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Echo delay versus spectral cues for temporal hyperacuity in the big brown bat, *Eptesicus fuscus*

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Abstract Big brown bats can discriminate between echoes that alternate in delay (jitter) by as little as 10–15 ns and echoes that are stationary in delay. This delay hyperacuity seems so extreme that it has been rejected in favor of an explanation in terms of artifacts in echoes, most likely spectral in nature, that presumably are correlated with delay. Using different combinations of digital, analog, and cable delays, we dissociated the overall delay of jittering echoes from the size of the analog component of delay, which alone is presumed to determine the strength of the apparatus artifact. The bats' performance remains invariant with respect to the overall delay of the jittering echoes, not with respect to the amount of analog delay. This result is not consistent with the possible use of delay-related artifacts produced by the analog delay devices. Moreover, both electronic and acoustic measurements disclose no spectral cues or impedance-mismatch reflections in delayed signals, just time-delays. The absence of artifacts from the apparatus and the failure of overlap and interference from reverberation to account for the 10-ns result means that closing the gap between the level of temporal accuracy plausibly explained from physiology and the level observed in behavior may require a better understanding of the physiology.

Keywords Bats · Delay hyperacuity · Echo delay · Echolocation · Target ranging

Abbreviations *FM* frequency-modulated · *XCR* cross-correlation function

Introduction

Big brown bats (*Eptesicus fuscus*) broadcast ultrasonic frequency-modulated (FM) biosonar sounds and perceive objects from echoes that return to their ears (Griffin 1958; Grinnell 1995; Neuweiler 2000). They determine target distance, or *range*, from echo delay (5.8 ms m^{-1} of *range*). In discrimination experiments—using two-alternative forced choice (2AFC), go/no-go, or yes/no paradigms—the bat's thresholds for perceiving differences in delay are mostly in the range of 40–80 μs (Simmons and Grinnell 1988; Moss and Schnitzler 1995). However, these thresholds are similar to the amount of uncertainty in delay introduced by the bat's head movements within or between trials, so they cannot be taken as valid measurements of the bat's underlying delay accuracy (Simmons et al. 1995) even though they are similar to the timing accuracy of responses in individual neurons (Pollak et al. 1977). To minimize this uncertainty, a new method was developed in which the arrival-time of echoes is varied (*jittered*) from one broadcast to the next over the much shorter interval between broadcasts rather than from one scan or one trial to the next (Simmons 1979). Figure 1 illustrates the procedure for the 2AFC version of jitter experiments (Simmons et al. 1990a). Echoes that alternate in delay are generated by picking up the bat's sonar sounds with microphones (m), passing the resulting electrical signals through electronic delay lines, and then reconstituting the delayed signals as acoustic echoes delivered back to the bat from loudspeakers (s). Figure 2 shows the signal path used to create the stimuli. By electronically switching delay lines from one broadcast to the next, successive echoes can be made to arrive at different delays. In experiments of this type, big brown bats can detect changes in delay of 0.5 μs or less (Simmons 1979; Menne et al. 1989; Moss and Schnitzler 1989). At an echo signal-to-noise ratio of 36 dB, the smallest detectable change in delay is about 0.04 μs , or 40 ns, and at 49 dB it is about 10 ns (Simmons et al.

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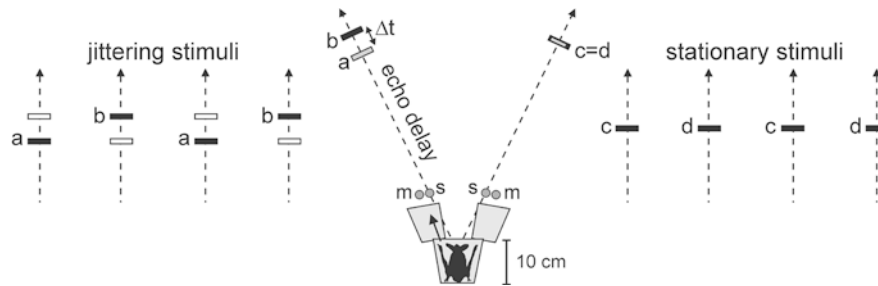


Fig. 1 Diagram of two-choice paradigm for jittering-echo experiments, showing bat on Y-shaped platform with microphones (*m*) and loudspeakers (*s*) (center), alternating delays of jittering echoes *a* and *b* (left), and fixed delays of alternating stationary or nonjittering echoes *c* and *d* (right). See Simmons et al. (1990a)

1990a). This exceptional sensitivity is termed *hyperacuity* for delay by analogy with the concept of hyperacuity in vision (Altes 1989; Simmons et al. 1990a). Here we report experimental evidence that the so-called “10-ns result” cannot be dismissed as due to artifacts, which suggests that conventional thinking about how the auditory system manages information about timing needs to be revised.

Objections to jitter results

It has been asserted that the 10-ns result is impossible—both because bats would have no conceivable biological purpose for registering submicrosecond changes in delay and because the thresholds seem too small for the auditory system to achieve (Pollak 1993; Beedholm and Møhl 1998; Menne et al. 1989). The result also has been described as impossible for information-theoretical reasons (Beedholm and Møhl 1998), but in fact the bat’s performance is within the bounds of delay accuracy for matched-filter reception of sonar echoes (Simmons et al. 1990a; Sanderson et al. 2003).

First, we take the biological purpose objection. It is true that the jitter experiment has no acoustic counterpart in nature, but this is true for *any scientific experiment* because the need to make measurements

necessarily imposes constraints on conditions. The jitter procedure was never *intended* to estimate how accurately the bat uses information about delay for guiding its flight while chasing insects (for factors influencing delay estimates in flight, see Boonman et al. 2003). For this reason the stimuli do not mimic echoes received from moving targets by flying bats any more than tone-bursts in frequency discrimination experiments with humans mimic natural sounds or speech. Instead, the jitter experiment was designed to measure the intrinsic delay sensitivity of the bat’s auditory system. The stimulus configuration emphasizes changes in delay while holding all other echo parameters constant or irrelevant to accomplishing the task. Contrary to what is asserted by critics (Pollak 1993; Beedholm and Møhl 1998), there has been no claim that the 10-ns result represents the bat’s ordinary acuity for delay, only its hyperacuity (Simmons et al. 1990a). Ordinary acuity has been estimated to be of the order of 1 μ s from echo-delay resolution results (Simmons et al. 1998), from analysis of performance in obstacle avoidance and airborne-target discrimination tests (Simmons et al. 1995, 1996), and from jitter experiments with echoes shifting over large intervals of absolute delay while they jitter (Masters et al. 1997). Thus, it is misleading to reject the 10-ns result as impossible by asserting that it is biologically without purpose, particularly without reference to the relevant material.

