

## REVIEW

K. Beedholm · B. Möhl

**Bat sonar: an alternative interpretation of the 10-ns jitter result**

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**Abstract** In 1990 Simmons et al. reported evidence of a time resolution hitherto unknown in any animal, namely a 10-ns jitter detection threshold in echolocating bats. This result is discussed. The calibration data from the original papers are examined. Observations indicating other cues than delay being presented to the bats are given. We offer an alternative explanation for the psychometric jitter function, based on the assumption of a subtle distortion due to impedance mismatch in the delay-producing apparatus. We also report that effects of impedance mismatch are detectable by a human subject in a model experiment.

**Key words** Echolocation · Psychophysics · Cross-correlation receiver · Range jitter · Impedance mismatch

**Abbreviations** *AD* analog to digital · *CCF* cross-correlation function · *DA* digital to analog · *FM* frequency modulated

**Introduction**

Comparing the performance of echolocating animals (bats and dolphins) with that of theoretical receivers has been used frequently to investigate the sonar systems of these animals. The value of this approach is that it yields a frame of reference that can be expressed in numerical terms. In most cases the psychophysical results of these investigations are evaluated as a degradation relative to the predictions of the receiver in question (e.g. Au and Pawlowsky 1989). However, in the literature there is at least one instance where psychophysical results *match*

(and even surpass) what is theoretically possible, namely in the paper by Simmons et al. (1990b). This outstanding result is the basis of our present paper.

The bats in the experiments of Simmons et al. (1990b) were trained to indicate from which one of two channels the delay of an electronically simulated echo changed back and forth (jitter) between successively emitted cries in order to obtain a food reward (Fig. 1). Since the threshold for detection of this jitter is as low as 10 ns (Fig. 2), this result has been taken as evidence of a coherent cross-correlation (or a mathematically equivalent) receiver in frequency-modulated (FM) bats. This receiver defines the theoretical limit for both detection and ranging purposes.

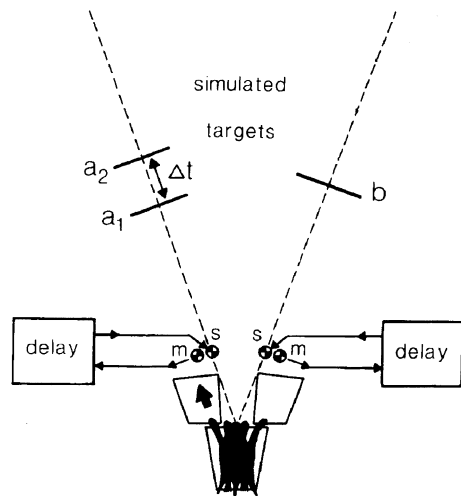
A coherent cross-correlation receiver operates on a delayed signal,  $e(t)$ , which is matched against a stored template,  $p(t)$ , at a time delay ( $\tau$ ).  $\tau$  is varied in (small) steps and tested for producing maximum similarity between the template and the delayed signal. The analog version of the cross-correlation function (CCF) is (Papoulis 1962):

$$R_{pe}(\tau) = \int_{-\infty}^{\infty} p(t) \cdot e(t + \tau) dt \quad (1)$$

Here  $p(t)$  and  $e(t)$  are functions of time,  $t$ ;  $R_{pe}(\tau)$  is the CCF between  $p(t)$  and  $e(t)$ . In the case of a bat,  $p(t)$  represents the pulse emitted and  $e(t)$  is the echo received.  $R(\tau)$  describes a *correlation value* as a function of time delay ( $\tau$ ). From this expression it can be seen that if the only difference between  $p(t)$  and  $e(t)$ , except for a scaling factor,  $\alpha$ , is a delay,  $d$ , so that  $e(t) = \alpha p(t-d)$ , then  $R_{pe}(\tau)$  will have a maximum at  $\tau = d$ . In a *coherent* acoustical receiver the elements  $p(t)$  and  $e(t)$  describe *pressure* values as a function of time, so that all information contained in the signals, including phase information, is utilized to produce the output. The value of  $\tau$  that yields the highest output is the maximum likelihood estimate of the delay between  $p(t)$  and  $e(t)$  (Altes 1984).

The possible existence of this processing mechanism in a mammal has far-reaching consequences for our understanding of the mechanisms of hearing and central

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**Fig. 1** Reproduced from Fig. 1 of Simmons et al. (1990b). *Original legend:* diagram of the two-choice discrimination procedure for studying perception of changes in the delay of echoes that simulate targets electronically. Bats choose between echoes ( $a_1$  and  $a_2$ ) that jitter by a controlled amount ( $\Delta t$ ) and echoes ( $b$ ) that arrive at a fixed delay. The bat's sonar sounds are picked up at microphones ( $m$ ), digitally delayed, and then returned to the bat from loudspeakers ( $s$ ) as echoes. Delay changes are introduced by a controller that resides in the delay system

nervous processing. The representation of all information in a signal containing frequencies of the order of 100 kHz cannot readily be accounted for with current theories of hearing (Kelly 1991).

