

CORRECTION

Echolocating Daubenton’s bats are resilient to broadband, ultrasonic masking noise during active target approaches

Ilias Foskolos, Michael Bjerre Pedersen, Kristian Beedholm, Astrid Særmark Uebel, Jamie Macaulay, Laura Stidsholt, Signe Brinkløv and Peter Teglberg Madsen

There was an error in *J. Exp. Biol.* (2022) 225, jeb242957 (doi:10.1242/jeb.242957). In Fig. 5, the left y-axis label was incorrect; the right y-axis label was missing. The corrected and original figure are shown below; both the online full-text and pdf versions have been corrected.

The authors apologise to readers for this error.

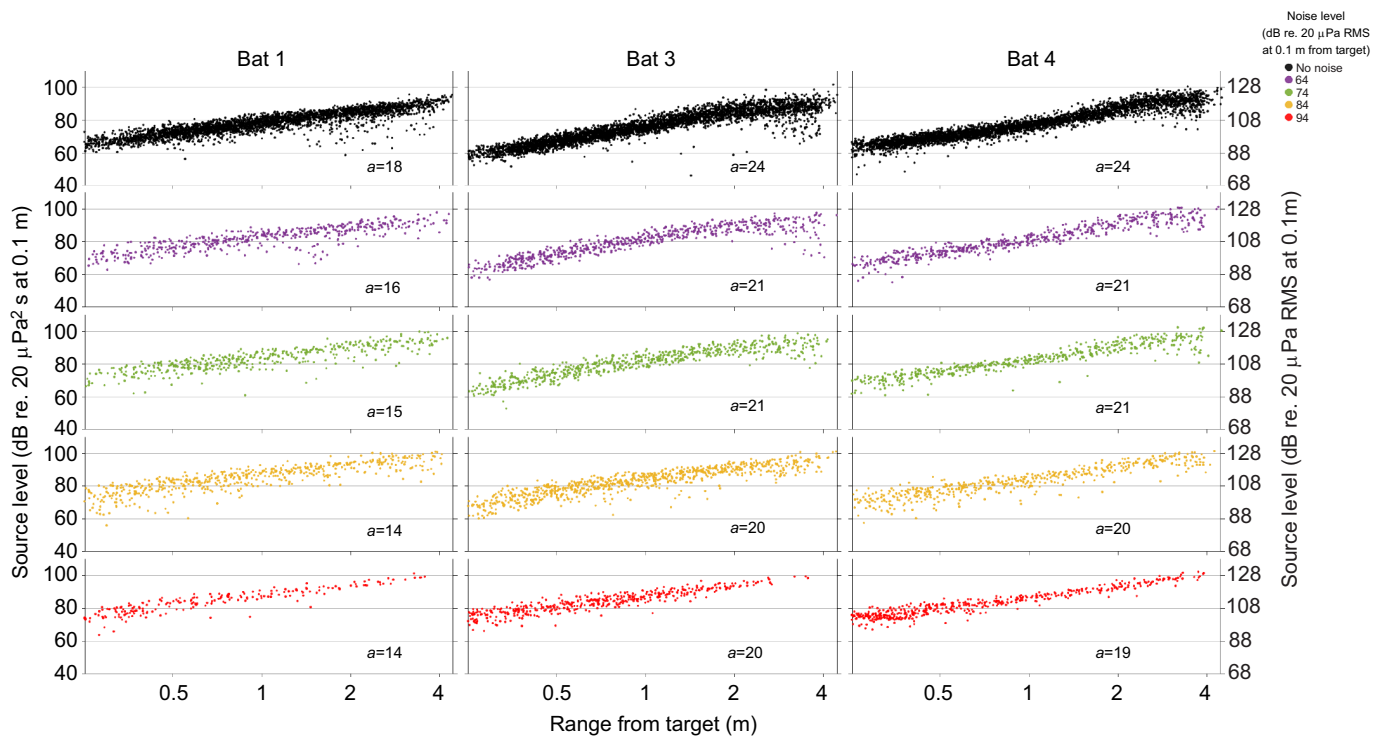


Fig. 5 (corrected). Rate of SL reduction with range to target for the different noise treatments and bats. SL (left y-axis: dB re. 20 μPa² s at 0.1 m, right y-axis: dB re. 20 μPa RMS at 0.1 m) of all the calls from successful trials is shown for bats 1, 3 and 4. *a*, rate of compensation with the decimal logarithm of range. *n*=17,408 calls.

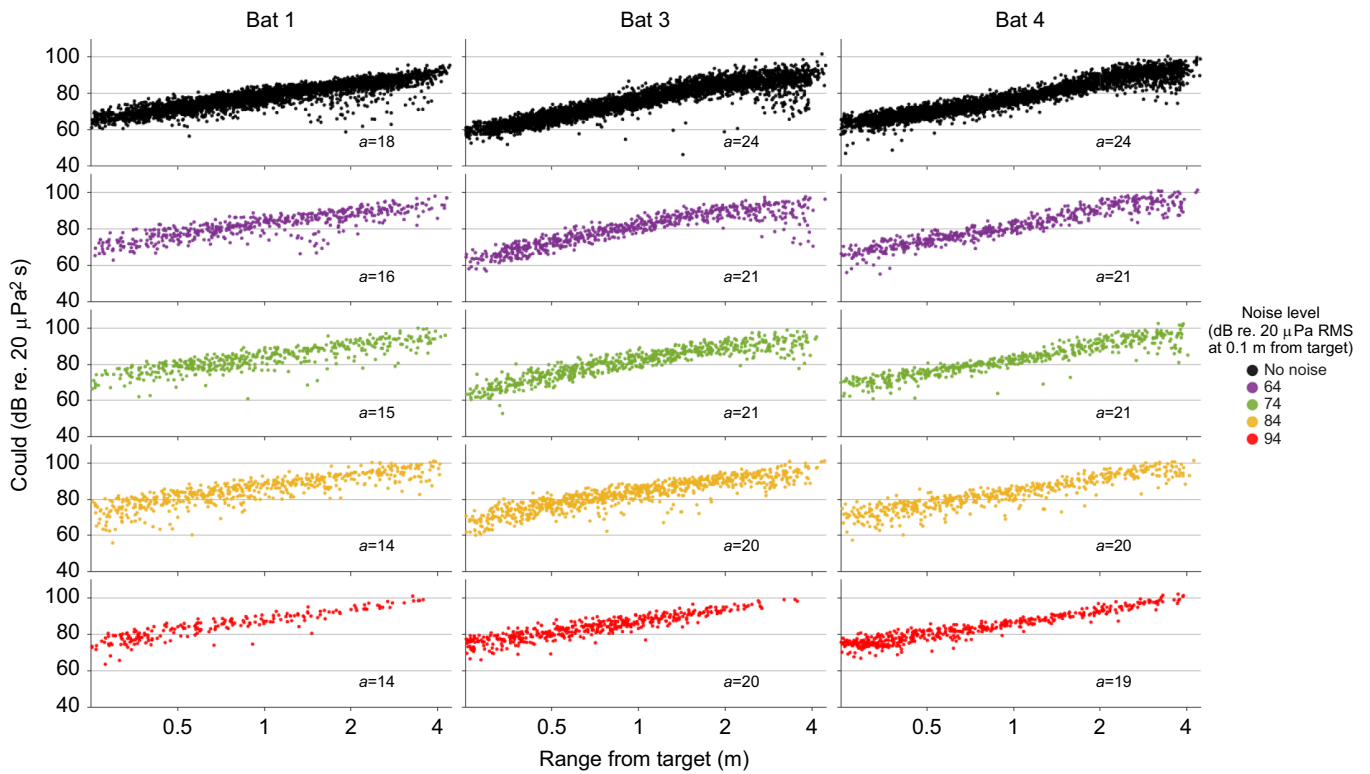


Fig. 5 (original). Rate of SL reduction with range to target for the different noise treatments and bats. SL (left y-axis: dB re. $20 \mu\text{Pa}^2 \text{ s}$ at 0.1 m, right y-axis: dB re. $20 \mu\text{Pa}$ RMS at 0.1 m) of all the calls from successful trials is shown for bats 1, 3 and 4. a , rate of compensation with the decimal logarithm of range. $n=17,408$ calls.

RESEARCH ARTICLE

Echolocating Daubenton's bats are resilient to broadband, ultrasonic masking noise during active target approaches

Ilias Foskolos^{1,*}, Michael Bjerre Pedersen¹, Kristian Beedholm¹, Astrid Særmark Uebel¹, Jamie Macaulay¹, Laura Stidsholt¹, Signe Brinkløv^{1,2} and Peter Teglberg Madsen^{1,3}

ABSTRACT

Echolocating bats hunt prey on the wing under conditions of poor lighting by emission of loud calls and subsequent auditory processing of weak returning echoes. To do so, they need adequate echo-to-noise ratios (ENRs) to detect and distinguish target echoes from masking noise. Early obstacle avoidance experiments report high resilience to masking in free-flying bats, but whether this is due to spectral or spatiotemporal release from masking, advanced auditory signal detection or an increase in call amplitude (Lombard effect) remains unresolved. We hypothesized that bats with no spectral, spatial or temporal release from masking noise defend a certain ENR via a Lombard effect. We trained four bats (*Myotis daubentonii*) to approach and land on a target that broadcasted broadband noise at four different levels. An array of seven microphones enabled acoustic localization of the bats and source level estimation of their approach calls. Call duration and peak frequency did not change, but average call source levels (SL_{RMS} , at 0.1 m as dB re. 20 μ Pa) increased, from 112 dB in the no-noise treatment, to 118 dB (maximum 129 dB) at the maximum noise level of 94 dB re. 20 μ Pa root mean square. The magnitude of the Lombard effect was small (0.13 dB SL_{RMS} dB⁻¹ of noise), resulting in mean broadband and narrowband ENRs of -11 and 8 dB, respectively, at the highest noise level. Despite these poor ENRs, the bats still performed echo-guided landings, making us conclude that they are very resilient to masking even when they cannot avoid it spectrally, spatially or temporally.

KEY WORDS: Echolocation, Chiroptera, Biosonar, Acoustic Interference, Lombard effect, Echo-to-noise ratio

INTRODUCTION

Animals experience the world through their sensory systems. To do so, they use these systems to extract information from their surroundings, but this information may be masked by other, less relevant signals. Acoustic masking is defined as any acoustic interference from sources other than the signals of interest, with the capability of impairing the detection and processing of such signals, including mating calls and sounds from prey or predators (Brumm and Slabbekoorn, 2005). The many vital functions served by auditory detection and processing of pertinent acoustic information from the environment are likely to pose a strong selective pressure

for ways to alleviate masking effects (Gomes et al., 2021), such as directional hearing, increased call amplitude (i.e. Lombard effect) or call rate and change of call frequency (for reviews, see Hotchkiss and Parks, 2013; Zollinger and Brumm, 2011).

Echolocating bats rely on their ability to detect faint prey echoes and may be particularly sensitive to masking. Yet, a seminal study by Griffin et al. (1963) reported that free-flying bats in darkness could detect and avoid small wires in the presence of intense ultrasonic, masking noise. Whether this was due to advanced auditory processing or a heterogeneous noise field that allowed for spectral or spatial release from masking (Sümer et al., 2009) remains unresolved. Despite this apparent resilience to masking, several noise sources (e.g. insects, conspecifics and heterospecifics, rain and anthropogenic noise) have the potential to compromise the biosonar performance of bats (Luo et al., 2015a; Roverud and Grinnell, 1985; Troest and Møhl, 1986). Recent studies have sought to investigate how masking noise affects echolocating bats in the absence of spectral and temporal release from masking (Luo et al., 2015b; Simmons, 2017; Tressler and Smotherman, 2009). Under these conditions, bats mainly increase call amplitude, but they may also compensate by increasing call duration, call rate and signal bandwidth (Luo et al., 2015b; Simmons, 2017; Tressler and Smotherman, 2009).

In an echo delay experiment with stationed big brown bats *Eptesicus fuscus* on a Y-shaped platform, Simmons (2017) found that the bats would increase their call amplitude in increasing masking noise until a point where poorer echo-to-noise ratios (ENRs) eventually deteriorated correct delay estimation. However, no study has so far evaluated the actual ENR defended by echolocating bats during the more ecologically relevant scenario of biosonar-guided active flights towards a target. ENR is critical for quantifying the potential effects of noise and for understanding how echolocating bats may compensate for noise to solve tasks with echolocation (Griffin et al., 1963; Luo et al., 2018). The auditory system of bats may operate at a certain ENR threshold for a detection task and presumably even higher ones for the tasks of target discrimination and ranging. It follows that: (i) if the perceived ENR deteriorates towards this threshold, bats may seek to improve the ENR via compensatory mechanisms; and (ii) bats will increasingly fail to solve these tasks if the ENR drops, on a statistical basis, below this threshold. The active sonar equation (Au and Penner, 1981) is a useful framework to estimate ENRs when enough parameters are known (Au, 1993a; Urick, 1983). In this way, it is possible to properly assess how bats adjust their biosonar when there is no spectral, spatial and temporal release from masking noise. Despite this, the equation is rarely used in bat literature with regards to masking noise (but see Møhl, 1988; Troest and Møhl, 1986).