Second, we take the auditory timing-accuracy objection, which is twofold. Disbelief about the 10-ns result is accompanied by disbelief about the other major finding from jitter experiments, which occurs on a more plausible microsecond, not nanosecond, time scale. As shown in Fig. 3, when the phase of echoes is shifted by 0° or 180° while delay is being jittered, big brown bats perceive the phase shift as equivalent to a change in delay of about ± 15 μ s. Moreover, bats easily discriminate between echoes that have phase shifts of 0° versus 180° (as in Fig. 3) or +90° versus −90° when delay jitter itself is zero (Menne et al. 1989; Simmons et al. 1990a; Moss and Simmons 1993). These demonstrations of “pure” phase sensitivity are important because, at signal-to-noise ratios of 36 or 49 dB, the bat’s respective jitter thresholds of 40 ns and 10 ns cannot be achieved without coherent processing of echoes (Simmons et al. 1990a; Sanderson et al. 2003). The phase-shift and 10-ns results are collectively dismissed as being physiologically impossible without

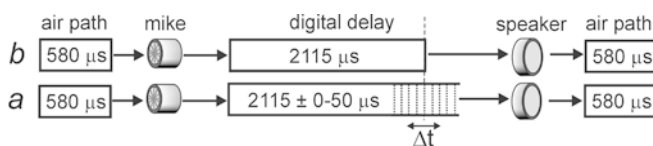


Fig. 2 Diagram of acoustic and digital electronic delays for echoes delivered to the bat in jittering-echo experiments (see Fig. 1). Microphones and loudspeakers are at distances of 20 cm for acoustic path-length delay of 580 μ s, augmented by digital delay lines to achieve a total average delay, including air-path and electronic delay, of ~ 3.275 ms. Jittering echoes (*a* and *b*) alternate between two delays determined by settings on digital delay lines, which are variable in steps of 1.3 μ s. The same system is used to control delays for stationary echoes (*c* and *d*) except that both electronic delays are fixed at 2,115 μ s

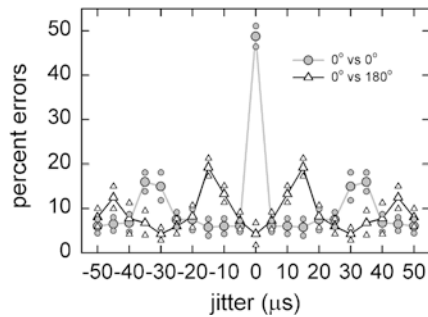


Fig. 3 Performance of bats in jitter experiments with changes in delay derived entirely from digital delay lines making 5- μ s delay steps combined with 0° or 180° change in echo phase for echoes *a* and *b*: Gray curves and circles show mean $\pm$ standard error of mean (SEM) for percentage errors by 4 bats (40–60 trials per bat per point) detecting jitter values from 0 to 50 μ s with 0° change in phase. Black curves and circles show mean $\pm$ SEM for percentage errors by 4 bats detecting jitter values from 0 to 50 μ s with 180° change in phase

citing any evidence besides a neuroscience textbook chapter that makes no mention of these phenomena in bats (Beedholm and Møhl 1998). Because the objections to both results are linked, they have to be addressed together to explain why we did the experiments reported here.

Phase sensitivity and the 10-ns result are thought to be well beyond the capacity of the auditory system to encode neurally (Menne et al. 1989; Pollak 1993; Beedholm and Møhl 1998). In mammals studied previously, phase sensitivity for coding of sounds by the inner ear extends no higher than 1–5 kHz (Weiss and Rose 1988; Koppl 1997), whereas the big brown bat's biosonar sounds are wholly at ultrasonic frequencies. Furthermore, although delay accuracy as small as 0.5 μ s is marginally plausible from present physiological knowledge (Schnitzler et al. 1985), the finding that hyperacuity may be in the range of tens of nanoseconds goes beyond any previous conception of the timing accuracy of the auditory system. Either the bat uses some acoustic cue other than delay in the jitter experiments, or essential capabilities of the bat's auditory nervous system are not yet appreciated. The former is possible, but the latter is virtually certain (for relevant aspects of what is unknown in auditory function, see Casseday and Covey 1995; Shamma and Klein 2000). Critical commentary about the jitter results has focused entirely on the likelihood of artifacts (e.g., Menne et al. 1989; Pollak 1993; Beedholm and Møhl 1998) without mentioning the need to examine the bat's auditory system more carefully, even though the most important physiological parameter (low-pass smoothing of receptor excitation) for auditory coding of the time of occurrence of FM sounds has not even been measured in bats (Simmons 1980).

Applicability of artifact hypothesis to phase result

Evidence for perception of echo phase shifts (0–180° or $\pm 90^\circ$) and for perception of delay changes from 50 μ s

down to about 1 μ s comes from jitter experiments that employ all-digital delay lines (Menne et al. 1989; Simmons et al. 1990a). These devices introduce no delay-related changes in echo spectra and thus are not susceptible to possible artifacts of the type potentially created by analog delay devices (see below). For example, jitter performance curves for 0° and 180° phase-shifted echoes (Fig. 3) are based on data collected for delay steps of 5–50 μ s, and there is scant basis for claiming that bats cannot perceive 5-, 10-, or 15- μ s changes in delay. The locations of the error peaks in the curves in Fig. 3 move left or right by ± 15 μ s, which is a difference in delay that bats manifestly can detect. The other source of spectral artifacts is overlap and interference between stimulus echoes and reverberation in the room. Acoustic measurements show no extraneous echoes from objects in the room that overlap with the jittering stimuli inside a critical time window of about 2.5 ms. Bats that use sounds shorter than 2.5 ms and bats that use sounds longer than 2.5 ms perform identically, which rules out spectral artifacts derived from reverberation in the room as a viable explanation for the results in Fig. 3 (for this and other reasons see Simmons 1993). The most important fact is that the locations of the error peaks in Fig. 3—in fact, the entire shape of the curve for either 0° or 180° phase shift—can be moved left or right along the delay axis according to predicted amplitude-latency trading (~ -15 μ s dB $^{-1}$; Simmons et al. 1990a). Big brown bats encode the phase-related difference in their jitter-detection performance from corresponding phase-related changes in the latencies of neural responses that jointly register echo arrival time and phase. The hypothesis that some artifact supplants delay and phase as joint cues for detecting jitter in steps of 5 μ s or changes in phase thus has been rejected (Simmons 1993). Instead of dwelling on this disproved hypothesis, physiological parameters already identified as determining the high-frequency limit for auditory coding of FM echo phase in relation to delay (Simmons 1980) need to be measured in bats. Computational modeling of auditory transduction reveals that, contrary to speculation (Beedholm and Møhl 1998), the most important factor—the low-pass cutoff frequency for smoothing the envelopes of excitation delivered to auditory neurons by hair cells—only has to be in the range of 8–10 kHz to achieve fully coherent processing of FM echoes in the 20–100 kHz band (Sanderson et al. 2003).

