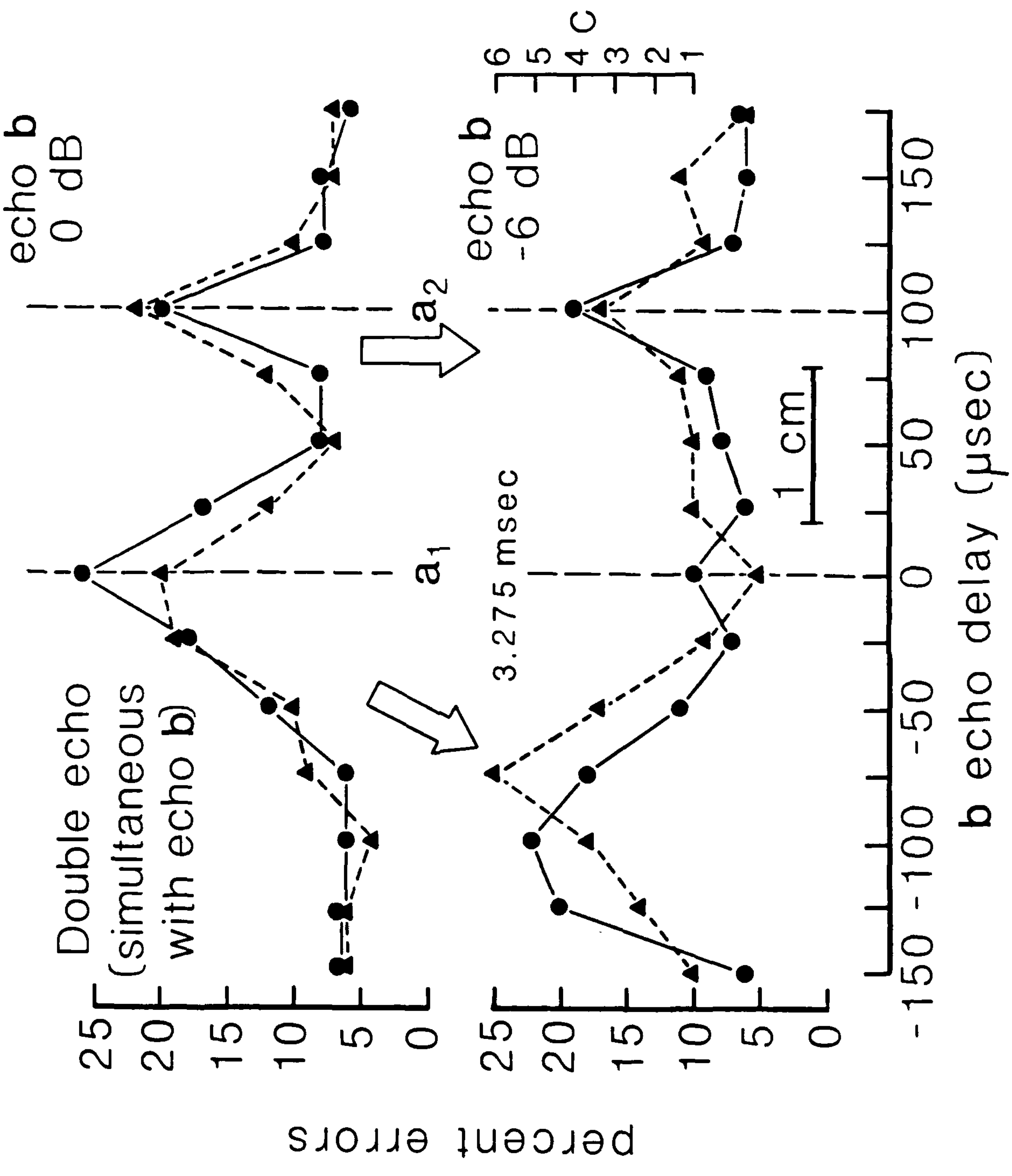

Double echo
(simultaneous
with echo b)
echo b
0 dB
echo b
-6 dB
a1
a2
3.275 msec
1 cm
percent errors
25
20
15
10
5
0
b echo delay (μsec)
-150
-100
-50
0
50
100
150
C
6
5
4
3
2
1

