

Detection of sonar signals in the presence of pulses of masking noise by the echolocating bat, *Eptesicus fuscus*

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Summary. Two big brown bats (*Eptesicus fuscus*) were trained to report the presence or absence of a virtual sonar target. The bats' sensitivity to transient masking was investigated by adding 5 ms pulses of white noise delayed from 0 to 16 ms relative to the target echo. When signal and masker occurred simultaneously, the bats required a signal energy to noise spectrum level ratio of 35 dB for 50% probability of detection. When the masker was delayed by 2 ms or more there was no significant masking and echo energy could be reduced by 30 dB for the same probability of detection. The average duration of the most energetic sonar signal of each trial was measured to be 1.7 ms and 2.4 ms for the two bats, but a simple relation between detection performance and pulse duration was not found.

In a different experiment the masking noise pulses coincided with the echo, and the duration of the masker was varied from 2 to 37.5 ms. The duration of the masker had little or no effect on the probability of detection.

The findings are consistent with an aural integration time constant of about 2 ms, which is comparable to the duration of the cries. This is an order of magnitude less than found in backward masking experiments with humans and may be an adaptation to the special constraints of echolocation. The short time of sensitivity to masking may indicate that the broad band clicks of arctiid moths produced as a countermeasure to bat predation are unlikely to function by masking the echo of the moth.

Introduction

Echolocating bats will often need to extract or filter out the echo of a single target, e.g. its prey, from a set of multiple echoes and background noise. The filtering takes place in several dimensions, such as direction, frequency, and time. The present paper deals with aspects of filtering in the time dimension.

A wide range of indications of the time resolution by echolocating bats appears in the literature depending on experimental paradigm. The estimates range from around 1 μ s to several ms. Jitter experiments showed that echolocating bats (*Eptesicus fuscus*) are capable of discriminating about 1 μ s of temporal jitter of a returning virtual target (Simmons 1979; Menne and Hackbarth 1986). In ranging experiments, different species of echolocating bats have discrimination thresholds between 8 and 40 mm in range corresponding to between 46 and 240 μ s. *Eptesicus fuscus* has a threshold of ca. 75 μ s both with real and phantom targets (Schnitzler and Henson 1980). Finally several other types of laboratory experiments have shown that the bat's ability to perceive targets is reduced by other echoes or noise pulses arriving within a much larger time window relative to the arrival of the target echo: some studies showed decreased performance when the disturbing sounds were within a spatial range of around 10 cm (0.6 ms) from the target (Joermann 1984; Simmons 1985) whereas other studies have demonstrated a critical interval of interference up to several ms from the target (McCarthy and Jen 1983; Troest and Møhl 1986).

Some arctiid moths produce clicks in response to the cries of bats. In some moth species the interval between the clicks is long (up to 180 ms, Sur-

Abbreviations: SPL sound pressure level; SD standard deviation; SE standard error; BW bandwidth

lykke and Miller 1985) and there is no phase locking to the bats' emissions. Hence, suggesting that the clicks increase those moths' chance of survival by interfering directly with the bat's sonar (Blest et al. 1963; Fullard et al. 1979) would imply that interference may occur in a time window as large as 10 to 100 ms around the echo.

To determine the size of the time frame within which an echolocating bat is sensitive to jamming, we carried out a set of simulated target detection experiments, where 5 ms noise pulses were presented at different delays relative to the echo. Essentially, this is a backward masking paradigm. In another set of experiments the onset of the noise pulse coincided with that of the echo and the duration of the noise pulse was varied. The findings from both experiments show that noise is an effective masker only when overlapping with the echo (forward masking experiments were not performed). Since the duration of the echo was controlled by the bats, this parameter was logged in some experiments.

The findings are discussed in relation to aural integration time.

Materials and methods

Subjects. Two adult *Eptesicus fuscus*, a 20 g female (bat F) and an 18 g male (bat M), were kept on a diet of mealworms, supplemented with vitamins and minerals. Food was given solely as reward during the experiments.