Applicability of artifact hypothesis to 10-ns result

Delay changes smaller than 0.5–1 μ s are produced with analog delay lines because digital sampling rates of less than 1 MHz preclude making finer digital adjustments of delay. Here there is scope for introduction of artifactual changes in echo spectra correlated with delay, and the artifact hypothesis may be relevant as an alternative explanation for very small jitter thresholds.

However, at present, only electronically produced artifacts remain viable as an alternative explanation of the 10-ns result because spectral artifacts caused by acoustic reverberation have been shown not to explain the results (Simmons 1993). Differences between channels in passive components, analog electronic switches, or analog operational-amplifier chips could have produced frequency-dependent changes in gain between jittering echoes if these variable components were switched along with delay. However, during system calibration, overall analog gain differences between channels were nulled out at 40 kHz using a precision analog voltmeter to reduce those differences to 0.3% (0.03 dB) or less. Following this adjustment, acoustic measurements of the output of the target simulator showed no frequency dependence of gain in the apparatus larger than 0.05–0.1 dB for different amounts of analog delay in the critical 0- to 50-ns range. Even these spectral differences are too small to detect in the presence of random spectral variations caused by the flat-spectrum ultrasonic noise deliberately added to the echoes to control the signal-to-noise ratio of echoes, which was approximately 49 dB in the conditions for the 10-ns result (Simmons 1993). Neither Beedholm and Møhl (1998) nor Pollak (1993) account for how the 10-ns result could be caused by these minuscule artifacts in the presence of random noise.

The only remaining source of delay-related artifacts is the analog delay lines or cables. These devices retard signals directly by having a propagation-time proportional to electronic length, and they conduct signals bidirectionally, which makes them susceptible to generation of spurious signals if their input or output impedances are not matched by the source or load. For example, if the output impedance of the analog delay line is not matched by the outgoing load, a reflection of the original signal is created proportional in strength to the impedance mismatch, and this reflection travels back and forth through the delay line to reappear at the output with an additional delay that is twice the intended delay of the original signal (Beedholm and Møhl 1998). The point of their objection is that the presence of the thrice-delayed reflection following the once-delayed signal converts the jitter task into detection of closely spaced overlapping reflections at different separations. With regard to this putative artifact, however, Beedholm and Møhl (1998) give no information about how a 10-ns + 30-ns pattern of echo delays is any easier for the bat to perceive than a 10-ns delay change. The bat's measured two-point resolution is about 1 μ s (Simmons et al. 1998), not the 20 ns required to make use of the putative reflection, which, as it happens, is impossible for information-theoretical reasons at a signal-to-noise ratio of 49 dB (Neretti et al. 2003). Moreover, it is a fact that the analog delay lines or cables were specifically terminated by their characteristic impedances (see Materials and methods). Nevertheless, to test for the presence of impedance-mismatch reflections using the same display format as Beedholm and Møhl (1998), we made measurements of delay line impulse responses at a

sampling rate of 0.5 ns using microwave equipment (see Fig. 5). The waveforms of short (80 ns) pulses delayed by the analog delay lines or the cables show no evidence whatsoever for any effect other than delay, so artifacts derived from impedance mismatches are not present.

As further evidence for their reflection artifacts, Beedholm and Møhl (1998) cite the presence of small distortions in the waveshape of a difference signal (Simmons 1993) computed to calibrate the delay lines. The method of calibration that yields this difference signal involved computing cross-correlation functions (XCRs) between FM test broadcasts and corresponding FM echoes for the jittering echoes *a* and *b* in Fig. 1. The *difference* between these XCRs was then determined for different small changes in delay (e.g., 0–25 ns; see Fig. 6A), and the resulting waveshape was used to estimate the difference in delay itself. This roundabout method was employed because the delay steps in the jitter experiment (0–50 ns) are very small compared to the sampling interval (2,000 ns for a 500-kHz sampling rate) for digitizing the signals prior to computing the XCRs. The waveshape for the difference function should approximate a 90° phase-shifted version of the XCR itself (Simmons 1993; Beedholm and Møhl 1998). As explained in Materials and methods, Fig. 6A illustrates the graded emergence of this phase-shifted difference function from the subtracted XCRs for jitter values of 0, 5, 10, 15, 20, and 25 ns. This plot also shows the level of noise in the method, which can be used to detect delay changes less than 10 ns, but not less than 5 ns. Small variations in a representative XCR difference function calculated for an 11-ns delay difference (Simmons 1993), were singled out by Beedholm and Møhl (1998) as evidence for impedance-mismatch reflections. However, Beedholm and Møhl (1998) did not attempt to use this method themselves; instead, they simulated it with noise-free XCRs, which unfairly creates a cartoon of the process, not the process itself. As Fig. 6A shows, variations in the XCR difference functions are caused by the noise intrinsic to making such small measurements of delay. To establish whether spectral artifacts are present, Fig. 6B shows a series of corresponding difference functions computed for the spectra of echoes *a* and *b* at delay changes of 0–25 ns in 5-ns steps. Examination of these spectral difference functions reveals the absence of any delay-related features that emerge as the amount of jitter increases from 0 to 25 ns. The plots in Fig. 6 demonstrate unambiguously that the jittering echoes differed only in delay due to the action of the analog delay lines, with no added reflections and no differences in their spectra, so the apparatus artifact hypothesis is rejected.

Alternative method for detecting whether apparatus artifacts are present

At the time the jitter experiments were carried out, the microwave equipment was unavailable for direct mea-

surements of nanosecond delays, so we designed and carried out “dissociation” experiments specifically to deal with the possibility of spectral artifacts in the delay lines that were not detected by our calibration procedures but might nevertheless be present in the sounds reaching the bat’s ears. These were not done specifically to control for the Beedholm and Møhl (1998) artifact, but nevertheless that is one of several delay-related artifacts covered by the outcome of the dissociation experiments. The overall arrival time of echoes at the bat’s ears is due to all the factors shown in Fig. 2. We produced jittering stimuli with different combinations of digital and analog delays, and then we observed whether the bats responded according to the overall delay of echoes or just to the analog delays which would produce the putative artifacts.