A number of objections exist against a coherent cross-correlation receiver model of echolocation in bats. These include the range-difference acuity predicted from this processing mechanism of only a few micrometres (Hackbarth 1986; Menne and Hackbarth 1986; Altes 1989; experimentally supported by the 10-ns result of Simmons et al. 1990b), which is paradoxically high for a biological system, and for which an evolutionary driving force is not evident, particularly, since in detection tasks the bats' performance seems best described by an energy detection mechanism (Møhl 1986; Troest and Møhl 1986; Masters and Jacobs 1989) where the receiver does not utilize signal phase information, or even information about frequency structure. In two wave-front discrimination tasks, the threshold is about  $1 \mu\text{s}$  ( $100 \cdot 10 \text{ ns}$ ) between wave fronts (Simmons et al. 1990a; Schmidt 1992). If bats can cross-correlate, they seem to choose not to do so for these tasks. Also, it is not clear whether detection of a variation in range of  $2 \mu\text{m}$  over a total range of  $5.4 \cdot 10^5 \mu\text{m}$  by acoustical delay measurement is physically possible when considering microturbulence and thermal inhomogeneities in the medium as well as movements of the bat's body caused by breathing and heartbeats. Such effects will cause variations in the animal's position considerably larger than  $2 \mu\text{m}$ , especially so in connection with the forced exhalations associated with the production of high sound pressure vocalizations. Several arguments of this kind were discussed by

Pollak (1993), Simmons (1993), and at the Sandbjerg Meeting.<sup>1</sup>

This paper is not intended as a part of that discussion. Although the objections mentioned are counterindicative of a coherent cross-correlation receiver, they do not explain the result of Simmons et al. (1990b). A threshold of 10 ns can *only* be interpreted as indicative of full utilization of echo information (R.A. Altes, personal communication at the Sandbjerg Meeting). If, on the other hand, the stimuli in these experiments varied in other respects than time delay, this interpretation is no longer valid and the discussion no longer relevant. Therefore, we re-examined the papers of Simmons et al. (1990b) and Simmons (1993) for information that would indicate the presence of other cues in the 10-ns jitter discrimination. This is possible only because of the extensive calibrational data given in these papers.

In psychophysical experiments there are at least two types of errors that can produce deceptive results. The most obvious is where some other cue, uncorrelated (except for the time of occurrence) with the parameter being tested, is the actual basis of the performance. The hallmark of an experiment in which this phenomenon is present is lack of a threshold region: the performance does not decline when the difficulty of the task is increased. A more difficult problem arises if the cue for discrimination is *correlated with*, but different from, the nominal parameter. This will produce a threshold, but possibly for the coupled cue. Whether such a cue will go undetected or not is likely to depend on whether the results of the experiment match the investigator's predictions.

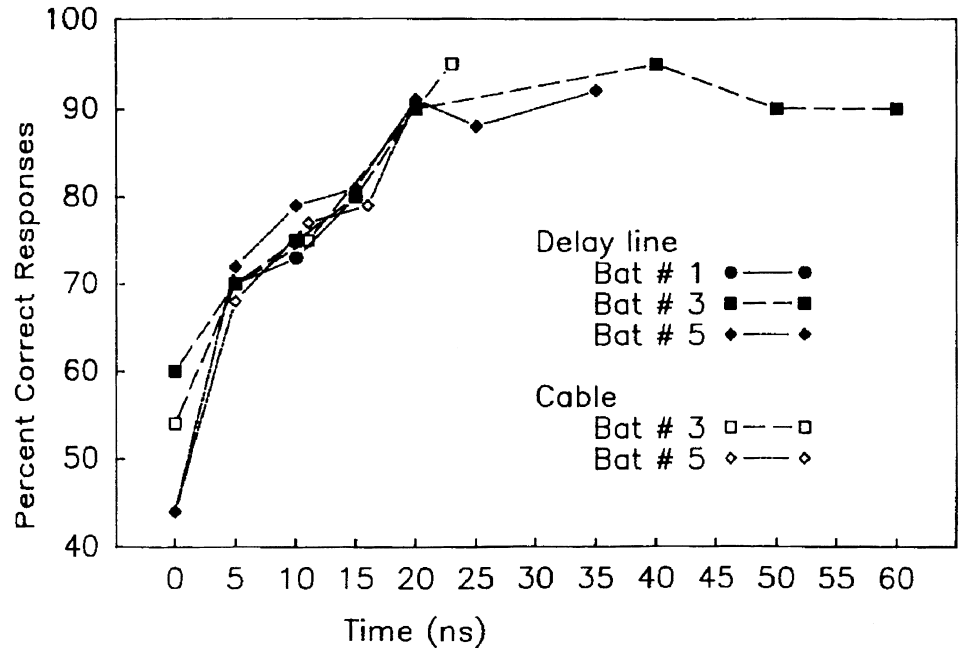
Since a threshold is obtained in Simmons et al. (1990b), our hypothesis was the existence of an error of the latter kind. In Simmons et al. (1990b) the delay devices were the only parts of the target simulator which were correlated with the jitter in the nanosecond range; therefore, it seems reasonable to look into the data given for this part of the apparatus.