To evaluate how echolocating Daubenton's bats (*Myotis daubentonii*) perform during an active landing task in noise-limited conditions, we designed an experimental setup that provided

¹Zoophysiology, Department of Biology, Aarhus University, 8000 Aarhus, Denmark. ²Department of Ecoscience - Wildlife Ecology, Aarhus University, 8410 Rønde, Denmark. ³Aarhus Institute of Advanced Studies, Aarhus University, 8000 Aarhus, Denmark.

*Author for correspondence (ilias.foskolos@bio.au.dk)

© I.F., 0000-0003-1951-9382; K.B., 0000-0001-5699-0849; J.M., 0000-0003-1309-4889; L.S., 0000-0002-2187-7835; P.T.M., 0000-0002-5208-5259

List of abbreviations

a	frequency-specific absorption loss constant
ASL	apparent source level, the emitted level of the calls 0.1 m in front of the bat irrespective of the acoustic axis, estimated as ASL_{RMS} or ASL_{EFD}
ASL_{EFD}	energy flux density apparent source level
ASL_{RMS}	root mean square apparent source level
D	call duration, defined by the -10 dB endpoints of the amplitude envelope
DFT	discrete Fourier transform, for estimating the frequency content of a signal
EFD	energy flux density, the acoustic energy flow per unit area
EL	level of returning echoes, estimated as EL_{RMS} or EL_{EFD}
EL_{EFD}	energy flux density level of returning echo
EL_{RMS}	root mean square level of returning echo
ENR	echo-to-noise ratio, estimated as ENR_{BB} , $ENR_{1/3}$ and ENR_{NB}
$ENR_{1/3}$	echo-to-noise ratio for 1/3 octave around the call peak frequency
ENR_{BB}	broadband echo-to-noise ratio
ENR_{NB}	echo energy to noise spectral density ratio (narrowband)
IPI	interpulse interval, the time between the end and start of successive calls
LMM	linear mixed-effect models
NL_{RMS}	broadband noise level at 0.1 m from the transducer estimated as root mean square
R_a	range from bat to recording microphone above the target
R_t	range from bat to the target
RL	received level of the calls at the recording microphone
RMS	root mean square, a measure of the average acoustic intensity
RNL	the received noise level at 0.1 m in front of the bat, estimated as RNL_{BB} or $RNL_{1/3}$
$RNL_{1/3}$	received noise level for 1/3 octave around the call peak frequency
RNL_{BB}	broadband received noise level
SL	source level, the emitted acoustic intensity of the on-axis calls 0.1 m in front of the bat, estimated as SL_{RMS} , $SL_{1/3}$ and SL_{EFD}
$SL_{1/3}$	source level at 1/3 octave around the call peak frequency
SL_{RMS}	root mean square source level
SL_{EFD}	energy flux density source level
SNR	signal-to-noise ratio
TL	transmission loss due to spherical spreading and absorption
TS	target strength of the ensonified target, the difference between the received and reflected acoustic intensity 0.1 m in front of the target

complete spectral, spatial and temporal overlap between the noise and echolocation calls, while offering measures of ENR for each call–echo pair. With the help of this setup, we tested the hypothesis that bats either defend a certain ENR threshold in masking noise by increasing their call amplitude or fail to solve the task. This was achieved by training Daubenton's bats to approach and land on a spherical hydrophone target that also acted as an omnidirectional sound source emitting broadband, ultrasonic noise. We show that the bats exhibited the Lombard effect to produce call source levels (SL) on a par with the highest SLs reported in the wild for their species. Despite this compensatory mechanism, the highest noise levels led to very poor ENRs, but the bats were nevertheless still able to solve the task, demonstrating their resilience to masking noise even in the absence of spectral, spatial or temporal release from it.

MATERIALS AND METHODS

Laboratory animals

We trained four adult males (bats 1–4, mean mass 8.1 g) of the trawling, insectivorous bat *Myotis daubentonii* (Kuhl 1819). The

bats were caught with mist nets over a stream in Odense, Denmark, and kept in temporary captivity at the bat facility of the Department of Biology at Aarhus University (12 h day/night cycle, 55% relative humidity and 20°C). They had continuous access to water and were kept on a diet of live mealworms (larvae of *Tenebrio molitor*), supplemented with vitamin paste (Nutri-cal Tomlyn, Fort Worth, TX, USA). They were allowed to fly and trawl mealworms from an indoor pond once a week during the captive period (5 months). At the end of this period, they were released back into the wild at the site of capture.

All experiments were approved by the Danish authorities (capture permit: MST-850-0064, issued by The Danish Nature Agency; permit to keep animals and conduct laboratory experiments: 2016-15-0201-00989, issued by The Animal Experiments Inspectorate).

Experimental setup

Over a 3 week training period, we trained the bats through positive reinforcement of natural behaviors to fly and land on a spherical hydrophone target [hereafter termed 'target'; HS26, Sonar Research and Development, Amersham, UK; 80 mm diameter, target strength (TS) -15 dB at 0.1 m] that was located at a height of 1.2 m and centered at the back end of an anechoic room ($5 \times 4 \times 2.5$ m; Fig. 1A). The room was lined with 0.15 m deep acoustic foam (-30 dB reflectivity re. hard wall at frequencies >10 kHz). The target was covered with a tight piece of black cloth to aid landing and was placed in front of a star-shaped array of six Knowles microphones (Fig. 1B; FG-3329, 2.6 mm diameter, Itasca, IL, USA) with an array aperture (maximum distance between any two microphones) of 0.6 m that was completely embedded in 0.15 m deep acoustic foam (Fig. 1B). We placed an extra Knowles microphone on the front surface of the target, 0.14 m in front of the array. To document the landing of bats and inform delivery of the bridging stimulus (a soft tongue click made by the handler) between the landing and a food reward, an infrared night vision camera mounted on the ceiling above the target was used to observe flight behavior (TV-IP310PI, Trendnet, Torrance, CA, USA). During the experiments, the room was kept dark, except for dim, red light from the computer screen at the recording station, which was oriented away from the target at the opposite end of the room. Although we cannot exclude the use of visual cues by the bats to aid the landing task, the small eye size and low visual acuity of Daubenton's bats (Cechetto et al., 2020; Eklöf et al., 2014) render this scenario unlikely.

The seven Knowles microphones were connected through a custom-built 30 dB amplifier with integrated band-pass filter (1-pole 1 kHz high-pass filter and 4-pole 100 kHz anti-alias filter, Aarhus University, Department of Biology Electronics Workshop) to A/D converter channels in a multipurpose USB device (USB-6356, National Instruments, Austin, TX, USA). The channels were sampled synchronously at a rate of 400 kHz per channel, with 16-bit resolution and a clipping level of 109 dB re. 20 μ Pa as calibrated relative to a 1/8 inch GRAS 40 DP microphone (GRAS Sound & Vibration, Holte, Denmark). The target transducer was connected to a 20 dB power amplifier (Marchand BE01 Piezo Transducer Amplifier, Rochester, NY, USA) outside the anechoic room. The transducer was either silent throughout a trial or generated one of four different levels of broadband noise [NL_{RMS} , 20–90 kHz, respectively 64, 74, 84 and 94 dB re. 20 μ Pa root mean square (RMS) at 0.1 m; Fig. 2A,B]. Noise emission from the same target that bats were trained to land on precluded any spatial release from masking. Recordings of bat calls (Fig. S1) and noise playbacks were

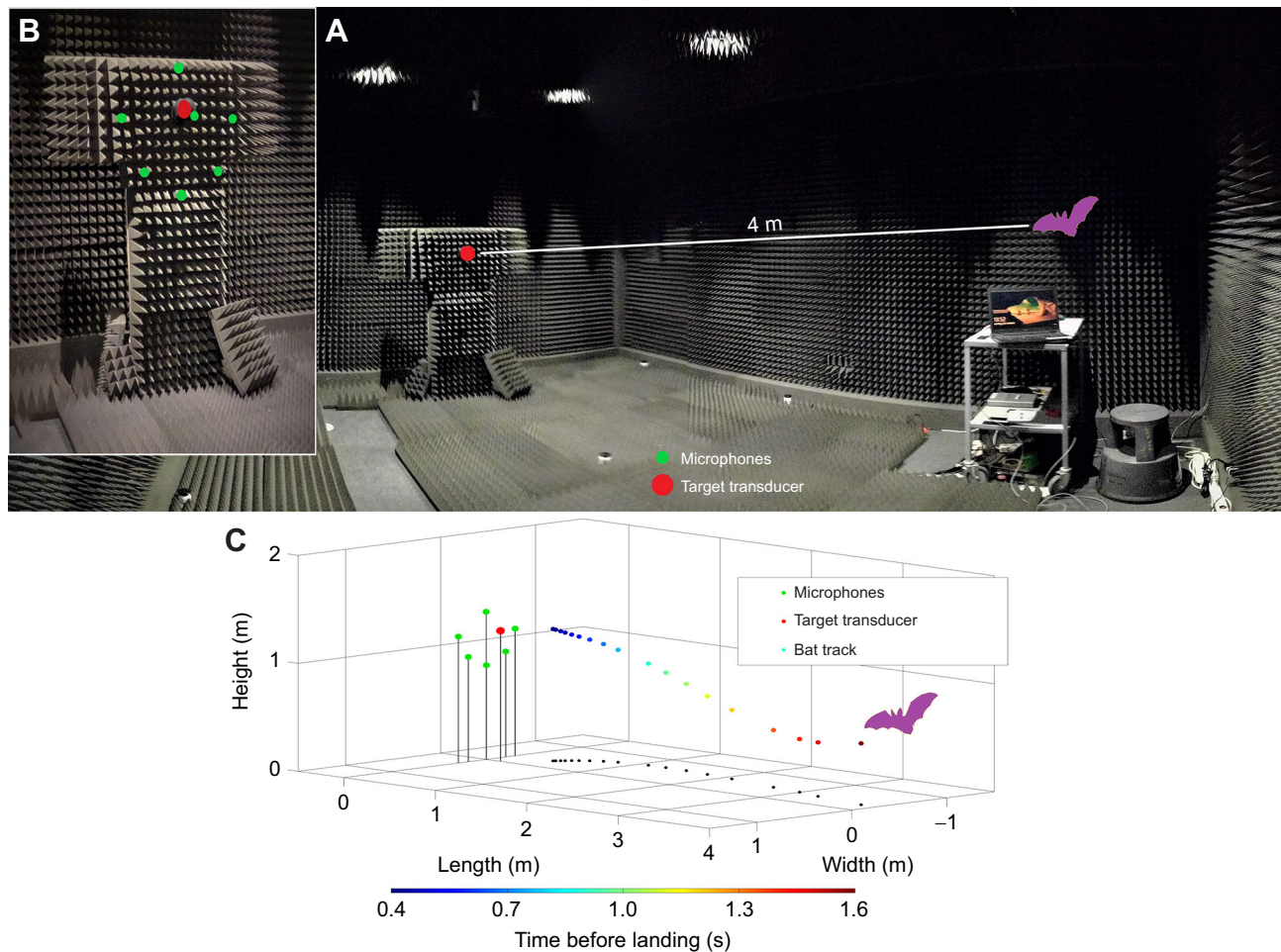


Fig. 1. The experimental setup used for the masking experiment. (A) The red circle (not to scale) indicates the noise-generating spherical transducer, where bats were trained to land. The bat (purple, not to scale) was released 4 m from the transducer. (B) Seven microphones (green) were embedded in the acoustic foam behind the target, along with one microphone on the target, to record the bat echolocation calls. (C) Example of a localization track (no-noise trial, bat 3) generated by the time of arrival differences for approach calls recorded by the microphone array. The localization points are projected onto the floor of the room with black dots to aid visualization. Note: buzz calls produced close to the target are not plotted.

controlled via a custom-written LabVIEW (National Instruments) program (K. Beedholm).

Training procedure

Training lasted for 3 weeks and took place in the same room and with the same setup as data collection. It followed a two-stage process where the staircase method (Levitt, 1970) was used to introduce the bats first to (i) the full distance to the target (i.e. 4 m) and then to (ii) the four different noise levels we used during the experiments. When bats could consistently fly the full distance and land on the target, we started at a level of 44 dB re. 20 μ Pa RMS at 0.1 m from the target and used 5 dB noise increments. The following criteria were used to maintain animal motivation: (i) a training session always started and ended with an easy trial (i.e. no noise from the target); and (ii) noise trials were interspersed with no-noise trials. Upon landing on the target, we used a soft tongue click to bridge each bat. Then, we could approach the bat and reward it with half a mealworm via a tweezer while it rested on the target. With the exception of bat 2, which refused to land at noise levels above 54 dB re. 20 μ Pa RMS at 0.1 m from the target, training was completed when a bat could land 90% of the time during trials of 94 dB re. 20 μ Pa RMS at 0.1 m from the target on a single day. Data collection for each bat started the day after training was considered complete.

