RESEARCH ARTICLE

Energy compensation and received echo level dynamics in constant-frequency bats during active target approaches

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ABSTRACT

Bats have been reported to adjust the energy of their outgoing vocalizations to target range (R) in a logarithmic fashion close to $20\log_{10}R$ which has been interpreted as providing one-way compensation for increasing echo levels during target approaches. However, it remains unknown how species using high-frequency calls, which are strongly affected by absorption, adjust their vocal outputs during approaches to point targets. We hypothesized that such species should compensate less than the $20\log_{10}R$ model predicts at longer distances and more at shorter distances as a consequence of the significant influence of absorption at longer ranges. Using a microphone array and an acoustic recording tag, we show that the output adjustments of two *Hipposideros pratti* and one *Hipposideros armiger* do not decrease logarithmically during approaches to different-sized targets. Consequently, received echo levels increase dramatically early in the approach phase with near-constant output levels, but level off late in the approach phase as a result of substantial output reductions. To improve echo-to-noise ratio, we suggest that bats using higher frequency vocalizations compensate less at longer ranges, where they are strongly affected by absorption. Close to the target, they decrease their output levels dramatically to mitigate reception of very high echo levels. This strategy maintains received echo levels between 6 and 40 dB re. 20 µPa^2 s across different target sizes. The bats partially compensated for target size, but not in a one-to-one dB fashion, showing that these bats do not seek to stabilize perceived echo levels, but may instead use them to gauge target size.

KEY WORDS: Microphone array, Intensity compensation, Source level, Echo level, CF bats, Atmospheric absorption

INTRODUCTION

Echolocating bats navigate and catch prey by auditory processing of the highly dynamic echoes returning from objects they have ensonified with powerful ultrasonic calls. To manage the complexity of such an actively generated acoustic scene, bats control the sensory flow by adjusting both the transmitting and receiving parts of their biosonar system. On the transmission side, bats can actively adjust the repetition rate (Wheeler et al., 2016;

Wilson and Moss, 2004), duration (Britton et al., 1997), intensity (Brinkløv et al., 2009; Waters and Jones, 1995), gaze (Ghose and Moss, 2003), directionality and bandwidth of their vocalizations to the task at hand (Fujioka et al., 2014; Kalko and Schnitzler, 1993). When approaching airborne prey, insectivorous bats follow a stereotyped search, approach and buzz phase strategy (Griffin et al., 1960). In the search phase, bats emit powerful and relatively invariant calls to detect prey. The approach phase is characterized by gradual reductions of call duration and source level (SL), as well as inter-call interval. Just before capturing prey, bats transition into a buzz consisting of a short train of calls with short duration, low SL and an extremely high repetition rate.

Range-dependent reductions in SLs have been ascribed to the need for echo levels (ELs) to return in a dynamic range matched to the hearing system of bats, i.e. with sufficient energy for detection and processing without exceeding comfortable levels (Denzinger and Schnitzler, 1998) – a phenomenon that has often been coined 'echo intensity compensation' or 'intensity compensation' (Budenz et al., 2018; Hartley, 1992a; Koblitz et al., 2011). Here, we use the term 'energy compensation' for SL adjustments during approach of a target, as the mammalian ear integrates intensity over time to detect energy (Green and Swets, 1966; Surlykke and Bojesen, 1996).