### The delay-producing apparatus in the set-up of Simmons et al. (1990b)

The set-up described in Simmons et al. (1990b) generates delays in a hybrid manner. The bulk of the delay is produced with four parallel digital delay lines. These are arranged so that two of them deliver the echoes at delays  $a_1$  and  $a_2$ , and the other two the reference echo at delay  $b$  (refer to Fig. 1). The reference delay,  $b$ , is set so that  $b = (a_1 + a_2)/2$ . When investigating the performance of the bats with jitter values below  $2/\text{clockrate}$ , analog delay devices are added in series. These are either

<sup>1</sup> The Sandbjerg Meeting 1994; this meeting was held to discuss results in this field of research and was titled "Bat echolocation: hard data and speculation". It was concerned with the 10-ns result in particular.

**Fig. 2** Reproduced from Fig. 7 of Simmons et al. (1990b). *Original legend:* performance of three bats discriminating echoes that jitter by very small amounts. Average acuity of the bats for jitter is about 10 ns. Two different delay-generating techniques were used – electronic delay lines and cables of calibrated lengths. Each data point is 40–60 trials



lumped constant-delay lines or coaxial cables. A lumped constant-delay line can be said to simulate a long cable. It utilizes the delaying properties of low-pass filters (RL or RC circuits with very high cut-off frequency) in series. The following discussion focuses on these two types of analog delay lines.

One reason for this approach is that the bats used by Simmons (1979) were not performing the same task as well as the bats used by Simmons et al. (1990b). In Simmons et al. (1990b) it is explained that the apparatus used in 1979 was not constructed for operation in the nanosecond range. The complete psychometric function with a much higher threshold of about 1.3  $\mu$ s in these earlier experiments was unexplained until the Sandbjerg Meeting, where Simmons explained that the bats had improved shortly after the original (1979) paper was published. In order to make this improvement possible, the nanosecond-delay apparatus appears to have been introduced (i.e. the system had been changed into that described in Simmons et al. 1990b). Thus, there seems to be a correlation between the bats' very low threshold for jitter discrimination and the presence of the nanosecond-delay devices.

### Observations on the analog part of the delay-producing apparatus

Observation 1: the signals differ in respects other than delay

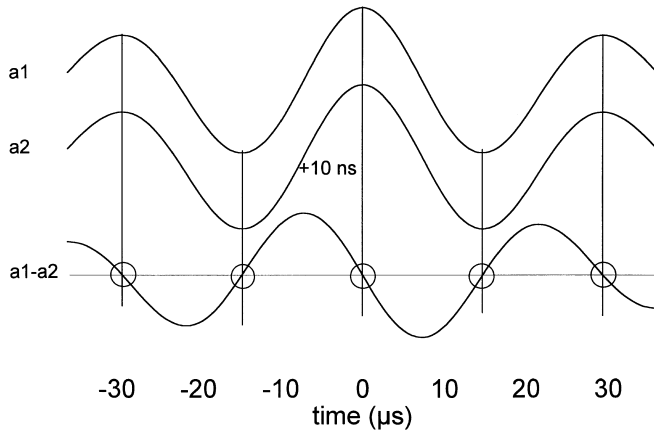
This observation stems from the answer (Simmons 1993) to the criticism made by Pollak (1993). It involves a simple property of subtraction of signals.

