Accuracy of target ranging in echolocating bats: acoustic information processing

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Summary. 1. Echolocating bats use the time delay between emitted sounds and returning echoes to determine the distance to an object. This study examined the accuracy of target ranging by bats and the effect of echo bandwidth on the bat’s performance in a ranging task.

2. Six big brown bats (Eptesicus fuscus) were trained in a yes-no procedure to discriminate between two phantom targets, one simulating a stationary target that reflected echoes at a fixed delay and another simulating a jittering target that reflected echoes undergoing small step-changes in delay.

3. Eptesicus fuscus emits a frequency modulated sonar sound whose first harmonic sweeps from approximately 55 to 25 kHz in about 2 ms. Sound energy is also present in the second and third harmonics, contributing to a broadband signal in which each frequency in the sound can provide a time marker for its arrival at the bat’s ears. We estimated range jitter discrimination in bats under conditions in which the echo information available to the bat was manipulated. Baseline performance with unfiltered echoes was compared to that with filtered echoes (low-pass filtered at 55 kHz and at 40 kHz; high-pass filtered at 40 kHz).

4. The results indicate that the low-frequency portion of the first harmonic (25–40 kHz) is sufficient for the bat to discriminate echo delay changes of 0.4 microseconds. This echo delay discrimination corresponds to a distance discrimination of less than 0.07 mm.

Introduction

An echolocating bat emits ultrasonic sounds and perceives its surroundings by listening to the returning echoes of these sounds (Griffin 1958). The features of the echoes carry various kinds of information about a target, such as range, size, and shape (Simmons and Vernon 1971; Simmons 1973; Schnitzler and Henson 1980). Target range is a particularly important parameter for tracking insect prey, and this information is conveyed by the time delay between a sonar emission and echo reception (Simmons 1973). It has been postulated that bats use the frequency modulated (FM) components of their echolocation sounds for target ranging (Griffin 1958; Strother 1961; McCue 1966; Schnitzler 1968, 1970, 1973; Simmons 1973). Several receiver models have been proposed to describe the process of echo ranging in bats (see for example, Altes 1976, 1980, 1984; Hackbarth 1984; Menne 1988; Simmons and Stein 1980). Here, we will briefly consider three such models, a semi-coherent ideal receiver, a coherent ideal receiver, and a matched filter bank receiver.

Both a coherent and a semi-coherent ideal receiver cross-correlate the transmitted signal with the returning echo by passing the echo through a receiver matched to the emitted signal. The cross-correlation function is a time-compressed representation of the sound and is used to estimate echo arrival time. A semi-coherent receiver cannot make use of the fine structure of the cross-correlation function (i.e. the instantaneous frequency and a constant, time-invariant phase shift of echoes) but instead uses the envelope of the function for echo arrival-time estimation (Woodward 1964). A co-

Abbreviation: ABB4 (design), see Methods

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herent ideal receiver operates like a semi-coherent receiver with the added capability of using the fine structure of the cross-correlation function to estimate echo arrival time (Woodward 1964). Echo ranging performance of both semi-coherent and coherent receivers depends on the bandwidth of the signal (centralized rms bandwidth for the semi-coherent receiver and rms bandwidth for the coherent receiver) and the signal-to-noise ratio (see Burdic 1968; Simmons 1968; Schnitzler and Henson 1980; Schnitzler et al. 1985; Menne and Hackbarth 1986). Performance of a filter-bank receiver (Hackbarth 1984; Menne 1988) also depends on the signal bandwidth and the signal-to-noise ratio, but differs from the classical ideal receivers in that it does not make optimal use of all information in the sonar sound for estimating target range. This receiver operates by passing the signal through a series of overlapping band-pass filters, followed by envelope detectors: the filter bandwidth is set to minimize timing error for a given frequency sweep rate, and the receiver averages the output across channels to estimate echo arrival time.