If bats did not perform energy compensation, the returning ELs for a given target would increase by up to ∼70 dB during an approach. This is illustrated in Fig. 1 for a bat emitting a constant-frequency call (call frequency of 68 kHz; hereafter, 'CF bat') approaching a point target (target strength, TS=−15 dB at 0.1 m) using different output level strategies. For a constant output level (Fig. 1, dark blue line), the sound will return to the bat with at least a $40\log_{10}(R)$ (where R is target range in units of the reference distance of 10 cm) loss of sound energy due to $20\log_{10}R$ geometrical spreading of sound in both the outward and return trip from a point target (Fig. 1, grey dashed line). In addition to this geometrical spreading loss, sound energy is also lost by acoustic absorption (i.e. friction between air molecules) (Griffin, 1971); this absorption increases linearly with range and in a more complex way with frequency. For example, in a CF bat species with 68 kHz calls (e.g. *Hipposideros armiger*), absorption adds 15 dB in transmission loss (TL) to the 59 dB of geometric spreading for a target at 3 m range (Fig. 1, grey shaded area). Thus, if the same bat closes in on a point target while emitting calls of constant SL, the ELs increase by up to 74 dB over an approach from 3 m to 0.1 m, greatly superseding the preferred dynamic range of the hearing system of some 40 dB (Denzinger and Schnitzler, 1998) (Fig. 1, light blue line). Varying target size will further add 20–30 dB to the overall dynamic range of ELs that bats receive over time. Probably to solve this dynamic range problem, bats have been shown to partially adjust both their receiving sensitivity and their output levels as functions of echo delay and therefore target range. Receiving sensitivity is reduced just before each call emission by a contraction of the middle ear muscles – a phenomenon termed 'automatic gain control' by a few

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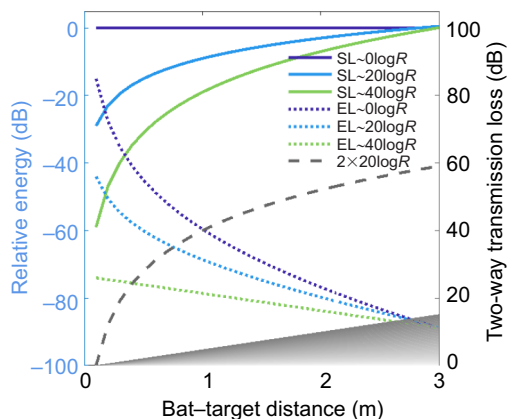*Author for correspondence (laura.stidsholt@bios.au.dk)

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> **List of symbols and abbreviations**
>
> CF bats   bat species using Doppler-shift compensation by emitting long, constant-frequency calls and evaluating the Doppler-shifted returning echoes
> EFD   energy flux density, the acoustic energy flow per unit area
> EL   energy level of the returning echoes
> ENR   echo-to-noise ratio
> FM bats   bat species using frequency-modulated sweeps
> R distance between the bat and the target of interest
> RMS   root mean square, a measure of the average acoustic intensity
> SL   source level, the emitted energy of the on-axis vocalizations 0.1 m in front of the bat
> TL   transmission loss due to spherical spreading and absorption
> TS   target strength of the ensonified target, the difference between the received and reflected acoustic energy 0.1 m in front of the target

studies showing an increase in sensitivity following roughly a 6 dB per doubling of range lasting up to 1 m in front of the bat (Hartley, 1992a; Patheiger, 1998).

Output level adjustments in bats have been investigated in several experiments using different methods, recording equipment and species (Koblitz et al., 2011). Most studies have used logarithmic models to describe the lowering of call SLs with decreasing target range, but have reached substantially different conclusions as to whether bats partially (Budenz et al., 2018; Hartley et al., 1989; Saillant et al., 2007; Lewanzik and Goerlitz, 2018) or fully (Hiryu et al., 2007; Kobler et al., 1985; Koblitz et al., 2011; Melcón et al., 2007) compensate for the reduced TL, and/or whether they rely on EL or just echo delay to inform the evoked SL changes (Boonman and Jones, 2002). For bats using frequency-modulated calls (hereafter, 'FM bats'), such studies have shown that they decrease their output levels by between 4 and 9 dB per halving of range when approaching both mirror targets (Hiryu et al., 2007; Koblitz et al., 2011; Melcón et al., 2007) and point targets (Boonman and Jones,