Figure 9

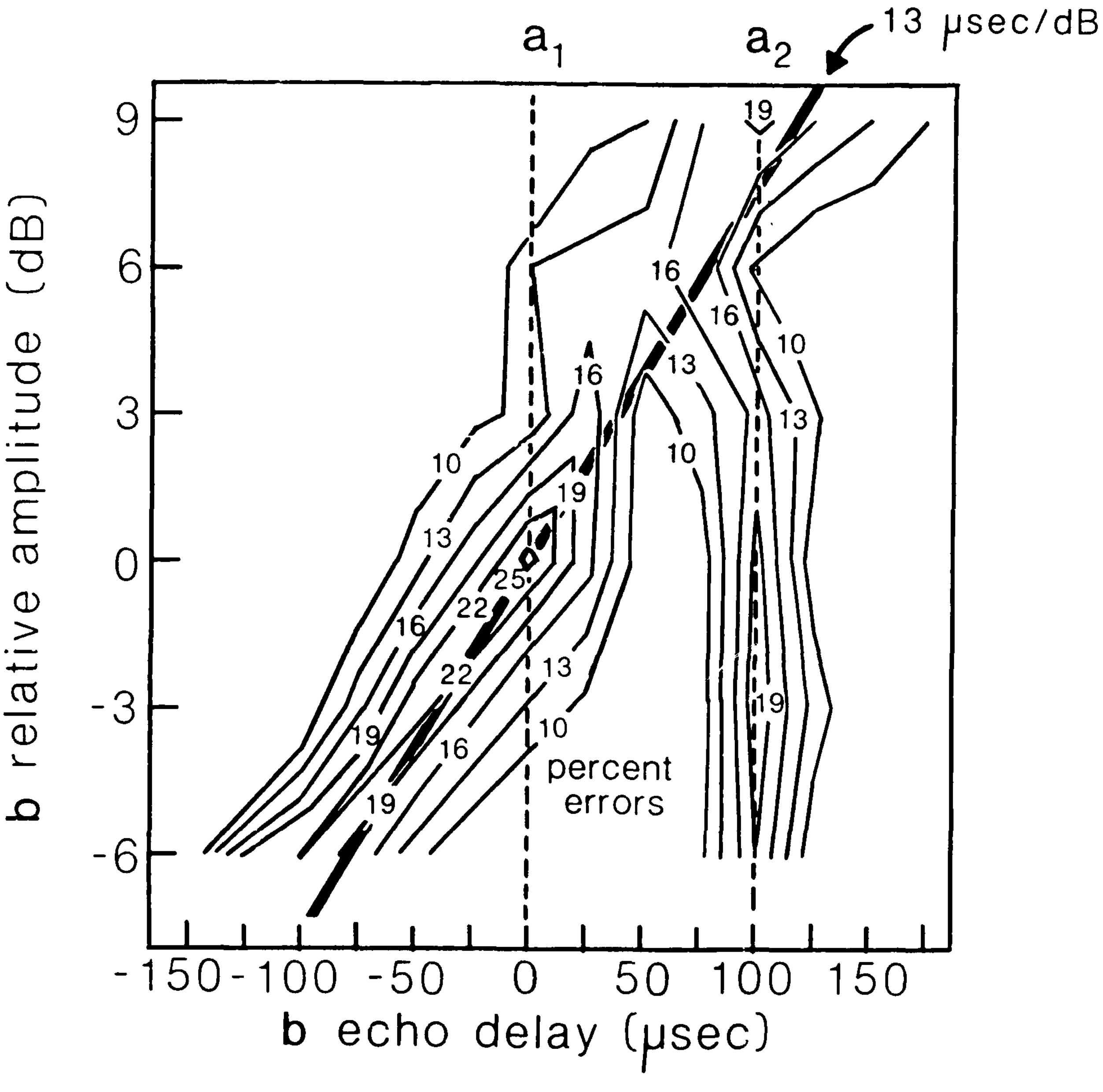

a1
a2
13 µsec/dB
9
6
3
0
-3
-6
b relative amplitude (dB)
-150
-100
-50
0
50
100
150
b echo delay (µsec)
10
13
16
19
22
25
percent errors