Experimental protocol

We collected data 4 days per week for 2 weeks and all noise treatments were part of each session with one session carried out per day for each bat. Before each daily session, the trial combinations were mixed in the same way for all bats via a pseudo-random Gellermann schedule (Gellermann, 1933). The same criteria for animal motivation were used during data collection as during training, until three trials per noise treatment and session were completed (Table 1). Two researchers were present in the room during trials. One triggered the emission of noise and the recording of echolocation calls, while the other researcher, coordinated by a verbal cue, released a bat from a fixed spot 4 m from the target. During some trials (mostly with noise), the bats circled the room several times while attempting to approach the target and land. We defined trials as successful if the bat had landed on the target within 50 s from release. The first researcher used the landing event to deliver the bridging stimulus while the second researcher terminated noise emission and sound recording via the LabVIEW program interface. During the trial, a digital switch was used to mark in the recording the time from release to completion of the landing task. At the end of a successful trial, the bat was rewarded with half a mealworm and retrieved from the target. During unsuccessful trials, in which bats did not land on the target but kept circling the room in

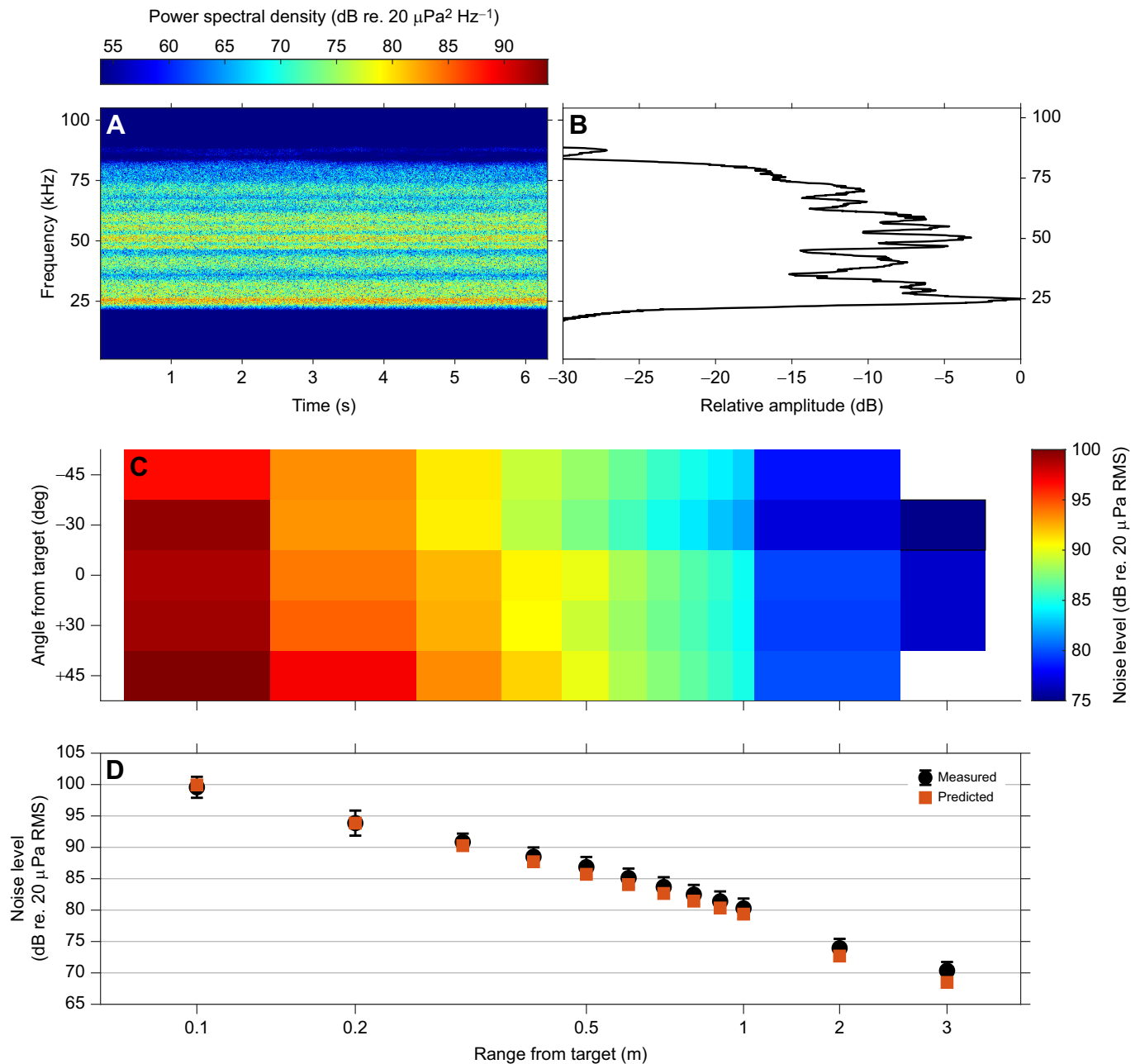


Fig. 2. Noise field of the experimental setup. (A) Spectrogram of emitted noise as recorded at 0.1 m from the target with a 1/8 inch GRAS microphone [400 kHz sampling rate, discrete Fourier transform (DFT) size 4000 points, Hamming window, 50% overlap, frequency resolution 0.1 kHz, time resolution 200 μs]. (B) Relative power spectrum of the same noise recording (400 kHz sampling rate, DFT size 4000 points, frequency resolution 100 Hz). (C) A noise level of 100 dB re. 20 μPa root mean square (RMS) at 0.1 m from the target was emitted and then measured at different distances and angles from the target. (D) The noise level was also predicted after assuming losses due to spherical spreading and absorption.

flight, the continuous noise exposure was halted after 50 s and the bats were not rewarded.

Localization and estimation of call parameters

For each successful trial, we used the PAMGuard click detector module (v. 2.01.03) (Gillespie et al., 2008) to detect and calculate time delay measurements via cross-correlation for all calls detected on a minimum of four microphones. A manual analyst marked all the calls belonging to the last approach phase that ended in landing. The approach phase was readily identifiable because it consisted of ca. 20 calls with sequentially decreasing range to the target that always preceded the single buzz produced during the trial. The

selected call waveforms and their associated metadata (e.g. time delay measurements) were then imported into MATLAB 2020a (The Mathworks Inc., Natick, MA, USA) using the PAMGuard MATLAB library (<https://sourceforge.net/projects/pamguard/>). Based on the interpulse interval (IPI) between the end and start of two consecutive calls, any buzz calls (IPI < 15 ms) (Geberl et al., 2015) were removed from the dataset. We did not use data from unsuccessful trials as they mostly consisted of off-axis calls with low signal-to-noise ratio (SNR) whose call parameters could not be reliably estimated. Thus, we only computed apparent source level (ASL) and ENR from trials where the bats did in fact solve the task (89% of all trials; Table 1).

Table 1. Number of successful trials (i.e. where landing on target occurred) out of total number of trials for each bat and noise treatment

Noise level (dB re. 20 μ Pa RMS at 0.1 m from target)	Bat 1	Bat 2	Bat 3	Bat 4
No-noise	207/208	254/254	208/208	214/214
64	32/33	3/31	31/31	32/32
74	29/30	0/30	30/30	30/30
84	28/31	0/27	31/31	29/30
94	11/30	0/27	21/30	28/31

One successful trial of bat 4 for the no-noise treatment did not contain any usable localizations and was discarded from further analysis.

The three-dimensional location of the bats for each selected call was calculated via acoustic localization using the associated time delay measurements and a simplex minimization algorithm (Nelder and Mead, 1965; White et al., 2006). We did not use these locations to describe the flight behavior of the bats, as the homogeneity of the noise field (Fig. 2C) could not have allowed any spatial release from masking. Instead, these locations were used to estimate the range to the target. The ASL could then be calculated from received levels (RL). As the microphone on the target had a very low SNR during noise trials, the closest microphone to the target microphone (0.16 m above it) was used to measure the RL and calculate ASL. We did so both as (i) RMS within the call duration, D (ASL_{RMS}); and (ii) as energy flux density (EFD, ASL_{EFD}) since the D call duration differed by a factor of 2 during the course of a full approach to the target (Madsen and Wahlberg, 2007).

To back-calculate ASL from RL, we estimated transmission loss (TL) after assuming losses due to spherical spreading and absorption [i.e. $20\log_{10}(R_a) + aR_a$, where R_a is range (in m) from the bat to the microphone above the target and a is the frequency-dependent absorption loss constant]. Estimating the term aR requires computation of the power spectrum of each call [discrete Fourier transform (DFT) size: 4000 (bin width: 100 Hz)]. Because the spectral characteristics of calls are noise sensitive, noise was removed from these spectra as follows: (i) for each trial, the first 500 ms of the audio file from the microphone above the target were used to compute the noise power spectrum, which was smoothed with a 10-point (1 kHz) moving average; (ii) this spectrum was then subtracted (in linear units) from the power spectrum of each bat call. To evaluate absorption across all frequencies and not just at call peak frequency, we then computed an absorption estimate a for each frequency bin using the formula of Bass et al. (1995) and assuming an ambient temperature of 22°C and range R_a . By multiplying these linearized absorption estimates with the call spectrum, the absorption-corrected call spectrum was generated. The difference in area of the spectrum before and after correcting for absorption is then aR_a . The call spectrum after noise correction was also used to estimate the call peak frequency, as this reflects the spectrum as emitted by the bat.

The broadband noise level received by the bats' ears (RNL_{BB}) was estimated by assuming losses due to spherical spreading and absorption from the target. For absorption losses, we followed the same approach as for call TL and used the noise power spectrum as recorded at 1 m from the target with a 1/8 inch GRAS microphone.

With ASL_{RMS} , range to the target R_t , TS and RNL_{BB} available, the broadband ENR (ENR_{BB}) received by the bats' ears was

estimated from the active sonar equation (Au, 1993a; Urick, 1983):

$$ENR_{BB} = (ASL_{RMS} - 2TL + TS) - RNL_{BB}, \quad (1)$$

where TS is -15 dB, TL is the transmission loss between the bat and the target microphone [$20\log_{10}(R_t) + aR_t$ where R_t is range (in m) from the bat to the microphone on the target] and $(ASL_{RMS} - 2TL + TS)$ is the echo RMS level (EL_{RMS}). For no-noise trials, the RNL_{BB} was assumed to be equal to the putative echo detection threshold (i.e. 20 dB re. 20 μ Pa RMS) in vespertilionid bats (Stilz and Schnitzler, 2012).

For each successful trial, the five calls with the highest ASL_{RMS} were chosen (hereafter termed ' SL_{RMS} ') as they represented the closest to on-axis calls. Based on the mean peak frequency of these calls from all successful trials (i.e. 56 kHz, Fig. 3C), a 1/3 octave filter with this center frequency (4-pole Butterworth, cut-off frequencies: 50 and 63 kHz) was applied to filter both each call and the noise. We then estimated $SL_{1/3}$ and $RNL_{1/3}$ and used Eqn 1 to compute the 1/3 octave ENR around the peak frequency ($ENR_{1/3}$) for all noise treatments, except for the no-noise treatment.

For these treatments, the echo energy to noise spectral density ratio (hereafter termed 'narrowband' ENR, ENR_{NB}) was also calculated following Au and Penner (1981):

$$ENR_{NB} = (SL_{EFD} - 2TL + TS) - RN_0, \quad (2)$$

where $(SL_{EFD} - 2TL + TS)$ is the echo energy (EL_{EFD}) and RN_0 is the noise power per 1 Hz bin received at the bats' ears [$RN_0 = RNL_{BB} - 10\log_{10}(BW)$ with BW denoting the bandwidth of noise in Hz (i.e. 70 kHz)]. While calculating all three measures of ENR, we did not correct for the directivity of the bats' auditory system (DI_R), as the noise in our setup was transmitted from the exact same bearing as the target echo.

All signal processing analyses were performed with custom-written scripts in MATLAB 2020a.

