J Comp Physiol A (1986) 159:559–567

Journal of Comparative Physiology A Sensory, Neural, and Behavioral Physiology

The detection of phantom targets in noise by serotine bats; negative evidence for the coherent receiver

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Accepted June 27, 1986

Summary. Using a target simulator three serotine bats, *Eptesicus serotinus*, were trained to judge whether a phantom target was present or absent. The echolocation sounds emitted by the bats during the detection were intercepted by a microphone, amplified and returned by a loudspeaker as an artificial echo, with a delay of 3.2 ms and a sound level determined by the overall gain and cry amplitude. The cry level of each pulse was measured and the echo level received by the bat was calculated. The target was presented in 50% of the trials and the gain adjusted using conventional up/down procedures. Under these conditions between 40 and 48 dB peSPL were required for 50% detection (Figs. 2, 3).

In a subsequent experiment the phantom target was masked with white noise (N_0) with a spectrum level of -113 dB re. 1 Pa·Hz$^{-1/2}$. The thresholds were increased by 7–14 dB. Energy density (S) of a single pulse was measured and used to estimate S/N_0, which ranged from 36–49 dB at threshold. Theoretically the coherent receiver model predicts the ratio between hits and false alarms observed for the bats at a S/N_0 of ca. 1–2 dB. Since the bats require 40–50 dB higher S/N_0 (Fig. 3), this is taken as negative evidence for coherent reception (cross correlation).

Furthermore, a strong sensitivity to clutter was found since there seemed to exist a fixed relationship between thresholds and clutter level.

Introduction

Performance of sensory systems, natural as well as man made, is limited by noise, ultimately. The mode of operation of a system may be revealed by the way it copes with noise. In the case of bats echolocating with frequency modulated pulses (FM-bats), a working hypothesis in the last two decades has been that they process echoes according to the principles of a coherent receiver (matched filter, ideal receiver, pulse compressor, crosscorrelator) (Simmons 1980; Strother 1961; Cahlander 1967). This principle is used in peak-power limited transmitters in radar- and sonar applications to obtain a high time resolution from pulses of relatively long duration. An increase of the duration of a signal will increase the signal to noise ratio (S/N), but decrease the time resolution. The coherent receiver is the optimal solution to simultaneous requirements of maximum signal detection ability and maximal time resolution. In bat sonar research a number of investigations (Simmons 1973, 1979, 1980; Wenstrup and Suthers 1984) deal with time resolution, while relatively few (Griffin et al. 1963; Simmons et al. 1978) are concerned with bats' ability to detect echoes in noise. However, this aspect is important, since it reveals whether the bats can operate under poor S/N conditions, and consequently whether it is likely that coherent processing is used in the sonar system of FM-bats.

In these previous experiments on signal detection in noise the S/N ratios can only be estimated indirectly since the echo is not measured but calculated. Furthermore, the noise field is not isotropic, so the bats may take advantage of the directionality of their sonar system in a manner hard to calculate (Grinnell 1967).

The S/N ratio of coherent receiver sonar systems, including biosonar or echolocation, can be obtained from the proper sonar equation (Urick 1975).

$$\mathrm{DT} = \mathrm{SL} - 2\mathrm{TL} + \mathrm{TS} - (\mathrm{N_o} - \mathrm{D}) \qquad (1)$$

where all parameters are in dB units.

Abbreviations: *C* clutter; N_{bw} noise in a specified bandwidth; N_0 noise in 1 Hz bandwidth; *peSPL* peak equivalent sound pressure level; *S* signal energy; *SD* standard deviation; *Y/N* Yes/No psychometry; *2AFC* two alternative forced choice psychometry

DT: detection threshold. SL: source level. TL: one way transmission loss. TS: target strength. N_o: noise spectrum level. D is a directionality parameter accounting for the fact that the masking efficiency of the noise depends on the direction of the noise relative to that of the signal. The sum of $SL-2TL+TS$ is the signal level, and the sum of N_o-D is the perceived noise level.

An independent estimate of the S/N ratio can be obtained using signal detection theory based on the observed proportion of hits and false alarms for the detection task (Swets et al. 1961). Thus, if the two estimates are close, coherent receiver operation is indicated.

In order to quantify all the elements of the sonar equation, detection experiments were performed with 3 serotine bats in a target simulator. The target is simulated electronically; the cry is intercepted and retransmitted as an artificial echo, a phantom target. In the setup, the phantom target level, i.e., the signal intensity $(SL-2TL+TS)$ and the noise intensity (N_o) are experimentally established and the effect of directionality cancelled, since noise and signal are always projected from the same point.

The results showed that, at threshold, a S/N_o ratio of about 50 dB was required, while estimates from the bats' performance indicated an effective S/N ratio of only about 2 dB. The results are thus inconsistent with the hypothesis of coherent reception but in line with expected performance from mammals in general.