Simmons (1973) presents behavioral data which suggest that target range discrimination by a bat is related to the bandwidth of its echolocation signal. He trained bats in a two-alternative forced-choice procedure to select the closer of two targets, and found that a species using comparatively narrowband sounds showed poorer range discrimination than a species using broadband sounds. For example, the CF-FM bat Rhinolophus ferrum-equinum successfully discriminated a range difference between two targets as small as 25 mm. This bat emits an 83 kHz CF sound followed by a shallow FM sweep from approximately 83 to 70 kHz. By contrast, the FM bat Eptesicus fuscus emits a three harmonic sound whose fundamental sweeps from approximately 55 to 25 kHz. This species successfully discriminated a 13 mm range difference between two targets.

Simmons (1973) also reports a close correspondence between the range discrimination performance of each species tested and the envelope of the autocorrelation function of that species’ echolocation sound. (For a stationary target that reflects well at all frequencies, the autocorrelation function is a good approximation to the cross-correlation function of the emitted sound and returning echo.) He uses this finding to suggest a hypothesis that the bat operates as a semi-coherent ideal receiver which uses some neurophysiological equivalent of cross-correlation processing. Simmons argues that the width of the envelope of the autocorrelation function is broader for a narrow-band sound than it is for a broadband sound, and the width of the function determines the extent to which a bat experiences ambiguity in a ranging task. Indeed, Eptesicus was able to discriminate a smaller range difference between two targets than Rhinolophus. The difference in range discrimination performance between the two species cannot, however, be used to confirm that bats use optimal filtering to estimate echo arrival time. The performance of an ideal receiver depends on the echo signal-to-noise ratio (Burdic 1968), and in Simmons’s experiment, it can be inferred from the structure of the echolocation sounds that performance for Rhinolophus and Eptesicus was measured at different signal-to-noise ratios (see Schnitzler and Henson 1980).

In an experiment on ranging accuracy by echolocating bats, Simmons (1979) trained Eptesicus to discriminate between two phantom targets, one simulating a stationary target that reflected echoes at a fixed delay and another simulating a jittering target that reflected echoes undergoing small step changes in delay. The bats successfully discriminated jitter of echo delay as small as 0.5 μs, suggesting that Eptesicus may be able to discriminate the distance to an object within a fraction of a millimeter. He also reports a parallel between the bat’s performance in an echo jitter discrimination task and the fine structure (half-wave rectified) of the autocorrelation function of the bat’s sonar sound. The fine structure of the autocorrelation function of Eptesicus’ echolocation sound shows a narrow central peak, flanked by side peaks separated by 30 μs intervals (the average period of the FM sweep). If the delay of the returning echo is jittered by 30 μs on alternating emissions, a bat that perceives the equivalent of the fine structure of the autocorrelation function would encounter ambiguity, confusing the central peak and the side peak. Indeed, Simmons reports an increase in the bat’s errors for discriminating 30 μs jitter compared to smaller and larger values. He offers this finding as evidence that the bat perceives the fine structure of the cross-correlation function and that this function describes the bat’s perceptual image of a target (Simmons 1987). These data do not, however, confirm that the bat operates as an ideal receiver, since the signal-to-noise ratio under which performance was measured is unknown. Furthermore, Simmons simulated the phantom targets in the jitter experiment with an analog delay line. The analog delay line may have introduced an acoustic artifact which could have aided the bats in the discrimination task and perhaps also contributed to the rise in errors at 30 μs jitter.
The behavioral experiments described above indicate that the accuracy of target ranging is remarkably high (Simmons 1979) and suggest that echolocation signal bandwidth may play a role in estimating echo arrival time (Simmons 1973). The data have important implications for assessing different receiver models of echolocation and elucidating the process of acoustic imaging by bats. Both of these findings, however, require further investigation: The analog delay line used to measure ranging accuracy may have introduced delay-related spectral changes, and the comparison of two different species at different signal-to-noise ratios leaves open the question of what effect echo bandwidth has on target ranging by a single species at the same signal-to-noise ratio.