Statistical modeling

During the statistical analysis, data from bat 2 were not used because it did not successfully complete 97% (112/115) of the noise trials (Table 1). For the three remaining bats and from the last approach phase of each successful trial, we created three datasets with the one, five and 10 loudest calls (SL_{RMS}) per trial to ensure a high SNR. These calls represented the loudest samples per trial for adequately quantifying the ENR required to solve the landing task in noisy conditions. Three linear mixed-effects models (LMMs) were then formulated to analyze how bats changed the: (i) SL_{RMS} , (ii) D call duration (hereafter termed 'call duration') and (iii) peak frequency of their calls with increasing noise level. Within-day and within-trial correlations in the response variables were treated with random intercepts, with trials nested within each day. As the number of bats used in this experiment was less than 10, animal ID was not treated as a random effect but was instead incorporated into the models as a categorical predictor (Supplementary Materials and Methods Eqns S1 and S2). To account for changes in SL_{RMS} with range to target, we introduced four logarithmically spaced intervals (0.6–1, 1–1.6, 1.6–2.5 and 2.5–4 m) as a categorical variable (Supplementary Materials and Methods Eqn S1). As the estimates of the models did not differ for the datasets with the one, five and 10 loudest calls per trial, we only used the one with the five loudest calls for the final modeling.

For each successful trial, a LMM was also formulated with the time to complete the landing task as the response variable (Supplementary Materials and Methods Eqn S3). To investigate

how bats adjusted their SL_{EFD} with range to target for the different noise treatments, all the calls belonging to the last approach leading to landing were used in a LMM along with the decimal logarithm of the range to the target as a covariate (Supplementary Materials and Methods Eqn S4).

All statistical analyses were made with RStudio (RStudio Team, 2021, version 1.43.17, <https://www.rstudio.com/>; Boston, MA, USA).

Control experiments

With the current setup, the bats could have solved the landing task by using: (i) the emitted noise from the target as a homing cue or (ii) spatial memory, as they were always released from the same spot. The following year, we designed two experiments (hereafter termed

‘control experiment 1’ and ‘control experiment 2’) to control for these confounding variables and used five different Daubenton’s bats (bats 5–9 with mean mass 8.1 g, caught in Hobro, Denmark). Training procedure for both control experiments was the same as with bats 1–4 in the main experiment.

In control experiment 1, the same type of broadband noise was transmitted at a NL_{RMS} of 94 dB re. 20 μ Pa at 0.1 m either from the target or from an Avisoft speaker (Vifa, Avisoft Bioacoustics, Glienicke/Nordbahn, Germany; frequency range 5–120 kHz; sensitivity 83 dB re. 20 μ Pa V^{-1} at 1 m; hereafter termed ‘speaker’). The speaker was embedded in foam and placed at two different positions relative to the target: (i) 0.35 m above and 0.3 m behind; and (ii) at the same height as the target (i.e. 1.2 m) but 2 m to the right and 1.4 m in front.

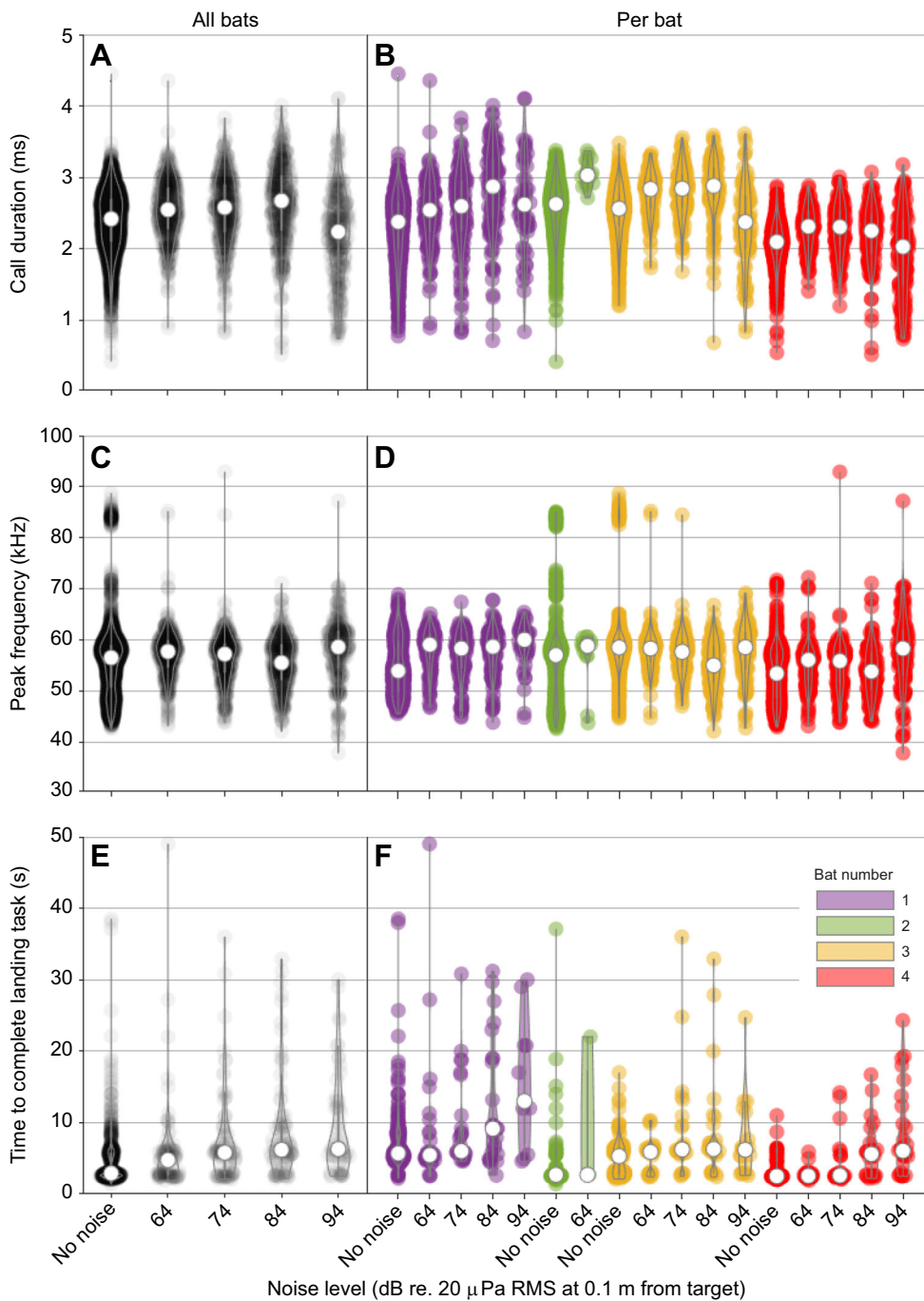


Fig. 3. Noise-induced behavioral adjustments for the different noise treatments and bats. (A,B) Call duration, (C,D) peak frequency and (E,F) time to complete the landing task between the different noise treatments for all bats (left) and per bat (right). Only data from the five loudest calls per trial are shown in A–D. Note: bat 2 successfully completed only three trials of the 64 dB noise treatment. $n=6062$ calls.

With the same experimental setup and protocol, data were collected on three consecutive days and all four treatments (i.e. no-noise and three sources of noise) were part of a session. We used the same pseudo-random Gellermann schedule and motivation criteria until six trials per treatment were completed per bat on each day (Table S3). By using the same localization routine, the ASL_{RMS} of each call and the broadband noise level received by the bats' ears (RNL_{BB}) were computed. For successful trials only (98% of all trials; Table S3), the five calls with the highest ASL_{RMS} (SL_{RMS}) per trial were selected and modelled with a LMM that allowed for treatment-dependent magnitudes of the Lombard effect (Supplementary Materials and Methods Eqn S5).

In control experiment 2, we put the array with the target on a moving platform (height of platform 0.2 m) that could move sideways between two possible locations (left/right, 1.5 m difference in distance). Instead of the target, only the Avisoft speaker was used to transmit the same type of broadband noise at NL_{RMS} of 74 dB re. 20 μ Pa at 0.1 m from the speaker. The speaker was at the same height as the target (i.e. 1.4 m) but 0.93 m behind it and in the middle of the two possible locations of the platform. With the same methodological approach and four bats (5–8), data were collected on two consecutive days with all four treatments (i.e. no-noise/left, no-noise/right, noise/left and noise/right) included in a session. With the same pseudo-random Gellermann schedule and motivation criteria, four trials per treatment and per bat were

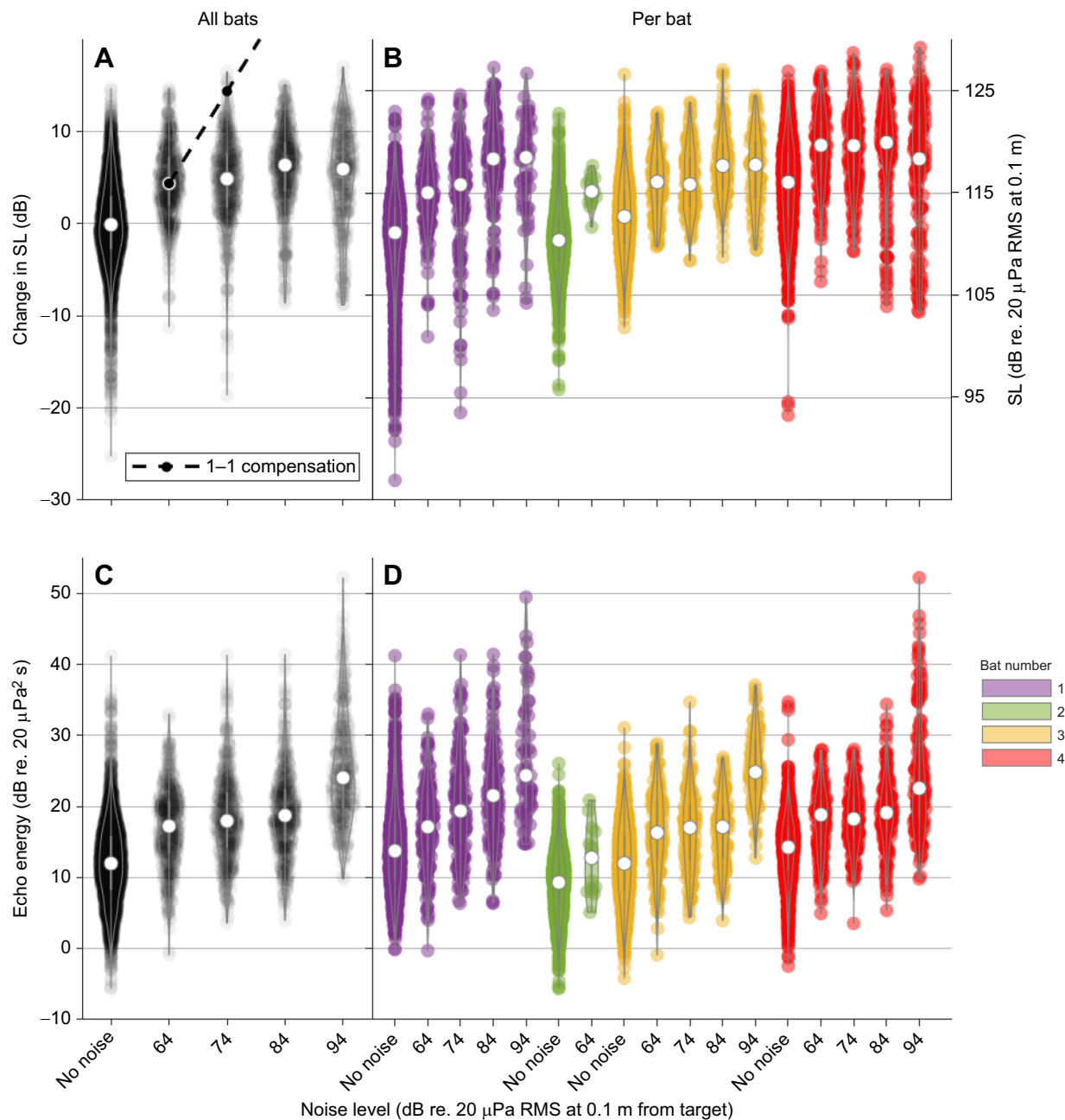


Fig. 4. Source and echo level dynamics for the different noise treatments and bats. (A) Change in source level (SL, all bats), (B) SL (per bat) and (C,D) echo energy (C, all bats; D, per bat). The dashed line in A indicates a Lombard effect magnitude equal to one. Only data from the five loudest calls per trial are shown. Note: bat 2 successfully completed only three trials of the 64 dB noise treatment. $n=6062$ calls.

completed on each day (Table S3). Across the different trials within a session, the target was alternated between the two positions following the pseudo-random schedule.