Figure 10

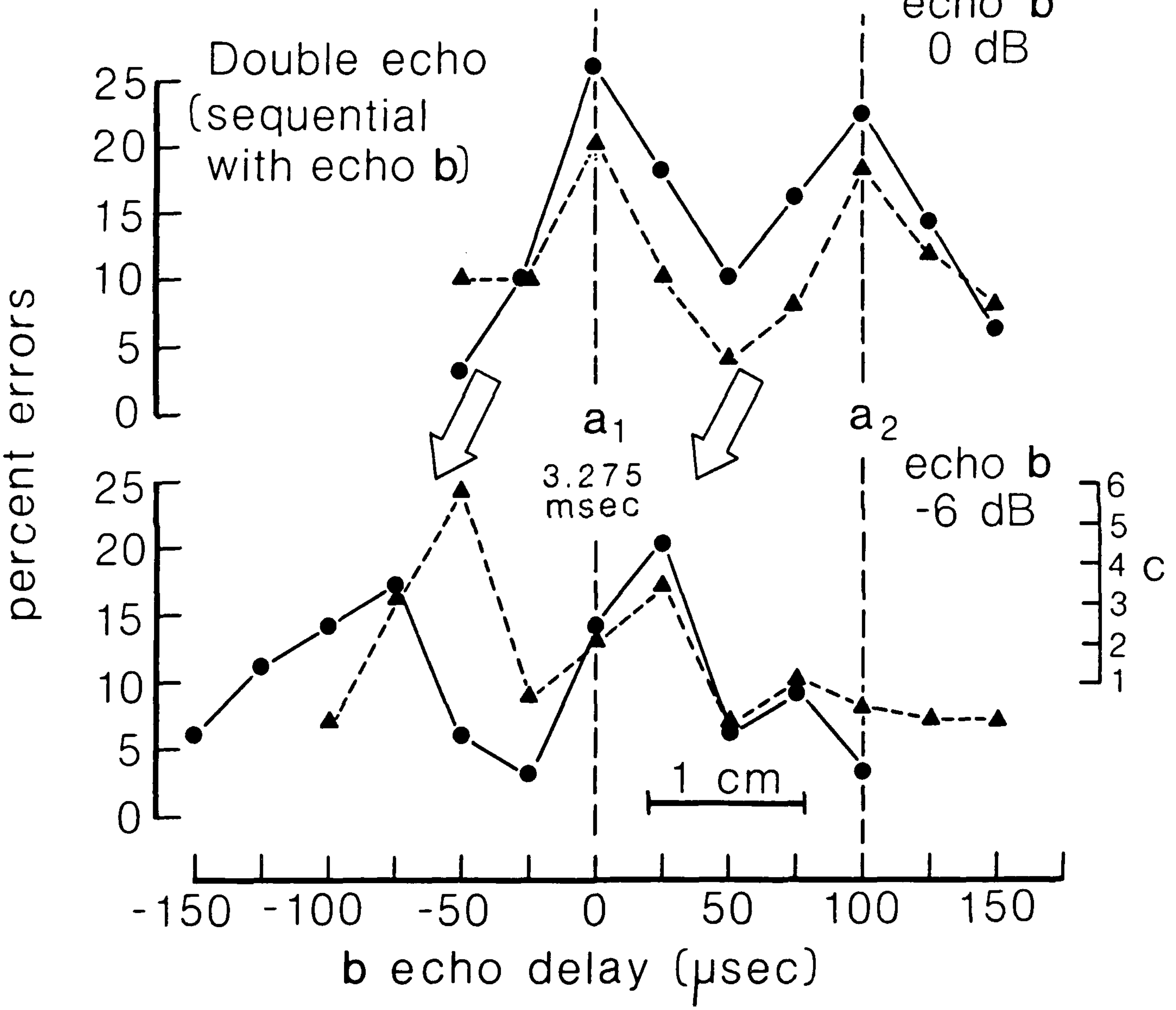