The purpose of this study was to address the issues raised above. We measured range accuracy performance in *Eptesicus fuscus* with a paradigm similar to that used by Simmons (1979), but instead used a digital delay system which permitted target simulation without introducing delay-dependent frequency artifacts. To carefully monitor response bias under different stimulus conditions, we also implemented a different psychophysical method than that used by Simmons. And finally, we compared the bat’s ranging performance with natural echolocation sounds and with filtered sounds to evaluate the effect of signal bandwidth on echo arrival time estimation in a single species.

### Methods

Six big brown bats were trained in a yes-no procedure to discriminate between two phantom targets, one that simulated a stationary target that reflected echoes at a fixed delay and another that simulated a jittering target that reflected echoes undergoing small step changes in delay (see Simmons 1979). Bats were trained to stand at the base of a Y-shaped observing platform and to emit sonar sounds into a 1.4” microphone (windscreen covering the diaphragm; Bruel & Kjaer, 4135) located at the end of the left arm of the platform, 15 cm from the bat. Sounds picked up by the microphone were amplified with a custom-built amplifier, digitized (12 bit ADC at a sampling rate of 250 kHz) and filtered (Medav GmbH FIRFIL 82 VO1, 37 coefficients). The digitized sounds could be delayed by variable amounts in steps of 0.4 μs, and the delays were set under computer control using software developed specifically for this system. Analog waveforms of the digitized sonar sounds were played back to the bats through a custom-built ultrasonic loudspeaker (designed by Lee Miller, Odense, Denmark) for calibration curve, see Fig. 1C) located at a distance of 1 m from the bat. The loudspeaker had a frequency response similar to those used in Simmons’s jitter experiment (Simmons, personal communication; see Simmons et al. 1979). These sounds simulated echoes returned by a phantom target positioned about mid-way between the bat and the loudspeaker (see Fig. 1A).

The distance to the phantom target depended upon the computer controlled delay of the playback sounds. On 50% of all trials, the sounds emitted by the bat were played back at a fixed delay of 3.67 ms, simulating a stationary target located 63.14 cm from the bat on its observing platform. On the remaining 50% of all trials, the sounds were played back at 3.67 ms on alternating emissions; for every other sound the bat emitted, a time value (ranging from 0.4 to 100 μs) was subtracted from the base echo delay of 3.67 ms. In these trials, the change in echo delay from one emission to the next simulated a target that jittered in space (see Fig. 1B), and the second echo (more distant reflecting element) from the jittering target occurred at the same delay as that from the non-jittering target. The spatial relation between the jittering and non-jittering targets differed in this experiment from the arrangement used by Simmons (1979). In his experiment, the jittering target was centered about the range (echo delay) of the non-jittering target.

The order of presentation of jitter and catch (no jitter) trials followed a pseudorandom schedule (Gellerman 1933). The subtracted time value was always the same on a given trial, i.e., the size of the jitter was fixed. While performing in the task, bats typically emitted sounds of about 1.8 ms in duration; echoes produced by sounds reflecting off the loudspeaker returned after 5.814 ms, more than 2.1 ms following the sound played back to the bat. The microphone at 15 cm produced an echo 2.5 ms earlier than the phantom target echo. Thus, there was rarely overlap between the simulated echoes played through the loudspeaker and the echoes reflecting off the microphone or loudspeaker; there was also no overlap between successive sound emissions and simulated target echoes.

When presented with sounds that returned at an alternating delay, bats learned to indicate a “yes” (jitter present) response by approaching the left arm of the platform, and when presented with sounds that returned at a fixed delay, they learned to indicate a “no” (jitter absent) response by approaching the right arm of the platform. The magnitude of the jitter was reduced from 100 μs to 0.4 μs in small steps (0.4–20 μs, the step size increasing with the jitter value) to estimate the smallest jitter that bats can reliably detect. Percentage hits (“yes” response, jitter present) and false alarms (“yes” response, jitter absent) were calculated for individual animals at each jitter magnitude tested.

