ORIGINAL PAPER

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The transfer function of a target limits the jitter detection threshold with signals of echolocating FM-bats

Abstract The delay jitter discrimination threshold in bats is a disputed subject. Some investigators have obtained results indicating that bats are able to discriminate alternations in delay down to 10 ns, which appears incredible for purely physical reasons. Using actual bat echolocation sequences recorded during an easy detection task to measure simulated delay jitter, it is shown here that jitter detection thresholds in the order of some tens of nanoseconds are actually physically realizable. However, if the transfer function of the target simulating apparatus is not perfect, the lowest thresholds are in the order of hundreds of nanoseconds and variable between individual bats. This phenomenon is shown to arise as a consequence of the variation in signal parameters from call to call. When the transfer function from a real jitter experiment was artificially applied to the echoes, the jitter detection thresholds again were several hundred nanoseconds. This is the first study to point out a limiting role of the transfer function of a system faced with variations in echolocation signal parameters, something that should be considered in evaluating all sonar systems with variable signal structure.

Keywords Bat echolocation · Cross-correlation · Jitter detection · Transfer function · Group delay

Abbreviations ADC: Analog to digital converter · RMS: Root mean square · B_{rms}: Frequency centroid (also called the non-centralized root mean square bandwidth) · cRMS BW: Centralized RMS bandwidth · CCF: Cross-correlation function · SNR: Signal to noise ratio · SD: Standard deviation · IPI: Interpulse interval

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Introduction

Echolocating microchiropteran bats emit trains of ultrasonic pulses and evaluate the returning echoes for a multitude of parameters (Griffin 1958; Pollak and Casseday 1989). Hartridge (1945) hypothesized that bats use echo delay to measure the distance between itself and echo-reflecting objects, similar to man-made systems of sonar and radar. Simmons (1971) then showed in a series of psychophysical experiments that bats were able to discern target distances down to about 1 cm. He finally settled this question by demonstrating that the bats were equally good at determining the distance to a virtual target, that is, the delay to an electronically produced replica of the outgoing pulse (Simmons 1973).

There has been a lengthy discussion concerning a phase-sensitive (coherent) cross-correlation receiver for modelling how bats might determine target distance (Simmons 1979; Menne and Hackbarth 1986; Hackbarth 1986; Altes 1981; Saillant et al. 1993). This receiver is optimal for target detection and range determination (Woodward 1955), and uses all the available information in the signals to arrive at an estimate.

It was shown by Schnitzler and Henson (1980) that with reasonable signal-to-noise ratios (SNR) in the laboratory, only range resolution in the area of 10 ns would constitute evidence of a coherent (phase-preserving) receiver. Therefore the question of whether bats use coherent reception is currently revolving around the credibility of the data later published by Simmons et al. (1990, 2003) showing the limit of the bats' ability to determine a change in delay between successive calls (jitter of simulated echoes) actually to be the predicted 10 ns – equivalent to 1.7 μm range difference (for discussion see Pollak 1993; Simmons 1993; Beedholm and Møhl 1998; Simmons et al. 2003).

The minimum standard deviation of range estimates obtainable with the coherent receiver can be calculated using the Woodward (1955) equation.

$$\sigma = \frac{1}{2\pi B_{rms} \sqrt{2E/N_0}}, \qquad (1)$$

where E is the energy of the echo, N_0 noise spectral density, and B_{rms} is the non-centralized "bandwidth" or frequency centroid. The formula is only valid for high SNRs (see Menne and Hackbarth 1986). If the bandwidth (in the usual sense of that term) is increased, then the range of SNRs for which the expression stays valid is expanded to lower values.

The present study provides an answer to this question of the minimum obtainable range accuracy using bat echolocation behaviour, but without actually putting the bats to the task. Instead both the outgoing sounds and returning (simulated) echoes are sampled in a "dummy" psychophysical experiment (easy target detection experiment) and it is investigated how accurately the delay between these two sound occurrences could be measured using optimal processing of the echolocation signals. It is found that the achievable accuracy is highly dependant on the transfer function of the playback system.