RESULTS

We exposed four Daubenton's bats (1–4) to broadband ultrasonic noise during active approaches to a landing target, to estimate, via a microphone array, the SL and the ENR as experienced by the bats at different noise levels (NL_{RMS}). During successful trials, the bats always landed on the target. Except for bat 2, which succeeded only in three trials at the lowest NL_{RMS} of 64 dB and was subsequently omitted from further statistical analyses, the other three bats could do the task at all noise levels (Table 1). The experimental treatment that proved most difficult for these three bats was the loudest, at 94 dB (Table 1). The pooled success rate of these three individuals was for each treatment: 99.8% (no-noise), 98.9% (64 dB noise), 98.8% (74 dB), 95.6% (84 dB) and 65.9% (94 dB). With a similar average IPI across all treatments (44–46 ms for all treatments combined), the bats increased the time to complete the landing task ($P<0.001$) and their call peak frequency ($P=0.001$) from the no-noise treatment (pooled median 2.9 s and 56.5 kHz, respectively) to 94 dB NL (pooled median 6.3 s and 58 kHz, respectively) but not their call duration ($P=0.1$, pooled median duration 2.4 ms and 2.2 ms, respectively; Fig. 3; Table S1). The pooled median measurements correspond to the five loudest calls per trial from all successful trials and bats combined. These calls were produced at similar distances from the target across all treatments (Fig. S2). The time to complete the landing task data are derived from all successful trials and bats combined.

The last approach phase leading to landing during successful trials was always followed by a buzz phase, the calls within which were excluded from analysis. After discarding 150 unsuccessful

trials and one successful trial with no usable localizations (Table 1), we localized 21,670 echolocation calls in total. These calls were reduced to 6062 after selecting the five loudest calls (SL_{RMS}) per trial. For each of these calls, the noise-limited active sonar equations (Eqns 1 and 2) were used to estimate: (i) echo level (EL) and (ii) ENR_{BB} , ENR_{NB} and $ENR_{1/3}$ around the mean call peak frequency (i.e. 56 kHz).

All bats increased their SL_{RMS} from the no-noise treatment (pooled median $SL_{RMS}=112$ re. 20 μPa , $SL_{EFD}=86$ dB re. 20 μPa^2 s; Fig. 4B) until 94 dB NL (pooled median $SL_{RMS}=118$ re. 20 μPa , $SL_{EFD}=92$ dB re. 20 μPa^2 s; Fig. 4B) up to a maximum of 129 re. 20 μPa RMS. After modeling the SL_{RMS} of bat calls as a function of received broadband NL (RNL_{BB}) at the bat (Supplementary Materials and Methods Eqn S1, Table S2), we estimated the magnitude of the Lombard effect at 0.13 dB SL_{RMS} dB^{-1} of noise (0.12–0.14 95% CI, $P<0.001$; Table S2). When approaching the target, bats did not change the peak frequency of their calls but instead decreased their SL_{EFD} by ≤ 6 dB per halving of range (Fig. 5). A comparison of the different slopes of the $\log_{10}(R)$ curves, showed that the rate of energy reduction was statistically different ($P<0.001$; Table S2) between the different noise treatments and decreased with increasing noise level at 0.1 m from the target ($P<0.001$; Table S2).

We calculated EL based on the sonar equation (Eqns 1 and 2) by using the SL, range to target and target strength. These computed EL_{RMS} (Fig. 4C,D) returned to the bats in a dynamic range between 21 dB re. 20 μPa (range to target: 4 m) and 82 dB re. 20 μPa (range to target: 0.2 m) ($EL_{EFD}=-6-52$ dB re. 20 μPa^2 s), but increased from the no-noise treatment (pooled median $EL_{RMS}=38$ dB re. 20 μPa , $EL_{EFD}=12$ dB re. 20 μPa^2 s) to the 94 dB NL_{RMS} (pooled median $EL_{RMS}=50$ dB re. 20 μPa , $EL_{EFD}=24$ dB re. 20 μPa^2 s).

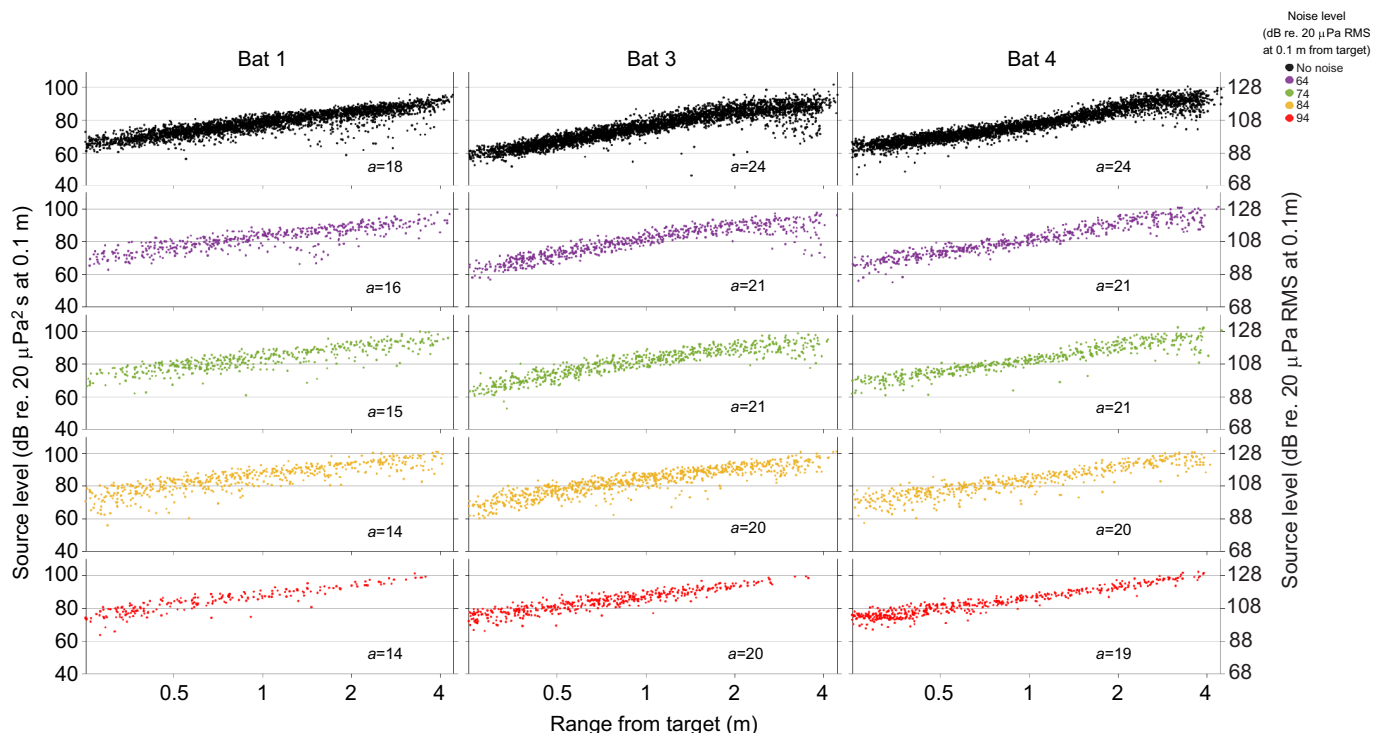


Fig. 5. Rate of SL reduction with range to target for the different noise treatments and bats. SL (left y-axis: dB re. 20 μPa^2 s at 0.1 m, right y-axis: dB re. 20 μPa RMS at 0.1 m) of all the calls from successful trials is shown for bats 1, 3 and 4. *a*, rate of compensation with the decimal logarithm of range. $n=17,408$ calls.

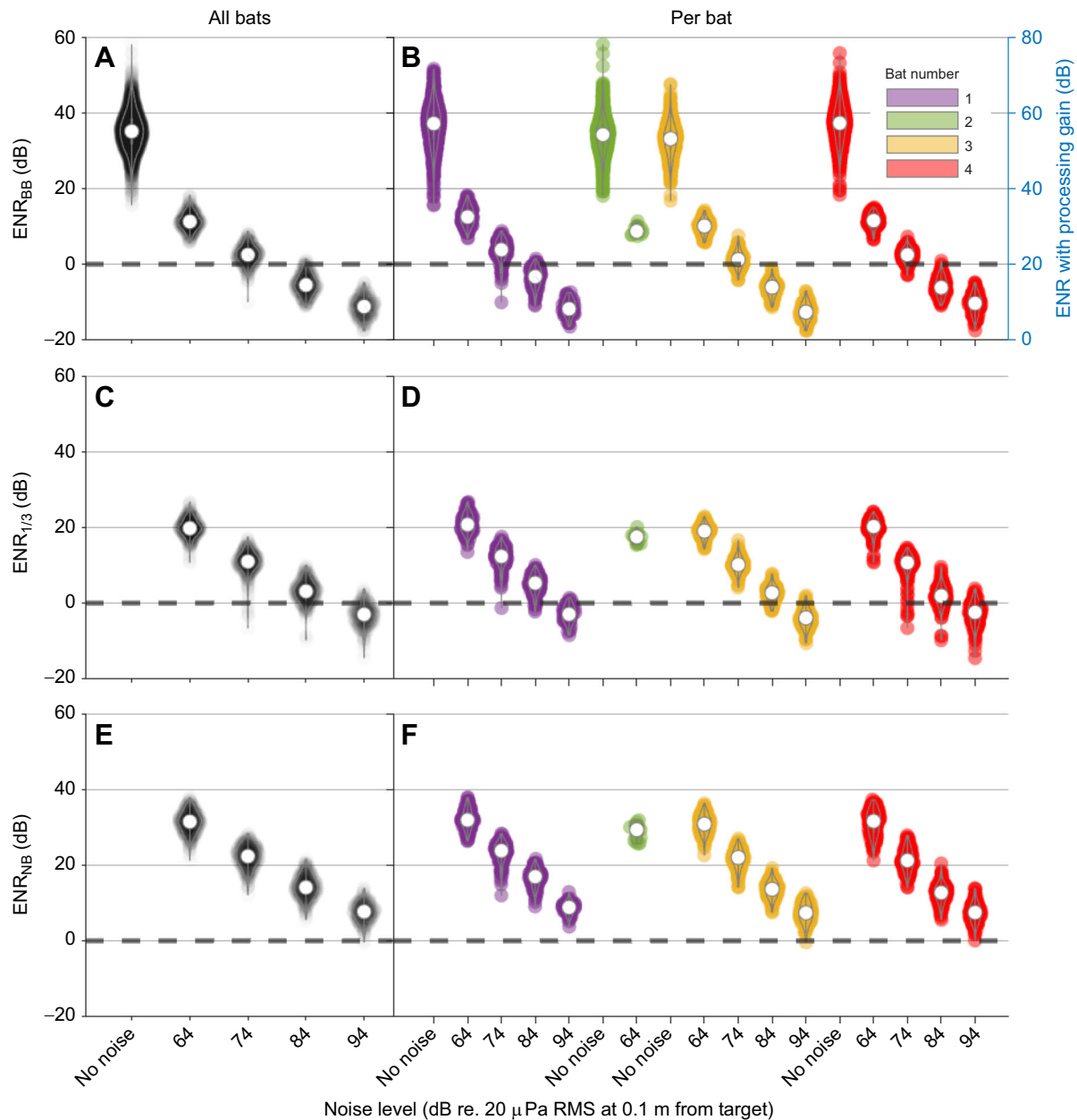


Fig. 6. Echo-to-noise ratio (ENR) between the different noise treatments. (A,B) Broadband ENR (ENR_{BB}), (C,D) 1/3 octave ENR ($ENR_{1/3}$) around mean call peak frequency (i.e. 56 kHz) and (E,F) echo energy to noise spectral density ratio ('narrowband', ENR_{NB}). The processing gain (B, second y axis) was calculated after assuming a call duration and bandwidth of 2 ms and 70 kHz (25–95 kHz), respectively: $10\log_{10}(0.002 \times 70,000) = 21$ dB. Dashed lines indicate ENR equal to zero. Only data from the five calls with the highest ENR_{BB} per trial are shown. Note: $ENR_{1/3}$ and ENR_{NB} were not estimated for the no-noise treatment and bat 2 successfully completed only three trials of the 64 dB noise treatment. $n=6062$ calls.

Both the magnitude of the Lombard effect and ENR estimates show that the SL adjustments did not fully compensate for the effect of masking noise. ENR reduced substantially from the no-noise treatment (pooled median $ENR_{BB}=35$ dB) until 94 dB NL_{RMS} (pooled median $ENR_{BB}=-11$, $ENR_{1/3}=-3$, $ENR_{NB}=8$; Fig. 6A,C,E). While the narrowband ENR_{NB} was positive for all noise treatments, ENR_{BB} was negative for 84 and 94 dB NL_{RMS} across all ranges from the target (Figs 7 and 8).