Animals were tested with only one jitter value on any given test day, following a modified descending method of limits. Each bat was first tested with 100 μs jitter, and if the bat performed with a minimum of 85% hits and a maximum of 20% false alarms on 3 consecutive test days, it was then tested on 2–3 consecutive test days with 80 μs jitter. Bats were then tested with smaller and smaller jitter values, over a minimum of 2 consecutive test days at each value. If the bat’s performance dropped below 75% hits on any test day, a larger jitter value was presented on the subsequent test day to ensure that the bat’s behavior reflected a change in stimulus discriminability and not in the bat’s motivation to participate in the task. Data collection at the smaller jitter value was then repeated on the following day. It was necessary to implement this rule for handling poor performance for only two bats. Moreover, the occasional poor performance of these two bats occurred only for jitter values greater than 40 μs, probably because the animals became more skilled at the task over time, and the testing of large jitter values preceded the testing of small values. In every case, performance improved on the subsequent test day, and the modified descending method of limits was continued. A minimum of 35 trials were run for each bat for each jitter value tested; however, most often between 50 and 100 trials were run. Following each correct response, animals were rewarded with a small piece of mealworm. Following each incorrect response, the animals received correction trials, which were excluded from the data analysis.
In order to assess the role of echo bandwidth in the bat’s performance in an echo ranging task, both unfiltered and filtered echolocation sounds were presented to the animals. *Eptesicus fuscus* emits a three-harmonic FM sound whose fundamental sweeps from approximately 55 to 25 kHz. To test the relative importance of selected components of the bat’s sound for range jitter discrimination, performance was measured under the following stimulus conditions: Echoes low-pass filtered at 55 kHz (leaving only the first harmonic), at 40 kHz (leaving only a portion of the first harmonic from 25–40 kHz), and echoes high-pass filtered at 40 kHz (leaving a portion of the first harmonic and the entire second and third harmonics). Digital filtering (Medav GmbH) permitted sharp attenuation of unwanted frequencies (exceeding 250 dB/octave) and avoided phase-shifts typical of analog filtering. Spectrograms of unfiltered and filtered echolocation sounds are shown in Fig. 2.

On a given test day, bats were tested in blocks of trials containing 12 trials each. Half of the blocks of trials contained filtered playback sounds and half contained unfiltered sounds; half of the trials in a given block contained echo jitter and half contained no jitter (catch trials). To ensure that a change in performance reflected a stimulus manipulation and not a change in motivation, blocks of filtered and unfiltered sound trials were counterbalanced following an ABBA design. Performance of individual bats for filtered and unfiltered sounds was compared at each jitter amplitude studied, and thus, each bat served as its own control.

Echolocation sounds of the bats performing in the task were picked up with the 1/4" Brüel & Kjeær microphone and taped using a Racal high-speed recorder (60 ips). The sounds were later played back at 3 3/4 ips and analyzed using a Medav Color Display Spectrum Analyzer (effective bandwidth 128 kHz). Recordings were also made of the filtered and unfiltered sounds played back to the bat (simulated echoes), picked up at the output of the delay apparatus to the speaker. The recordings of the bat’s emissions and the playback sound were digitized for cross-correlation and further spectral analysis (Interactive Laboratory System Modules; Signal Technology, Inc.).
C.F. Moss and H.-U. Schnitzler: Target ranging accuracy in bats

Fig. 2. Spectrograms of natural and filtered echolocation sounds. The natural echolocation sound (left) contains 3 harmonics: the first sweeping from approximately 55 to 25 kHz in about 2 ms. For the 55 kHz low-pass filtered sound, the second and third harmonics have been removed; for the 40 kHz low-pass filtered sound, all but the low-frequency portion of the first harmonic have been removed; and for the 40 kHz high-pass filtered sound, all but the low-frequency portion of the first harmonic have been retained.

Fig. 3. Sequence of echolocation sounds emitted by Eptesicus fuscus shortly before making its decision in the jitter discrimination task. During this sequence, the bat was presented with 0.8 μs jitter and a 40 kHz low-pass filtered echo (dotted outline). Frequency (kHz) is plotted on the ordinate and time (ms) on the abscissa.

Results

The echolocation behavior of the bats performing in this task showed no reliable change across conditions. A typical sequence of echolocation sounds emitted by a bat shortly before making its decision are shown in Fig. 3. Bats typically emitted between 10 and 40 sounds/s, increasing the sound repetition rate before indicating a 'yes' or 'no' response.