Methods

Animals and training

Four big brown bats, *Eptesicus fuscus* (two males, two females, one of each sex caught in the wild, the other two born in captivity) were initially trained over a period of more than 2 years, typically 5 days a week, mostly in a jitter task with real targets, which, however, they never learned. They were therefore switched to a detection task, which all bats learned within a single experimental day.

During collection of the data the bats were performing in a Yes/No psychophysical detection experiment with simulated targets (see e.g. Møhl 1986; Troest and Møhl 1986). The data presented here were collected when the bats were very well trained and never made any mistakes at high gain settings. The normal training usually started with high playback gain and, in order to get as high an SNR as possible, a setting of −16 dB at the recording microphone was chosen for the present analysis. The bats behaved like they did during normal trials with very little hesitation in reaching a decision.

Apparatus

The echo playback set-up consisted of analogue equipment only, that is, a microphone, attenuators, amplifiers, analog filters, and a loudspeaker (Fig. 1). The microphone, a 1/8in. B&K (model 4138) was mounted
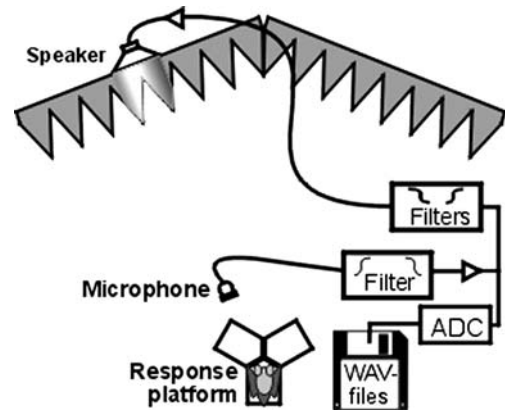

Fig. 1 Schematic of the set-up used for collecting vocalizations and echoes of the bats during the trials. ADC analogue to digital converter

vertically 10 cm in front of the response platform. Mounting was mechanically independent of the response platform. The electrostatic loudspeaker (Polaroid) that delivered the played back echoes was placed 1.5 m from the microphone. Echoes thus simulated a target distance of 0.75 m, resulting in a propagation delay of about 4.4 ms.

The speaker was driven by a power amplifier, producing a 90° phase turn as voltage was converted into current. The loudspeaker itself was resonant and had a transfer function with a peak around 60 kHz. This response was equalized by means of a Krohn–Hite filter (model 2650) set to band reject around 60 kHz and a first-order passive high-pass filter with −3 dB cut-off at 60 kHz. The resulting combined frequency response was flat within 6 dB over the most relevant range of 25–100 kHz. There was a phase shift in the loudspeaker amplifier of $\pi/2$ due to a voltage to current converter.

The experimenter started a continuous sampling process (480 kHz, 16 bit, ADC in Fig. 1) at the beginning of a trial. Sampling was stopped manually when the bat had made a decision and the samples taken in the preceding 2 seconds were saved (WAV-files in Fig. 1). Most bats responded within two seconds. For each bat, four target present trials were run with these conditions.

Offline signal treatment

The sampled trial-sequences were split up so that all sequences consisted of consecutively emitted signals with a recorded echo level in excess of 87 dB peSPL RMS (= 96 dB peak-to-peak) and no overlap between pulse and echo. Signals below this level, or signals so long that overlap between pulse and echo occurred, were not analysed further. This resulted in 7 sequences for bat 1 and 2, 8 for bat 3, and 4 for bat 4. Emitted sounds were analysed for frequency centroid, centralized RMS bandwidth (cRMS BW), energy, interpulse interval (IPI), and duration. Duration was measured as the time

interval containing 95% of the energy of the signal (Madsen et al. 2004).