Materials and methods

Jitter procedure

The animals in our experiments were big brown bats, *E. fuscus* (Chiroptera: Vespertilionidae; see Kurta and Baker 1990), obtained as adults from the attics of houses in Rhode Island. Figure 1 shows the experimental paradigm we used for studying the accuracy of echo-delay perception. The procedure (center of Fig. 1) is to present the bat with echoes of its sonar broadcasts that either jitter in delay from one broadcast to the next (left side of Fig. 1) or are stationary in delay (right side of Fig. 1) and to determine the smallest amount of jitter (Δt) which the bat can detect. (See Simmons et al. 1990a and Simmons 1993 for details about apparatus and methods.) Each bat was trained to sit on an elevated Y-shaped platform (shaded in Fig. 1) and broadcast sonar sounds into two Bruel and Kjaer Model 4138 condenser microphones (m) located approximately 10 cm (Fig. 4C, D) or 20 cm (Fig. 4A, B) from the bat’s position, one on the bat’s left and one on the right. The signals produced by the microphones were led to delay lines, and the delayed signals were returned to the bat as artificially generated echoes delivered from corresponding RCA type 112343 electrostatic loudspeakers (s) located next to the microphones and also 10 cm or 20 cm away from the bat. (Calculations of delay below are based on a nominal 10-cm or 20-cm distance from the bat to the microphones and from the loudspeakers back to the bat; actual distances varied according to the bat’s position; see Fig. 4.) The electronic apparatus which picked up the bat’s broadcasts, delayed them, and determined whether the left or the right loudspeaker was to be activated, constitutes a dual-channel target simulator. The angle separating the microphone/loudspeaker assemblies (m, s) on the left and right was 40°. The effective bandwidth of the system was about 20 to 80 kHz, with reduced output especially at frequencies from 80 to 100 kHz. Variations between channels depended on the loudspeakers and ranged from zero to as much as ± 1 to ± 4 dB depending on frequency (Simmons et al. 1990a).

Psychophysical data on detection of jittering echoes were collected with a 2AFC procedure. The bat’s task was to determine whether electronically delayed echoes of successive biosonar broadcasts changed in delay from one sonar broadcast to the next (“jittering stimuli” *a* and *b* at left in Fig. 1) or were constant in delay (“stationary stimuli” *c* and *d* at right), and to choose which of the two loudspeakers (left or right) delivered the echoes that changed in delay on that particular trial. The bat indicated its choice by moving forward towards the correct loudspeaker (producing jittering echoes) and onto the left or right arm of the Y-shaped platform (arrow in Fig. 1), where it received a piece of mealworm (*Tenebrio* larva) offered with forceps. If the bat moved towards the wrong loudspeaker (producing stationary, nonjittering echoes), it received no reward and was kept on the platform while

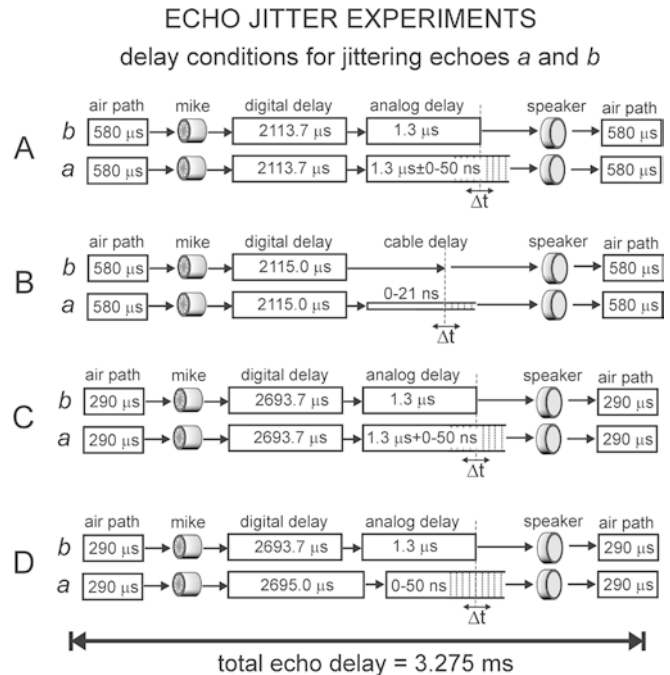


Fig. 4A–D Alternative methods for producing changes in electronic echo delay smaller than 1.3 μ s (see Fig. 1): total delays for jittering echoes *a* and *b* at zero jitter ($\Delta t = 0$) and for stationary echoes *c* and *d* are ~ 3.275 ms. Microphones and loudspeakers are at distances of 20 cm for acoustic delay of 580 μ s in **A, B** and 10 cm for delay of 290 μ s in **C, D**. **A** Combination of delay lines with *a* and *b* digital delays of fixed same size (2,113.7 μ s) and analog delays of equal size (1.3 μ s) at zero jitter. **B** Combination of digital delay lines of fixed same size (2,115.0 μ s) and variable cable delays (fine delay increments depend on cable length; see Table 1). **C** Combination of delay lines with *a* and *b* digital delays of fixed same size (2,693.7 μ s) and analog delays of equal size (1.3 μ s) at zero jitter. **D** Combination of delay lines with *a* and *b* digital delays of different size (2,693.7 μ s and 2,695.0 μ s) and analog delays of different size (1.3 μ s and 0.0 μ s) at zero jitter. Analog delays are 0–50 ns in increments of 5 ns. In **D**, equal analog delays occur at *nonzero* jitter, whereas in **C** equal analog delays occur at *zero* jitter. **C** and **D** dissociate the null point of any potential analog-delay artifact (Beedholm and Møhl 1998) away from zero jitter and should displace performance curves away from zero if bats use this artifact to detect jitter rather than perceive the delay change itself

the experiment halted for a brief time-out period. In these experiments, the amount of jitter (Δt in Fig. 1) ranged from ± 50 ns down to zero around a mean delay of 3.275 ms, which also was the delay of the stationary echoes (Simmons et al. 1990a). The apparatus for generating stationary echoes was the same as that for generating jittering echoes except that the delay difference (Δt) between *c* and *d* was set to zero. It is important that the jittering and stationary echoes be presented at the same mean delay ($[(a + b)/2 = c = d]$) because the bat’s performance is degraded by masking that occurs when the value of *c* or *d* is equal to either *a* or *b* (see Fig. 23 in Simmons et al. 1990a). The mean delay of both the jittering and the stationary echoes is equivalent to a simulated target range of about 56 cm.

The correct (jittering) stimulus appeared on the left or right from one trial to the next according to a pseudorandom schedule (Simmons et al. 1990a). At each stimulus condition described below, 40–60 trials were conducted. Perfect performance was 100% correct choices (0% errors), chance performance was 50% correct choices (50% errors), and threshold performance was arbitrarily set at 75% correct choices (25% errors). The psychophysical method of limits was used, i.e., the size of the jitter interval (Δt) was

decreased in small steps from a value the bat easily could detect to values too small for the bat to detect. In the course of reducing the amount of jitter, the delays of *a* and *b* always were adjusted to keep the mean delay at 3.275 ms. The data are presented as plots showing percentage of correct responses achieved by each bat at different values of the jitter interval (Δt).