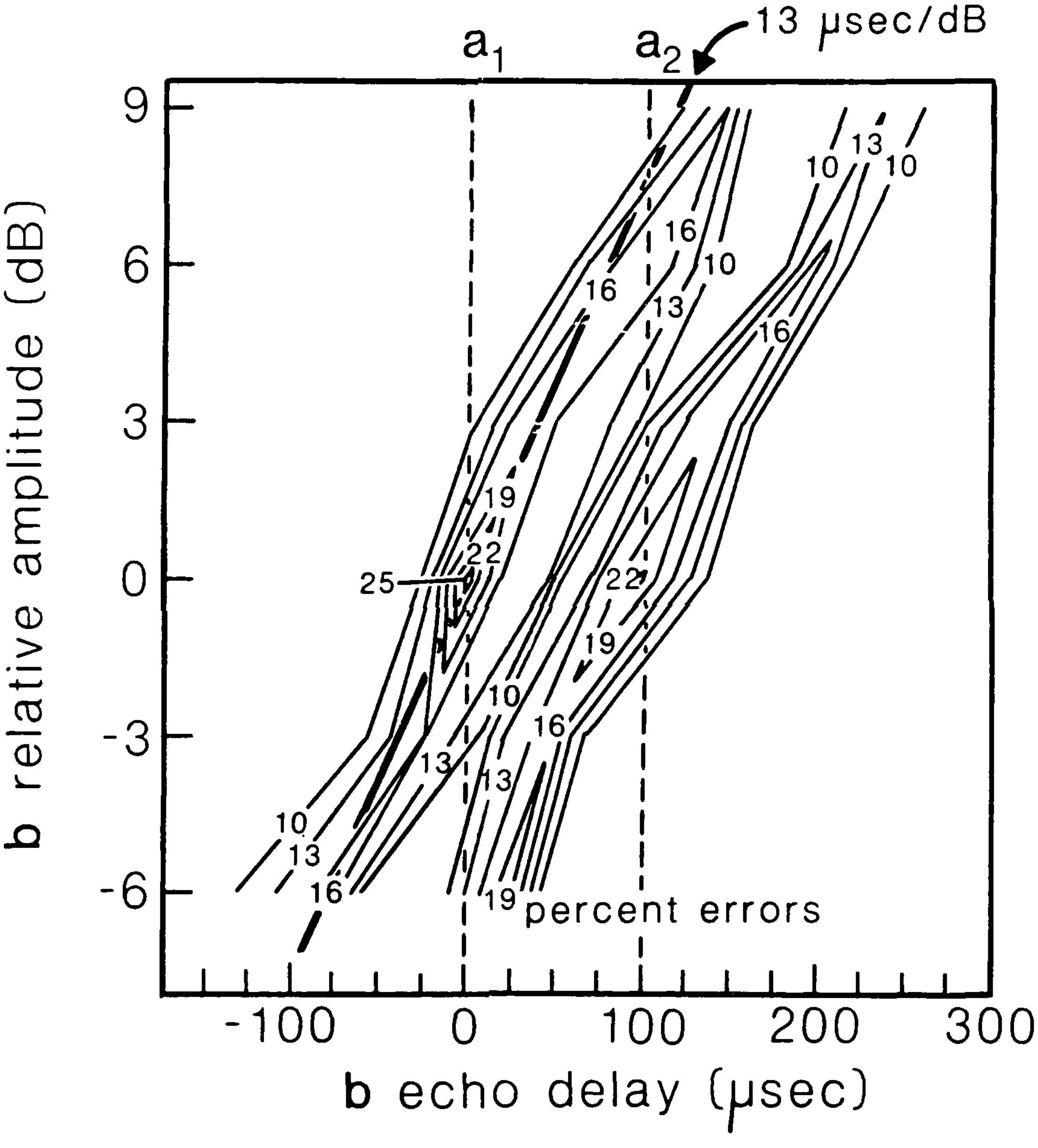

