

Theories About Target Ranging in Bat Sonar

James A. Simmons

Postal:

Department of Neuroscience
Brown University
Providence, Rhode Island 02912
USA

Email:
james_simmons@brown.edu

The frequency-modulated biosonar sounds transmitted by bats are well-suited to the accurate determination of target range and target.

Introduction

Echolocating animals achieve high levels of performance for guidance, orientation, and target finding in surroundings that go from simple, open spaces to densely cluttered scenes. Developing man-made radar and sonar systems that can perform at comparable levels has been an important motivation for studying echolocation from the time of its discovery (Griffin, 1958) to the present (Au and Simmons, 2007; Simmons et al., 2017). The most obvious comparison with man-made systems is with *target ranging*, determining the distance to an object from the outward and returning travel time of echoes. **Figure 1** illustrates the problem of determining target range from echo delay. The earliest theories of echolocation recognized the distinction between a pulse and a chirp to explain target ranging. Inspired by these theories, behavioral studies established that bats do indeed perceive target range from echo delay (Simmons et al., 1995). Furthermore, they exploit the properties of their frequency-modulated (FM) signals to work back from long chirps to brief pulses (Simmons et al., 1996).

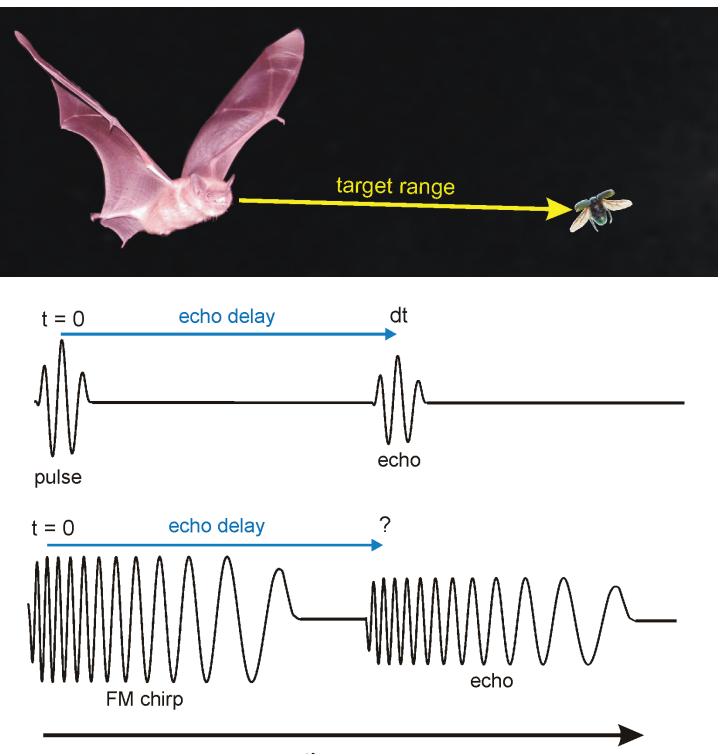
Discovering Echolocation

The first theory, of course, is that animal sonar exists at all. The full story leading to the discovery of echolocation and subsequent research has been described in detail elsewhere (Griffin, 1958; Grinnell et al., 2017). Beginning with Spallanzani and Jurine in the late 18th century and extending into the first years of the 20th century, experiments had established that these animals guided flight in the dark using their ears, not vision. Lacking knowledge about ultrasonic sounds, early researchers did not consider the bat as the source of signals. This idea was proposed by Sir Hiram Maxim in 1912 (see Griffin, 1958). He asserted that bats radiated low-frequency sounds and picked up echoes from objects as a way to avoid collisions.

In 1920, Hamilton Hartridge reported a series of observations on bats flying from room to room where the lights could be turned on or off and obstacles placed in their path (see Griffin, 1958; Grinnell et al., 2017). He concluded that bats must be able to perceive objects when they are a considerable distance away, most likely by emitted high-frequency sounds inaudible to humans, and listening for echoes returning to their ears. The crucial part of Hartridge's argument was acoustical, that obstacles typically encountered by bats do not cast "shadows" of audible sounds (i.e., low-frequency sounds heard by humans) nor do they return strong reflections of these sounds because the wavelengths are too long. However, if the sounds are of high frequency so that their wavelengths are short, then an obstacle will intercept an appreciable part of each incident sound, creating a sound shadow behind it and returning the intercepted part of the sound to the front as a reflection.

Armed with a newly developed electronic device for picking up ultrasonic sounds and rendering them into audible signals, Donald R. Griffin and Robert Galambos

Figure 1. Top: To determine target range, the bat has to clock the time that elapses between the emission of each broadcast and reception of the target's echo. **Middle:** If the signal is a brief pulse, the moment of transmission (time [$t = 0$]) and the arrival time of the echo (time difference [dt]) are unambiguous events in time. However, the pulse has limited energy because it is so brief, which restricts the bat's operating range. Extending the operating range requires emitting more energy by lengthening the broadcast, but the bandwidth has to remain wide to retain the delay acuity provided by the pulse. **Bottom:** The bat emits a long-duration frequency-modulated (FM) chirp that retains the pulse's wide bandwidth and increases the energy, but the FM signal has numerous peaks that fill much of the time between the emission of the broadcast and reception of the echo. The moment of broadcast and the moment of echo reception are ambiguous ("?") from the numerous peaks taken by themselves. Although the brief onsets of the broadcast and the echo could be registered to determine delay, the enhanced energy built into the entire FM sweep is lost. To exploit the FM chirp's full bandwidth and energy, the short duration of the pulse has to be recovered by compressing the FM sweep into a synthetic pulse.