Sequential activation of channels

Even though the procedure nominally was a two-choice *simultaneous* discrimination task, the appearance of jittering or stationary echoes on the left and right channels actually was *sequential* (as described in Simmons et al. 1990b) because the simulator apparatus prevented the bat from actually receiving echoes through both the left and the right channels at the same time (see Fig. 2 in Simmons et al. 1990a). During trials, the bat on the platform scanned its head to the left and right, activating one channel at a time and each channel in succession. The bat's echolocation signals are moderately directional (Hartley and Suthers 1989), and the broadcast beam is steered by these head-scanning movements. Consequently, the sound impinging on the microphone the bat aims its head towards will be stronger than the sound impinging on the microphone off to the side. Head scanning causes amplitude differences between the microphones of up to 10–15 dB (see Fig. 6 in Simmons and Vernon 1971). Activation of one channel over the other was determined by electronic comparison of the envelopes of the signals from the microphones to select whichever microphone's signal was stronger (in operational terms, whether the left or right envelope crossed a preset amplitude threshold first; see Simmons et al. 1990a). We dealt with the special case of the bat aiming its broadcasts exactly half-way between the two microphones, so that the sounds impinging on them would cross both comparator's thresholds at the same instant, by incorporating a narrow "dead-zone" in the microphone-selecting circuit that shut both loudspeakers off for that case (see Fig. 2 in Simmons 1993).

Signals received by the left and right microphones and the signals delivered to the left and right loudspeakers (in Fig. 1) were recorded on a Racal Store-4 instrumentation tape recorder (tape speed 76 cm s⁻¹) to serve as an acoustic log of representative experimental trials. After the experiments, we examined recordings in which the bat responded correctly to very small jitters (jitter Δt s of 5–20 ns, which are too small for the bat to detect according to conventional wisdom—see Schnitzler et al. 1985; Pollak 1993; Beedholm and Möhl 1998). A summary of the content of these plots has been published (Simmons 1993; Simmons et al. 1990a), together with a representative plot (Fig. 16 in Simmons et al. 1990a), and their content was described at the 1994 Sandbjerg workshop on echolocation. For further analysis, we played the recordings at 8:1 reduced tape speed (from 76 to 9.5 cm s⁻¹) into a stereo sound board (SoundBlaster 16) in a PC-type 486 computer, digitized each channel at a 44-kHz sampling rate (equivalent to 352-kHz effective sampling rate at the original tape speed). We then clipped out most of the silent interval between successive broadcast sounds to reduce the computer files to manageable size, converted the two channels of signals into two-channel spectrograms (using GoldStar v1.52), and displayed the spectrograms side by side. We found no occasion where the target simulator delivered an echo to the bat from both the left and the right loudspeakers on the same broadcast.

Generation of echo delays

The echo delays shown in Fig. 1 (*a*, *b*, *c*, *d*; mean value of 3.275) were compounded in Fig. 2 from the air-path travel time of the bat's sound to the microphone (290 μ s or 580 μ s over a nominal path length of 10 cm or 20 cm), a variable electronic delay generated by the apparatus (approximately 2,115 μ s or 2,695 μ s), and the travel-time of the bat's sound back from the loudspeaker (290 μ s or 580 μ s over a nominal path length of 10 cm or 20 cm). Figure 4 shows different combinations of hardware devices used to

Table 1 Lengths and delays of RG58U coaxial cable used for small delay steps (see Fig. 4B)

Cable length	Calculated delay (1 ns/20 cm)	Measured delay (counter method; ± 3 ns)	Measured delay (oscilloscope; ± 2 ns)
152 cm	7.6 ns	5 ns	7 ns
244 cm	12.2 ns	11 ns	12 ns
336 cm	16.8 ns	16 ns	18 ns
427 cm	21.3 ns	23 ns	21 ns

produce the electronic delays in the jitter experiments described here and elsewhere. The configurations shown in Fig. 4A, B are from experiments reported previously (Simmons et al. 1990a), and the configurations shown in Fig. 4C, D are from the experiments reported in this paper. In Fig. 4, the particular devices used to adjust the delay of jittering echo *a* relative to echo *b* are marked " Δt ." Identical delay devices were used to produce the stationary delays of echoes *c* and *d*, only the value of Δt was zero.

The signal picked up by each microphone (*m* in Fig. 1) was amplified, filtered to a passband of 20 and 100 kHz (Wavetek/Rockland Model 442 variable Butterworth band-pass filter; 24 dB/octave) and then fed simultaneously into two specially built digital delay lines corresponding to delays *a* and *b* for one microphone and into delay lines corresponding to delays *c* and *d* for the other microphone. Each digital delay line used an A-to-D sampling rate of 750 kHz (12-bit accuracy) to supply delay values in nominal steps of 1.3 μ s from 0 to 42 ms using a solid-state memory that was read out by a D-to-A converter through a 50- Ω buffer amplifier to reconstitute the delayed, digitized echo as an analog signal. To manipulate the delay of electronic echoes in steps smaller than the minimum digital step-size of 1.3 μ s, each digital delay line was supplemented by either a switch-variable analog "lumped-constant" delay line or by different lengths of coaxial cable. In Fig. 4A (Simmons et al. 1990a), the analog delay lines were Ad-Yu Electronics Model 801b1 (500 Ω impedance, input and output matched with 500- Ω resistors and then buffered by operational amplifiers to have a 10-k Ω input impedance and a 50- Ω output impedance). In Fig. 4B (Simmons et al. 1990a), the analog delay devices were different lengths of coaxial cable (see Table 1; RG58U, 50 Ω impedance, driven by the 50- Ω buffered output of the digital delay line and terminated by 50 Ω into a 10-k Ω operational amplifier prior to being switched electronically). In Fig. 4C, D for the experiments reported here, the analog delay devices were Ad-Yu delay lines for 0 or 1.3 μ s, in series with switch-selectable Allen Avionics delay lines supplying 1-ns steps (75 Ω impedance, input and output matched with resistors and then buffered with operational amplifiers).