After possible off-line modification to the echo waveform, described next, the cross-correlation function (CCF) was determined for each pulse–echo pair, and the delay was estimated in the following way: the location of the peak was found by expanding the sampling rate to 7.7 MHz and then interpolating the peak of the CCF and the two neighbouring samples with a second-order Lagrange polynomial. The first of these steps is done by zero-padding the DFT beyond the Nyquist frequency and then transforming the signal back into the time domain. This reliably yields the sample values that would have been obtained, had the signal been sampled at this rate in the first place. The polynomial method on the other hand is only an estimate and it was therefore checked in a Monte-Carlo procedure with artificially generated pulse–echo pairs that these methods combined gave accurate results down to at least 5 ns.

For all series of consecutively emitted cries that met the afore mentioned criteria, the result was an array of N range estimates. For each estimate — except for the first one — the difference to the previous estimate was calculated, resulting in $N-1$ estimates of the delay *differences* from call to call. For each bat these arrays of delay difference estimates were pooled across all cry series.

In order to determine the effect of the transfer function on the delay stability, it was also investigated how two modifications to the echo waveform — applied before cross-correlation — affected the thresholds. One modification removed the residual frequency dependency of the transfer function that remained after the analogue equalization described previously, and also the overall phase shift of $\pi/2$ due to the loudspeaker amplifier. The other modification reintroduced imperfections into the transfer function to facilitate direct comparisons with the published jitter thresholds (Simmons et al. 1990, 2003).

To make these modifications, the transfer function of the system was first determined from eight pulse–echo pairs that were not part of the other parts of the analysis. The Fourier transform of the echo was divided by the Fourier transform of the pulse. The resulting transfer function was then represented by high–degree (18) polynomials in the relevant frequency range: one polynomial for the amplitude and one for the phase (without the average phase slope representing the pure delay). The use of polynomials to represent the amplitude and phase parts of the transfer functions instead of just the raw data served to eliminate noise.

In the first modification, the transfer function was corrected with the data determined as described previously. These corrections rendered the phase shift and the group delays of the system approximately zero (see Fig. 2) and the frequency response completely flat.

To make the second modification, the right channel of the system used by Simmons et al. (1990, Fig. 5) was chosen as a representative of a more typical transfer function than the partly equalized one used here (see
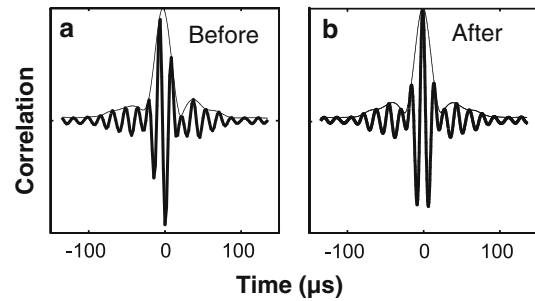

Fig. 2 Example of CCF before and after corrections to the transfer function. *Thick line* CCF, *thin line*, envelope of CCF

Fig. 3). The phase part of the transfer function of that system was calculated by using the so-called minimum phase property: the phase spectrum of a system like this one can be calculated as the Hilbert transform of the natural logarithm of the amplitude spectrum (Oppenheim and Schaeffer 1989). By convolving the otherwise corrected echoes with the impulse response of this non-flat spectrum before cross-correlation, it was possible to evaluate the delay stability of that system given the call sequences here (but excluding any possible constant phase shift as the one caused by the voltage to current converter in our system).

All methods were verified in Monte-Carlo simulations using computer-generated sequences of calls in noise for which the parameters were known.