(see Griffin, 1958; Grinnell et al., 2017) carried out classic experiments at Harvard University in 1940 to demonstrate that (1) flying bats indeed do broadcast ultrasonic sounds, (2) the pattern of these sounds changes when the bat is engaged in swerving to avoid obstacles, and (3) the bat's inner ear is sensitive to ultrasonic frequencies by generating correspondingly ultrasonic cochlear microphonic responses. This trifecta of experimental findings constitutes the discovery of echolocation and stands as a model for scientific inquiry.

Theories of Frequency-Modulated Echolocation

Theorizing about the echolocation of bats depends on knowing what the bat's sounds are like (Pye, 1980). **Figure 2** shows spectrograms for a recording of echolocation sounds emitted by a big brown bat, *Eptesicus fuscus*, searching for and then detecting, tracking, approaching, and finally capturing a flying beetle. Efforts up through the 1950s to characterize echolocation sounds were impeded by several factors. First, the sensitivity of the available microphones only partially extended to frequencies above 15-20 kHz, with relatively uneven frequency-response curves above the critical minimal region from 20 to 40 kHz and negligible sensitivity to 100 kHz. Second, available methods for recording and displaying the sounds were far from current acoustic analysis technology. Until the sound spectrograph was developed, the waveforms of echolocation sounds could only be observed on an oscilloscope screen. The fleeting nature of these traces and the limitations of oscilloscope photorecording meant

that the full extent of frequency modulation in echolocation sounds was underappreciated until the 1960s.

Marking Time

Figure 3 shows a downsweeping FM transmitted sound followed by an echo that is somewhat lower in amplitude than the broadcast and also has a more irregular envelope due to changes in the target's reflective strength at different frequencies. The target's range is conveyed by the time (t) that elapses between the broadcast (**Figure 3**, $t = 0$) and reception of its echo (difference in time [dt]). Each meter of added distance increased the echo's delay by about 6 ms. Marking the beginning of the delay interval can be done by simply taking the instant the transmitter is activated to start counting time until an echo is received. Or the transmitted signal itself can be routed to the receiver and used to register the beginning of the delay interval, which starts the counting of time until an echo is received. **Figure 3** shows several representations that could be used to mark the arrival time of echoes: the time-series waveform itself (**black**), the time-frequency structure or spectrogram (**green**), and the envelope (**orange**).

The Spectrogram Theory

Griffin and Galambos (see Griffin, 1958; Grinnell et al., 2017) had demonstrated experimentally that active ultrasonic sonar, echolocation, was the solution to the Spallanzani "bat problem." They elaborated on several issues they identified as relevant to understanding the inner mechanisms of echolocation (Griffin, 1958). These issues all were concerned with the time axis that begins with each broadcast ($t = 0$) and

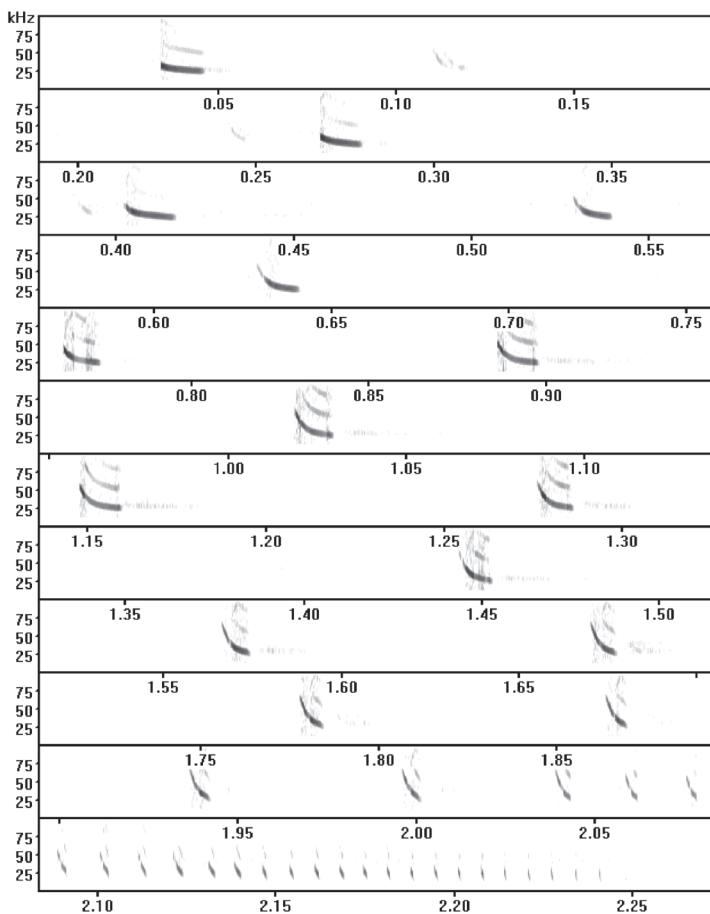


Figure 2. Spectrograms for a series of FM echolocation sounds emitted by a big brown bat during an aerial interception. Time is in seconds; frequency is in kilohertz. Most of the information illustrated by these spectrograms would have been available to anyone thinking about echolocation by the late 1950s (see Griffin, 1958, Plate 8). The sounds shorten in duration from 20 ms down to 0.3 ms as the maneuver progresses and the bat flies closer to its target. The bat likely detects the insect from the echo of the broadcast that occurs at about 0.27–0.28 s because subsequent broadcasts have more gradual onsets and increase progressively in the slope of the FM sweep at the very beginning of the sound. Each sound contains several harmonics (**curved sloping ridges**), with the strongest shown as the **darkest**. The 1st harmonic changes from shallow FM sweeps in the 25- to 30-kHz region to wide FM sweeps from 60 to 25 kHz.

extends far enough to encompass the arrival of echoes from objects at different distances (dt).