Procedure. The bats were trained in an electronic target simulator (Simmons 1971) to interrogate a virtual (phantom) target with their sonar and report its presence or absence in a Y/N paradigm by moving to one platform for target present, and to another for target absent (Møhl 1986). Correct responses (hits and correct rejections) were rewarded with a piece of mealworm. Masking noise pulses were time locked to the bats' sonar emissions and present in all trials (except for reference sessions). The target was present in only half of the trials, the sequence being pseudo-randomized in a Gellerman series with a maximum of 3 consecutive trials of the same type. A session was limited to 60 trials. Fewer trials were used if the bats were not motivated.

The strength of the virtual target was varied in steps according to an up-down procedure: 2 dB reduction following a hit, 4 dB increase following a miss. In this way the bulk of the trials become concentrated just above the 50% detection level, but still widely distributed due to the variable output of the bat.

When computing thresholds, only sessions with 70% or higher correct rejections were used. The data from sessions with identical conditions were pooled and sorted in bins by energy level, varying the bin width to obtain approximately the same number of trials in each bin across the psychometric function. Data outside the threshold zone (bins with 0 or 100% detection) were omitted. Following NED-transformation (normal equivalent deviate, Finney 1971), the energy level for 50% detection probability was estimated by linear regression and the S.D.

(standard deviation) from the slope of the regression line. Thus, the data were essentially treated as if obtained by a method of constant stimuli (Guilford 1954).

Set-up. The experimental set-up was basically as in Troest and Møhl (1986). Briefly, it is a single channel target simulator where the bat's sonar signals are intercepted by a 1/4" recording microphone (Brüel & Kjær 4135 without protection grid), placed 24 cm in front of the bat, attenuated and projected back by a loudspeaker. The modification from the previous set-up included a device for measuring pulse energy and the facility for mixing a noise pulse into the projected signal. The frequency response was flat within ± 3 dB from 30 to 120 kHz. The electrostatic speaker (designed by L.A. Miller) had a diameter of 15 mm; it was placed 68 cm from the bat's observation position. The virtual target was presented 46 cm from the bat, corresponding to a delay of 2.7 ms between the bat's emission and reception of the sonar signal. The speaker was the major determinant of frequency response and clutter interference.

The energy of the returning echo was a function of the gain in the electronic circuitry and the energy produced by the bats. The energy of the bat pulses varied and had to be measured. Consequently, we logged the energy (rather than intensity) of each pulse emitted and defined the effective stimulus level of a given trial as the mean of the three most energetic pulses. Pulse energy was measured by analog squaring and integration of the signal from the recording microphone and reading the output of the integrator with an A/D-converter 8 ms after onset of the pulse. A signal from an auxiliary microphone, placed 2 cm closer to the bat than the recording microphone, triggered the reading sequence by resetting the integrator.

Noise pulses were generated by gating the output from a white noise generator (Brüel & Kjær 1405, -3 dB at 100 kHz). The gate was controlled by a crystal clock to provide well defined delays and durations (accuracy in the μ s range). Rise and fall-times were linear over 4 decades of intensity and set to 0.4 ms. The gate was opened by the signal from the auxiliary microphone and the noise pulse mixed into the simulator circuit at the input of the loudspeaker amplifier.

Monitoring sonar behavior of the bats. To measure the variation of sonar pulses produced by the bats, their signals were recorded at 30 ips on a Racal Store 7 instrumentation recorder during 15 sessions. The envelope of the pulses was extracted and sampled by an A/D-converter. Pulse duration was obtained by measuring the time the pulse intensity would exceed a fixed threshold set at twice the level of the system noise. A measure linearly proportional to energy was obtained by squaring and integrating the samples defining the envelope. The time of occurrence of each pulse was time stamped to give the repetition rate.

Reference thresholds. Reference sessions without noise pulses were interlaced with masking sessions to test for stability in performance and to establish the difference between the masked and the unmasked threshold. The residual noise of the system had a level of -28 dB SPL/ $\sqrt{\text{Hz}}$.