Simulation procedures

The data sets were the basis for simulated two alternative forced choice jitter discrimination experiments (Simmons et al. 1990). For each bat and for each of the modifications to the echoes mentioned previously, a performance curve was generated using the following procedure: the computer picked two random items, A
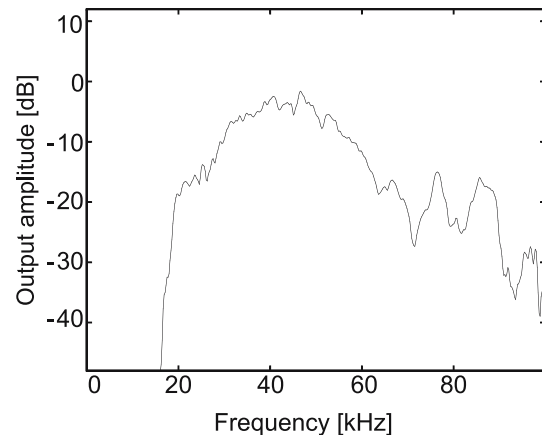

Fig. 3 The amplitude part of the transfer function used as a representative of a "typical" system without any corrective measures taken. The data were grabbed from Simmons et al. (1990, Fig. 5 *right channel*)

and C, from the relevant data set of measured delay differences. The decision rule was that if

$$|A + Jitter| > |C|, \tag{2}$$

a correct decision was counted. This was done 10,000 times for each jitter value and the probability of answering correctly was determined from the ratio of correct decisions to this number of trials. The jitter values were spaced 5 ns apart.

Without corrections to the transfer function and with the "typical" transfer function applied, some delay estimate differences became very large and they were excluded from the analysis. The threshold for exclusion was set to 1.2 µs.

A "theoretical" 75% correct threshold was calculated based on average values of echo energy, centre frequencies, and a measured N_0 of -7.5 dB // 20 µPa $Hz^{-1/2}$. These parameters were used to generate an array of delay estimates with a standard deviation, σ, by plugging the relevant quantities into the Woodward equation (Eq. 1). The artificial array was then treated in the same way as the pool of measured delay values for the bat call–echo pairs. The simulation procedure as described previously was then followed with the artificial distribution of estimate differences.

Results

The signals from these trials do not differ noticeably from the ones the bats usually used to solve the more difficult detection tasks. They contain three harmonics with appreciable energy. For all four bats the last part of the second harmonic was usually the most powerful signal component and most of the energy was typically found around 65 kHz. Interpulse intervals ranged between 24 and 181 ms, which is typical for laboratory behaviour of *E. fuscus* (Surlykke and Moss 2000). Relevant statistics of the call parameters are given in Table 1.

For each bat there is a variable number of calls in each data set due to differences in echolocation behaviour. Bat #3 at some point used calls over 5 ms long and therefore had many calls eliminated. Bats #1 and #2 had some calls below the amplitude criterion, leaving a larger number of shorter call sequences. Bat #4 behaved perfectly in these respects and had no sounds excluded.

Simulated performance curves are shown in Fig. 4 and the evaluated 75% thresholds are summarized in
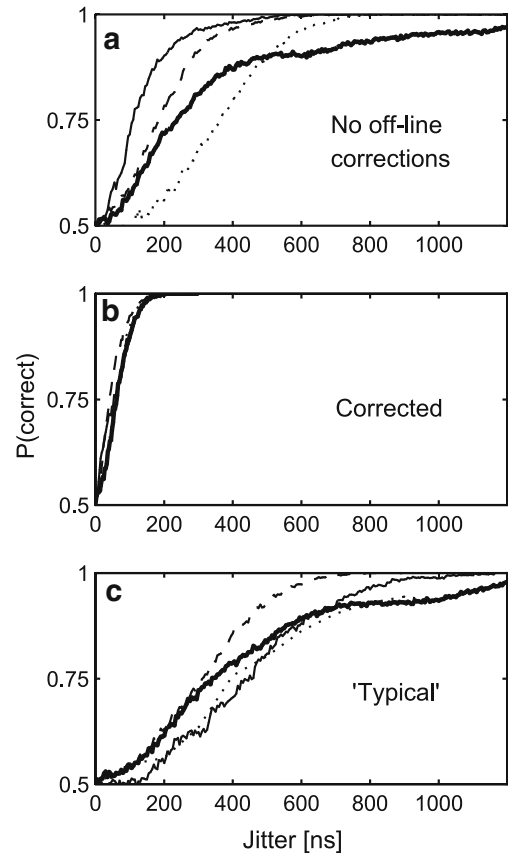

Fig. 4 Simulated performance curves with and without off-line modifications to the echoes. *Dotted line*: Bat #1, *dashed line* Bat #2, *thin, fully drawn line* Bat #3, *thick line* Bat #4

Table 2. The theoretical threshold, based on the average signal parameters and the spectral noise level, was 7.4 ns.