2002; Hartley, 1992b; Melcón et al., 2007). For CF–FM bats using Doppler-shift compensation, SL reduction towards mirror targets has shown similar reductions in output levels of approximately 6 dB per distance halved (Hiryu et al., 2008; Kobler et al., 1985; Tian and Schnitzler, 1997). Thus, the SL compensation when CF–FM and FM bats approach both mirror and point targets appears to be around 6 dB per distance halved (dB/dh). This results in a roughly constant received EL for mirror targets, but an increase of 3–8 dB per halving of range when approaching point targets (Fig. 1, light blue dotted line). It has been proposed that the combined effect of transmitting and receiving side adjustments renders fairly constant perceived ELs for point targets (Hartley, 1992b). In an extreme version of such a scenario in which the perceived EL is maintained strictly constant, bats would only know something about the size of the ensonified target by keeping track of the call-by-call compensatory changes in SLs and auditory sensitivity. While such rapid feedback is used to adjust call frequency in Doppler-compensating CF bats to gauge prey movements (Schnitzler, 1973), there is little evidence to suggest that bats evoke a similar closed loop feedback on ELs (Budenz et al., 2018). Rather, Budenz and co-workers (2018) have argued that the low output levels emitted when bats are close to objects would perhaps not result in a contraction of the middle ear muscles large enough to affect the sensitivity to the following echoes. Instead, they argue that FM bats use the differences in EL development during target approach to differentiate between point and mirror targets.

Even though many studies of SL adjustments with range interpret their data as evidence for an overall 6 dB/dh or $20\log_{10}R$ reduction, there are often large deviations from these predictions and a substantial spread between studies. This might be ascribed to differences in experimental design (stationary versus free-flying bats, point targets versus mirror targets, simple versus complex echoic scenes, or field versus captive studies), the species chosen (CF versus FM species) as well as a low number of repetitions per animal (typically between 3 and 10 flights). In addition, there may be wide variations in the clutter level in these studies [e.g. from recording equipment directly behind a target (Budenz et al., 2018; Hartley et al., 1989; Saillant et al., 2007) or from nearby structures in the flight room such as walls and ceiling], potentially influencing the energy compensation strategy used by bats.

Given these large variations, it may be speculated that biosonar output dynamics as a function of range are not entirely explained by control models based only on geometric spreading losses (Norum et al., 2012). Most energy compensation studies have used either species that emit low-frequency pulses or an experimental setup with short operating distances. In both situations, acoustic absorption has often been neglected as the effect is fairly small under these circumstances. However, for species using vocalizations with higher frequency, e.g. 68 kHz in Fig. 1, differences in absorption at longer versus shorter ranges will lead to developments in ELs during target approaches that cannot be compensated for by adjusting the SL in an $x\log_{10}R$ fashion (Fig. 1, light blue and green lines).

Thus, the call frequency of the species in question and the experimental setup are predicted to have an effect on the relationship between output levels and range, and hence on the echo energy available to the animals. This will affect how we understand the bats' adjustments of their emitted energy and therefore how they may organize echo information perceptually. In this study, we sought to understand how CF bats that are subject to significant acoustic absorption perform range-dependent adjustments in call output for different target sizes. Specifically, we hypothesized that as a result of absorption, these bats would delay the onset of SL adjustment so as to increase the possibility of detecting echoes at

Fig. 1. Calculated echo level (EL) dependency on source level (SL) adjustments and transmission loss (TL) for a bat emitting constant-frequency calls (CF bat) at 68 kHz. SLs (solid lines, left-hand axis) with no target range (R) adjustment (dark blue), $20\log_{10}R$ (light blue) or $40\log_{10}R$ (green) adjustment, and corresponding ELs (dotted lines). The calculations are based on the sonar equation (Urick, 1983) using a point target with a target strength of −15 dB. The grey right-hand axis shows the two-way TL due to geometric spreading ($2\times20\log_{10}R$; grey dashed line) and acoustic absorption ($2\times\alpha\times R$, where α is the absorption coefficient; grey shaded area). Absorption increases with frequency and this is indicated by the grey colour scale from white (0 kHz) to dark grey (70 kHz). All dB values are relative.

long ranges, but would then reduce call output levels with decreasing range by more than what has been measured in lower-frequency species under similar experimental settings. We further hypothesized that bats would not compensate their output levels for target size and so would receive useful information on target movement and size based on relative changes in ELs.