Dissociation of analog delays

In the first dissociation experiment, shown in Fig. 4C, the digital delay lines were both set to 2,113.7 μ s, and the analog delay lines were both set to 1.3 μ s, plus fine delay changes of 0–50 ns. The second dissociation experiment, shown in Fig. 4D, carried the procedure in Fig. 4C a step further by deliberately offsetting the size of the digital contributions to delays *a* and *b*. This offset was matched by a countervailing offset in the analog contributions to these same delays. In Fig. 4D, the digital delays are not identical, in this case one (*a*) being 1.3 μ s longer than the other (*b*). Differences between the jittering echoes were adjusted by first increasing the amount of delay on the analog delay line in series with the shorter digital delay by 1.3 μ s to make the total electronic delay the same for both echoes *a* and *b*. Then, the analog delay line was used to make fine delay changes of 0–50 ns. Through use of different amounts of analog delay offset by different amounts of digital delay for *a* and *b*, any putative artifactual effects of the analog delay lines could be dissociated from the actual delay values for the echoes delivered to the bat. In particular, when the *total* difference in the

delay of echoes a and b (Δt) is reduced to zero, the difference in the amount of *analog* contribution to those delays would still be 1.3 μ s. Any delay-correlated artifact caused by the different sizes of the analog delays (e.g., reflections due to delay line impedance mismatch) should still be available to the bats. If the bats perceived the arrival times of the echoes to detect the jitter, their performance should be the same in the experiments shown in Fig. 4C and D. That is, the bats' percentage of correct responses should decline to chance levels at jitter interval $\Delta t = 0$ for both experiments, regardless of whether one of the echoes still had a substantial amount of analog delay. However, if the bats used the effects of analog delay artifacts rather than delay itself, their performance curves should remain uniformly high at all delay values in the range of 0–50 ns for the configuration Fig. 4D because the 1.3- μ s analog delay difference always is present and its collateral artifact always is available.

Calibration of delayed signals

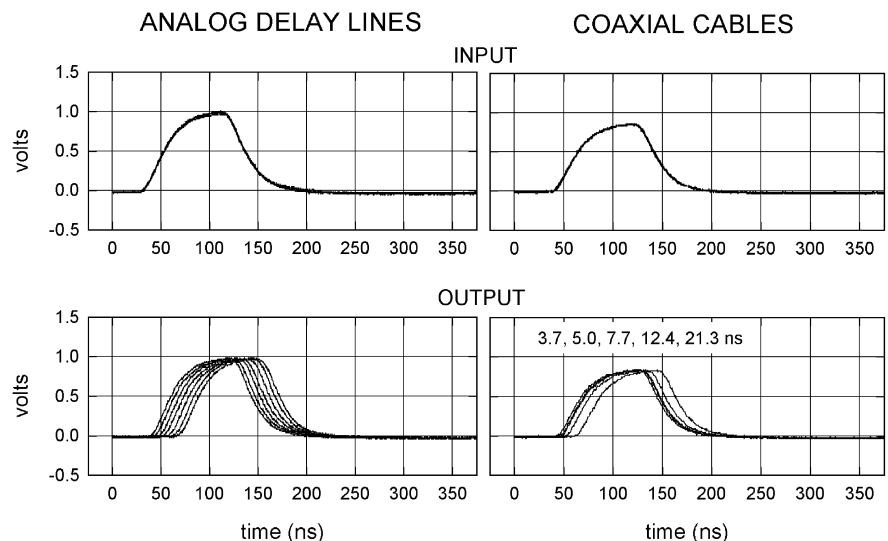
For the analog delay lines, nominal delay values were set each day using the switches, but values of delay actually used to specify the stimuli were measured directly instead of relying on reading the switch dials. The most recent method for determining the amount of delay produced by the delay lines used short 80-ns input pulses, with display of delayed signals on a microwave-frequency digital oscilloscope at a 0.5-ns sampling interval. This method yields results that confirm the calibrations reported previously (Simmons et al. 1990a; Simmons 1993). Figure 5 (left) shows the delayed signals for these short pulses traveling through the analog delay lines in the configuration of Fig. 4C, D. The illustrated output pulses are delayed by steps of 5 ns and separated by steps of 5 ns, which was the nominal size of the increment in delay used for the experiments. The series of output pulses in Fig. 5 contain no distortion or stretching of shape caused by changes in the frequency-response of the delay lines or the presence of reflections in proportion to delay. That is, no delay-correlated changes in the phase or spectrum of the signals are present, just changes in delay itself. For the cables, their lengths were cut by crudely calculating the propagation delay using an approximation of 1 ns/foot (1 ns/30.5 cm) as a "rule-of-thumb." As described at the Sandbjerg meeting in 1994, these values were not used to specify the stimuli, however, just to make the cables. Measured values for cable delays are closer to 1 ns/20 cm, but even these depend on proper impedance matching (see Beedholm and Möhl 1998), so we also relied on direct measurements for cable delays. Table 1 gives the increments in length for the four RG58U cables used here, together with their theoretical differences in delay and actual differences measured

electronically with a digital counter at the time the experiments were conducted or more recently with a microwave-frequency oscilloscope. Figure 5 (right) shows the delayed signals for the short (80 ns) pulses traveling through the cables in the configuration of Fig. 4B. There is no indication of spectral artifacts or stretching of the output waveform due to reflections at multiple delays. Differences between calculated and measured delays in Table 1 are within the ± 3 -ns range we found to be our measurement accuracy from repeated measurements of the same delay.

These same calibration measurements examined whether spectral artifacts accompany the delays. Detailed information about calibration of delays is given elsewhere (Simmons et al. 1990a, Simmons 1993). Here, we give a summary of yet other new measurements to establish further that the delay system produced no delay-related spectral artifacts. The total electronic delays which have to be measured are 2,115 μ s (Fig. 4A, B) or 2,695 μ s (Fig. 4C, D), while the accuracy needed to describe the stimuli is about ± 0.003 μ s (± 3 ns), so even for purely electronic measurements (not including the acoustic delays) the desired accuracy is about 10^{-6} or 1 ppm. This poses special problems because not only the digital delay lines, which supply a large part of the delay to be measured, but also the available measuring devices (oscilloscopes, analog-to-digital converters, digital counters) rely upon internal time-base oscillators to serve as a time standard. Over time, the frequency of the reference oscillator in any of these measuring devices drifts with temperature by several parts per million relative to the corresponding oscillator in the delay lines, and it is difficult to ensure that measurements of nanosecond-sized time steps made more than a few minutes apart are not confounded by this time drift. Our original delay estimates drifted progressively larger by the order of 10 ns over a period of 30 min, which we found when we carried out faster measurements of electronic delays over only a few minutes to minimize this drift to less than 3 ns. (This time-base drift was misinterpreted by Beedholm and Möhl 1998 as evidence for an impedance mismatch in the delay lines or cables. Inspection of the spectra of signals confirms that no such cues are present.) Such slow drift does not materially affect stimulus jitter because the bat's broadcast sounds are emitted at intervals of only 20–50 ms.