Without off-line modifications to the transfer function the jitter thresholds vary among the individual bats. Bat #3 had the lowest jitter detection threshold with 110 ns, whereas bat #4 had the highest with 365 ns. The average, weighted according to the number of estimates contributed by each bat, was 198 ns. Using *F* tests on the distributions of the delay difference data and testing the bats against each other, it was found that Bats #2 and #3 were not significantly different from each other at the 95% level, but the other bat combinations were. Bat #3 had one difference value above the 1.2 µs threshold, whereas Bat #4 had six. These outliers did not contribute to these statistical tests.

Table 1 Average call parameters ($\pm$SD)

Bat #	N	Amplitude (dB peRMS SPL)	Energy (dB // 20 µPa·s)	95% dur. (ms)	IPI (ms)	cRMS BW (kHz)	Frequency centroid (kHz)
1	33	91.5 ± 2.4	61.3 ± 2.3	2.3 ± 0.4	89 ± 28	15.0 ± 2.9	58 ± 8.2
2	89	95.9 ± 3.4	64.4 ± 3.3	1.8 ± 0.2	53 ± 14	16.1 ± 1.4	67 ± 3.7
3	43	92.2 ± 3.0	61.2 ± 3.4	2.1 ± 0.7	56 ± 33	15.2 ± 1.9	70 ± 5.9
4	44	96.3 ± 3.6	67.2 ± 3.7	2.8 ± 0.6	65 ± 32	15.1 ± 1.9	57 ± 8.0

Table 2 Thresholds and number of delay estimate differences (N)

Bat #	N	No corr. Thr [ns]	Corr. Thr [ns]	"Typical" Thr [ns]
1	26	365	65	394
2	82	185	40	312
3	34	110	60	432
4	40	237	62	339

With the off-line correction of the transfer function the differences between the bats disappeared according to the F test method described previously. The weighted average threshold in this case was 56 ns. No estimate differences were excluded as no difference values above 1.2 μs were observed.

With the transfer function of the right channel from Simmons et al. (1990) applied on top of the corrections to the transfer function, thresholds increased to between 312 (Bat #2) and 432 ns (Bat #3) with a weighted average of 355. The thresholds were not significantly different from each other. In the case of this modification the number of excluded differences due to the 1.2 μs limit were as follows: Bat #1: 1, Bat #2: 12, Bat #3: 15, and Bat #4: 1.

Without the exclusions the thresholds were highly different with, for example, Bat #3 having a 75% threshold of 16 μs. In this case they were also not normally distributed.

Discussion

The measurements made here are independent of head movements as the stationary microphone, not the bat, is the point of reception of both the copies of the sound used in forming the CCF. As argued in the following, the results would not have been achieved in a similar experiment using artificial signals simulating the bat calls, since such signals would lack the variation in the calls by the bats.

The most interesting finding here is the strong dependence of the jitter threshold on the degree to which the transfer function of the system has been corrected. This effect is treated next and the results are compared with psychophysically obtained jitter thresholds, in particular the Simmons et al. (1990, 2003) studies.

Effects of an imperfect transfer function on the jitter thresholds

Why are the jitter thresholds so much higher without corrections to the transfer function than with them? Normally one would expect that the transfer function would affect all echoes equally and therefore be of no consequence. But this is only the case if the transmitted signals affected by the system are always exactly the same. If they are not, as is the case with a real bat, the differences between the calls translate into differences in the location of the peak of the CCF. The simplest case is the one where there is a 90° phase shift present in the transfer function as was the case here. In the following, the consequences of such a characteristic is explained as an example of the influence of transfer function on the estimate stability in combination with signal variations.