Double echo
(sequential
with echo b)
echo b
0 dB
echo b
-6 dB
percent errors
25
20
15
10
5
0
a1
a2
3.275
msec
1 cm
6
5
4
3
2
1
c
-150
-100
-50
0
50
100
150
b echo delay (µsec)

Figure 11



a1
a2
13 μsec/dB
9
6
3
0
-3
-6
b relative amplitude (dB)
-100
0
100
200
300
b echo delay (μsec)
10
13
16
19
22
25
percent errors

Figure 12

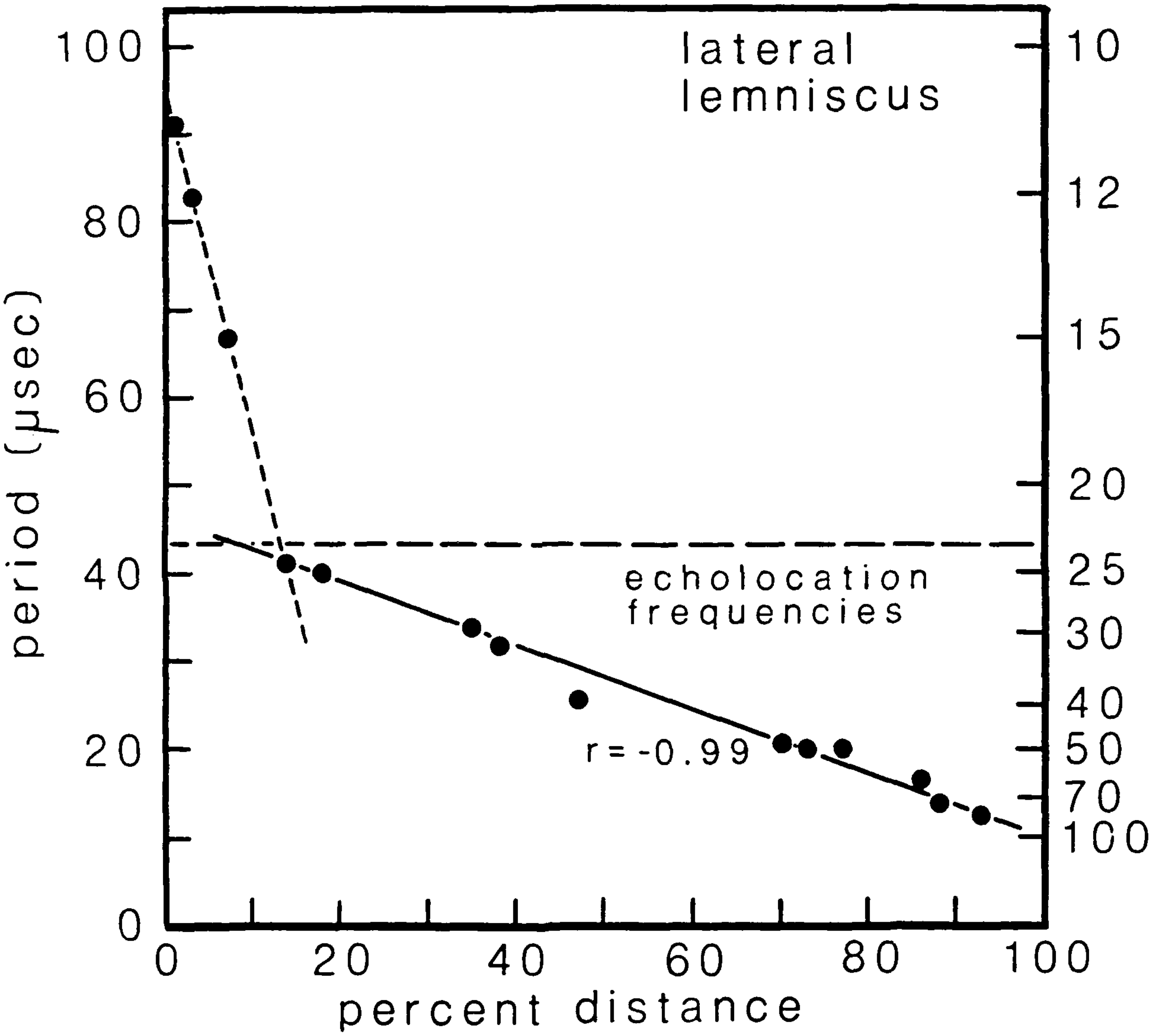

lateral
lemniscus
echolocation
frequencies
r = -0.99
period (µsec)
frequency (kHz)
percent distance
0
20
40
60
80
100
10
12
15
20
25
30
40
50
70
100