Materials and methods

The animals. Three serotine bats (*Eptesicus serotinus*) (one male and two females designated E1, E2 and E3) with body weights from 15 to 23 g were used. One bat was caught in a mistnet, the others were taken during hibernation. The age at capture was unknown. The bats were only fed on the mealworms given as rewards during the experiments; vitamins were added to the food.

The bat's task. The bats were trained for target detection. Using a two choice paradigm they had to judge whether a phantom target was present (signal trial) or absent (catch trial) under various noise conditions and report their decisions by moving from an observation platform to one of two response platforms (yes and no platforms, Fig. 1). In signal trials the bat made a hit by going to the yes-platform and a miss by going to the no-platform. In the catch trial situation, the bat made a false alarm by going to the yes-platform and a correct rejection by going to the no-platform. A correct response was rewarded with food while an incorrect response resulted in a mild punishment (a punch on the nose with the forceps). The under scori probability of a target present was 0.5. The distribution of signal and catch trials was pseudorandomized (Gellerman schedule), with a maximum of 3 consecutive trials of the same type.

Experiments. All experimental animals were used in two different experiments. In the first experiment the detection threshold for the simulated target was determined with no noise added (unmasked thresholds). In the second experiment white noise was added and a masked threshold for target detection was determined (masked thresholds). In these experiments a loudspeaker with a diameter of 75 mm was used.

In addition, an unmasked threshold was determined for bat E3, using a loudspeaker of a diameter of 15 mm.

Sessions. Each session, usually one a day, consisted of up to 60 trials or less if the bat flew from the platform. The first 10 trials of each session were considered warm-up-trials at a constant echo level well above threshold. If the bat made less than 3 errors in the warm-up period, tracking after the up/down-method (see below) was initiated and continued to the end of the session. Otherwise, the session was terminated and no data collected nor any reward given that day. The attenuator steps were held constant within any session, but 2, 3 and 4 dB steps were used.

Simulator principle. The echolocation sounds emitted by the bats during the detection task were intercepted by a microphone, amplified and returned by a loudspeaker. The bats thus received an echo which was very much like their own cry, with a delay determined by the relative positions of the bat, the microphone and the loudspeaker. The sound level was determined by the overall gain (including transmission losses) and the cry amplitude, the latter being outside the experiment's control. Thus cry amplitudes had to be measured for each emitted sound in order to obtain the actual signal level. Sound pressure levels are stated in dB peSPL defined as the root mean square sound pressure level of a continuous pure tone having the same amplitude as the transient (Stapells et al. 1982). A similar setup was used in range discrimination experiments by Simmons (1973, 1979, 1980). The present simulator differs from those previously used mainly by having one channel only.

Setup. The experiments were carried out in a 100 m^3 anechoic room (Kremer principle) with a reflection coefficient of less than 0.1 in the 500–100,000 Hz range. The ambient noise was measurable up to 4 kHz with a Brüel & Kjaer (B & K) 4179 1/1 inch microphone, a B & K 2660 preamplifier, and a B & K 2112 spectrometer. The 1/1 octave levels had a slope of −20 dB/decade, passing the 20 μPa level (0 dB SPL) near 3 kHz.

As shown in Fig. 1 the signal from the microphone is passed via a signal-catch trial switch to an amplifier/bandpass filter combination open from 10 to 150 kHz, and followed by a digital attenuator. This device is controlled by a computer according to the up/down method, which require the gain (and hence the signal level) in the trial following a hit to be decreased by one step, while a miss causes an increase. The outcome of catch trials is not affecting the gain. Finally the signal is passed to a power amplifier/loudspeaker combination.

The frequency response of the setup was flat (±3 dB) in the 30–120 kHz range.

In the masking experiments, white noise at a constant level was added to the signal before the power amplifier. Thus the noise level was constant throughout a session and independent of signal attenuation. To ensure that the system noise was as close as possible to being the same in both trial and catch trial situations, an acoustically blocked, 'dummy' microphone-preamplifier combination, identical with the cry intercepting unit, served as input for the signal path during catch trial. The system noise was measured with a B & K 2010 heterodyne analyzer (1,000 Hz bandwidth) and a B & K 2305 level recorder.