Backward masking. In the backward masking experiments a noise pulse of 5 ms duration was played back at a delay relative to the onset of the echo. The delay was kept constant within any given session, but sessions with different delays were interlaced. The intensity of the noise was measured with the gate open and adjusted to 16 dB SPL/ $\sqrt{\text{Hz}}$ (except at the shortest delays, see Results).

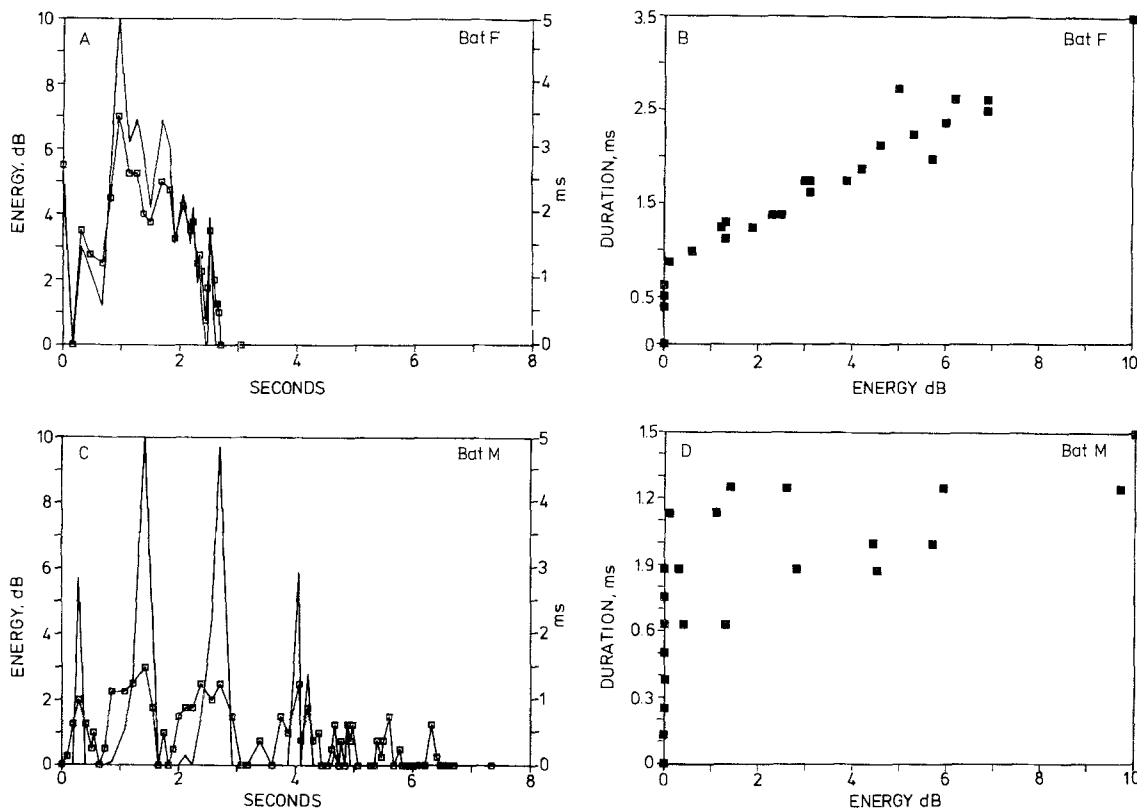


Fig. 1 A–D. Sonar behavior in typical trials of two *E. fuscus*. A and C show how pulse duration (—□—) and relative pulse energy (—) varies from trial start until a decision has been reached. The energy is depicted relative to the most energetic pulse of the trial which was arbitrarily set to 10 dB. B and D show the duration of the pulses as a function of their relative energy

Table 1. Sonar behavior statistics. The table shows average numbers from the analyzed trials of 15 different sessions. n is the number of trials analyzed. The average duration of the pulse is measured for the most energetic pulse of each analyzed trial

	No. of pulses per trial		Duration of pulse		Duration of trial	
	No.	SD (n)	ms	SD (n)	s	SD (n)
Bat F	40	18 (20)	2.5	0.7 (27)	3.9	2.3 (20)
Bat M	66	39 (20)	1.7	0.5 (37)	7.1	5.2 (20)

Simultaneous masking. The masker in this series was noise pulses of constant level (-5 dB SPL/ $\sqrt{\text{Hz}}$) and with no delay but with durations from 2 to 37.5 ms.