There exists a simple relationship between the frequency centroid and the deviation of the position of the peak in the CCF relative to a pure delay in the case of a 90° phase change: the distance between the peak and the first zero-crossing in the CCF between a signal and a delayed copy of itself, is the reciprocal of four times the frequency centroid. So if the frequency weight of a signal changes, then the position of the zero-crossings of this CCF changes too. If a 90° phase shift is applied to the delayed copy, then the peak of the CCF between them will occur where the zero-crossing was before. Therefore, a change in the frequency centroid between consecutively emitted signals translates into a change in the peak of the CCF (Fig. 5).

As explained in the Methods section, the amplitude part of a transfer function is for most systems linked to the phase function. The slope of the phase part of the transfer function determines the delay of the frequency components, the so-called group delay. If the group
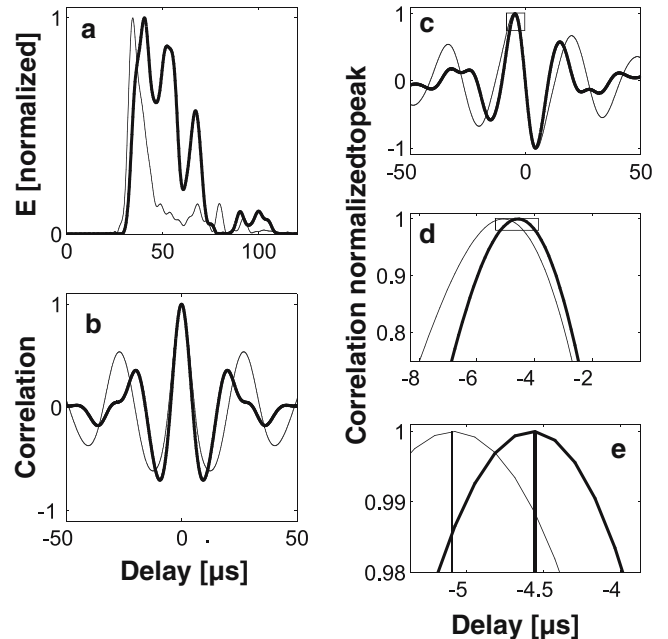

Fig. 5 The effect of phase shifting the transfer function on the peak location of the CCF between outgoing and returning signal. *Thick* and *thin solid curves* represent data for two signals emitted consecutively by Bat #4. **a** Energy spectra (normalized, linear ordinate axis). The frequency centroids of the calls (the value dividing the area below the spectrum in half) were 54 and 49 kHz. **b** Normalized ACFs. **c–e** CCF between one copy of the signal phase shifted −90° relative to an undistorted one. *Squares* in **c** and **d** delimit the display range covered by the graph in the next panel. The *vertical lines* in **e** are at $1/(4 \times$ frequency centroid)

delay of the system is not zero, meaning that all frequencies are delayed by the same amount, then this also has as a consequence that changes in frequency content of the call will translate into a change in the location of the peak of the CCF between pulse and echo. This effect is less easy to predict quantitatively than the effect of the phase shift.

The fact that the individual bats achieve different thresholds without the corrections to the transfer function is then understandable since the bats would have different degrees of variation from call to call. Also the fact that introducing the corrections removed the differences between individual bats is in good agreement with the notion that if the transfer function is perfect, it is inconsequential for the stability, even if the signals differ from call to call.

The large estimate differences above 1.2 μs present in the simulations with the imperfect transfer functions represent cases where the Woodward equation (Eq. 1) breaks down. This shows itself in that many estimates occur around the delays corresponding to the side lobes of the CCF (not shown).

Comparisons with the theoretical threshold

The theoretically obtainable threshold given values of echo energy, noise spectral density, and bandwidth of 7.4 ns was not reached even when the transfer function was corrected. This might be due to imperfections of the air path, such as small degrees of turbulence caused by movements of the trainer and the bats.