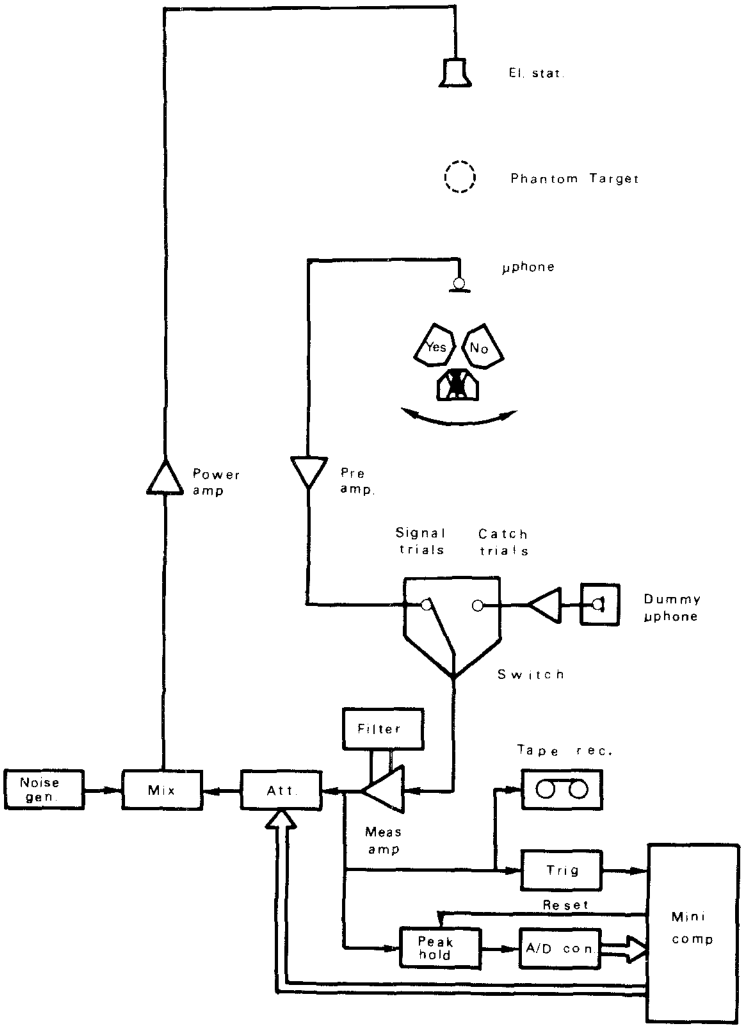

Fig. 1. Diagram of the target simulator. The bats cries are intercepted by the microphone, passed through gain controlling circuitry and returned by the loudspeaker. Peak amplitude of each cry is logged by the computer, which also controls the gain control according to the up/down logic. *A/D-con* analog to digital converter, 8 bit; *Att* digitally controlled step attenuator, accuracy better than 0.5 dB; *Dummy µphone* acoustically blocked B & K 4135, 1/4 inch condenser microphone, followed by a B & K 2619 preamplifier; *El. stat* electrostatic speaker; *Filter* Krohn-Hite 3550 band pass filter, 10–150 kHz, 24 dB/oct; *Meas. amp* B & K 2606, measuring amplifier; *µphone* B & K 4135, 1/4 inch condenser microphone without grid, near normal to sound direction; *Minicomp* NOVA 1200 minicomputer; *Mix* passive, resistive mixer for noise and signal; *No* 'Target absent' platform; *Noise gen.* B & K 1405 noise generator; *Peak hold* B & K 2425 voltmeter; *Power amp.* driver for electrostatic speaker; *Pre. amp.* B & K 2619 preamplifier; *Switch* B & K 2807 two channel microphone power supply and line driver; *Tape rec.* Racal Store-7-D (30 ips, −3 dB at 150 kHz); *Trig* trigger facility on Tektronix 5100 oscilloscope; *Yes* 'Target present' platform

In the 1–150 kHz range it amounted to a spectrum level of −48 dB SPL. The masking noise level for each session was measured in the 1/1 octave around 63 kHz with a B & K 1614 band pass filter set and a B & K 2608 measuring amplifier.

The peak pressure of each cry was obtained by a peakmeter in peakhold mode, which passed a DC-signal proportional to the peak amplitude to an A/D-converter. The reading was stored in a computer and the peakmeter reset after each cry. The dynamic range of this peakmeter-A/D-converter combination was 20 dB. This system operated satisfactorily up to 50 pulses/s, well above the repetition rate in the probing phase of the bats. The overall reliability of the peak reading measurements was checked by comparing it with conventional storage-oscillography of tape recorded cries played back one pulse at a time at slow speed. No difference beyond measuring accuracy (1 dB) was found in 3 recorded sessions. Tape recordings were also used to examine the duration of the cries and to supply time series for spectrum analysis. The microphones were calibrated by a B & K Sound Level Calibrator, type 4230.

A recording of the sound field near the bat was carried out by placing a B & K 4135 1/4 inch condenser microphone immediately behind the observation platform, in line with the loudspeaker and the bat. The microphone passed the signal to a B & K 2608 measuring amplifier with a Krohn-Hite filter (band pass 10–150 kHz) and the signal was then recorded. From this recording the intensity of real echoes from the setup ('clutter') was estimated. The loudspeaker clearly was the main source of clutter.