Units. Sound pressure level is given as dB SPL implying a reference of $20 \mu\text{Pa}$ rms. The energy measuring procedure weighs variations in cry intensity, duration and envelope in a defined manner, and is a prerequisite for calculating the signal-to-noise ratio of pulsed signals. Energy is given as dB re. $1 \text{ Pa}^2 \cdot \text{s}$. Assuming a square envelope a 1 ms cry of 94 dB SPL intensity has an energy level of -30 dB re. $1 \text{ Pa}^2 \cdot \text{s}$. The noise levels are given as spectrum levels in units of dB SPL/ $\sqrt{\text{Hz}}$, i.e. the level in a bandwidth of 1 Hz referred to the SPL reference level. The intensity of the noise in a given bandwidth, BW, is found by integrating over this BW.

Results

Sonar behavior

The two bats differed somewhat in the ways they used their sonar. Pulse energy, pulse duration, number of pulses, and pulse repetition rate are all

variables controlled by the bat and they all have an effect, major or minor, on the likelihood of the bat making a correct decision. To get an impression of this variability, we analyzed taped sessions for the mentioned quantities (Table 1, Fig. 1).

The duration was measured of all pulses of the taped sessions, and Table 1 gives the average duration of the single most energetic pulse of each trial. It appears that bat F had the more stable routine, used less time and fewer pulses to reach a decision; it used pulses that on average were just short of the two way transit time of 2.7 ms. Bat M used significantly shorter pulses ($P < 0.005$, t -test), but emitted a larger number of pulses and used more time per trial (Fig. 1A, C). A positive correlation

between pulse duration and intensity was evident for both bats since the results clearly showed more than 3 dB increase in energy per doubling of cry duration (Fig. 1 B, D). Mean repetition rates for both bats were close to 10 pulses per s. The intensity of the cries was around 94 dB SPL at the recording microphone.

Reference thresholds

The threshold energy at this condition for bat F was -79 dB re. $1 \text{ Pa}^2 \cdot \text{s}$ and -82 dB re. $1 \text{ Pa}^2 \cdot \text{s}$ for bat M. The standard deviations (SD) of these measures were 5 and 14 dB, respectively. The number of trials, n , in the threshold area was 257 for bat F and 186 for bat M, giving standard errors ($\text{SE} = \text{SD}/\sqrt{n-1}$) of 0.3 and 1.0 dB, respectively.

An estimate of the intensity of the virtual echoes at the reference threshold can be obtained from the energy values and cry durations (Table 1) assuming very short rise and fall times. This estimate is 38 dB SPL for bat F and 37 dB SPL for bat M.

Backward masking

Figure 2 shows the relative echo energy level required for a 50% detection probability as a function of the delay of the masker relative to onset of the echo from the virtual target. The 5 ms masking noise had a constant level of $16 \text{ dB SPL}/\sqrt{\text{Hz}}$. Bat F would not perform at the two shortest delays at this noise level. Consequently the noise was reduced by 15 dB at 0.4 ms delay and by 21 dB at 0 ms delay for both bats. For consistency with the bulk of the data the threshold values are corrected with these differences assuming a linear proportionality between masker and threshold intensity. The main feature of the function is that it shows that in order to affect the threshold the masker must be delayed no more than ca. 2 ms with respect to the echo. The thresholds for the two bats are 3 to 4 dB within each other throughout the range, except at 0.4 ms delay where bat M has a threshold almost as high as at zero delay and 14 dB above that of bat F. The SE of the data in Fig. 2 ranged from 0.4 to 1.5 dB, except for the results at 1 ms, where a low number of trials (20) gave a SE of about 4 dB.

Simultaneous masking

In the simultaneous masking experiments the delay between onset of the echo and the noise pulse was 0 ms and the noise level was kept at

$-5 \text{ dB SPL}/\sqrt{\text{Hz}}$.