To test for the possibility that the bats were using the noise as a homing cue for solving the landing task, we conducted a subsequent control experiment with five different Daubenton's bats (bats 5–9). These bats were exposed to the same type of broadband noise (94 dB NL_{RMS}) that was transmitted from three different locations:

the target and a different speaker above or on the side of the target (control experiment 1). During all treatments, the bats always landed on the target and the pooled success rate (%) of these five individuals for each treatment (Table S3) was: 97.7% (no-noise), 96.6% (noise from target), 98.8% (noise from speaker above) and 100% (noise from speaker on the side). We estimated the magnitudes of the Lombard effect (Table S2) at: 0.15 dB SL_{RMS} dB^{-1} of noise (target, 95% CI 0.09–0.19 dB SL_{RMS} dB^{-1} , $P=0.005$), 0.11 dB SL_{RMS} dB^{-1} of noise (speaker above, 95% CI 0.08–0.12 dB SL_{RMS} dB^{-1} , $P<0.001$) and 0.08 dB SL_{RMS} dB^{-1} of noise (speaker on the side, 95% CI 0.02–0.09 dB SL_{RMS} dB^{-1} , $P=0.03$). To further test whether bats 5–8 could use spatial memory to locate the target, we transmitted the same noise at 74 dB NL_{RMS}

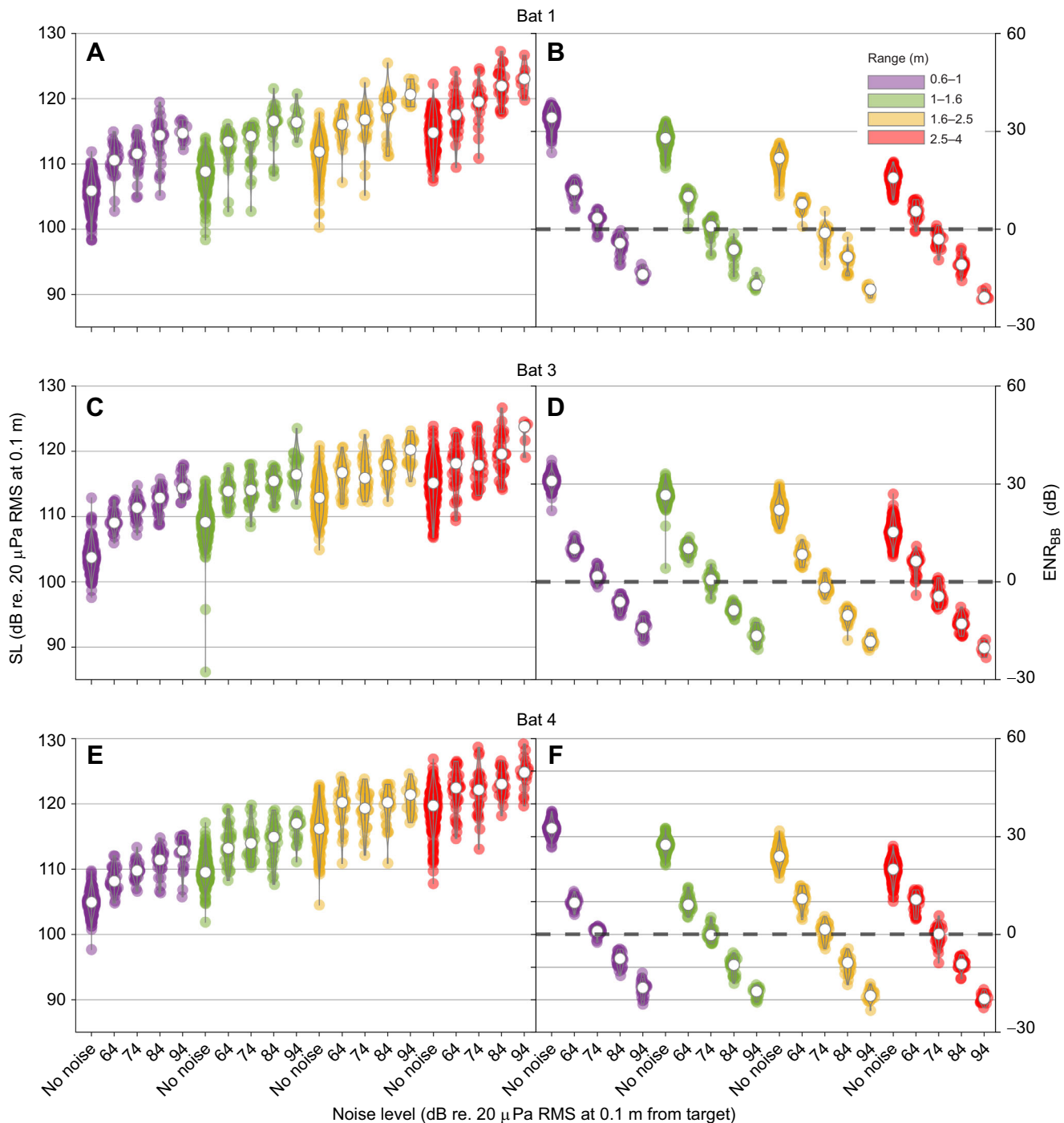


Fig. 7. SL and ENR dynamics for the different noise treatments, target ranges and bats. For each successful trial of bats 1, 3 and 4, the call with the highest SL (A,C,E) and ENR_{BB} (B,D,F) in logarithmically spaced range intervals (0.6–1, 1–1.6, 1.6–2.5 and 2.5–4 m) is plotted between the different noise treatments. $n=5874$ calls.

from the speaker while moving the landing target between two possible locations (control experiment 2). Irrespective of target location, the bats always landed on the target while using echolocation (Table S3).

DISCUSSION

Acoustic masking is a common challenge for animals that rely on sound to forage or communicate. Masking from a discrete noise source occurs whenever noise overlaps spectrally, spatially and temporally with auditory cues of interest, and is on a par with or

exceeds prevailing ambient noise levels and the hearing thresholds of animals. While some studies have investigated masking in bats (e.g. Hage et al., 2013; Luo et al., 2015b; Simmons, 2017; Tressler and Smotherman, 2009), no study has to our knowledge addressed the concomitant effects of spectral, spatial and temporal masking during an active echolocation task where the parameters of the sonar equation can be quantified. Instead, the consequences of masking are often indirectly inferred from a reduction in foraging efficiency (Domer et al., 2021; Finch et al., 2020; Luo et al., 2015a) that in turn may stem from behavioral disturbance caused by the noise, rather

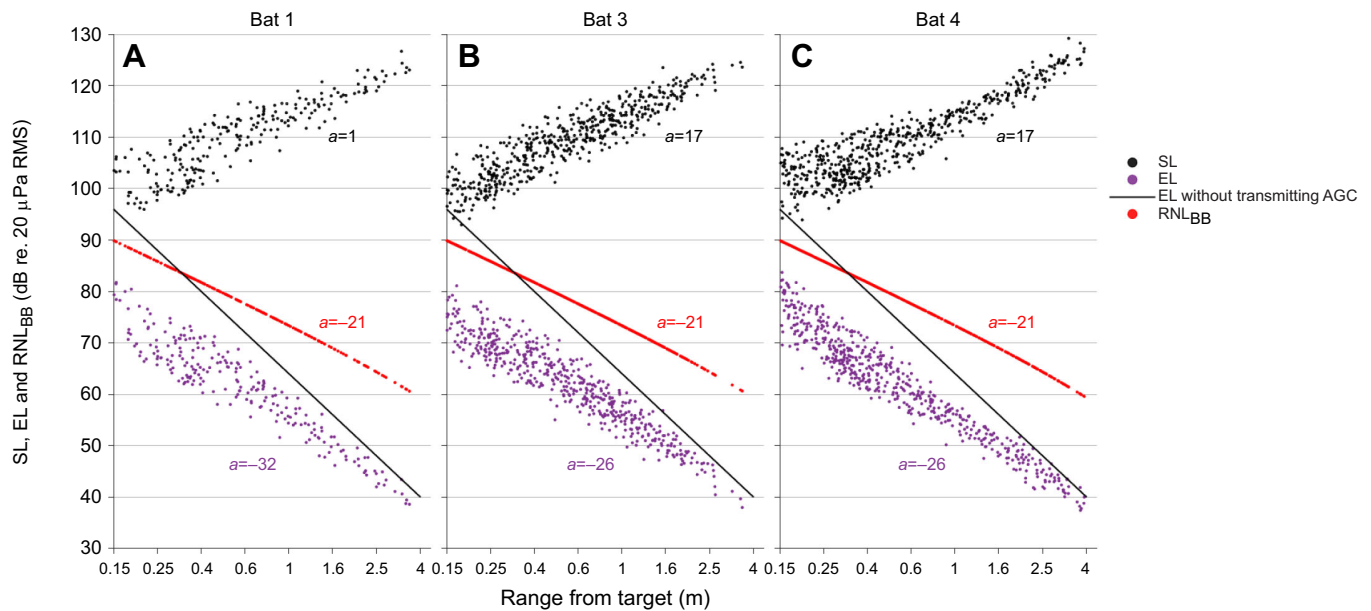


Fig. 8. Call, echo and noise dynamics with range to target for the different bats during the treatment of 94 dB re. 20 μ Pa RMS at 0.1 m from the target. Source level (SL; dB re. 20 μ Pa RMS at 0.1 m), echo level (EL; dB re. 20 μ Pa RMS) and received broadband noise level (RNL_{BB} ; dB re. 20 μ Pa RMS at 0.1 m from the bat) of all the calls from successful trials are shown for bats 1, 3 and 4. *a*, rate of change with the decimal logarithm of range. The solid black line depicts the echo level if the bats did not change their SL with target range (automatic gain control, AGC; Hartley, 1992a). $n=246$, 545 and 644 calls for bats 1, 3 and 4, respectively.

than actual masking effects. Prompted by observations by Griffin et al. (1963) that bats apparently are highly resilient to masking, we designed an experiment to test this hypothesis by investigating the masking impact of broadband, high-frequency noise (20–90 kHz) that overlapped spectrally, spatially and temporally with the echolocation calls of four Daubenton's bats. The bats were able to move freely while echolocating to detect, approach and land on a noise-transmitting target. Thus, since this experimental design did not offer the bats any room for spectral, spatial or temporal release from masking, we could test the hypothesis that they indeed are resilient to noise and not just good at evoking compensatory mechanisms other than the Lombard effect.

Although exposure to increasing masking from noise with source levels from 64 to 94 dB re. 20 μ Pa from the target led to a drop in landing success rate (Table 1), our hypothesis is generally supported as three out of four bats solved the landing task even at the highest NL_{RMS} (94 dB) treatment. The absence of any spectral, spatial and temporal release from masking (Sümer et al., 2009) left the bats with one main option for improving ENR: to increase their SL_{RMS} , which they did by some 10 dB compared with no-noise trials, with a maximum of 129 dB re. 20 μ Pa in the 94 dB NL_{RMS} treatment (Fig. 4B). Given the drop in success rate at the high noise levels, we conclude that a compensatory adjustment of SL cannot defend the ENRs of the no-noise treatment. The Lombard effect as a coping strategy when exposed to masking noise has previously been reported in bats that use frequency-modulated (FM) calls, with the magnitude of the effect ranging from 0.1 to 0.4 dB SL dB^{-1} of noise (Currie et al., 2020; Luo et al., 2015b; Tressler and Smotherman, 2009), and up to what appears to be almost a 1 dB SL/dB of noise in Simmons (2017). The low magnitude of the effect in our study of 0.13 dB SL_{RMS} dB^{-1} of noise was probably the result of the already high SL_{RMS} used by the bats during the no-noise treatment (Fig. 4B), compared to the low SLs of stationary bats in for example Simmons (2017). The increased SL_{RMS} that bats employed while exposed to 94 dB NL_{RMS} at 0.1 m from the target matches well with

the maximum SL_{RMS} values (i.e. 119–122 dB re. 20 μ Pa at 0.1 m) reported for Daubenton's bats in the laboratory and in the wild (Jakobsen et al., 2015; Surlykke et al., 2009). In this study, the maximum SL_{RMS} of 129 dB re. 20 μ Pa is to our knowledge the highest ever documented for this species, and unusually high for any bat echolocating in a lab setting (Surlykke and Kalko, 2008). Thus, irrespective of the NL_{RMS} , these high SL_{RMS} probably represent the upper limit of what these bats can produce with their larynx (Jakobsen et al., 2021) at high energetic costs (Currie et al., 2020), which would explain the moderate Lombard effect.

To test whether the bats used noise as a homing and landing cue, we emitted the same broadband noise at 94 dB NL_{RMS} from either the target or a different speaker above or on the side of the target. Irrespective of the noise source, bats always landed on the target and displayed a different magnitude of the Lombard effect depending on the noise source. The lower magnitudes when the noise was decoupled from the target, and especially when the speaker was on the side of the target, highlight that spatial release from masking (Sümer et al., 2009; Taub and Yovel, 2020) is important to the animal and needs to be carefully addressed in studies of noise effects on wildlife. By moving the landing target between successive trials and using the speaker to emit the same noise, we could also exclude the possibility that the bats used their spatial memory instead of their biosonar to solve the landing task.