A major concern for Griffin and Galambos was the potential deleterious effect of intense outgoing broadcasts on sensitivity to weak echoes arriving immediately thereafter. Radar systems “blank” the receiver at the moment of transmission to avoid blinding the system to weak reflections from targets (Skolnik, 1980). The mammalian auditory system does have a mechanical means, the middle ear muscles, to attenuate sounds traveling from the external ears to the highly sensitive

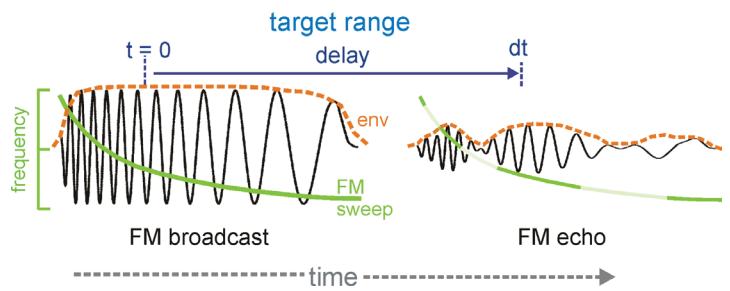


Figure 3. Diagram of information in a bat-like downsweeping FM echolocation broadcast and an echo relevant to determining target range. FM sweep is from 90 kHz to 10 kHz. The wide bandwidth of bat sounds favors accurate determination of distance from delay. The broadcast is emitted (at $t = 0$) to propagate outward, impinge on an object, and return as an echo (at dt). Two-way travel time is 6 ms/m of target range. The bat has to clock the sound’s travel time (one operation) and then register target range on a perceptual scale from near to far (a different operation). For large objects such as background vegetation, operating ranges are up to 20–30 m or delays of 120–180 ms (Stilz and Schnitzler, 2012). For small objects such as flying insects, operating ranges are only about 3–5 m or delays of 18–30 ms. Broadcasts and echoes (**black**), the envelopes (**orange**), or the spectrograms (**green**) supply the information used by bats. Central to these theories is the nature of the time-measurement process for target ranging and the time origin ($t = 0$). For a receiver that utilizes the envelopes, the onsets or the offsets are the prominent markers in both the broadcast and the echo. Other than delay, most information about the target’s effect on echo waveforms is lost.

receptors of the inner ears, but can they contract to suppress the broadcast while relaxing quickly enough to allow weak echoes to pass through? Eventually, both physiological and behavioral tests clarified the role of the middle ear muscles for attenuating broadcasts and also for regulating sensitivity to echoes (Pollak and Casseday, 1989; Neuweiler, 2000).

However, although masking of weak echoes by the preceding strong broadcast is a serious worry, the masking effect of one echo on another has to be considered as well. If several echoes arrive close together in time, can the bat resolve them as separate sounds well enough to perceive the corresponding objects? The newly available sonograms of the bat’s FM sounds suggested a solution to the echo-on-echo masking problem. Each of the bat’s FM sounds is milliseconds long (20 ms down to 2 ms during the course of most of the interception in **Figure 2**). In contrast, the spectrogram of each sound consists of sloping ridges that trace the frequency sweep from high to low over time. Importantly, the width of this ridge along the time axis of the spectrogram is roughly half a millisecond, substantially shorter than the duration of the sound itself. If the bat receives only one echo following each broadcast, the echo in isolation would stand out well enough to represent a discrete object that could be avoided or tracked and intercepted.

But bats also can fly with little difficulty through vegetation, in scenes that contain many sources of echoes from objects that require anything from dodging maneuvers to deciding if prey might be present (Moss and Surlykke, 2010). In these conditions, bats necessarily receive multiple echoes that often arrive quite close together in time. The ability to distinguish among the corresponding objects is at a premium if obstacles are to be located and avoided by following a path through them. If the bat's auditory system converted the echo time-amplitude pressure waveform received by the external ears (**Figure 3, black**) into a time-frequency representation similar to a spectrogram (**Figure 3, green**), then two echoes could arrive closer together than the overall duration of the original broadcast and still be registered as separate reflections from two objects located at slightly different distances (Griffin, 1958).

Frequency-Modulated Pulse Compression

Once it had been established that bat echolocation sounds were FM, comparisons with then new FM chirp radar (Skolnik, 1980) were compelling. The goal of chirp radar, also called *pulse-compression* radar, is to solve the problem posed in **Figure 1** by the difference between pulse and chirp signals. For a pulse transmission, the location of the echo's peak (**Figure 1, dt**) directly registers the target's range. The brief pulse sharply marks the echo's delay, but its brevity is the source of a different problem. The energy transmitted in each pulse is the product of amplitude squared (i.e., power) times duration. For the pulse, the radiated energy, which determines the echo's detectability at long range, is limited by its short duration. Because engineered devices inevitably reach a limit on the peak amplitude they can handle, increasing the broadcast energy beyond this power limit means lengthening duration, but a longer pulse duration also means a narrower frequency bandwidth with a concomitant loss of delay acuity due to reduced sharpness on the display. By sweeping the frequencies in the signal over the desired bandwidth (from high to low or low to high), the same broad span of frequencies can be spread out to occupy a much longer duration than the equivalent brief pulse, thus achieving the desired wide bandwidth and high radiated energy.