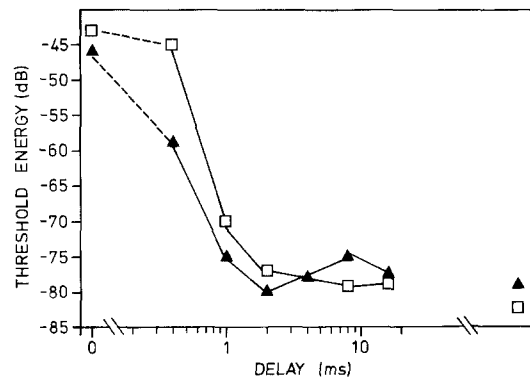


Fig. 2. Backward masking. The echo threshold energy as a function of the delay between echo and noise pulse masker. The points to the right are reference thresholds without added noise. The ordinate is referenced to $1 \text{ Pa}^2 \cdot \text{s}$. \blacktriangle bat F; \square bat M

Table 2. Average thresholds at different masker durations (simultaneous masking). The masking noise level was $-5 \text{ dB SPL}/\sqrt{\text{Hz}}$. For direct comparison with the threshold results shown in Fig. 2 one should add 21 dB to the threshold values in this table since a standard noise level of $16 \text{ dB SPL}/\sqrt{\text{Hz}}$ was used in the backward masking experiments. The thresholds are referred to $1 \text{ Pa}^2 \cdot \text{s}$ and n is the number of trials contributing to each threshold

Masker duration ms	Bat F Threshold		Bat M Threshold	
	dB	SD (n)	dB	SD(n)
2	-69	6.3 (97)		
5	-67	7.3 (97)	-64	6.7 (115)
10	-66	7.5 (90)	-61	9.9 (116)
32			-63	11.0 (74)
37.5	-63	6.1 (31)		

The duration of the masker was varied from 2 to 37.5 ms. The thresholds were raised by about 15 dB relative to the reference level (Table 2). For bat M, the threshold remained close to the reference value for all durations tested (5, 10 and 32 ms). Bat F was tested with a duration of the masker from 2 to 37.5 ms and a small increase in threshold with increasing masker duration was seen. The 2 ms duration data might not be comparable to the rest of the data, since this bat used cry durations that on average were 2.5 ms (Table 1), thus exceeding the duration of the masker.

Discussion

The two bats used somewhat different sonar strategies (Table 1, Fig. 1), but common to both bats was a correlation between intensity and duration, i.e., the most intense cries were also the longest cries. This is consistent with the behavior of a bat pursuing an insect in the field where the short ter-

minal phase cries are of low intensity compared to the longer search and approach cries. This may reflect constraints in the laryngeal mechanics. The differences in behavior of the two bats did not result in major differences in threshold. The only delay at which a noticeable difference was found was 0.4 ms but we have found no evidence in the bats' behavioral data to explain this difference.

The reference thresholds are required to determine if a particular masking condition is limiting detection. Reference thresholds are measures of the lowest echo energy detectable by the bats in this system, not a measure of their absolute sensitivity. The reference thresholds themselves are limited, either by clutter (the real echo from the loudspeaker) or by system noise. Since the thresholds in the experiment with simultaneous masking noise pulses were not raised in proportion to the difference in spectrum level between system and masking noise, we regard the reference thresholds to be limited by clutter.

The threshold function from the backward masking experiments (Fig. 2) may be divided in two regions. The first region extends from zero to 2 ms. Here, the threshold decreases with increased delay. In the second region, above 2 ms, the slope is essentially zero and the level only marginally different from reference level. Our interpretation is that detection is limited by the masker in the first area and by clutter in the second area. The transition takes place at the delay where overlap between echo and masker ceases. The observation can be explained by proposing a time window with a lower limit – or integration constant – of 2 to 3 ms. A precise determination of the transition point is hardly feasible with the present set-up, due to variations in cry duration, envelope and triggering of the noise pulse. The transition point might depend on the absolute masking level unlike the critical interval (integration time) found in time/intensity trade experiments, where the critical interval (the time in which the signal threshold depends on the signal duration) is around 200 ms independent of noise level (de Boer 1985).