For bats in general, vocal modifications induced by broadband noise include an increase in call duration and redundancy as well as changes in call spectral characteristics (e.g. Amichai et al., 2015; Luo and Wiegrebe, 2016; Luo et al., 2015b; Tressler and Smotherman, 2009). While the bats did not increase call duration in this study, there was a twofold increase in the time to complete the landing task (Table S1; Fig. 3A,E) which was associated with more attempts to land on the target. Although there was a statistically significant increase in the call peak frequency with increasing noise (Table S1; Fig. 3C), we posit that a difference of just 1.5 kHz (95% CI 0.5–2 kHz) between the no-noise and the 94 dB NL_{RMS}

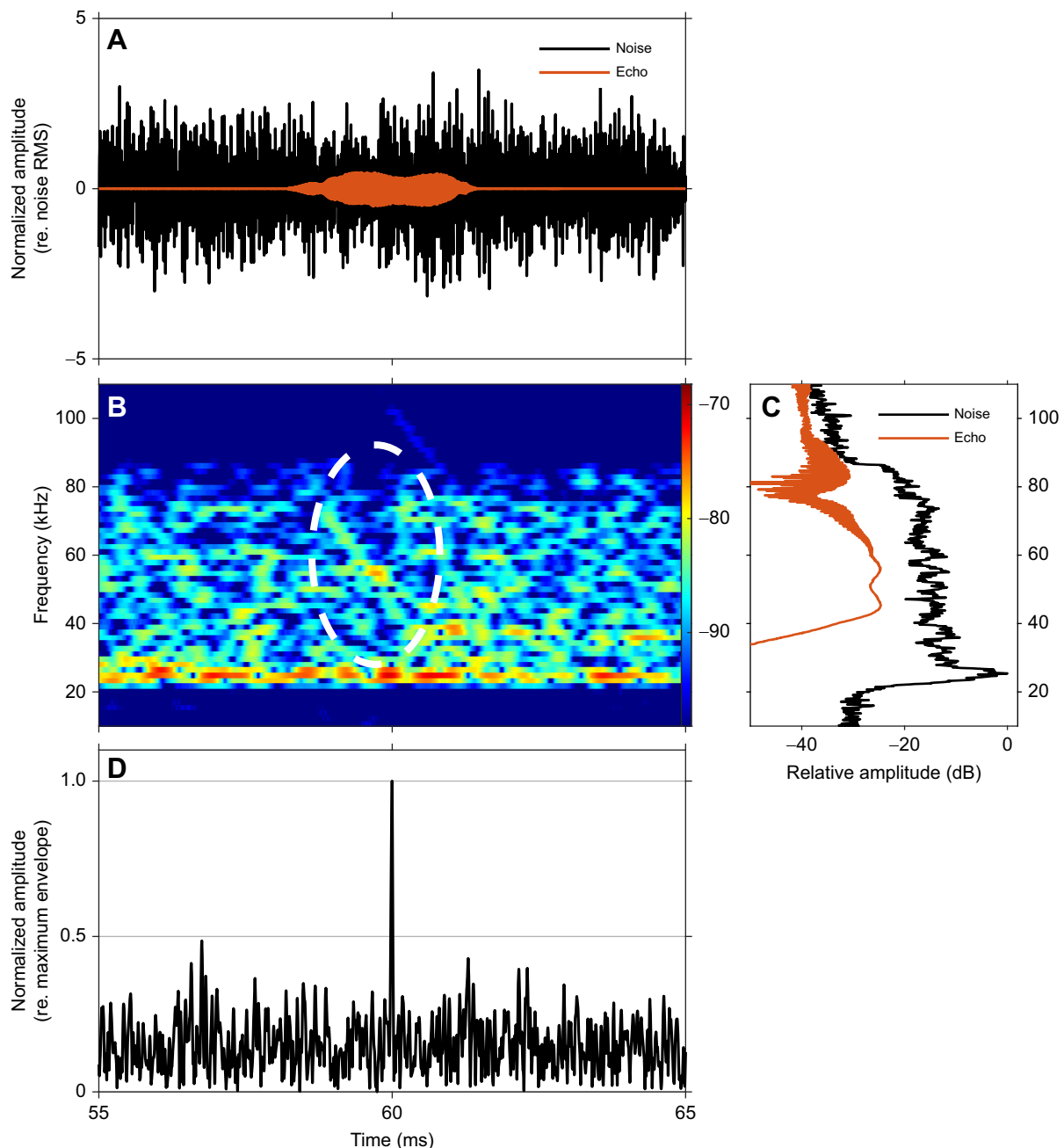


Fig. 9. Simulated echo with the lowest average observed ENR. (A) Waveform, (B) spectrogram (400 kHz sampling rate, DFT size 256 points, Hamming window, 98% overlap, frequency resolution 1.56 kHz, time resolution 12.8 μ s) and (C) spectrum (400 kHz sampling rate, DFT size 4000 points, frequency resolution 100 Hz) of simulated echo and noise with $ENR_{BB} = -11$ dB. Color in B shows the relative amplitude in dB while the dashed ellipse highlights the simulated echo. (D) Envelope of cross-correlation plot for the same echo. The processing gain after harnessing the time–frequency structure of this echo is 20 dB.

treatment is biologically insignificant given the broadband nature of the masker, and could as well be attributed to small changes in aspect with regards to the recording microphone or higher driving pressures of the vocal folds (Elemans et al., 2011).

A major issue for echolocating bats is to contain received ELs within a dynamic range that matches that of their auditory system (Denzinger and Schnitzler, 1998). To do so, bats can reduce both their receiving (by contraction of middle ear muscles; Hartley, 1992a) and transmitting sensitivity (i.e. SL), as a function of decreasing echo delay and therefore target range and transmission loss (Koblitz et al., 2011). On the transmitting side, studied bats generally reduce their SL by ca. 6 dB per halving of target range for

short target ranges (Boonman and Jones, 2002; Hartley, 1992b; Hiryu et al., 2007; Koblitz et al., 2011). While a reduction in SL_{EFD} by 6 dB per halving of target range will render a received EL of ca. 6 dB higher for a point target, the concurrent increase of 6 dB in noise level reaching the bats' ears due to spherical spreading in our experiment will result in an ENR that remains constant with diminishing range. Thus, an advantageous strategy under masking noise in our setup would be to dispense with SL adjustments to target range. Given a stable SL, for every halving of range, the EL increases fourfold while the noise increases only twofold; thereby, ENRs would improve by 6 dB per halving of target range as the bats home in on the target. Surprisingly, given these virtues of

dispensing with output gain control, the bats in this experiment kept on reducing their SL_{EFD} with the same slope as in the no-noise trials (Fig. 5). We speculate that the bats perhaps were not able to maintain the same high SL across a whole approach because of the decoupling of call emission and wingbeats at close ranges that seemingly dictates lower SL at higher wingbeat frequencies (Stidsholt et al., 2021). In that light, our findings imply that echo information redundancy via higher biosonar sampling rates when closing on a target is more important to the bat than improving ENRs in noise.

To better understand echolocation performance under the influence of masking noise, the quantification of ENR is critical (Au and Penner, 1981; Au et al., 1988), as it is a measure of the relationship between echoes and noise available to the auditory system (Luo et al., 2018; Simmons, 2017). Although the drop in success rate with increasing noise level could have been the result of noise being an unpleasant stimulus, our ENR calculations along with the SL compensation of the bats suggest that masking was indeed the underlying cause of this drop. All bats started increasing their SL_{RMS} at 64 dB NL_{RMS} (Fig. 4A), indicating that they tried to defend a broadband ENR_{BB} of at least 10 dB (Fig. 6A). Their increased SLs gave rise to higher target ELs during exposure to noise (Fig. 4C,D). The lower ELs from the no-noise treatment were comparable to ELs recorded by archival sound recording tags attached to bats using constant-frequency calls that were also tasked with approaching spherical targets in the lab (Stidsholt et al., 2020). Although ELs were higher in noise, they were not enough to improve ENR_{BB} , which in the case of the 94 dB NL_{RMS} treatment deteriorated to -11 dB (Fig. 6A). So, even though the bats exhibited the Lombard effect in masking noise, ENRs were more unfavorable while approaching the target during the 84 and 94 dB NL_{RMS} treatments, which were characterized by negative broadband ENR_{BB} across the whole approach (Fig. 7).

Despite such poor ENRs that in big brown bats lead to poorer ranging performance (Simmons, 2017), our bats were able to perform echo-guided landings at these noise levels. While broadband ENR_{BB} was negative for the 94 dB NL_{RMS} noise treatment (Fig. 6A,B), the narrowband ENR_{NB} was on average 8 dB (Fig. 6E). For bottlenose dolphins (*Tursiops truncatus*) whose auditory system can be explained by the performance of an energy detector, the minimum ENR_{NB} for 75% correct detection is 5–7 dB (Au, 1993b). The similarity between these dolphin ENRs in noise and the ENR_{NB} at 94 dB NL_{RMS} implies that the bats could have completed the task using a similar energy detector. Owing to the frequency modulation of the call and hence echoes, the ENR can be improved by substantial processing gain of some 20 dB (Fig. 9) if processed by a matched filter type receiver as some studies have claimed for bats (Simmons, 1979; Strother, 1961). {The potential processing gain for a rectangular pulse with a linear sweep is $10\log_{10}(0.002 \times 70,000) = 21$ dB [with the nominal values of a Daubenton's bat call, average duration 2 ms and bandwidth 70 kHz (25–95 kHz) to form the time–bandwidth product]. The biosonar calls from Daubenton's bats are not rectangular or linear (or without harmonics), but the values calculated in this way are remarkably close to what is found by actually calculating the processing gain (Fig. 9).} Our experimental design cannot resolve whether such a receiver is indeed used by the bats. Despite this, comparable ENRs to those of toothed whales along with the observation that human listeners can detect slowed down echoes with an ENR_{BB} of -11 dB (Audio 1) prompt us to opt for the parsimonious explanation that the auditory performance of bats during target detection in noise can be explained with the model of

an incoherent energy detector like that of toothed whales (Au, 1993b).

In conclusion, we have demonstrated that bat species using FM calls in a captive setting were resilient to the masking effects of broadband ultrasonic noise when performing a landing task (Griffin et al., 1963). Such resilience may be augmented for bats in the wild where spatial release from masking might be readily available and where, as a result of high absorption, the bats are rarely if ever exposed to such high levels of ultrasonic noise except perhaps when leaving the roost or close to streams. In our experimental setting, a reduction of broadband ENR_{BB} to 10 dB was enough to trigger a weak Lombard effect, probably limited by metabolic or biomechanical constraints of an already loud sound production system. This inadequate output adjustment and a varying transmitting gain with target range led to unfavorable ENR_{BB} which, however, did not prevent the bats from solving the task. Despite this resilience to masking in target interception tasks, noise can still be a substantial sensory pollutant, compromising the fitness of bats. Their foraging and mating efficiency can be reduced if noise affects social communication or other parts of the biosonar process (tracking of moving targets or discrimination) by distracting them (Allen et al., 2021) and/or causing aversion (Luo et al., 2015a). It is therefore clear that the effects of noise on bats are multifactorial, thus necessitating a multi-pronged approach to study them and the conservation problems they face.

Acknowledgements

We thank the Zoophysiology workshop at Aarhus University (John Svane Jensen, Jesper Riedel Voetmann, Niels Kristiansen and Lasse Vestergaard Sørensen) and Per Gulddammer Henriksen for technical support while building the experimental setup. We also thank Jakob Tougaard for helpful discussions.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: I.F., P.T.M.; Methodology: I.F., P.T.M.; Software: K.B., J.M.; Validation: I.F., M.B.P., P.T.M.; Formal analysis: I.F., M.B.P., J.M.; Investigation: I.F., M.B.P., A.S.U., L.S., S.B.; Resources: I.F., K.B., J.M., S.B., P.T.M.; Data curation: I.F., J.M.; Writing - original draft: I.F., P.T.M.; Writing - review & editing: I.F., M.B.P., K.B., A.S.U., J.M., L.S., S.B., P.T.M.; Visualization: I.F., K.B., J.M.; Supervision: P.T.M.; Project administration: I.F., P.T.M.; Funding acquisition: P.T.M.

Funding

This study was funded by a Carlsberg Semper Ardens grant to P.T.M.

Data availability

Data are available in the Dryad digital repository (Foskolos et al., 2022): dryad.ngf1vhhv3.