The loudspeaker used was an electrostatic speaker of the Kuhl et al. (1954) type with fixed dielectricum, 75 mm in diameter and provided with a cap of polyurethane foam 7 cm thick to reduce clutter. In the experiment with bat E3 for studying clutter (Tables 1 and 2, lower lines), the loudspeaker was changed to a similar loudspeaker 15 mm in diameter and without cap. The target strength of the loudspeakers was determined with 0.5 ms pulses of 30 kHz sinewaves (using that $TS = RL + 2TL - SL$, RL being the level of the reverberated signal or clutter (C), see eq. 1). All sound pressures are referred to a distance of 0.1 m.

The distance from the edge of the observation platform (the average position of the head of the bats during trials) to the microphone and to the loudspeaker was 22 cm and 88 cm, respectively. This results in a delay of the signal of 3.2 ms, corresponding to a target distance of 55 cm.

Psychophysics. The up/down method requires that following a hit the overall gain is decreased, while a miss has the opposite effect. The system only allowed for control of overall gain. Since the signal level is the sum of the gain and the cry level, the bat could to a certain degree blur the effect of the up/down

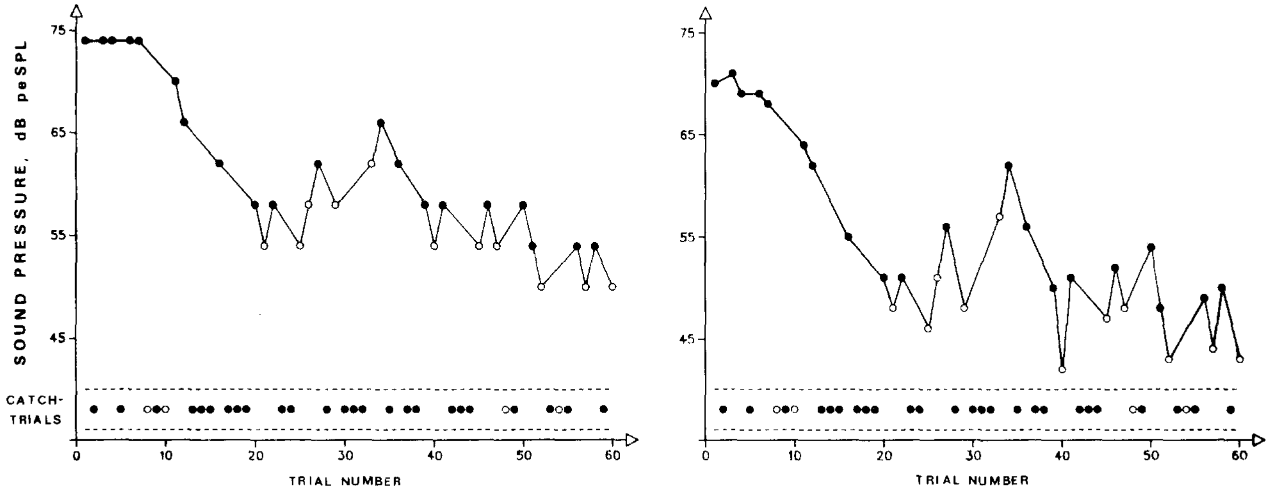

Fig. 2. A session for bat E1 in the unmasked experiment, raw data (left), and cry level corrected data (right). Closed circles signify correct, open circles incorrect response. For the raw data a constant cry source level of 104 dB peSPL in 0.1 m is assumed. This graph shows how gain is changed during a session. The figure on the right shows the data after taking into account the bat's actual cry intensity

scheme by changing the cry level. However, several hits or misses in a row would change the gain considerably and consequently the signal level.

Only sessions in which the false alarm rate was less than 25% are used in the threshold determination. Such sessions constitute 90% of the total number of sessions. The signal level at the bats position in any given trial is operationally defined as the mean of the three most powerful signals for that trial. As the number of trials at each signal level is often less than 10, the computed signal levels from all sessions of a given experiment (here defined as a series of sessions with the same detection problem for the same bat) were grouped in classes spanning signal levels of 3 dB. At the extremes of the distribution very few observations were obtained, and the class width increased accordingly. The data were treated as constant stimuli data (Guilford 1954). The reason for doing this is that the conventional up/down strategy breaks down, when the bat's cry level is not stable from trial to trial. The probability of detection is calculated as the number of 'hits' in a class divided by the total number of trials in that class. Thus, the psychometry is a hybrid between the up/down-method and the constant stimuli method.