Figure 4A illustrates in current signal-processing terms how long-duration FM signals can be compressed to form the equivalent short pulse for determining delay without sacrificing the enhanced energy provided by the long duration. Here, the transmitted signal is a downward FM sweep (90

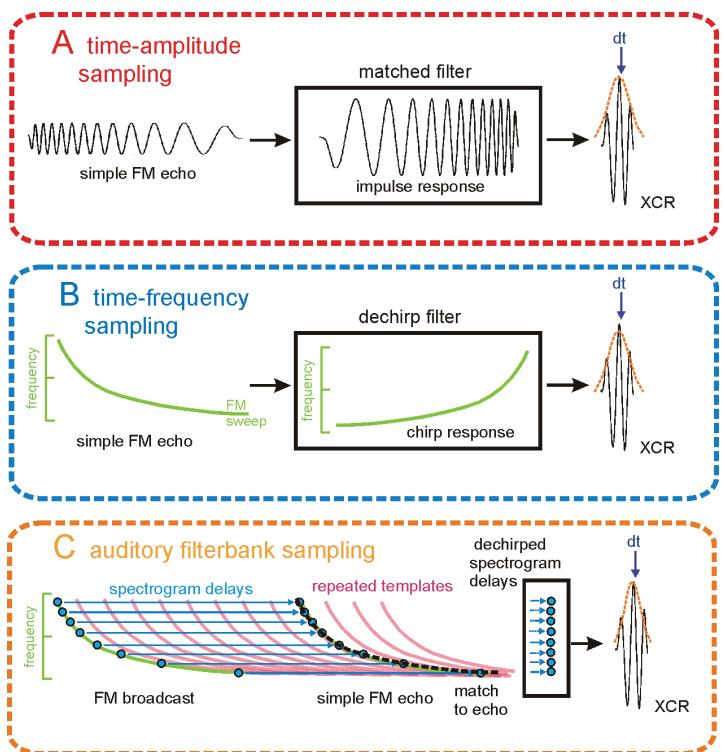


Figure 4. Diagrams illustrating three types of receivers capable of utilizing essentially all of the information contained in the waveforms of a FM broadcast and an echo to determine target range and shape. **A:** A matched-filter receiver implemented by contemporary digital signal-processing (DSP) methods. The FM echo is received and digitized into multiple-bit samples at a fixed sampling rate and then passed through the matched filter, which has as its impulse response a time-reversed version of the original FM broadcast. For a single reflection (a simple FM echo is a delayed replica of the broadcast), the output is the cross-correlation function (XCR) of the received echo with the broadcast template embodied in the time-reversed impulse response. Echo delay is unambiguously registered by the main peak of the XCR. **B:** Pulse compression, or chirp, receiver that operates on the time-frequency pattern of the FM broadcast instead of using the impulse response of a digital filter. Countervailing frequency-dependent delays inside the receiver compress the FM sweeps of echoes into XCR pulses. **C:** Spectrogram correlation process in which the broadcast FM sweep is registered and then propagated along neural delay lines to be available whenever an echo is received. The match between the FM sweep in the echo and the propagating trace of the sweep in the broadcast replaces the chirp receiver's compression of the sweep.

kHz to 10 kHz). The FM echo returns at a delay that corresponds to the target range (dt). This method for converting FM echoes into a display of delay is to pass them through a *matched filter*, a receiver that has as its impulse response a time-reversed version of the FM broadcast itself. The receiver uses knowledge about the original broadcast to telescope the FM sweep into the equivalent pulse, hence, pulse "compression," which "dechirps" the FM sweep.

The Chirp Radar Theory

Figure 4B illustrates the principle of pulse compression for a chirp radar receiver in the 1960s, which was based on analog electronics, not digital methods (as in Figure 4A). The broadcast signal sweeps from high frequency to low frequency, and the receiver breaks the entire frequency span of the sweep into multiple, closely-spaced frequency channels using band-pass filters. It imposes an electronic delay on each frequency in inverse relation to its place in the sweep. The highest frequencies are delayed the longest, the middle frequencies are delayed less long, and the lowest frequencies are delayed the least. As a result, the frequencies all emerge from the receiver's parallel delay elements at the same instant in time to form a compressed pulse. In this scheme, the receiver contains a frozen time-reversed template of the FM sweep (a time-frequency template; Figure 4B) instead of a time-reversed impulse response (a time-amplitude template; Figure 4A).

The 1960s-era chirp radar theory is an extension of the spectrogram theory of Griffin and Galambos (see Griffin, 1958) into how the spectrograms might actually be processed to achieve very sharp delay registration. The segmentation of frequencies with band-pass filters before applying different delays in a chirp radar receiver resembles the segmentation of frequencies by the parallel, frequency-tuned receptors and auditory nerve cells of the mammalian cochlea (inner ear), a fact known by that time (von Békésy, 1960).

Advent of Neurophysiology

A crucial part of the original evidence for the existence of echolocation was the finding that the cochlea of the bat responded to the same ultrasonic frequencies that were present in the sounds the bat emitted. This inaugurated an intensive neurophysiological research effort that has now spanned many decades and constitutes the larger part of published work (Neuweiler, 2000; Surlykke et al., 2014; Fenton et al., 2016). The salient discoveries specific to echolocation theory were that (1) neural responses to the second of two sounds, the “echo,” recovered swiftly and strongly from the effects of the first sound, the “broadcast,” clarifying that bats are not in fact at a disadvantage when listening for echoes that follow broadcasts; (2) middle ear attenuation of broadcasts preceded auditory transduction of broadcasts by the inner ear, so that sensitivity to the emitted sound is substantially reduced while sensitivity to echoes recovers in a graded fashion; (3) neural responses at successive levels of the bat’s auditory system incorporate additional neural gain control for further reducing responses to broadcasts in favor of echoes; (4) neurons at all levels of the bat auditory system are tuned to

specific frequencies somewhere in the range of echolocation sounds, thus confirming that cochlear frequency tuning and subsequent tonotopic representation encode the FM sweeps of echolocation sounds; and (5) the action of neurons in the bat’s auditory system to short-duration FM sounds that mimic echolocation signals are restricted almost entirely to single-spike, phasic-on responses.