Comparison with psychophysical jitter experiments

The closed loop jitter experiments made by Simmons (1979), Moss and Schnitzler (1989), and Menne et al. (1989) had their lowest detected jitter values above 0.4 μs. Consequently, these bats were for the most part performing just outside the range of limits given earlier. The jitter experiments of Simmons et al. (1990, 2003) yielded thresholds of 10–15 ns, which are the prime concern here. Although the results may have been influenced by other factors (Beedholm and Møhl 1998), it is found here that this accuracy is actually marginally physically attainable under conditions like the ones in the laboratory used here. The 56 ns are obtained with the minimum number of estimates to reach a decision (Eq. 2), and with a higher number of echoes going into the estimate, a reduction is possible. Also, it might well be that the longer air path used here has a negative effect on the stability of the estimates. If small disturbances are indeed the limiting factor, and if such phenomena are distributed equally along the signal path, then a longer air path will affect the threshold negatively and a shorter delay caused by the air path like the one used in Simmons et al. (1990) might reduce the threshold enough to make that result feasible in principle.

However, given the echolocation behaviour of the bats in the present experiment, 10 ns is not a realistic threshold if the system is not perfectly equalized. The thresholds reached under application of the transfer function of Simmons et al. (1990) show that the bats in this study would not have been able to detect a jitter even in the order of 100 ns. Several estimate differences were excluded from the jitter simulation due to the limit of 1.2 μs when the "typical" transfer function was applied. Without this criterion the thresholds would have been even larger.

It could well be argued that because the task in this study was one of detection, and an extraordinarily easy one at that, the bats were not compelled to keep the variation in centre frequency and bandwidth as low as they would have done if they were performing in a jitter task. For one signal parameter, namely frequency centroid and its standard deviation, SD, an estimate can be derived from Figure 20B of Simmons et al. 1990, showing an average autocorrelation function of 50 calls emitted by one bat. By scanning this graph, evaluating the points around the zero-crossings on one side of the peak (Fig. 6), and applying the rule that the frequency centroid is the inverse of four times the delay relative to the peak of the "mean" zero-crossing trace (see Fig. 5), the resulting estimate is 58 kHz, which is close to the corresponding values for Bats #1 and #4 in this detection experiment (see Table 1) and close to the value of 55 kHz stated in Simmons et al. (1990, p 598). The corresponding delays of the zero-crossings of the SD curves correspond to frequencies of 52 and 64, ca. 6 kHz from the mean. When this procedure of data reconstruction and analysis was followed for a small graph of
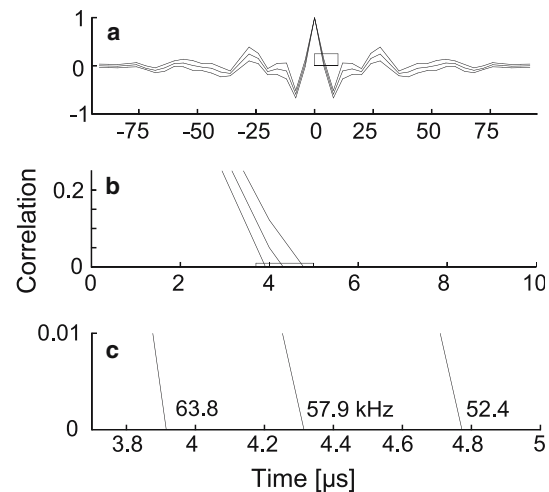

Fig. 6 Method for evaluating the variation in frequency centroid of the calls in the jitter experiment by Simmons et al. (1990). **a** Data from Simmons et al. (1990, Fig. 20b). It shows mean normalized ACFs of 50 calls ±1SD. **b** The same data in the area delimited by the rectangle in (**a**). **c** The data contained in the rectangle in (**b**). The frequencies shown by the zero crossings are calculated as 1/(4 × t(zero)). The middle value corresponds to the frequency centroid, the ones by the traces to the left and right are estimates of the frequency centroid plus and minus its standard deviation

CCFs ±1SD with 50 signals from Bat #2, the exact value for the mean frequency centroid was found, and the SD was underestimated slightly relative to the value in Table 1. It therefore appears that estimating the SD in this — not completely sound — way gives a conservative estimate of the SD. The value of 6 kHz for the SD of the frequency centroid in Simmons et al. (1990) fits very well with the values found here, which had a weighted average of 5.8 kHz taken over all bats.