Since thresholds inherently are of a stochastical nature they can be described only in a statistical way. The probability of detection in each class is transformed to the corresponding probits in a normal distribution with a mean at 5 and a standard deviation of 1, since constant stimuli data are assumed to be normally distributed (Swets et al. 1961). This is called 'probit analysis' (Guilford 1954; Finney 1971). The relation between the probits and their assorted signal level is established by linear regression. In essence, this method utilizes all the data in the estimation of the threshold, which is defined as the 50% correct detection level. Further it provides a measure of the standard deviation (SD), which is the slope of the regression line. The thresholds under ambient and added noise for each animal are tested pairwise for similarity using 'comparison between two lines of regression' (Blaesild 1985), which successively tests for equal variance, slope, and level of the two lines. The significance level for equal variance and slope was chosen to 10%. The assumption of normal distribution is only partly true because the requirement of identical variance in each class is not completely fulfilled. However, this error is negligible as the number of trials in each class is large.

Results

The bat's behavior in simulator

A trial was initiated with the bat sitting at the observation platform (Fig. 1) with its back to the microphone. When it had finished eating its reward from the previous trial it turned around and faced the microphone, emitting cries to detect presence or absence of the phantom target. After having made its decision it moved to the response platform to get its reward. While the bat was eating, the platform was rotated to bring the bat in proper position for the next trial. The simulator was turned off when the bat was eating.

During the trial the properties of the cries changed except for duration, which was around 3.2 ms. The number of pulses used by the bat per trial varied considerably, but 10–30 pulses were most commonly used. Pulses were distributed in a definite pattern. First 1–10 well separated (60 ms interval), intense (94–104 dB peSPL) cries, presumably detection cries, followed by 10–30 less intense (84–94 dB peSPL) cries, often in pairs, separated with about 30 ms within pairs. These cries we assume to be navigational, related to the crawling on the platforms and the localizing of the reward. This interpretation was supported by video recordings of the bat's movements during a few sessions. The video recordings also confirmed the experimenter's impression that only a few, one to five,

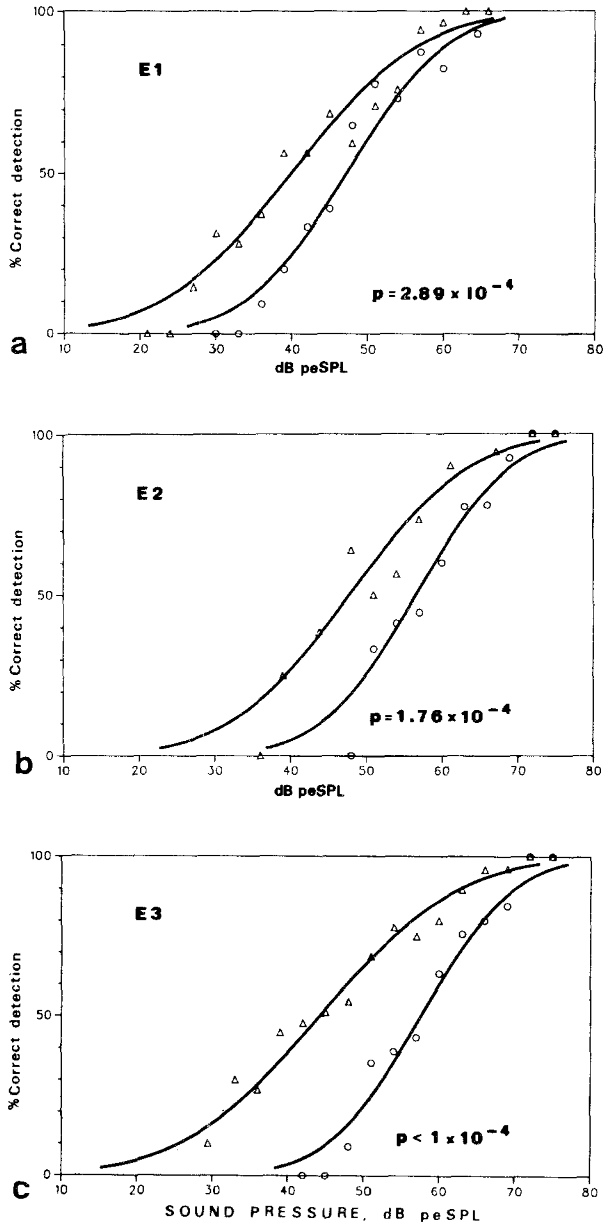

Fig. 3A–C. Performance of three bats (E1, E2, E3) in the target detection experiment under conditions of ambient (triangles) and added noise (open circles). p is the probability that the added noise has no masking effect

cries seem to be used before the bat started to move towards the response platform.