When from a wave form  $s(t)$ , a delayed replica  $s(t-\Delta t)$  is subtracted, one gets an increasingly good approxi-

mation to the first derivative,  $ds(t)/d(t)$  of  $s(t)$ , when  $\Delta t \rightarrow 0$  (except for a scaling factor of  $1/\Delta t$ ). This approximation will be quite good whenever  $\Delta t < 1/(4*f_{\max})$ , where  $f_{\max}$  is the highest frequency component in  $s(t)$ . For a first derivative,  $ds(t)/d(t)$  of a signal  $s(t)$  it is obviously true that if  $s(t_0)$  is a "peak" or extremum<sup>2</sup> then  $ds(t)/dt = 0$ . Figure 3 illustrates this property.

In Fig. 4, reproduced from Simmons (1993), the result of cross-correlating a probe signal (artificial bat cry) with the same signal sampled after two different delays is shown. The purpose of the graph is to demonstrate that delay differences are detectable in the 10-ns jitter stimulus. The wave form marked "a2" has passed through analog delay calibrated to produce 11-ns more delay than the signal marked "a1". Also the difference between these two CCFs is shown, scaled up to the amplitude of the CCFs. Using the above argument this graph can be used to determine directly whether the wave forms are identical apart from the 11-ns difference in delay. If this is the case, then whenever the *slope* of the top traces is zero the "diff." trace should also be zero. A  $\Delta t$  of 11 ns will certainly yield a very nice approximation to the first derivative when  $s(t)$  has a  $f_{\max}$  of 100 kHz, which is the case here. Figure 4 is reproduced by scanning the original graph. Pixel counting was used to determine whether the extrema of the CCFs correspond to zero crossings in the "diff." trace. This is clearly not the case. In fact, the time of identical correlation values seems to vary considerably ( $\mu$ s) between the top traces of Fig. 4. The method used is not precise due to the crude way of "digitizing", but it is more than sufficient to observe the deviations. The figure is reproduced without

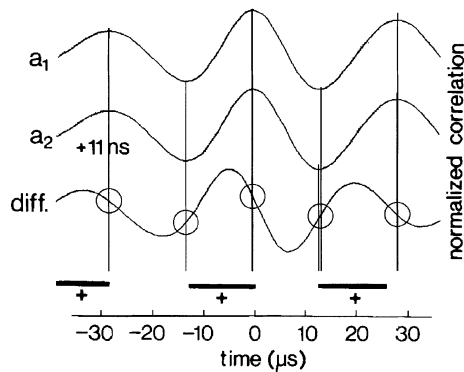
<sup>2</sup>  $s(t_0-dt) > s(t_0) < s(t_0+dt)$  or  $s(t_0-dt) < s(t_0) > s(t_0+dt)$



**Fig. 3** Similarity between a delay-and-subtract result and the first derivative of the “mother functions”. The “a1” function is a shaped (Gaussian) cosine with a base frequency of 30 kHz. “a2” is a delayed (10-ns) version of the same function. The subtraction product is scaled up by a factor of 400. The vertical lines placed at the extrema (“peaks”) of a1 and a2 pass exactly through the zero crossings of the resulting difference trace, indicated by circles. The functions are generated with a 500-kHz “sampling rate”, and the interpolation is performed by a standard spreadsheet program (MS Excel)

the grey bars of the original figure, the edges of which do not correspond well to the extrema of the functions.

Since the zero crossings of the difference trace are not aligned with the extrema of the CCFs, the conclusion is that the reference signal differs from the delayed signal in respects other than delay.



**Fig. 4** Reproduced from Fig. 8 of Simmons (1993). *Original legend:* cross-correlation function for echo a<sub>1</sub> at delay of 3.275 ms and echo a<sub>2</sub> at 11 ns longer delay (...). The sampling rate for these signals is 500 kHz. Although the spectra of the echoes are indistinguishable, thus eliminating spectral artifacts, the cross-correlation functions are readily shown to be offset by a small time shift. The difference between these cross-correlation functions shows a 90° leftward phase shift as a measure of the time disparity. This figure illustrates that the sampling rate does not have to be as high as 100 MHz to allow time accuracies of 10–11 ns. *Addition to original legend:* this graph has been modified compared to the original figure in that the grey bars have been erased. Moreover, some lines and circles have been added to demonstrate points of interest. The long vertical lines mark where we have determined the extrema of the upper two traces to be. The circles indicate the alignment of the extrema of the upper curves with the “diff.” trace. Compare with Fig. 3