Figure 13

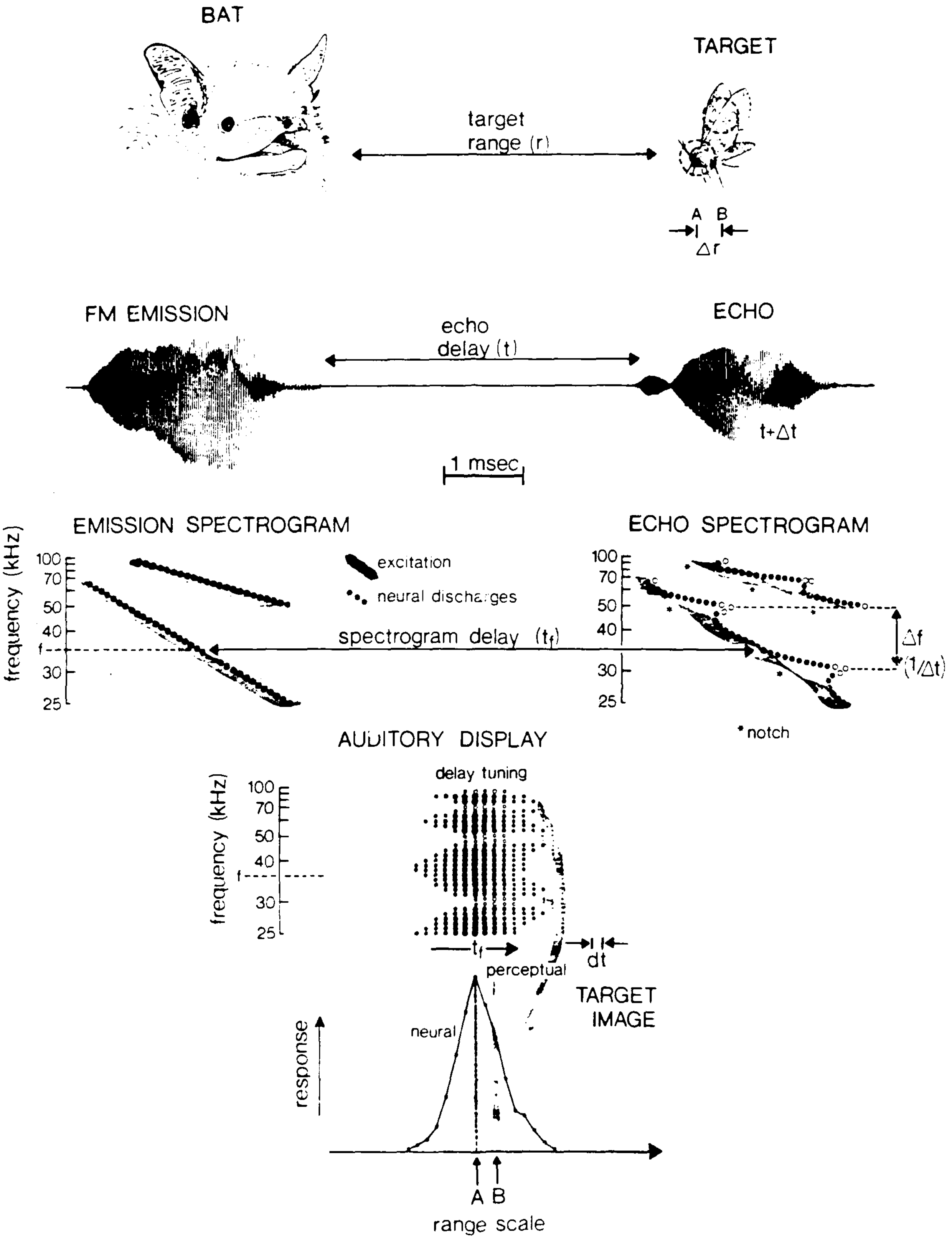

BAT
TARGET
target range (r)
A B
Δr
FM EMISSION
ECHO
echo delay (t)
t+Δt
1 msec
EMISSION SPECTROGRAM
ECHO SPECTROGRAM
frequency (kHz)
100
70
50
40
f
30
25
excitation
neural discharges
spectrogram delay (t_f)
Δf
(1/Δt)
* notch
AUDITORY DISPLAY
delay tuning
t_f
dt
perceptual
neural
TARGET IMAGE
response
A B
range scale

Figure 14