For this paper, a new calibration of delays was done using an R.C. Electronics ISC-16 data-acquisition board with a 1-MHz sampling-rate limit to achieve simultaneous recording of input and output, each at a 500-kHz sampling rate. We generated 1-ms FM signals sweeping from 115 kHz down to 15 kHz (linear FM), digitally synthesized with 16-bit accuracy at a 500-kHz sampling rate with a Tucker-Davis Model QC2 waveform-generator board. These FM signals were supplied as input to the delay lines by the electronic filter used in the target simulator (Wavetek/Rockland Model 442 bandpass filter), and both the input and the output of

Fig. 5 Electronic calibration of fine delays: waveforms of input impulse and output impulses from analog delay lines in Fig. 4C, D for delay steps of 0 to 30 ns in 5-ns steps (*left*) and from coaxial cables in Fig. 4B for delays of 0 to 21.3 ns (*right*). There are no discernable distortions of waveform shape or rightward shift in delay values which would indicate the presence either of spectral artifacts or of reflections due to impedance mismatch (Beedholm and Möhl 1998)



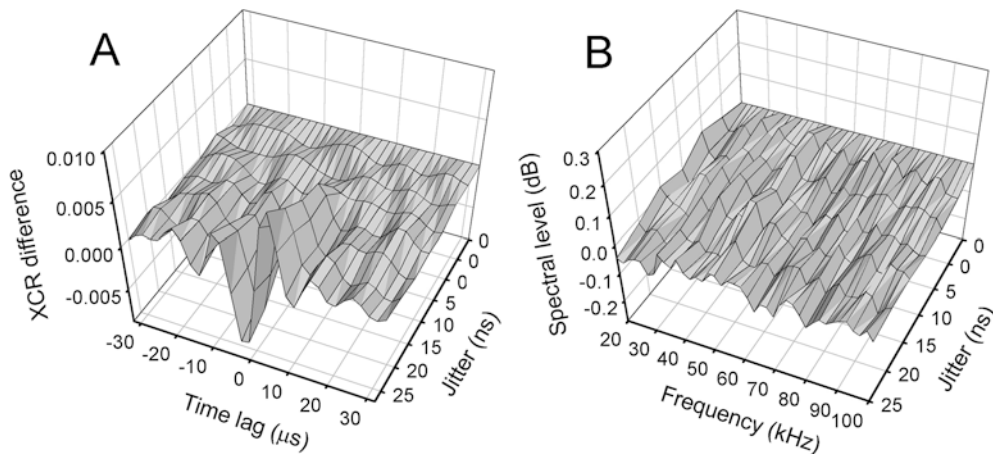


Fig. 6A, B Electronic calibration of analog delay lines. **A** Cross-correlation (XCR) difference functions between echoes *a* and *b* for jitter Δt values of 0–25 ns (see Fig. 4C, D). Three different difference functions are shown for zero jitter to illustrate variability of functions in the absence of any actual time difference (first 0 jitter slice is for identical XCRs so is flat in magnitude). *Vertical scale* is numerical value of difference between the two XCRs. **B** Corresponding spectral difference functions between amplitude spectra of echoes *a* and *b* for jitter Δt values of 0–25 ns. In this case, two different difference functions are shown for zero jitter. While the spectral differences in **B** show no delay-dependent changes in spectra that increase as jitter increases, the XCR differences in **A** show the progressive emergence from the noise of a waveform that is a 90° phase-shifted version of the XCR as jitter increases. Together, these plots show that the only difference between echoes *a* and *b* within the limits imposed by the noise is a difference in delay

the delay system was recorded on the data-acquisition board without averaging to insure that time-base drift did not affect the measurements. The resulting digitized input and output signals were processed in MatLab to obtain the XCR in the time domain and the transfer function in the frequency domain for each delay setting used in the jitter experiments. Figure 6A plots values of differences between the XCR of echo *b* and the XCR of echo *a* relative to the FM test “broadcast” for jitter Δt values of 0–25 ns. Figure 6B plots corresponding differences between the transfer function of echo *b* and the transfer function of echo *a* relative to the FM test “broadcast.” As the amount of jitter increases, the subtracted XCRs in Fig. 6A show the gradual rise of a difference function that is a 90° phase-shifted version of the XCR. This difference function is obvious at 10 and 15 ns jitter, and it can be discerned for jitter values down to 5–10 ns. Whereas the XCR differences show a progressive increase in height as the size of the jitter interval (Δt) increases, the spectral differences in Fig. 6B show no such progressive change in frequency response related to delay. This graded emergence of a well-defined series of peaks in the XCR differences in Fig. 6A, coupled with the absence of any comparable emergence of peaks in the spectral differences in Fig. 6B, shows, as far as is methodologically possible, that the electronic equipment did not create delay-related spectral artifacts or changes in waveform shape which could be used by the bats as a substitute for perception of echo delay. Instead, the delay lines just delayed the signals (as in Fig. 5).

Results

Jitter performance for different delay configurations

Two big brown bats (bat no. 3 and bat no. 5 from Simmons et al. 1990a) completed all four experimental

protocols shown in Fig. 4A–D, yielding comparable sets of data for each condition. Figure 7A–D plots the percentage of correct responses achieved by each bat in the four different experiments. The first experiment (from Fig. 4A) used equal-length digital delay lines supplemented by analog delay lines to generate the delays of the stimuli. The bats’ performance shown in Fig. 7A remained high (above 75% correct responses) for jitter intervals from 60 ns down to 20 ns. Then, as the size of the jitter interval declined to 15, 10, and 5 ns, the bats’ performance also declined, reaching near-chance levels at 0 ns. In alternative versions of this basic jitter detection task (Fig. 4B–D), the bats’ performance was substantially the same as in the initial version. In Fig. 7B, for the experiment using coaxial cable delay as a supplement to the digital delay line (Fig. 4B), the percentage of correct responses achieved by both bats declined smoothly as the size of the jitter interval declined from 21 ns, passing through the 75%-correct threshold at about 10–12 ns and reaching chance at 0 ns. The experiments shown in Fig. 4C–D used a different distance from the bat to the microphones and loudspeakers (10 cm instead of 20 cm). In Fig. 7C, for the first of two experiments which modified the amount of digital and analog contributions to total delay (Fig. 4C), the performance of the bats remained above 75% correct responses for jitter intervals from 20 ns down to 10 ns, and then it declined for smaller intervals, passing through the 75%-correct threshold at 8–10 ns and reaching chance at 0 ns. In Fig. 7D, for the experiment that deliberately offset the amount of digital delay by 1.3 μ s so that the analog delay was also offset but in the opposing direction (Fig. 4D), the bats’ performance remained high for jitter intervals from 40–50 ns down to 20 ns, declining through the 75% threshold at 8–12 ns. The results from the basic jitter experiment (Fig. 7A) thus were replicated with three alternative methods for generating electronic delay differences (Fig. 7B–D). Most important is the fact that performance is the same as seen in Fig. 7C, D, with either *zero difference in analog delay* or 1.3 μ s difference in analog delay between echoes *a* and *b* at the condition where the jitter interval itself is zero. This dissociation of analog delay from