Thresholds

Primary data from a session from an unmasked experiment are shown in Fig. 2. Figure 3a, b and c shows the performance of the 3 bats during target detection under conditions of ambient and added noise. The likelihood that noise has no effect on the detectability is given in Fig. 3a–c.

The curves fitted to the observations in Fig. 3a–c correspond to the transformed lines obtained by probit analysis. Table 1 summarizes the results of all the experiments. The correlation coefficient is a measure of the acceptability of the assumption that the psychometric function is normally distributed. The precision of the thresholds can be estimated by dividing the SD with the square root of the number of trials (SE). The SE for all experiments is close to 1 dB.

S/N-ratios

In order to determine the S/N ratio, the energy of the phantom echo and the noise must be known. An estimate of signal energy was obtained by integrating instantaneous pressure squared over the duration of a selected, typical cry from the probing phase of bat E1 (Fig. 4). The energy of other cries was assumed to differ proportionally to amplitude only. The relationship established was that a signal with an amplitude of 1 Pa (=94 dB peSPL) had an energy of −30 dB re 1 $\mathrm{Pa}^2 \cdot \mathrm{s}$. Doubling or halving the duration changes this figure by 3 dB. At threshold, the energy, S, of a signal (Fig. 4) with a pressure of 47 dB peSPL for bat E1 is derived as:

$$S = 47 - 94 - 30 = -77 \text{ dB re } 1\ \mathrm{Pa}^2 \cdot \mathrm{s}.$$

(where −94 is the conversion figure from SPL to Pascal and −30 is the above mentioned conversion

Table 1. Psychophysical data for all 3 bats under ambient (S) and added noise (S+N) conditions

Loudsp Dim	Bat	Condition	Threshold 50% dB peSPL	SD dB	No of Signal-trials	Corr coef	N_0 dB re 1 $\mathrm{Pa} \cdot \mathrm{Hz}^{-1/2}$	S/N_0 dB	S/N_{bw} dB	correct reject
75 mm	E1	S	40	13.4	437	0.958				85
+cap		S+N	47	10.5	165	0.965	−19	36	−8	93
	E2	S	48	12.6	403	0.956				85
		S+N	57	10.0	93	0.974	−22	49	5	84
	E3	S	44	14.4	523	0.981				84
		S+N	58	9.7	162	0.966	−19	47	3	85
15 mm	E3	S	24	10.8	149	0.870				86

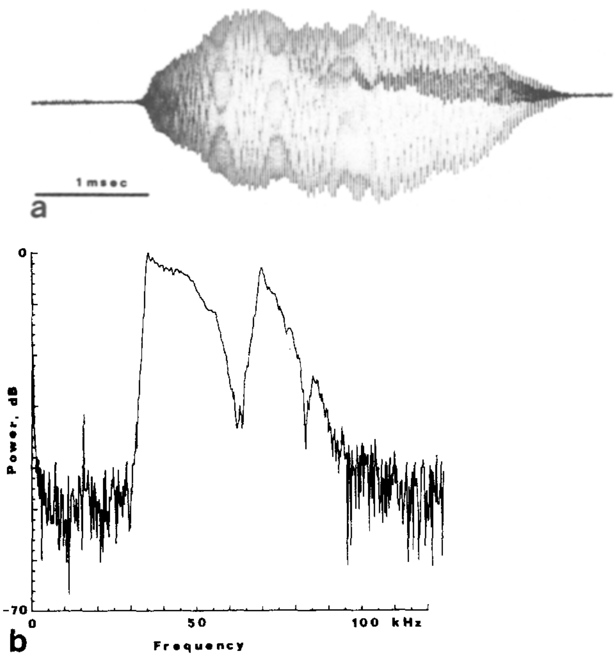

Fig. 4A, B. Detection cry. **A** Oscillogram. **B** Power spectrum (FFT)

figure from pressure to energy units for a typical cry). Noise is measured in a specified bandwidth and converted to the equivalent power density in 1 Hz bandwidth, N_o. The noise power density of -19 dB SPL (Table 1, E1) converts to:

$N_o = -19 - 94 = -113$ dB re 1 Pa$\cdot$Hz$^{-1/2}$.

Thus, the signal to noise ratio is: $S/N_o = -77 - (-113) = 36$ dB. A widely used model for the auditory system of mammals is that of a bank of filters, followed by a square law detector (Urick 1975). In such a receiver the noise will interfere with the receiver in a bandwidth approximately equal to the bandwidth of the signal.

The -10 dB bandwidth of the cry in Fig. 4 is 25 kHz (35–60 kHz). The power of the noise received in this bandwidth is:

$N_{bw} = -113 + 10 \cdot \log(25{,}000) = -69$ dB re 1 Pa$\cdot$Hz$^{-1/2}$ and the S/N ratio is then: $S/N_{bw} = -77 - (-69) = -8$ dB. The S/N-ratios for the other bats are computed likewise. Table 2 shows the level of the cries used by the bats for target detection at threshold, together with the calculated levels of clutter from the two loudspeakers. The measured target strength of the loudspeakers are within 3 dB of predicted values for circular, planar targets (Urick 75).