Results from backward masking experiments in humans showed that the detection of a 250 μ s click was masked by noise pulses (duration from 1 ms to 125 ms) starting at delays up to 30 ms relative to the onset of the click (Penner 1974). The masking levels used were comparable to those of the present study. Hence, for bats the interference time is shorter by an order of magnitude relative to that of humans. This is obviously seen as an adaptation to echolocation.

The observation of a limited period of sensitivi-

ty to masking may have some relevance for the discussion of the function of the clicks of arctiid moths. It has been proposed that the clicks, which are elicited by ultrasound, could increase the arctiid moth's chance of survival by concealing the echo from the moth in a number of false echoes (Blest et al. 1963; Fullard et al. 1979). The function in Fig. 2 suggests that in order to mask or jam the bat's sonar the clicks should arrive at the bat within 1 ms of the echo. Arctiid moths may produce single clicks or trains of clicks depending on the structure of their tymbal (click producing) organs. Arctiid moths with smooth tymbals produce single clicks with intervals from 10 to around 200 ms arriving at the bat at random relative to the echo (Surlykke and Miller 1985), so the clicks are likely to be far separated in time from the echoes. Thus it is unlikely that at least those arctiid moths that produce single clicks can jam the bat's sonar by masking. However, it should be noted that the present experiment is completely devoid of the surprise factor often seen in clicking insect-bat interactions (Møhl and Miller 1976). The noise pulses occurred perfectly predictably in a 1:1 ratio with the cries and at a constant delay within any session.

When the noise pulse coincided with the return from the virtual target (simultaneous masking) there was an apparent effect of masker duration for bat F. However, the effect was only minor compared to results from similar experiments with humans, where the pure tone detection threshold was increased by around 50 dB when the masker duration was increased from 10 ms to around 200 ms (Weber and Green 1978). The threshold of bat M remained unchanged when the masker duration was increased. Our interpretation of the combined data therefore is that the effect of masker duration is slight or non-existent above a value that is equal to the duration of the cry.

The rise in threshold relative to reference confirms that the bats were limited by the masker in this experiment. The ratio of signal energy to noise spectrum level was computed and found to be about 35 dB. This value is close to the range of 36 to 49 dB found for detection in a constant background of white noise in 3 specimens of *E. serotinus* (Troest and Møhl 1986). The consistency in S/N with constant noise and short noise pulses offers additional evidence supporting the interpretation of a critical interval of masking of a few ms.

When discussing the results in relation to aural integration time the basic assumption is that noise and signal are integrated in the same locus over equal time. However, a vast body of data from

the psychophysical literature (reviewed by Green 1985; Yost 1980) indicate a variety of integration times spanning several orders of magnitude depending on the experimental paradigm. It seems that each integration time can best be regarded as an ad hoc model (de Boer 1985). In this sense, the 2 ms interval of interference sensitivity found in this study can be said to represent an integrator. The 2 ms value is an order of magnitude above the one found in multiple click detection experiments in echolocating dolphins (Au and Moore 1988) and two orders of magnitude below the classical one found in intensity-duration trade experiments over a wide range of mammals, including dolphins (reviewed by Brown and Maloney 1986). But the 2 ms value is fairly well adapted to the present detection task, where perfect adaptation would show integration times equal to signal duration.

The durations, entirely set by the bats, may reflect constraints given by the two way transit time of 2.7 ms. Durations above this value cause overlap between the outgoing and the returning signal, a condition generally avoided by FM-bats (Cahlander et al. 1964; Schnitzler et al. 1987). Hunting *E. fuscus* are known to generate much longer cries (10 ms, Simmons et al. 1978) in the search phase, a behaviour that increases detection probability by increasing the signal to noise ratio. To exploit this effect, however, integration time should be increased correspondingly (Surlykke 1988). This raises the question about integration time being a fixed value, or adaptable to the duration of the cries. The present experiment has no relevant information on this matter.

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