Range-jitter discrimination of unfiltered echoes

Figure 4A shows the performance of two individual bats for jitter values between 0.4 and 4.8 μs. In this and subsequent Figs., percentage hits are plotted with filled symbols (left ordinate), and percentage false alarms are plotted with open symbols (right ordinate). Discrimination performance for jitter values larger than 4.8 μs are not shown; however, hits remain consistently above 85% and false alarms at or below 20% for the larger jitter values. Figure 4 shows that the bats discriminated between time-jittered and stable echoes for jitter values down to 0.4 μs, for which the percentage hits is at or above 80% and false alarms at or below 20%. Unfortunately, the apparatus could not produce jitter values smaller than 0.4 μs; and therefore, it was not possible to assign an arbitrary threshold (e.g., 75% hits), where performance would fall between 100% (clear discrimination) and 50% (chance). There is for bat 17, however, a 15% decrease in percentage hits between 3.2 and 0.4 μs jitter. This observation, along with data from Simons (1979) showing jitter discrimination thresholds for Eptesicus of about 0.5 μs, suggests that an arbitrary threshold estimate of 75% hits might fall just below 0.4 μs for at least one animal tested.

The zero value on the abscissa in Fig. 4 represents a condition in which the bat was never presented with jittered echoes and was rewarded according to a random schedule. Since no echoes were temporally jittered, no hits could be scored. Every time the bat moved to the left arm of the platform, indicating a 'yes' (jitter present) re-
response, a false alarm was scored. This condition was run to control for any hidden artifact in our apparatus, and indeed, the data show how infrequently the bats indicated 'yes' when no jitter was introduced across an entire block of trials. Care was taken to limit the number of trials in this condition on any day to less than 20 to avoid confusing the bat.

Range-jitter discrimination of filtered echoes

In these conditions, the bats discriminated between jittered and stable phantom targets which were simulated with filtered electronically-delayed echo-location sounds. Individual performance curves for two bats presented with the first harmonic alone (55 kHz low-pass filtered sounds) are shown in Fig. 4B. For bat 12 performance under filtered sound conditions remains virtually unchanged from unfiltered conditions. This bat discriminates jitter of only 0.4 μs in approximately 90% of all trials. Bat 17 shows a different pattern in performance: For jitter values at or greater than 0.8 μs, performance under filtered and unfiltered conditions is essentially the same; however, at the smallest jitter value tested (0.4 μs), performance under the filtered condition drops below that under the unfiltered condition to 69.6%. For this animal under the 55 kHz low-pass filtered condition, an arbitrary threshold (75% hits) can be assigned at 0.56 μs. It should be noted that bat 17 was the only animal tested whose performance dropped below 75% under either filtered or unfiltered conditions.

Overall, the jitter discrimination performance under the 55 kHz low-pass filtered-echo condition does not differ from that under the unfiltered-echo condition. This is illustrated by the group average
data from six bats shown in Fig. 5. Data collected under unfiltered conditions are plotted with triangles and those collected under 55 kHz low-pass filtered conditions with circles: Discrimination curves for the two conditions are shown for jitter values out to 30 μs, and the two curves essentially overlap. Even for 0.4 μs jitter, the average performance is at 80% under both filtered and unfiltered conditions. At all jitter values tested, the average false alarm rate is at or below 20%, indicating that the bat’s response bias remained stable.

One bat was also tested with 40 kHz low-pass filtered echoes. This animal discriminated between jittered and stable phantom targets with only the low-frequency portion of the first harmonic of its echolocation sound. Figure 6 shows the performance curve for bat 5 under these conditions for jitter values between 0.4 and 4.8 μs (circles). Also plotted are jitter discrimination data under unfiltered conditions (triangles). This figure illustrates that jitter discrimination remains undisturbed by 40 kHz low-pass filtering, even for a jitter value of 0.4 μs.