Discussion

Methodology

The psychometric method used (a modified up/down, yes/no or Y/N, hybridized with the method of constant stimuli) differ from standard practice in bat sonar detection experiments, which largely can be classified as wire avoidance or as right/left, two alternative forced choice techniques (2AFC). When thresholds, rather than psychometric functions are sought, Y/N techniques tend to be more efficient, since most of the trials are either just above or just below the threshold. The use of catch trials is a consequence of the Y/N logic. They provide information on the nature of the criterion (strict or lax) used by the bat in the decision process, and allow estimates on the perceived difficulty ('perceived S/N') of the detection task. Further, this technique provides estimates on the precision of the threshold determinations as required for tests on the significance of threshold shifts. Thresholds obtained by a Y/N paradigm tends to be higher than those obtained by 2AFC methods (Swets et al. 1961).

Inherent properties of target simulation in masking experiments solve some technical problems but create others. Among the advantages is the complete elimination of directionality effects, the control of noise and echo level, a defined geo-

Table 2. Signal to clutter ratios (S/C) at the various experimental conditions. The average cry level at 0.1 m emitted by the bats under ambient (S) and added noise (S+N) conditions. TS is the target strength of the loudspeaker at 30 kHz. Thresholds from Table 1

Loudsp dim	Bat Nr	Stim type	Cry level dB peSPL	TS dB	Threshold dB peSPL	Clutter dB SPL	S/C dB
75 mm	E1	S	98	4	40	64	−24
+cap		S+N	102	4	47	68	−21
	E2	S	105	4	48	71	−23
		S+N	113	4	57	79	−22
	E3	S	102	4	44	68	−24
		S+N	111	4	58	77	−19
15 mm	E3	S	104	−14	24	52	−28

metry, and the fact that no visual cues are present. Disadvantages are the clutter from the loudspeaker which is hard to avoid and a limited dynamic range. A course of concern is whether the 'purification' of the measuring situation has made it unrealistic for the bat's sonar system. We have found no way to test this question.

The S/N ratio at threshold

The thresholds in the masked experiment were 7 to 14 dB above the unmasked thresholds. This rise is statistically significant at the 10% level. This implies that the masked thresholds are indeed set by the added white noise since all other parameters are held constant. Thus, the S/N ratio for noise limited thresholds can be calculated.

For a transient signal and a coherent receiver, the signal term should be given as a measure of energy flux density and the noise term simply as its spectrum level, N_0 (Urick 1975). Accordingly, the S/N_0 ratios at the masked thresholds of bat's E1 to E3 averaged 44 dB (Table 1). The detectability index (d) is 3 dB higher ($d = 2 \times S/N_0$, Urick 1975). The latter values can be compared directly with theoretically obtained values from receiver operating characteristic curves (ROC) (Altes 1984) using the false alarm rates against detection probability (Table 1). This results in detectability indices of 2 dB, 1 dB and 1 dB, respectively. Thus, the measured S/N ratio at threshold is roughly 40 to 50 dB higher than required by an ideal coherent receiver at the same performance in terms of hits and false alarms. Hence, our results do not indicate coherent reception.

If, instead, the bats' auditory system detects broad band signals masked by noise as does the auditory system of man (Jeffress 1970) the noise will interfere with the signal (echo) in a frequency range approximately equal to the bandwidth of the signal. Calculated this way the signal to noise ratios, S/N_{bw} at threshold were -8 dB, 4 dB and 3 dB, respectively, for our bats. This is within an order of magnitude of the estimates using the ROC-technique. Therefore our data do not indicate detection processes in the serotine bat's auditory system which in principle differ from that of other mammals, including echolocating dolphins, where Au and Snyder (1980) found a S/N_{bw} of 3.8 dB.

The above discussion is based on the assumption that only a single pulse is used for detection. However, the bats emit a train of pulses. Inspections of video- and tape-recordings of the bats in the simulator gave the impression that less than 10 pulses were used for detection. Knowledge of integration time and number of pulses used might alter the estimate of the S/N ratio. However, this effect is probably of minor importance, rule of thumb from sonar is an improvement in S/N of $5 \cdot \log$ (number of pulses) (Urick 1975). Estimations of the effects of integration over several pulses and of noise in the time between the pulses are sensitive to assumptions about integration time, which is presently unknown. Values from humans range from a few to 300 ms, dependent on the detection task (Yost 1980). An evaluation of the effect of integration was not attempted.