References

- Allen, L. C., Hristov, N. I., Rubin, J. J., Lightsey, J. T. and Barber, J. R. (2021). Noise distracts foraging bats. *Proc. R. Soc. B Biol. Sci.* **288**, 20202689. doi:10.1098/rspb.2020.2689
- Amichai, E., Blumrosen, G. and Yovel, Y. (2015). Calling louder and longer: How bats use biosonar under severe acoustic interference from other bats. *Proc. R. Soc. B Biol. Sci.* **282**, 20152064. doi:10.1098/rspb.2015.2064
- Au, W. W. L. (1993a). *The Sonar of Dolphins*. New York, NY: Springer.
- Au, W. W. L. (1993b). *Signal Processing and Signal Processing Models*. In *The Sonar of Dolphins*, pp. 216–241. New York, NY: Springer.
- Au, W. W. L. and Penner, R. H. (1981). Target detection in noise by echolocating Atlantic bottlenose dolphins. *J. Acoust. Soc. Am.* **70**, 687–693. doi:10.1121/1.386931
- Au, W. W. L., Moore, P. W. B. and Pawloski, D. A. (1988). Detection of complex echoes in noise by an echolocating dolphin. *J. Acoust. Soc. Am.* **83**, 662–668. doi:10.1121/1.396161
- Bass, H. E., Sutherland, L. C., Zuckerwar, A. J., Blackstock, D. T. and Hester, D. M. (1995). Atmospheric absorption of sound: Further developments. *J. Acoust. Soc. Am.* **97**, 680–683. doi:10.1121/1.412989

- Boonman, A. and Jones, G.** (2002). Intensity control during target approach in echolocating bats; stereotypical sensori-motor behaviour in Daubenton's bats, *Myotis daubentonii*. *J. Exp. Biol.* **205**, 2865-2874.
- Brumm, H. and Slabbekoorn, H.** (2005). Acoustic Communication in Noise. In *Advances in the Study of Behavior*, pp. 151-209. Academic Press.
- Cechetto, C., De Busserolles, F., Jakobsen, L. and Warrant, E. J.** (2020). Retinal ganglion cell topography and spatial resolving power in echolocating and non-echolocating bats. *Brain. Behav. Evol.* **95**, 58-68. doi:10.1159/000508863
- Currie, S. E., Boonman, A., Troxell, S., Yovel, Y. and Voigt, C. C.** (2020). Echolocation at high intensity imposes metabolic costs on flying bats. *Nat. Ecol. Evol.* **4**, 1174-1177. doi:10.1038/s41559-020-1249-8
- Denzinger, A. and Schnitzler, H.-U.** (1998). Echo SPL, training experience, and experimental procedure influence the ranging performance in the big brown bat, *Eptesicus fuscus*. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **183**, 213-224. doi:10.1007/s003590050249
- Domer, A., Korine, C., Slack, M., Rojas, I., Mathieu, D., Mayo, A. and Russo, D.** (2021). Adverse effects of noise pollution on foraging and drinking behaviour of insectivorous desert bats. *Mamm. Biol.* **1**, 3. doi:10.1007/s42991-021-00101-w
- Eklöf, J., Šuba, J. and Rydell, J.** (2014). Visual acuity and eye size in five European bat species in relation to foraging and migration strategies. *Environ. Exp. Biol.* **12**, 1-6.
- Elemans, C. P. H., Mead, A. F., Jakobsen, L. and Ratcliffe, J. M.** (2011). Superfast muscles set maximum call rate in echolocating bats. *Science* **333**, 1885-1888. doi:10.1126/science.1207309
- Finch, D., Schofield, H. and Mathews, F.** (2020). Traffic noise playback reduces the activity and feeding behaviour of free-living bats. *Environ. Pollut.* **263**, 114405. doi:10.1016/j.envpol.2020.114405
- Foskolos, I., Pedersen, M. B., Beedholm, K., Uebel, A. S., Macaulay, J., Stidsholt, L., Brinklov, S. and Madsen, P. T.** (2022) Echolocation call parameters from Daubenton's bats during exposure to masking noise. *Dryad Dataset*. doi:10.5061/dryad.ngf1vhhv3
- Geberl, C., Brinklov, S., Wiegrebe, L. and Surlykke, A.** (2015). Fast sensory-motor reactions in echolocating bats to sudden changes during the final buzz and prey intercept. *Proc. Natl. Acad. Sci. USA* **112**, 4122-4127. doi:10.1073/pnas.1424457112
- Gellermann, L. W.** (1933). Chance orders of alternating stimuli in visual discrimination experiments. *Pedagog. Semin. J. Genet. Psychol.* **42**, 206-208. doi:10.1080/08856559.1933.10534237
- Gillespie, D., Gordon, J. C. D., McHugh, R., McLaren, D., Mellinger, D. K., Redmond, P., Thode, A. M., Trinder, P. and Deng, X. Y.** (2008). PAMGUARD: Semiautomated, open source software for real-time acoustic detection and localisation of cetaceans. In *Proceedings of the Institute of Acoustics*, pp. 54-62. Acoustical Society of America.
- Gomes, D. G. E., Francis, C. D. and Barber, J. R.** (2021). Using the Past to Understand the Present: Coping with Natural and Anthropogenic Noise. *Bioscience* **71**, 223-234. doi:10.1093/biosci/biaa161
- Griffin, D. R., McCue, J. J. G. and Grinnell, A. D.** (1963). The resistance of bats to jamming. *J. Exp. Zool.* **152**, 229-250.
- Hage, S. R., Jiang, T., Berquist, S. W., Feng, J. and Metzner, W.** (2013). Ambient noise induces independent shifts in call frequency and amplitude within the Lombard effect in echolocating bats. *Proc. Natl. Acad. Sci. USA* **110**, 4063-4068. doi:10.1073/pnas.1211533110
- Hartley, D. J.** (1992a). Stabilization of perceived echo amplitudes in echolocating bats. I. Echo detection and automatic gain control in the big brown bat, *Eptesicus fuscus*, and the fishing bat, *Noctilio leporinus*. *J. Acoust. Soc. Am.* **91**, 1120-1132. doi:10.1121/1.402639
- Hartley, D. J.** (1992b). Stabilization of perceived echo amplitudes in echolocating bats. II. The acoustic behavior of the big brown bat, *Eptesicus fuscus*, when tracking moving prey. *J. Acoust. Soc. Am.* **91**, 1133-1149. doi:10.1121/1.402640
- Hiryu, S., Hagino, T., Riquimaroux, H. and Watanabe, Y.** (2007). Echo-intensity compensation in echolocating bats (*Pipistrellus abramus*) during flight measured by a telemetry microphone. *J. Acoust. Soc. Am.* **121**, 1749-1757. doi:10.1121/1.2431337
- Hotchkiss, C. and Parks, S. E.** (2013). The Lombard effect and other noise-induced vocal modifications: insight from mammalian communication systems. *Biol. Rev.* **88**, 809-824. doi:10.1111/brv.12026
- Jakobsen, L., Olsen, M. N. and Surlykke, A.** (2015). Dynamics of the echolocation beam during prey pursuit in aerial hawking bats. *Proc. Natl. Acad. Sci. USA* **112**, 8118-8123. doi:10.1073/pnas.1419943112
- Jakobsen, L., Christensen-Dalsgaard, J., Juhl, P. M. and Elemans, C. P. H.** (2021). How Loud Can you go? Physical and Physiological Constraints to Producing High Sound Pressures in Animal Vocalizations. *Front. Ecol. Evol.* **9**, 325. doi:10.3389/fevo.2021.657254
- Koblitz, J. C., Stitz, P., Pflästerer, W., Melcón, M. L. and Schnitzler, H.-U.** (2011). Source level reduction and sonar beam aiming in landing big brown bats (*Eptesicus fuscus*). *J. Acoust. Soc. Am.* **130**, 3090-3099. doi:10.1121/1.3628345
- Levitt, H.** (1970). Transformed Up-Down Methods in Psychoacoustics. *J. Acoust. Soc. Am.* **49**, 467-477. doi:10.1121/1.1912375
- Luo, J. and Wiegrebe, L.** (2016). Biomechanical control of vocal plasticity in an echolocating bat. *J. Exp. Biol.* **219**, 878-886. doi:10.1242/jeb.134957
- Luo, J., Siemers, B. M. and Koselj, K.** (2015a). How anthropogenic noise affects foraging. *Glob. Chang. Biol.* **21**, 3278-3289. doi:10.1111/gcb.12997
- Luo, J., Goerlitz, H. R., Brumm, H. and Wiegrebe, L.** (2015b). Linking the sender to the receiver: Vocal adjustments by bats to maintain signal detection in noise. *Sci. Rep.* **5**, 1-11. doi:10.1038/srep18556
- Luo, J., Hage, S. R. and Moss, C. F.** (2018). The Lombard Effect: From Acoustics to Neural Mechanisms. *Trends Neurosci.* **41**, 938-949. doi:10.1016/j.tins.2018.07.011
- Madsen, P. T. and Wahlberg, M.** (2007). Recording and quantification of ultrasonic echolocation clicks from free-ranging toothed whales. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **54**, 1421-1444. doi:10.1016/j.dsr.2007.04.020
- Möhl, B.** (1988). Target Detection by Echolocating Bats. In *Animal Sonar: Processes and Performance* (ed. Nachtigall, P. E. and Moore, P. W. B.), pp. 435-450. Boston, MA: Springer US.
- Nelder, J. A. and Mead, R.** (1965). A Simplex Method for Function Minimization. *Comput. J.* **7**, 308-313. doi:10.1093/comjnl/7.4.308
- Roverud, R. C. and Grinnell, A. D.** (1985). Echolocation sound features processed to provide distance information in the CF/FM bat, *Noctilio albigentris*: evidence for a gated time window utilizing both CF and FM components. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **156**, 457-469. doi:10.1007/BF00613970
- Simmons, J. A.** (1979). Perception of echo phase information in bat sonar. *Science* **204**, 1336-1338. doi:10.1126/science.451543
- Simmons, J. A.** (2017). Noise interference with echo delay discrimination in bat biosonar. *J. Acoust. Soc. Am.* **142**, 2942-2952. doi:10.1121/1.5010159
- Stidsholt, L., Müller, R., Beedholm, K., Ma, H., Johnson, M. and Madsen, P. T.** (2020). Energy compensation and received echo level dynamics in constant-frequency bats during active target approaches. *J. Exp. Biol.* **223**, jeb217109. doi:10.1242/jeb.217109
- Stidsholt, L., Johnson, M., Goerlitz, H. R. and Madsen, P. T.** (2021). Wild bats briefly decouple sound production from wingbeats to increase sensory flow during prey captures. *iScience* **24**, 102896. doi:10.1016/j.isci.2021.102896
- Stitz, P. and Schnitzler, H.-U.** (2012). Estimation of the acoustic range of bat echolocation for extended targets. *J. Acoust. Soc. Am.* **132**, 1765-1775. doi:10.1121/1.4733537
- Strother, G. K.** (1961). Note on the Possible Use of Ultrasonic Pulse Compression by Bats. *J. Acoust. Soc. Am.* **33**, 696-697. doi:10.1121/1.1908771
- Sümer, S., Denzinger, A. and Schnitzler, H.-U.** (2009). Spatial unmasking in the echolocating Big Brown Bat, *Eptesicus fuscus*. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **195**, 463-472. doi:10.1007/s00359-009-0424-9
- Surlykke, A. and Kalko, E. K. V.** (2008). Echolocating Bats Cry Out Loud to Detect Their Prey. *PLoS One* **3**, e2036. doi:10.1371/journal.pone.0002036
- Surlykke, A., Boel Pedersen, S. and Jakobsen, L.** (2009). Echolocating bats emit a highly directional sonar sound beam in the field. *Proc. R. Soc. B Biol. Sci.* **276**, 853-860. doi:10.1098/rspb.2008.1505
- Taub, M. and Yovel, Y.** (2020). Segregating signal from noise through movement in echolocating bats. *Sci. Rep.* **10**, 1-10. doi:10.1038/s41598-019-57346-2
- Tressler, J. and Smotherman, M. S.** (2009). Context-dependent effects of noise on echolocation pulse characteristics in free-tailed bats. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **195**, 923-934. doi:10.1007/s00359-009-0468-x
- Troest, N. and Möhl, B.** (1986). The detection of phantom targets in noise by serotine bats; negative evidence for the coherent receiver. *J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol.* **159**, 559-567. doi:10.1007/BF00604175
- Urick, R. J.** (1983). *Principles of underwater sound*, 3rd edn. Los Altos: Peninsula Pub.
- White, P. R., Leighton, T. G., Finfer, D. C., Powles, C. and Baumann, O. N.** (2006). Localisation of sperm whales using bottom-mounted sensors. *Appl. Acoust.* **67**, 1074-1090. doi:10.1016/j.apacoust.2006.05.002
- Zollinger, S. A. and Brumm, H.** (2011). The evolution of the Lombard effect: 100 years of psychoacoustic research. *Behaviour* **148**, 1173-1198. doi:10.2307/41445240