**Observation 2: conduction velocities above the speed of light**

The delays reported by Simmons et al. (1990b) are generated by propagating the signals through varying lengths of standard coaxial cable. The authors state that “From our delay measurements (...), the RG-58/U cable we used required 35 cm to produce a delay increment of 1 ns” (Simmons et al. (1990b)). The inverse of this delay per length is a speed of propagation equal to 350 000 km s<sup>-1</sup>, which is well above the speed of light in a vacuum ( $c = 300\,000\text{ km s}^{-1}$ ). The value disagrees with the basis of the special theory of relativity (Einstein 1905). The usually quoted maximum conduction speed of good-quality coaxial cable of this type is  $(2/3)c$  ( $= 20\text{ cm ns}^{-1}$ ) and the delay produced accordingly is 1 ns per 20 cm. This is now understood to be due to a printing error. The speed of conduction reported should have been 1 ns per 30.5 cm (J.A. Simmons, personal communication) which, however, is still slightly above the speed of light in a vacuum and also clearly above the expected value for coaxial cable of the type used. The calibration value in Simmons et al. (1990b) is obtained by measuring the phase changes produced in a steady-state sine wave (40 kHz) passing through the cable. This method includes any phase shifts that might occur, and it is possible, based on the non-realizable calibration value, that such a shift in phase occurs within the system.

**Observation 3: signals with identical nominal delays differ in transfer function**

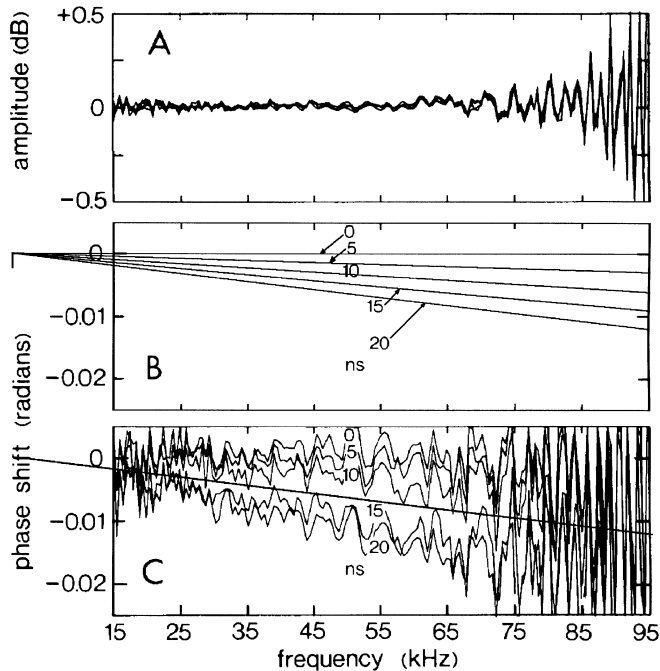
First we should like to give a short explanation of Fig. 5 taken from Simmons et al. (1990b). The amplitude part of these transfer functions (Fig. 5A) is presumably the relationship between the amplitude spectra of signals after different amounts of delay. This operation can be summarized as

$$\text{Amplitude spectrum (dB)}_{a_2/a_1} = 20 \log \frac{|S_{a_2}(f)|}{|S_{a_1}(f)|} \quad (2)$$

where  $|S_{a_1}(f)|$  and  $|S_{a_2}(f)|$  are the magnitudes of the Fourier transforms of the sweep signals that are sampled after having passed the delay line with delay a<sub>1</sub> and a<sub>2</sub>, respectively; a<sub>1</sub> refers, as in Simmons et al. (1990b), to the shorter of the jittering delays, and a<sub>2</sub> to the longer one (as in Fig. 1). Similarly the phase part of the transfer functions (Fig. 5C) is given by the expression:

$$\text{Phase spectrum}_{a_2/a_1} = \tan^{-1} \left[ \frac{\text{imag } S_{a_1}(f)}{\text{real } S_{a_1}(f)} \right] - \tan^{-1} \left[ \frac{\text{imag } S_{a_2}(f)}{\text{real } S_{a_2}(f)} \right] \quad (3)$$

It is important to note that in Fig. 5C the delay difference of zero is included as a separate trace. It seems reasonable to assume that this is also the case for the



**Fig. 5A–C** Reproduced from Fig. 4. of Simmons et al. (1990b). *Original legend:* graph showing the amplitude (A) and phase (C) components of the transfer function of the simulator for changes in delay of 0 ns, 5 ns, 10 ns, 15 ns and 20 ns. The frequency response of the system is effectively independent of delay, and the accumulating phase lags approximate the expected values (see text). The ripples in the curves are a consequence of digital sampling and analysis; they are not attributable to the delay system itself. *Addition to original legend:* part B of the original graph (not shown) has been replaced by a graph (B) showing the expected phase spectra for the delays indicated. The relative position of the nominal delay values is identical to that of C. Also, the phase spectrum for a delay of 20 ns has been drawn into C (straight line)

amplitude functions (Fig. 5A), but it is not essential to the following argument. From the expressions above (Eqs. 2, 3), deviations from a straight line are not expected when the signals have the same delay. The fact is that there are ripples with approximately the *same amplitude* at the *same frequencies* for *all delay settings*, which increase with frequency. The similarity of the ripples between settings points against the possibility of random noise as the source.