We tested these hypotheses by conducting a target approach experiment using two CF species, the great roundleaf bat (*Hipposideros armiger*) and Pratt's roundleaf bat (*Hipposideros pratti*), approaching four different target sizes. We show that such CF bats using higher frequency vocalizations do not use a logarithmic decrease in output levels with range. Instead, they maintain the returning ELs within a dynamic range of around 34 dB by emitting calls with a nearly constant output level at long distances and dramatically decreasing their output levels close to the target.

MATERIALS AND METHODS
Experimental setup
This work was carried out under Institutional Animal Care and Use Committee Permit No. 15-067. Two *Hipposideros pratti* Thomas 1891 (73 and 93 g) and one *Hipposideros armiger* (Hodgson 1835) (63 g) were used for the study. The bats were trained to fly diagonally across a flight room (4×3.5×3.5 m; Shandong University, China) and land on target spheres of different sizes. Four plastic spheres (diameter: 0.30, 0.20, 0.12, 0.07 m; TS: −3, −6, −10, −15 dB) were wrapped with thin cloth to facilitate landing and placed in a corner of the flight room at 2 m height. A star-shaped array of six Knowles microphones (FG-3329, 2.6 mm diameter) spaced at 0.25 and 0.5 m were placed behind the target spheres and completely embedded in 30 cm deep pyramidal acoustic foam (Fig. 2). The surfaces of the room were covered with 5 cm deep acoustic foam and the room was kept dark during the experiments except for dim computer light used for running the set-up and for handling of the bats (Fig. 2).

The six Knowles microphones were connected through a custom-built 30 dB amplifier and filter box (a 1-pole 1 kHz high-pass filter and a 4-pole 100 kHz anti-alias filter) to an A/D converter (USB-6356, National Instruments, Houston, TX, USA) and sampled synchronously at a rate of 250 kHz per channel, with 16-bit

Fig. 2. Side view of the experimental setup. The microphone array was placed at 2 m height and embedded in anechoic foam. Knowles array microphones are marked in red; the Knowles microphone on the tag is shown in yellow on top of the bat.

resolution and with a clipping level of 106 dB re. 20 μPa pk. The echolocation calls were recorded by the array when manually triggered, and stored in 5 s files for each landing. An archival sound recording tag (Stidsholt et al., 2018) was attached to the back of the bats with Velcro and glue (Ökonorm Pro) during trials to continuously record the echolocation pulses and echoes. The tag measured 14×33×6 mm and weighed 2.6 g. The tag audio data were recorded at a sampling rate of 187.5 kHz, with 16 bit resolution and a clipping level of 121 dB re. 20 μPa pk. The tag included a 10 kHz 1-pole high-pass filter and an 80 kHz 4-pole anti-aliasing filter. The frequency responses of the Knowles microphones (FG-3329) both in the array and on the tag were corrected prior to analysis by convolving the recorded signals with the predetermined impulse response of the recording system (Stidsholt et al., 2018).
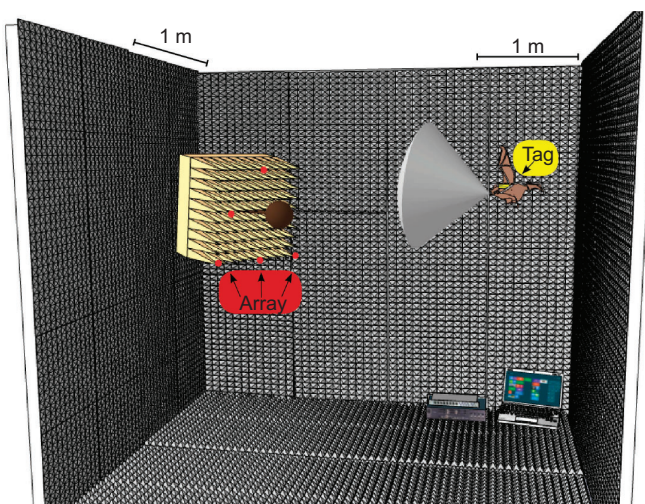
Each bat was instrumented with the tag for approximately 4 h in total over four experimental days (maximum duration of 60 min per session). As the tag weighed 2.6 g, the loading did not exceed 5% of the mass of any of the bats (63–93 g). The tag did not appear to adversely influence the flight performance over the short flight paths studied here and the bats were carefully observed during the flights for any sign of fatigue. The three bats completed between 20 and 45 landings on each target (354 flights analysed; Table 1). Because of the time required to change targets, a single target size was used per day. When a bat landed on a target, a synchronization sound unique for each trial (400 ms and frequency content between 1 and 8 kHz) was emitted by a small speaker embedded in the array. This sound was recorded on both the array and the tag, thus facilitating synchronization. The emission of the synchronization sound also served as a bridge signal, indicating a successful trial, and the bat was subsequently fed a mealworm.