Some other call parameters can be compared: amplitudes of the calls were comparable. The signals were reported to be 96–102 dB peak-to-peak SPL in Simmons et al. (1990, p.597) equivalent to 87–93 peRMS SPL. This should be compared with the values in Table 1, 91–96 dB peRMS SPL mean values among the bats. The differences should not have any influence on the thresholds, as these were presumably not limited by the SNR but by the transfer function of the system.

Repetition rates do differ relative to Simmons et al. (1990). We found interpulse intervals of 27 to almost 200 ms. Mean values are given in Table 1. In Simmons et al. (1990) values of 15–70 ms are reported, depending on which part of the trial is concerned. Judging from Fig. 16 of Simmons et al. (1990), it seems that in the ''scan'' period of trials the bats made sounds with intervals even shorter than 15 ms. Given that in the mentioned experiment some bats made use of signals of upto 3.5 ms in duration this is a rather unusual behaviour for *Eptesicus*. The differences, however, should not affect the comparison with the results of the current investigation, since the stability of the echo delay estimate should be independent of the time between estimates. This is assuming that slow changes to the air path is not the limiting factor. This would have made a higher repetition rate an advantage, as it would reduce call-to-call changes in delay. But again, since correcting the transfer function removed most of the timing error, it is unlikely that features of the air-path limited the uncorrected and ''typical'' transfer function thresholds.

To achieve the 10 ns jitter threshold in the face of the transfer function of the target simulator of Simmons et al. (1990), the bats would have had to use unusually stable signal parameters compared with bats in this study if they were to overcome the pronounced group delays of the system. This analysis on frequency centroid variation strongly suggests that it was comparable with what was seen here. The errors can therefore also be expected to have been about the same. If the bats in a jitter experiment used echoes from objects in the room as a time reference, the result would have been exactly the same, unless the acoustic transfer function of these objects were the same as the speaker in the target simulator, which is unlikely.

Implications of the results

One biological implication of the current result is that it is difficult to imagine an ecological driving force for the generation of coherent reception in echolocating bats, at least if the implied phase preserving hearing were to evolve to increase the range determination accuracy. Insects differ from, for example, an iron sphere in that they have transfer functions that are far from being flat (Miller and Pedersen 1988). The use of the type of processing applied in this study should therefore generate the same kinds of errors by converting signal variability into delay estimate variations. Bat echolocation signals are notoriously variable, which fact seems to contradict the biological implementation of the coherent sonar receiver, since it would not result in range determination capabilities above what can be achieved with more standard auditory models (Menne 1988), and presumably not lead to increased hunting success.

The fact that a non-flat transfer function affects delay estimation stability in the face of variable echolocation calls may also be of interest to practical applications of radar/sonar with adaptive signals. If very high precision in the delay measurements is called for then it may not be a good idea to use adaptive echolocation signals, that is, signals that change frequency content as a target is approached, as such changes in parameters will lead to errors in the range determination, given that the target is not for example, a smooth sphere.

Implications for the jitter experiments of Simmons et al. (1990, 2003) are that the bats could not have used delay as a cue to solve the task: it cannot be done using echolocation sequences like the ones recorded here, which were shown to vary to the same degree as the ones reported on in the 1990 study, at least with respect to frequency centroid. This confirms our earlier conclusion (Beedholm and Møhl 1998) that the bats must have had some other cue, correlated with delay to solve the 10 ns jitter discrimination task.

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