An explanation for these ripples is offered in Simmons et al. (1990b) based on sampling errors and the windowing function<sup>3</sup> (see also the legend to Fig. 5 in this paper). Indeed, the interference between a sampled signal, varying in delay, and the windowing function is a possible source of ripples for the *non-zero* delay transfer

functions: the window will be positioned at a fixed delay (sample), so when the analog signals to be sampled are delayed relative to one another by amounts smaller than the sampling interval, it will cause different weighting from the window. This can cause something like the ripples observed, but when the signals have *identical* delays (Fig. 5B) the result should be *uniformly zero* according to *both* Eq. 2 and Eq. 3.

In Simmons (1993) it is said of the graph reproduced here as Fig. 5: “These measurements include all electronic equipment but not the air path from the loudspeaker to the bat ...”. In Simmons et al. (1990b) no other evidence is presented for the crucial prerequisite to the conclusions that no effects apart from delay result from varying the analog delay devices. At first sight the high degree of similarity between these functions appears to strengthen their statement of this being the case; however, questions arise when one tries to understand how this graph was created.

The absence of random noise mentioned above is in itself interesting. The inclusion of all the devices of the set-up (possibly without microphones and loudspeakers; see the above quote) should result in some noise notably from the amplifiers and active filters. Since it does not, it is possible that averaging of test signals has been performed to raise the signal-to-noise ratio. The notion that noise is present at some point in the measuring process is supported by the authors’ use of a Hamming window. A time window should only be used to limit the influence of noise occurring before and after the signal of interest.

Hence, this graph (Fig. 5) alone gave two reasons for concern: first, the difference from zero at zero delay, and secondly the similarity of the ripples at all delays (absence of noise). Thus, we cannot conclude that changes other than delay are excluded from the lumped constant-delay apparatus. The effect of averaging signals will be dealt with later.

#### Observation 4: results of calibration methods differ

In this observation we have looked at the slopes of the transfer functions of Fig. 5C, taken from Simmons et al. (1990b); see also observation 3 above. This graph describes the phase lags produced by the lumped constant-delay line at different settings. The slopes of these curves can be translated into a delay. The setting of the delay apparatus is indicated at each of the lines.

In Fig. 5B the expected phase spectra for delays of 0 ns, 5 ns, 10 ns, 15 ns and 20 ns are given. By comparing the expected lines with the position of the nominal delay values copied from Fig. 5C, it is relatively clear that the delay values that can be estimated from the slopes of Fig. 5C do not correspond well to the values stated. The text in the graph states the delay values for two of the functions to be 15 ns and 20 ns, but the slopes would indicate that they are of the order of 30–40 ns (and practically indistinguishable). In Fig. 5C we have also drawn the line which the trace marked “20” is ex-

<sup>3</sup> Simmons et al. (1990b) chose to use a so-called Hamming window. It is customary to use a windowing function when an approximation to the spectrum of a continuous signal is desired. In this case it has been applied to a signal of finite duration. Sometimes, when noise is a problem, it is desirable to attenuate or zero-out those values obtained during sampling of a transient signal that are clearly outside the time window in which the signal of interest occurs before the spectrum is computed.

pected to follow. This line is clearly less steep than either of the lines labelled “15” and “20”.

The explanation for the graph (Simmons et al. 1990b) states that these two delay values were 16 ns and 22 ns and that the values were “cross-checked with the digital counter method” (Simmons et al. 1990b; see also observation 2). Thus, delay estimates derived from the slopes of Fig. 5C do not agree with the results from the digital counter method (which read 16 and 22 for the two traces 15 and 20). The digital counter method for calibrating delays can be said to yield a single point (at 40 kHz) in a phase plot like Fig. 5B or 5C; therefore, the two methods should yield the same values at this frequency.

#### Summary of the conclusions to the above observations

The following conclusions can be drawn from our observations:

1. Differences exist other than a pure delay between echoes a1 and a2 (observation 1).
2. At least one difference between echo a1 and echo a2 shows up as a slight phase difference (observation 2) when the delay is calibrated with a pure tone.
3. When other means of delay calibration (sweeps) are employed, unexplained differences between the results of identical settings exist.
4. When sweeps are used to probe the system, phase plots (Fig. 5C) indicate too-high delay values at certain settings, but not with pure-tone calibration (observation 4).