The performance of three bats was also studied under conditions of 40 kHz high-pass filtering. These bats were required to discriminate temporal jitter without the low-frequency portion of the first harmonic. Under these conditions, bats failed to perform: After 3–4 trials, the animals refused to make a choice, either remaining at the base of the observing platform or flying away. This behavior occurred immediately following performance of approximately 90% hits with unfiltered or low-pass filtered echoes. Each bat was tested, however, only once in the high-pass filtering condition.

**Discussion**

The results of this study show that *Eptesicus* is indeed sensitive to small changes in echo delay. They further suggest that the low-frequency portion of the first harmonic of *Eptesicus*’ echolocation sound is sufficient for the bat to discriminate jitter of echo delay down to 0.4 μs, corresponding to a target distance discrimination of less than 0.07 mm. Such fine accuracy of distance measurement is consistent with data reported by Simmons (1979), who also measured echo delay discrimination in bats presented with unfiltered echoes of their sonar sounds.

In this study, the emitted sounds and electronically-delayed phantom target echoes never overlapped. There was rarely overlap between the phantom target echoes and clutter echoes from objects such as the loudspeaker and microphone. The bat’s sonar emissions, the phantom target echoes, and clutter echoes were, however, correlated, with a delay separation of about 3.67 ms between each emission and phantom echo, a separation of about 2.1 ms between the phantom echo and the speaker reflection, and a separation of about 2.8 ms between the microphone reflection and the phantom echo. The time separations between the bat’s sonar emission, the phantom target echo and the clutter echoes may have provided acoustic cues which could give rise to the psychological phenomenon of pitch (typically referred to as time-separation pitch or repetition pitch; see for example, Thurlow and Small 1955; Bilsen and Ritsma 1969/1970; de
Boer 1976), and these acoustic cues may have conceivably aided in the bat’s discrimination of the echo jitter. We consider this possibility unlikely, however, since the pitch changes that might be associated with echo jitter in the microsecond range would be extremely small if time-separation pitch operates in bats as it does in humans.

The bat evidently can discriminate range differences of less than 0.07 mm using only the low frequency portion (25–40 kHz) of its echolocation sound. Substantially reducing the overall bandwidth of the echoes returning to Eptesicus thus does not interfere with this level of fine distance discrimination. Although each frequency in the broadband FM sound provides a potential marker for the time of occurrence of a returning echo, the low-frequencies provide sufficient information for fine range discrimination of 0.07 mm. Perhaps filtering out the higher frequencies would have disrupted range discrimination closer to threshold (i.e. distance changes smaller than 0.07 mm or echo delay changes of less than 0.4 μs). A suggestion of this possibility comes from data from the single animal (bat 17) whose discrimination performance under the 55 kHz low-pass filter condition began to break down for the jitter value of 0.4 μs. Clearly, however, a large reduction in echo bandwidth (retaining only the low-frequency portion of the first harmonic) does not disturb range discrimination for echo delay changes greater than 0.4 μs.

For Eptesicus, a large portion of the sound energy that returns in echoes from distant targets is contained between 25 and 40 kHz. Therefore, it is perhaps not surprising that bats can make fine distance discriminations while listening to echoes containing only these frequencies. Simmons and Grinnell (1988) propose that frequencies between about 25 and 40 kHz may be particularly useful for marking the echo time of arrival, since the periods of these sound frequencies are longer than those of the higher frequencies. Although phase-locking of primary auditory nerve fibers to pure tones has never been reported at ultrasonic frequencies, the relatively longer periods of the lower frequencies of the first harmonic may make these frequencies especially significant in carrying a temporal code for broadband transients.