Data analysis
The tag and array data were synchronized within an error of a few milliseconds by cross-correlating with the unique synchronization sound recorded on both the array and tag for each trial. All calls were automatically detected by a custom-written call detector. Only the second and strongest harmonic of the calls and echoes were extracted for analysis by digitally filtering the data with an 8-pole band-pass Butterworth filter with low-frequency cut off at 50 kHz and 47 kHz, and high-frequency cut off at 70 kHz and 65 kHz, respectively, for *H. armiger* and *H. pratti*.

Localization and SL estimation
The location of the bat was determined by acoustic localization using time of arrival differences between the array microphones for each recorded call. Time of arrival differences were found by cross-correlating the downward FM sweep of each call. A simplex minimization algorithm (Macaulay et al., 2017; Nelder and Mead, 1965) was used to estimate the location of the bat based on the time delays between calls. A Kalman filter was used to smooth the location estimates across successive calls. The received levels (RLs) at each microphone were calculated and calls with RL 10 dB above the noise floor were chosen for further analysis. The in-band noise floor of the array was 25 dB re. 20 μPa RMS for *H. armiger* and 24 dB re. 20 μPa for *H. pratti*. To back-calculate the RL to a SL at 0.1 m, TL was compensated for by assuming spherical spreading loss, i.e. $20\log_{10}R$, plus a frequency-dependent absorption loss (*sensu* Jakobsen et al., 2012). The localization and SL estimates were validated by transmitting a broad-band sweep from an Avisoft ultrasonic dynamic speaker (frequency range: 5–120 kHz; sensitivity: −83 dB re. 1 V/20 μPa at 1 m) at distances from 0.5, 1, 2 and 3 m perpendicular to the array and the target. SLs were

Table 1. Biosonar parameters during each trial for each bat

| Diameter (cm) | ID | Species | No. flights | dB decrease/dh | | $x\log_{10}R$ | | r^2 |
				EFD	RMS	EFD	RMS	
30	Bald	*H. armiger*	23	9	8	30	25	0.72
	King	*H. pratti*	42	11	10	35	33	0.74
	T	*H. pratti*	34	6	5	20	17	0.33
20	Bald	*H. armiger*	21	11	9	36	31	0.67
	King	*H. pratti*	23	11	10	35	33	0.69
	T	*H. pratti*	34	5	4	16	13	0.23
12	Bald	*H. armiger*	43	12	10	39	34	0.72
	King	*H. pratti*	42	12	11	41	38	0.81
	T	*H. pratti*	22	7	6	22	20	0.61
7	Bald	*H. armiger*	31	6	5	20	16	0.49
	King	*H. pratti*	34	10	9	32	31	0.69
	T	*H. pratti*	24	8	7	26	23	0.33

The mean decrease in source level (SL) in dB per distance halved (dB decrease/dh) as well as the mean of the fitted $x\log_{10}R$ curves in the last 2 m before landing are reported for each bat (ID) and target diameter (*D*) and in both energy flux density (EFD) and root mean square (RMS) for comparison. The species and number of flights are shown for each session. r^2-values are shown for the $x\log_{10}R$ fits to the EFD.

calculated as energy flux density (EFD), i.e. acoustic energy per unit area, expressed in dB re. 20 μPa² s. The RMS SL, expressed in dB re. 20 μPa² was also calculated for comparison with previous studies. Both EFD and RMS were measured over the −6 dB window of the envelope of each call.