#### Elaborations and a possible alternative explanation

Observations 1 and 2 are the most important in this context, since they directly indicate in a qualitative manner the existence of differences other than delay between echoes at delay a1 and a2. The nature of these differences can only be guessed at. One of the problems faced in trying to understand these phenomena is that the calibration values seem to contradict each other as mentioned in observation 4. The slopes in Fig. 5C, which have little connection with the delay values they are predicted to yield, can perhaps be explained as a result of slight instabilities in crystals controlling the digital delay line or the analog to digital (AD) system used to sample them. We have experienced problems with obtaining stable delay values from phase plots in a comparable set-up.

As mentioned in observation 2, the non-realizable value of 1 ns per 30.5 cm of cable indicates that a phase distortion results from delaying the signals with analog apparatus. The magnitude of this phase distortion, however, is in itself too small to be the basis of the bats’ discrimination.

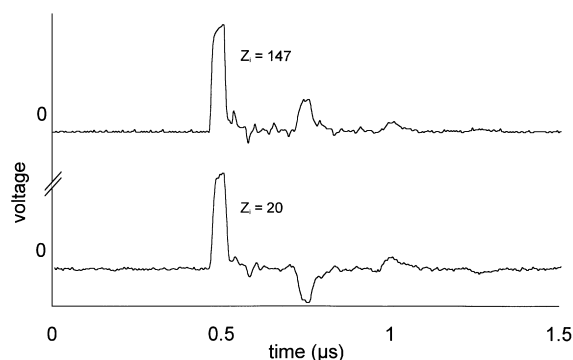
Below is a suggestion of what the bats’ cue could have been is presented, together with a rather informal test on the feasibility of this guess.

#### Impedance mismatch as a possible cue

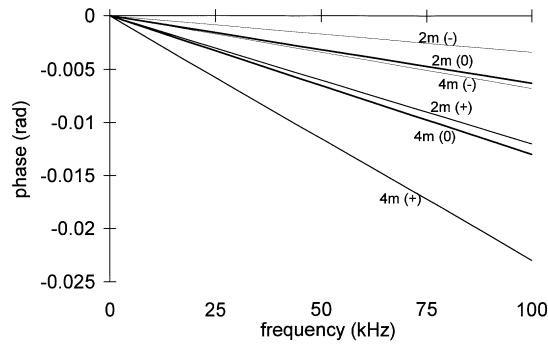
Passing a signal relatively undistorted through any length of cable requires that the impedance is matched at the termination points. Improper impedance matching will cause reflections of signals within the cables (see Fig. 6), which will produce a sometimes rather complicated filtering effect (see legend to Fig. 7).

For frequencies below several megahertz the degree of distortion will increase with the amount of incorrectly terminated cable (nominal delay). In Fig. 7 we show that deviations from the expected delay can be an indication of impedance mismatch. As the delay calibration of the cables in Simmons et al. (1990b) indeed shows deviations from the expected (or even physically realizable) delays, we take it as evidence pointing to impedance mismatch as a possible source of a cue for the nanosecond discrimination performed by the bats.

For unfiltered signals generated by a digital to analog (DA) converter, non-linear elements in the circuit – such as a loudspeaker – will produce low-level distortions within the hearing range of bats. The frequencies most distorted in such a system are the high-frequency components of the steplike signals of the DA converter. For this reason, averaging of signals will eliminate most of such distortion products if the sampling is not in phase with the output clockrate (i.e. the steps are not positioned at the same point in the signal every time). This could help to explain why, if present, the effects were not discovered during calibrations (see observations 1 and 3).



**Fig. 6** Effect on signals of passing through cables with poor impedance matching. A short pulse, approximating a  $\delta$ -function, was passed through approximately 25 m of RG-58/U cable with characteristic impedance of 50  $\Omega$  facing 1 M $\Omega$  at the output end and either 147  $\Omega$  (top trace) or 20  $\Omega$  (lower trace) at the input end. The two traces are not to scale. To produce the  $Z = 20 \Omega$  trace, averaging was performed over 256 signals, and furthermore a running average over three samples was made. Sampling was performed using a digital oscilloscope (250 MHz, 8-bit). One can easily see the reflections resulting from terminating impedances different from the characteristic impedance of the cable. When the input terminal impedance  $Z_i$  is lower than the impedance of the cable (lower trace) the reflection products are negative. Time between reflections is  $2 \cdot 25 \text{ m}/0.20 \text{ m/ns} = 250 \text{ ns}$ . The time-domain transfer function of a system with such reflections is  $h(t) = \sum_{n=0}^{\infty} R^n \cdot \delta(t - 2nt - T)$ , where  $t$  is time,  $R$  is the amplitude of each reflection;  $\delta(t)$  is the delta function, and  $T$  is the delay induced by the cable. Compare with Fig. 7