Simmons (1973) asserts that it is unlikely that the bat extracts target distance information directly from time-domain cross-correlation processing but rather reduces sound emissions and echoes into neural displays of spectrograms before deriving the equivalent of the cross-correlation function. Altes (1980, 1981, 1984) has elaborated on this notion to show mathematically that the correlation function of a sonar emission and echo may be reconstructed from spectrogram representations if each frequency in the FM sweep is registered with sharply-tuned impulses in parallel, overlapping frequency-tuned channels. Spectrogram formation destroys phase information; however, Altes (1980) demonstrates that the fine structure of the cross-correlation function can be reconstructed from emission and echo spectrograms (revealing the side-peaks) if a phase measurement at the output of any single filter can be made. Thus, a bat may perceive the equivalent of the fine structure of the correlation function without necessarily operating with a classical matched filter. If indeed the bat does use a spectrogram-correlation process for target ranging, the phase information needed to reconstruct the fine structure of the correlation function may be carried by the low-frequency portion of the first harmonic; the periods of these frequencies are longer than those of the higher frequencies, and a phase measurement seems to require that the timing of nerve impulses representing any one frequency have a distribution narrower than the period of that frequency (Simmons and Grinnell 1988).

The hypothesis that the bat perceives the equivalent of fine structure information in sonar emissions and echoes is based on a comparison of the bat’s performance curve in the echo jitter discrimination task and the shape of the half-wave rectified autocorrelation function. Specifically, Simmons (1979, 1987) observed an increase in the bat’s errors for discriminating 30 μs jitter, a stimulus condition that would produce perceptual ambiguity for an ideal coherent receiver. In the present study, we found no rise in errors for 30 μs echo jitter compared to larger and smaller values. Moreover, the filtering manipulation changes the cross-correlation function such that one would predict a pronounced increase in errors for 30 μs jitter if indeed this function represents the bat’s perceptual image:

The low-pass filtering does not change the location of the side-peaks of the cross-correlation function; it does, however, raise the height of the side-peaks with respect to the central peak. The discrepancy in echo jitter discrimination performance at 30 μs between our findings and those reported by Simmons is difficult to explain, but it may be due to differences in the spatial arrangement of the jittering target with respect to the non-jittering target. In Simmons’s experiment, the jittering target was centered in range about the non-jittering target; whereas, in our experiment, the more distant reflecting element of the jittering target was presented at the same range as the non-jittering target.
A comparison of the absolute performance of the bats in the two experiments shows that errors are greater in the target range configuration used in the present experiment than in that used by Simmons. The data reported by Simmons (1979) show the bat’s discrimination performance at 10–20, 40–50, and again at 70–80 µs to be about 94–100% correct. By contrast, our group data show discrimination performance to be about 86–90% correct (combining hits and correct rejections) for these same jitter values, the lowest value differing by only 2% from that reported by Simmons (1979) at 30 µs (84% correct). Although it seems possible that the differences in results between the two experiments could be attributed to differences in the equipment and psychophysical procedures, Simmons et al. (in preparation) have found that placement of the non-jittering target at the same range as either the first or second reflecting element of the jittering target indeed reduces the bat’s overall discrimination performance below that measured with the non-jittering target centered within the jitter interval. Such a reduction in discrimination performance may have therefore obscured the presence of the side peaks at 30 µs in our data.

In contrast to a coherent cross-correlation receiver model of echolocation, a matched filter bank model does not propose the use of fine structure information (Hackbart 1984; Menne 1988). Rather, a filter bank model incorporates a series of overlapping bandpass filters whose frequency range encompasses the entire echolocation signal. An FM sweep successively activates each filter when the frequency components of the sweep correspond to the bandpass frequency. An envelope detector follows each filter, and activation of each separate channel serves as a marker of echo arrival time. This model assumes that the bandwidth of the filters is matched to the frequency sweep rate of the echolocation signal to minimize timing error at the output of each channel, and that an echo delay estimate is based on an average across channels. Timing error by a matched filter bank receiver depends on the bandwidth of the echolocation signal, yet it is conceivable that performance would remain relatively undisturbed by low-pass filtering at favorable signal-to-noise ratios.