The Neural Spectrogram Code

Segmentation of FM sweeps into numerous, parallel frequency-tuned neural channels is the auditory system’s way to create spectrograms. Individual auditory receptors and then individual neurons at all levels of the bat’s auditory system (in the brain) are tuned to specific frequencies, accompanied by clear topographic mapping of frequency that mimics the cochlea’s frequency map. When the acoustic stimuli are brief FM sweeps that mimic echolocation broadcasts and echoes, the vast majority of neurons in the bat’s cochlear nucleus (the first stage of auditory neural processing in the brain), the inferior colliculus (the principle neural integrating center in the auditory pathway), and the auditory cortex (the highest stage of neural processing and, in effect, a kind of display) react with an average of just one neural action potential (“spike”) for each sound (phasic-on response; Pollak and Casseday, 1989). This representation is a time-frequency point process, an auditory spectrogram. In physiological terms, auditory computations based on frequency consist largely of local *inhibitory* connections between neighboring frequency channels that feed forward to sharpen the registration of frequency and create responses that are selective for downward or upward FM sweeps at different sweep rates and long-distance *facilitatory* connections that link widely separated frequency channels tuned to harmonic frequencies (e.g., 1st harmonic with 2nd harmonic) to create responses that require the simultaneous presence of both harmonics.

To carry out computations on spike timing, the spikes have to be arranged at different latencies in different neurons. Spikes that occur at short latencies have to be preserved, remembered, so that they can be made available to compare with spikes that occur later. The problem with a single-spike code is that once a spike has occurred, the information it conveys evaporates. Having an auditory memory for the timing of single spikes means repeating that spike in different neurons at progressively longer latencies to carry its information forward so it will be available at a later time when it is needed. The particular details of latency registration are crucial for understanding auditory computations in biosonar (Simmons and Simmons, 2010; Simmons, 2012, 2014).

Delay Lines for Target Ranging

In **Figure 4, A and B**, the receiver incorporates a fixed template of the broadcast that is reversed in time. Because the template is specific to each transmitted signal's waveform and it is hardwired or programmed into the receiver, changing the broadcast requires making a different receiver for each new broadcast, which might be practical if there is a small number of potential transmitted signals in the repertoire, but it is cumbersome if there are many possible broadcasts that have to be accommodated. The spectrograms in **Figure 2** show that the big brown bat changes its broadcasts virtually continuously along the dimension of duration, which means FM sweep rate and frequency. To accommodate these changes, the bat must listen to each transmitted sound as it is sent out and create a new template "on the fly."

Figure 4C illustrates an auditory version of the spectrogram theory that takes each new broadcast into account for determining echo delay (Suga et al., 1990; Simmons et al., 1996; Wiegrefe, 2008). The bat transmits an FM sound and receives it at the inner ear at the moment it is sent out. Reception of the broadcast stimulates auditory receptors tuned to different frequencies along the sweep in succession, which evoke a single well-synchronized spike in each auditory neuron serving that receptor. Although secondary spikes are likely to occur in auditory nerve fibers when this excitation occurs, the cochlear nucleus must strip them out of subsequent stages of the auditory pathway because the single-spike phasic-on response pattern dominates responses recorded from all higher levels if the stimuli are brief FM chirps that mimic broadcasts or echoes. In the big brown bat's inferior colliculus, response latencies in different neurons spread densely over a range from about 4-5 ms (the minimum required for excitatory responses to ascend through the auditory brainstem) to about 30-35 ms and then more sparsely to longer latencies of 50 ms or more. Each of these neurons has a characteristic latency as well as a tuned frequency. Its single-spike response registers the corresponding time-frequency sampling point in the FM sweep, but, in addition, it retains it for the length of its latency.

Taken together, the ensemble of inferior colliculus neurons tuned to an individual frequency has a spectrum of latencies that resembles a frequency-tuned *delay line*. Each cell's particular response latency is created by a combination of inhibitory and excitatory inputs that first prevent a response from occurring until the inhibition has ceased and then triggers the response at a latency that is characteristic of that cell.

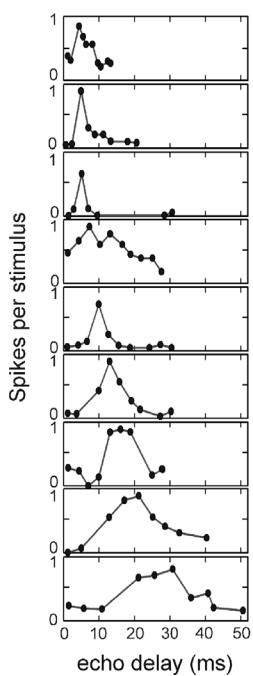
The spread of inhibitory durations determines the spread of neural delays. **Figure 4C** illustrates how this system of frequency-tuned delay lines responds in succession to the arrival of different frequencies in the broadcast and then repeats the initial registration of each time-frequency point over and over from one cell to the next. Across neurons tuned to different frequencies, the shape of the FM sweep is preserved as a traveling template analogous to the fixed templates in **Figure 4, A and B**, but it is updated for each new broadcast.