**Fig. 7** Differences between expected and “actual” phase slopes resulting from impedance mismatch (reflections) for cables having a length of 2 m and 4 m. In the frequency domain the transfer function described in Fig. 6 is  $H(f) = e^{-j2\pi fT} / (1 - R \cdot e^{-j4\pi fT})$ , where  $f$  is frequency,  $j$  is  $\sqrt{-1}$ , and the other symbols are as in the legend to Fig. 6. The lines in this graph represent the phase part of this transfer function with different values of  $T$  and  $R$ . When reflections are present, the absolute value of  $R$  is set to  $1/3$  to correspond to what can be observed in Fig. 6. *Thick lines:* perfect impedance matching (expected values) – marked (0). *Medium lines:*  $R = 1/3$  – marked (+). *Thin lines:*  $R = -1/3$  – marked (-). It can be seen that when  $R$  is negative, the slopes are less steep than expected from a system with perfect impedance matching (no reflections). When  $R$  is positive, it results in steeper slopes than expected (i.e. more apparent delay)

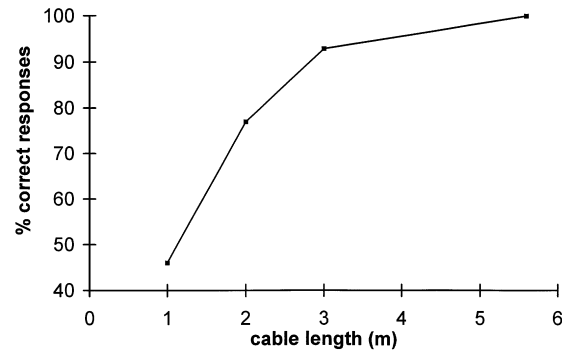
We know that averaging was performed during sampling in Fig. 4, and in Fig. 5 the absence of random noise points in the same direction.

Most importantly, the impedance mismatch explanation meets the condition that the amount of nominal delay introduced increases the amount of distortion, so that a complete psychometric function will result when the delay is varied.

With more assumptions about the set-up (which we shall abstain from making) it is also possible that the impedance mismatch hypothesis will explain why different methods of calibration do not produce the same results, as is the case with the digital counter method (see observation 2) being in better agreement with the nominal values of the lumped-constant device than are the slopes of the phase plot of Fig. 5C (observation 4): if the different calibration devices do not have the same impedances, or are not present during all the calibrations, then this will yield different results.

#### A model experiment with a human subject

We have conducted a model experiment to determine whether humans can detect an artificial bat cry (linear sweep from 50 kHz to 20 kHz in 1 ms with a second harmonic) passed through various lengths of cable with grossly inappropriate termination. The test signals were sampled at a clockrate of 1 MHz after small cable delays and interpolation filtering. These sampled signals were then presented with a 50-kHz clockrate, lowering the involved frequencies by a factor of 20. With terminal impedances of 10 K $\Omega$  the cables (RG 58 c/u,  $z=50 \Omega$ ) function like a first-order low-pass filter with cut-off



**Fig. 8** The performance of one human observer discriminating “jittering” signals as a function of the length of coaxial cable prior to sampling of the original (100–20 kHz) signals (see text). Each data point represents 100 trials

frequencies dropping for longer cables. Our subject reported the cue to be subtle differences in sound quality, but was unable to define the nature of this precisely. The cue is difficult to determine, since an approximation to a jitter experiment was used in which only overall changes in signal quality are needed to solve the task. Both amplitude and frequency distribution changes with increasing cable length. The threshold for detecting a difference in cable length that the signals had passed prior to sampling was around 2 m of cable (Fig. 8). This corresponds to the amount of cable needed to produce a delay of 10 ns in a well-functioning system.

#### Conclusion

As in all psychophysical experiments the conclusions of the jitter experiment of Simmons et al. (1990b) are valid only if no cue apart from the experimental variable is present. The fact that detection of nanosecond delays of ultrasonic signals is beyond the sensory capabilities of the human observers conducting the experiments is a complicating factor. The papers discussed accordingly supply an outstanding richness of calibration data, which have made the present analysis possible.

We have presented evidence for differences other than delay being available to the bats in the 10-ns experiment of Simmons et al. (1990b). A direct indication of impedance mismatch in the system are the too-small delay values from the cables.

In summary, we find that the studies reported by Simmons et al. (1990b) and Simmons (1993) contain sufficient evidence to demonstrate that the essential condition of a psychophysical experiment, as outlined above, has not been met, and that explanations other than the 10-ns jitter discrimination abilities can potentially account for the data.

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