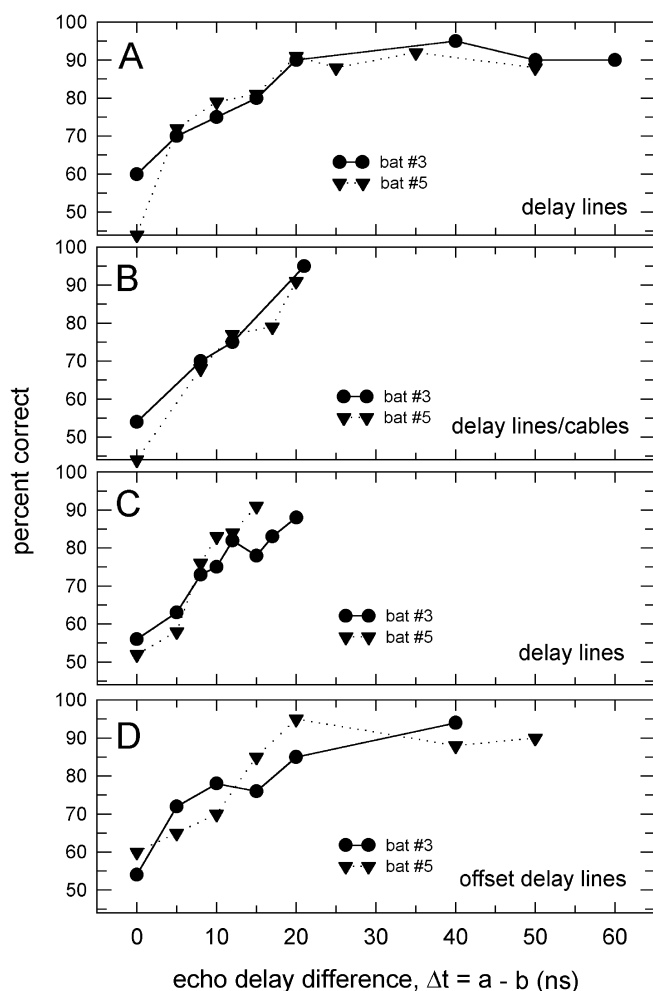


Fig. 7A–D Performance of bat no. 3 and no. 5 in four experiments using different configurations of delay lines from Fig. 4A–D. Each data-point is from 40–60 trials. Different replications of the jittering echo experiment all yield threshold levels for 75% correct responses at about 7–15 ns. Comparison of plots C and D show no effect related to changes in numerical values of analog delay for echoes a and b , whether they are equal at zero jitter or are different by 1.3 μ s at zero jitter, only the effect of changes in overall delay

performance demonstrates that no delay-related analog-delay artifact is involved in determining the bats' performance.

Discussion

Jittering-echo experiments employing four different electronic ways to regulate the delay of simulated echoes (Fig. 4A–D) have produced substantially the same results: *Eptesicus* can detect changes in the arrival-time of jittering echoes as small as 10–15 ns with high performance of 80–85% correct responses or better (Fig. 7A–D). The performance of the bats declines for smaller amounts of jitter, reaching threshold at 75% correct responses for jitter intervals of about 10 ns, and reaching chance performance at zero jitter. Given the

extreme temporal sensitivity implied by the results shown in Fig. 7, there is concern that the bat's performance might be due to some artifact that manifests itself in easier-to-detect changes in the spectrum or stretched waveform of jittering echoes instead of perception of jitter in delay itself (Simmons 1979, 1993; Schnitzler et al. 1985; Menne et al. 1989; Simmons et al. 1990a; Pollak 1993; Beedholm and Möhl 1998). However, the signals delayed by the apparatus do not contain delay-related changes in their waveforms or spectra, only changes in delay (Figs. 5 and 6). Moreover, bats that use sonar sounds of different durations nevertheless perform the same in the jitter task, indicating that overlap of stimulus echoes with background reverberation is neither required nor quantitatively decisive for achieving sub-microsecond jitter acuity (Simmons et al. 1990a; Simmons 1993). As presently formulated, none of the artifact hypotheses (Pollak 1993; Beedholm and Möhl 1998) can accommodate the full of results shown in Fig. 7A–D, and thus they can be rejected. *Eptesicus* indeed seems capable of perceiving changes as small as 10 ns in the arrival time of successive sonar echoes regardless of the exact size or type of analog contribution to the total delay of echoes.

The bat's sensitivity to small changes in echo delay is extraordinary; the closest performance observed in other animals is of the order of 1 μ s for the electroreception system of the weakly electric fish, *Eigenmannia* (Heiligenberg 1991), and for binaural time-difference orientation in barn owls (Moiseff and Konishi 1981). For both electric fish and owls, however, the behavioral procedures are different from that used for presentation of jittering stimuli to bats, so it is not clear to what extent the data are comparable—perhaps these other animals could also perform in the submicrosecond range if presented with jittering stimuli (Altes 1989). Another factor to consider is the unusually broad bandwidth of the biosonar sounds emitted by *Eptesicus* (about 80 kHz) and the correspondingly broad bandwidth of the echoes the bats process in order to achieve their submicrosecond delay acuity. The sounds used as stimuli in experiments on passive sound localization by barn owls have 3-dB bandwidths of only a few kilohertz at most, while *Eptesicus* is stimulated by sounds with bandwidths 10–40 times greater. We conclude that the bat's submicrosecond performance may be compatible with the poorer auditory temporal acuity of other animals when the bat's very large bandwidth is taken into account. The inability of other animals to perform better than about 1 μ s is not good evidence that the bat's 10-ns hyperacuity is biologically "impossible" and must therefore be due to artifacts.

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in echolocation. Much of the discussion focused on issues surrounding observations of jitter hyperacuity by bats, and results from additional jitter experiments and control procedures were presented at that meeting. Pursuant to requests from several workshop participants, this paper gathers together findings relevant to whether echo delay or spectral differences can explain the bats' performance. We thank colleagues at the Sandbjerg workshop for their constructive suggestions about these experiments. Care and use of the animals was supervised by Brown University veterinarians and the Institutional Animal Care and Use Committee in accordance with *Principles of Animal Care* no. 86-23 (revised 1985) of the US National Institutes of Health Publication.

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