Registration of Echo Delay by Spectrogram Correlation

In **Figure 4C**, when an echo is received, it evokes a new pattern of single-spike responses in neurons tuned to successive frequencies in its FM sweep. This pattern resembles the pattern already in progress from the original broadcast and moving step-by-step to longer latencies (repeated occurrences of the same template). Responses to the echo coincide in time with one of the templates composed of ongoing responses to the broadcast. In each frequency channel (spectrogram delays in **Figure 4C**), the temporal coincidence of long-latency responses to the broadcast and short-latency responses to the echo is registered by neurons at higher levels of processing, in the medial geniculate and auditory cortex. Each such coincidence evokes a time-locked spike in neurons that receive inputs from neurons that have different characteristic response latencies along one of the delay lines. Coincidence-detecting neurons are "tuned" to the particular echo delay calibrated by the difference in time between the longer latency response to the broadcast and the shorter latency response to the echo. In big brown bats, delay-tuned neurons in the auditory cortex cover delays from 2 to 28 ms (Simmons, 2012), which fits well with the span of latencies found along the delay lines in the inferior colliculus. **Figure 5A** illustrates delay-tuning curves recorded from neurons in the auditory cortex of the big brown bat (Sanderson and Simmons, 2003). These delay-tuned cells encode a target range from about 30 cm to 5 m. A separate system of delay-tuned neurons is found in the superior colliculus (Wohlgemuth et al., 2016). It is important to note, however, that the fact of delay tuning does not constitute an explanation of a perceived target range because delay tuning is too imprecise to support the bat's behavioral delay acuity (Pollak, 1980).

Unlike the fixed template designs in **Figure 4, A and B**, the delay line structure in **Figure 4C** can adapt to changes in the broadcasts and still determine the delay of echoes. Successive broadcasts can shorten in duration and thus become steeper in FM sweep rate, but the separation of delay computations

A delay tuning curves



B behavioral performance in delay tests

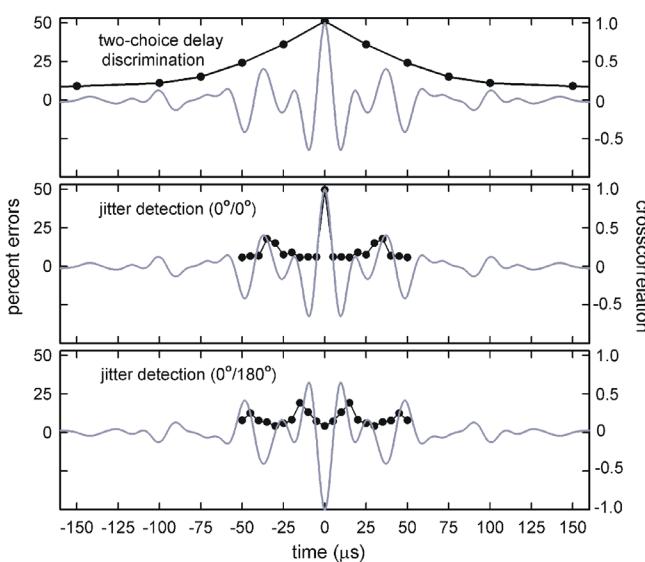


Figure 5. Comparison of neural delay tuning with behavioral tests of echo delay acuity in big brown bats. **A:** Delay-tuning curves measured in the auditory cortex of big brown bats. **B:** Performance (in percent errors) in two-choice delay discrimination tests with electronically generated echoes (bat “virtual reality”; **top**), and performance in tests of delay-jitter detection with alternating electronic echoes in the same phase ($0^\circ/0^\circ$; **middle**) or inverting phases ($0^\circ/180^\circ$; **bottom**). Neural delay-tuning sharpness is measured in milliseconds or tens of milliseconds, whereas behavioral discrimination is measured in tens of microseconds and delay-jitter detection involves changes of only a few microseconds.

into parallel frequency channels before registering the final overall delay allows the system to accommodate changes in the broadcasts. This process is spectrogram correlation, the first stage in a two-stage computational model of target ranging and target shape perception (Simmons et al., 1996, 2017). The performance of auditory spectrogram correlation has been evaluated along with the performance of a matched-filter receiver in a large simulation (Sanderson et al., 2003). The process of spectrogram correlation achieved the same performance levels as a matched-filter receiver across a wide span of echo signal-to-noise ratios.

Perception of Target Range

At this last juncture, the critical question is whether echolocating bats can perceive a target range using the delay of echoes as the principal acoustic cue. The regular decrease in broadcast duration with declining distance to the target (**Figure 2**) is very suggestive, but what is needed is psycho-physical evidence that the distance to a target and the delay of echoes are equivalent auditory dimensions. The first demonstration of target range perception was a series of discrimination experiments in which bats of several species (including big brown bats) were trained to sit on an elevated platform and broadcast echolocation sounds in the direction

to about 1 cm or the delay of the echoes up to about 60 ms. Because the bat’s discrimination thresholds are of similar size, the bat might be able to perceive small changes in delay that these experiments would not be able to determine.

A new procedure trained bats to detect small changes in delay that alternate or jitter from one broadcast-echo pair to the next. In the jitter detection task, big brown bats easily determined that the delay was changing by about 1 ms, and under some conditions, they could detect changes of a small fraction of a microsecond (Simmons et al., 1995, 1996). This ultimate sensitivity roughly matches what can be achieved by a matched filter using the same signals at the same signal-to-noise ratios (Sanderson et al., 2003).