For a given signal-to-noise ratio, the predicted accuracy of target ranging differs for the cross-correlation and filter bank receiver models described above. Assuming a signal-to-noise ratio of about 30 dB, the predicted accuracy of echo arrival time estimation by *Eptesicus fuscus* is 0.45 µs for a semi-coherent receiver, 0.006 µs for a coherent receiver (Menne and Hackbart 1986) and 1.2 µs for a matched filter bank receiver (Menne 1988). These predictions provide some basis for evaluating which receiver model may describe echo ranging in bats. Our data show that bats can discriminate jitter of echo delay down to 0.4 µs, a value somewhat better than that predicted for both a semi-coherent ideal receiver and a matched filter bank receiver. Although 0.4 µs is well above the predicted accuracy for a coherent ideal receiver, our apparatus did not permit us to measure performance with smaller jitter values. Therefore, we are unfortunately unable to conclusively accept or reject any one of these receiver models based on the accuracy of time delay estimation.

The mechanisms of target ranging have been studied electrophysiologically in several different species of bats, and the response properties of single neurons cannot yet account for the behavioral accuracy measured in *Eptesicus fuscus*. At the level of the inferior colliculus, there are neurons whose latency of response is considerably stable from one stimulus presentation to the next. These cells, identified in the FM bat, *Tadarida brasiliensis mexicana*, have been termed constant latency responders, and show a variability of response latency on the order of 100–200 µs (Pollak et al. 1977; Bodenhammer et al. 1979). This variability, although low, is still several orders of magnitude greater than the ranging accuracy of *Eptesicus fuscus* (present study; Simmons 1979). In the mid-brain of *Eptesicus fuscus*, some neurons respond only to pulse-echo pairs, not to a single sound. Moreover, such cells are selectively responsive to a particular time interval between the pulse and echo, suggesting that they code target range (Feng et al. 1978). Range-tuned cells have also been identified in the auditory cortex of the FM bat *Myotis lucifugus* (Sullivan 1982a, b; Wong and Shannon 1988) and the CF-FM bat *Pteronotus parnellii* (Suga and O’Neill 1979; O’Neill and Suga 1979). For all three species, the width of the delay tuning curves is in the ms range; whereas the behavioral estimates of echo delay discrimination (measured only for *Eptesicus*) are in the fractional-µs range. Although there is a discrepancy between the single cell data and the bat’s performance, it is possible to account for high behavioral accuracy with broadly tuned receptive fields by invoking mechanisms of ensemble coding (see for example McIlwain 1976; Heiligenberg 1987). That is, central sharpening of acoustic images may arise from the activation of many broadly tuned range-sensitive neurons, operating in parallel.
When bats catch insects, they estimate the location of their prey with an accuracy of approximately 1–3 cm (Webster and Griffin 1962; Trappe 1982). They use the tail membrane or wing to scoop up insects in flight, and this relatively large surface area facilitates the capture of prey without requiring range accuracy of less than a millimeter. Furthermore, our finding that bats can discriminate jitter of echo delay down to 0.4 μs with only the low frequency portion of the first harmonic strongly suggests that the full bandwidth of Eptesicus’ echolocation sound is not necessary for the capture of prey under natural conditions. If a bat can discriminate echo delay changes of 0.4 μs without the frequency components of its echolocation sound above 40 kHz, what is the importance of the broadband echolocation signal? The higher frequency portion of the sonar sound may play an important function in the localization and discrimination of natural insect prey in the approach stage of insect pursuit, when the bandwidth of the echolocation sound is the broadest. Natural stimuli have depth structure, containing many reflecting surfaces, and at the high frequency components of the bat’s sounds may convey important spectral information about target shape. For example, the echolocation sound of Eptesicus is 1.5–2 ms in duration. If the spatial separation of the multiple reflecting surfaces of a target is less than a couple of centimeters, the multiple echo reflections will be largely overlapping, resulting in cancellations and reinforcement at particular frequencies of a composite echo spectrum. This information may be used by the bat to discriminate target shape (e.g. Simmons et al. 1974; Schnitzler, et al. 1985), and the higher frequencies of the bat’s echolocation sound would add richness to this information.

The results of this study demonstrate not only that the big brown bat is capable of making very fine distance discriminations but also that it can do so with echoes containing only the low-frequency portion of its first harmonic. That this capability is so robust suggests its potential importance to the sophisticated acoustic imaging system of the echolocating bat.

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C.F. Moss and H.-U. Schnitzler: Target ranging accuracy in bats

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