Previous estimates of the S/N_0 ratio for bats at detection threshold have been obtained in a wire avoidance experiment (Griffin et al. 1963). They reported that *Plecotus* makes detections rather successfully at a S/N_0 of -5 dB at 30 kHz with a false alarm rate of 0.01%. In theory, this is not possible. However, they observed that the bats always approached the wires in an angle relative to the incidence of the noise, and raised the estimate of S/N_0 to 10 dB and possibly more, due to directionality of hearing as required by detection theory. This adjustment was justified by the nature and number of assumptions needed to calculate the effective S/N at the bat's ear at the moment of detection of the wires. The present experiment yields values about 35 dB higher. Here, the S/N is measured directly (barring the assumption of a fixed conversion ratio between measured peak amplitude and pulse energy). To wich extent the difference of 35 dB between the results of the wire avoidance experiment and the present experiment can be explained by differences in methods, including differences in the bat's task in the two experiments, is not evident.

An experiment by Simmons et al. (1978) on range discrimination of planar targets in noise by *Eptesicus fuscus*, gave 75% correct performance at a target range difference of 2 cm. Taking into account the target strength of the plates and their distance from the bat, and assuming a source level of 109 dB (10 cm) we estimate a S/N_0 ratio of about 60 dB. In that experiment signals and noise come from separate sources, so the bats may have some advantage of the directionality of their sonar system (Kick and Simmons 1984). This tends to increase the estimate of the effective S/N_0 beyond the 60 dB given above, the implication being that target ranging requires a considerably higher S/N ratio than does target detection.

The presently obtained masked thresholds and S/N ratios are in general agreement with results from an experiment with a *Pipistrellus pipistrellus* obtained in a different target simulator (Møhl 1986). In that study, the bats' cries triggered the playback of a previously recorded, stored echolocation signal, while in our experiment the actual bat cry is retransmitted directly. The S/N_0 values in the present work tend to be somewhat lower than the S/N_0 of 50 dB for the pipistrelle bat, possibly reflecting the larger bandwidth of the echolocation pulses of that species. The expected difference from the bandwidth effect is 4 dB which brings the pipistrelle result within the range of the *Eptesicus* data reported here. This indicates that the two principally different implementations of the target simulator produce compatible results.

Clutter

The added noise was in the order of 30 dB above system noise in the unmasked situation. Since the threshold was raised by about 10 dB only, it follows that the threshold in the unmasked experiment was set by either internal noise in the bat's auditory system, or interfering echoes from the equipment, i.e. clutter, external acoustical noise being much lower than system noise. Internal noise is contra-indicated by reference to the work of Kick (1982), who obtained detection thresholds 40 to 50 dB below our results in a clutter and noise free environment. A number of observations makes it likely that clutter limits the thresholds in our unmasked experiments:

1. The planar surface of the electrostatic speaker did indeed produce a specular reflection of the bat's cry (trailing the transmitted signal by 2 ms, but with a level some 20 dB above that of the projected signal at threshold amplitude).
2. While the individual thresholds of the three bats in terms of peSPL were significantly different from each other, the S/C ratio at threshold were not (Table 2).
3. When a phantom target detection threshold was obtained using a smaller loudspeaker, the threshold decreased proportionally to the target strength of the clutter (20 and 18 dB, respectively).
4. The threshold seems to be correlated to the average cry level (Table 2).

With regard to this point it is observed that in a target simulator of the present type, clutter level and signal level are decoupled. Signal level is the sum of cry level and system gain which means that a certain level can be obtained by low cry level and high amplification and by high cry level and low amplification. The perceived signal level will be the same in the two situations whereas the clutter level would be low in the first and high in the second situation. It appears as if bat E1 tried to maximize its profits by exploiting this peculiarity of the experimental design by reducing its output. The lower thresholds of E1 compared to E2 and E3 may reflect her generally lower cry levels.

An intriguing question is how clutter can possibly be a limiting factor in the present detection experiment, when the clutter is delayed by about 2 ms relative to the phantom target. This is two orders of magnitude above range determination and 4 orders of magnitude above range resolution for this type of bat sonar (Simmons 1971, 1979). Both of these ranging results have been interpreted to indicate different kinds of optimal receiver properties in bats. This interpretation has been challenged on theoretical grounds by Schnitzler and Henson (1980) and Menne and Hackbarth (1986). Simmons' results were obtained under highly favourable S/N conditions. However, the advantage of using an ideal receiver is manifest only at limiting conditions (poor S/N or S/C ratio). Our results, obtained under such conditions, do not indicate ideal receiver operations.

Acknowledgements. We thank A. Surlykke and L.A. Miller for discussions and comments and C.D. Pedersen for statistical assistance. This work is supported by the Danish Natural Science Research Council and by the Carlsberg Foundation.

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