Figure 5B shows the mean performance of four big brown bats detecting jitter in echo delay accompanied by no phase jitter ($0^\circ/0^\circ$) or by 180° phase jitter ($0^\circ/180^\circ$). These results are compared with delay tuning in neurons of the big brown bat’s auditory cortex (**Figure 5A**). The discrepancy between delay tuning at the neural level and delay acuity in behavioral tests is striking. It is barely plausible that the $\sim 60\text{-}\mu\text{s}$ accuracy obtained in two-choice tests can be explained by neural tuning, whereas delay acuity and phase sensitivity obtained in jittered-echo tests is well beyond plausible accounting. The

of two flat targets, one to its left and the other to its right (Simmons, 1973). The bat’s task was to move toward the nearer of the two targets. The bats were able to perceive changes in distance of about 1-2 cm. When the physical targets were replaced by an electronic echo-generating system, a “virtual reality” version of the same task, big brown bats could perceive changes of about 50-70 μs . **Figure 5B, top**, shows the mean performance of two big brown bats discriminating differences in echo delay during such a virtual reality experiment (Simmons, 1973). The ability to discriminate changes of about 1 cm or 60 μs has been found to be ubiquitous across different species of bats (Simmons and Grinnell, 1988).

Two-choice range or delay discrimination experiments involve the bat scanning with the aim of its head and broadcasting to the left and right during each trial. These movements introduced changes in the apparent distance to the targets of up

spectrogram correlation process is capable of achieving delay accuracies comparable to a matched filter, but the properties of delay-tuned neurons created by this mechanism do not appear to be the vehicle for achieving the bat's actual performance (Pollak, 1980). How is this difference to be explained?

The obvious place to look is at the timing of the spikes instead of the delay-tuning curves themselves. Although delay tuning is manifested in milliseconds, the latencies of the spikes vary by only a few hundred microseconds in most cells, a reduction in timing errors of up to 100 times (Simmons et al., 1996). **Figure 4C** shows the delay lines for spectrogram correlation just schematically and very qualitatively, whereas the actual numerical values of the spike latencies, the phasic-on responses that constitute the delay taps, are arranged periodically at intervals of about 2 to 3 milliseconds (Simmons and Simmons, 2010). This periodicity is present in the latencies of responses evoked by both broadcasts and echoes (Simmons et al., 1996). Its presence points to underlying oscillatory signals in the representation of the broadcasts and echoes that provides a way for fine delay changes to affect how these oscillatory signals interact and interfere with each other. These oscillations suggest that a neural heterodyning process may be manifested in the inferior colliculus and its subsequent neuronal circuits to register small, microsecond-scale changes in echo delay as shifts in interference patterns across the time (i.e., latency) dimension. This would render seemingly microscopic changes in echo delay into large changes in response probability and latency that would be recognizable by the much more sluggish responses of neurons. The hallmark of a vernier-like interference process is the magnification of small changes in timing into larger changes in the product of the interference, which has been observed in big brown bats (Simmons et al., 1996). This mechanism may explain the big brown bats extraordinary submicrosecond sensitivity to changes in echo delay.

Implications for Hearing in General

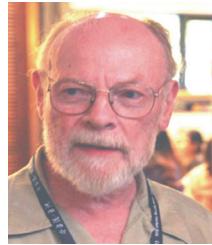
The periodic organization of single-spike on-response latencies and their role in registering the timing of sounds are not restricted to big brown bats; it is present, too, in the inferior colliculus of bullfrogs and of cats (Simmons and Simmons, 2010). The auditory cortex, at the top of the auditory processing pathway, is thought of as a display of information for perception, but it also feeds information back to the integrating center of the inferior colliculus, which is responsible for the distributed nature of spike latencies. The time lags asso-

ciated with this excitatory feedback may produce the periodic pattern of latencies, which maybe critical for the fine perception of echo delay. This, in turn, means that the concepts of display and processing are intermingled across levels in the auditory system, which raises the possibility that the superior performance echolocation may require radical new technology to replicate.

Acknowledgments

The computational studies for this article were supported by Office of Naval Research Grant N00014-14-1-05880. I am grateful for the assistance of the *Acoustics Today* editor in preparing this work.

Biosketch



Jim Simmons was an undergraduate at Union Junior College in New Jersey and Lafayette College in Pennsylvania. He was a graduate student of E. G. Wever at Princeton University where he began working with echolocating bats. He taught at Washington University in St.

Louis for 10 years, where his colleagues were Nobuo Suga and the many members of the auditory community at the Central Institute for the Deaf. He moved to the University of Oregon for four years as part of a group of neuroethologists and has been at Brown University since 1985 in psychology and then in neuroscience.

References

- Au, W. W. L., and Simmons, J. A. (2007). Echolocation in dolphins and bats. *Physics Today* 60, 40-45.
- Fenton, M. B., Grinnell, A. D., Popper, A. N., and Fay, R. R. (Eds.). (2016). *Bat Bioacoustics*. Springer-Verlag, New York.
- Griffin, D. R. (1958). *Listening in the Dark*. Yale University Press, New Haven, CT; reprinted by Cornell University Press, Ithaca, NY, 1986.
- Grinnell, A. D., Gould, E., and Fenton, M. B. (2017). A history of the study of echolocation. In Fenton, M. B., Grinnell, A. D., Popper, A. N., and Fay, R. R. (Eds.), *Bat Bioacoustics*. Springer-Verlag, New York, pp 1-24.
- Moss, C. F., and Surlykke, A. (2010). Probing the natural scene by echolocation in bats. *Frontiers in Behavioral Neuroscience* 4, 33. doi:10.3389/fnbeh.2010.00033.
- Neuweiler, G. (2000). *The Biology of Bats*. Oxford University Press, New York.
- Pollak, G. D. (1980). Organizational and encoding features of single neurons in the inferior colliculus of bats. In Busnel, R.-G., and Fish, J. F. (Eds.), *Animal Sonar Systems*. Plenum, New York, pp. 549-587.
- Pollak, G. D., and Casseday, J. H. (1989). *The Neural Basis of Echolocation in Bats*. Springer-Verlag, Berlin Heidelberg.

- Pye, J. D. (1980). Echolocation signals and echoes in air. In Busnel, R.-G., and Fish, J. F. (Eds.), *Animal Sonar Systems*. Plenum, New York, pp. 309-353.
- Sanderson, M. I., and Simmons, J. A. (2003). Selectivity for echo spectral shape and delay in the auditory cortex of the big brown bat, *Eptesicus fuscus*. *Journal of Neurophysiology* 87, 2823-2834.
- Sanderson, M. I., Neretti, N., Intrator, N., and Simmons, J. A. (2003). Evaluation of an auditory model for echo delay accuracy in wideband biosonar. *The Journal of the Acoustical Society of America* 114, 1648-1659.
- Simmons, J. A. (1973). Resolution of target range by echolocating bats. *The Journal of the Acoustical Society of America* 54, 157-173.
- Simmons, J. A. (2012). Bats use a neuronally implemented computational acoustic model to form sonar images. *Current Opinion in Neurobiology* 22, 311-319.
- Simmons, J. A. (2014). Temporal binding of neural responses for focused attention in biosonar. *Journal of Experimental Biology* 217, 2834-2843.
- Simmons, J. A., and Grinnell, A. D. (1988). The performance of echolocation: Acoustic images perceived by echolocating bats. In Nachtigall, P., and Moore, P. W. B. (Eds.), *Animal Sonar Systems: Processing and Performance*. Plenum, New York, pp. 353-385.
- Simmons, J. A., and Simmons, A. M. (2010). Bats and frogs and animals in between: Evidence for a common central timing mechanism to extract periodicity pitch. *Journal of Comparative Physiology A* 197, 585-594.
- Simmons, J. A., Ferragamo, M. J., Saillant, P. A., Haresign, T., Wotton, J. M., Dear, S. P., and Lee, D. N. (1995). Auditory dimensions of acoustic images in echolocation. In Popper, A. N., and Fay, R. R. (Eds.), *Hearing by Bats*. Springer-Verlag, New York, pp. 146-190.
- Simmons, J. A., Saillant, P. A., Ferragamo, M. J., Haresign, T., Dear, S. P., Fritz, J. B., and McMullen, T. A. (1996). Auditory computations for acoustic imaging in bat sonar. In Hawkins, H. L., McMullen, T. A., Popper, A. N., and Fay, R. R. (Eds.), *Auditory Computation*. Springer-Verlag, New York, pp. 401-468.
- Simmons, J. A., Gaudette, J. A., and Warnecke, M. (2017). Biosonar inspired signal processing and acoustic imaging from echolocating bats. In Ballieri, A. (Ed.), *Biologically Inspired Radar and Sonar: Lessons from Nature*. IET Press, London, pp. 5-36.
- Skolnik, M. I. (1980). *Introduction to Radar Systems*, 2nd ed. McGraw-Hill, New York.
- Stilz, W.-P., and Schnitzler, H.-U. (2012). Estimation of the acoustic range of bat echolocation for extended targets. *The Journal of the Acoustical Society of America* 132, 1765-1775.
- Suga, N., Olsen, J. F., and Butman, J. A. (1990). Specialized subsystems for processing biologically important complex sounds: Cross-correlation analysis for ranging in the bat's brain. *Cold Spring Harbor Symposium on Quantitative Biology* 55, 585-597.
- Surlykke, A., Nachtigall, P. E., Fay, R. R., and Popper, A. N. (Eds.) (2014). *Biosonar*. Springer-Verlag, New York.
- von Békésy, G. (1960). *Experiments in Hearing*. McGraw-Hill, New York.
- Wiegreb, L. (2008) An autocorrelation model of bat sonar. *Biological Cybernetics* 98, 587-595.
- Wohlgemuth, M. J., Luo, J., and Moss, C. F. (2016) Three-dimensional auditory localization in the echolocating bat. *Current Opinion in Neurobiology* 41, 78-86.

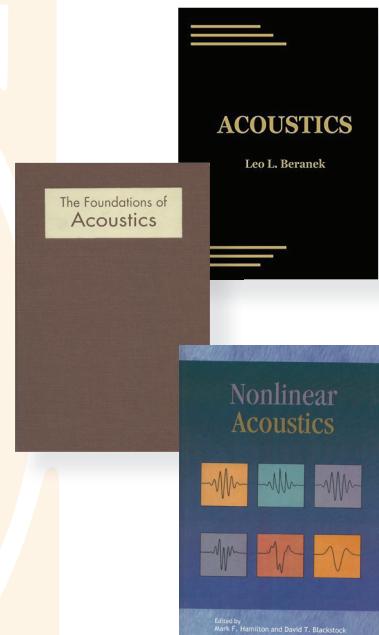
ASA Press Books available through Amazon.com

The ASA Press offers a select group of Acoustical Society of America titles at low member prices on Amazon.com with shipping costs as low as \$3.99 per book.

Amazon Prime members can receive two-day delivery and free shipping.

To purchase ASA Press books quickly and easily follow these steps:
visit www.Amazon.com > select Books > enter Title in Search bar >
press on Title then New > choose the ASA Press listing.

For more information and updates about ASA Press books on Amazon,
please contact the ASA Publications Office at **508-362-1211**.



ASA Press

ASA Press - Publications Office
17 High School Road
Hyannis, MA 02601
508-362-1211