To identify calls where the acoustic beam axis was directed towards the target, calls were only extracted for further analysis if their RLs were highest on any of the three microphones closest to the target.

Tag

We extracted echo information from the tag when the bat was within 0.6–1.5 m of the target. At shorter distances, the target echoes overlapped with the emitted call, and at greater distances, the target echoes were masked by echoes from the walls, as verified by visual inspection of call–echo spectrograms and echograms (Stidsholt et al., 2018).

To determine target echo energy, each call–echo pair was separated in time based on the FM downward sweep from the call applied as a matched filter to find the end of the call and the end of the echo. Target echoes with less than 10 dB in-band signal-to-noise ratio were rejected to ensure accurate energy measurement. The in-band noise floor of the tag was predetermined to be 4 dB re. 20 μPa RMS (*H. armiger*) and 2 dB re. 20 μPa RMS (*H. pratti*). As the calls in the array and tag recordings were synchronized, the target range could be calculated for each call–echo pair detected on the tag. Thus, for each call, we measured the SL (from the array), the EL (on the tag) and the range to the target (by acoustic localization). SL results for each session were fitted to the logarithm of range, *R*. To test the hypothesis that bats do not adjust SL in a fixed logarithmic manner throughout target approaches, we fitted $x\log10R$ curves in logarithmically spaced bins (0.6–1, 1–1.6, 1.6–2.5 and 2.5–4 m). If our hypothesis is true and dissimilar slopes occur between the bins, we expect to find the highest slopes when the bat is closest to its target because the ELs rise faster close to the target.

The ELs received by the bat were predicted using the sonar equation based on target range (*R*), call SL and calculated TS of the spheres (Urick, 1983) and compared with the measured EL recorded by the tag for the largest target. TS of the spheres was not measured by ensonification, but calculated from the equation provided by Urick (1983).

All analyses were performed with custom scripts in Matlab 2018a.

Statistical analysis

To investigate how SL is reduced during the last 2 m of target approaches, the SLs were first fitted to target range, by linear fit of SL (measured in EFD and RMS) to $\log_{10}R$. $x\log_{10}R$ slopes were estimated for each individual for each target size for comparison with previous studies. Next, all SLs (EFD) were modelled using a generalized linear mixed-effects model (GLME, Matlab function: 'fitglme') using $\log_{10}R$ and target size as fixed effects and bat ID and individual flight trials as random effects (Table 2). The residuals of the full model were plotted and visually inspected for signs of non-normality and heteroscedasticity.

To investigate whether the bats adjusted SL according to the size of different targets, a three-way ANOVA (Matlab function: 'anovan') was performed to test for any changes between the measured ELs from the different targets. Here, we used target size, bat ID and range as explanatory variables and used ELs received between 0.6 and 1.5 m distance to avoid overlap with masking echoes. A model comparison (Matlab function: 'multcompare') between the output from the two-way ANOVA was used to determine significant differences between ELs for different target sizes and individual bats.

All SL (both EFD and RMS) and EL measurements were normally distributed (Anderson–Darling test, Matlab function: 'adtest').

RESULTS

We recorded the vocalizations and echo returns of three hipposiderid bats approaching targets of four different sizes. For

Table 2. Generalized linear mixed-effect model analysis for the relationship between source level (SL) and target range ($\log_{10}R$)

	Name	Estimate	*t*	d.f.	*P*-value
Fixed effects coefficients	(Intercept)	71.3	48.52	4551	0
	$\log_{10}R$	28.2	57.90	4551	0
	TS	2.1	11.42	4551	0
Random effects covariance parameters	Name 1	Name 2	Type	Estimate	
ID (3 levels)	(Intercept)	(Intercept)	s.d.	2.4	
Trial (354 levels)	(Intercept)	(Intercept)	s.d.	3.3	
Model fit statistics	AIC	BIC	r^2		
	27423	27462	0.63		

Model: SL~1+$\log_{10}R$+TS+(1|trial)+(1|ID). Target size (TS) was a fixed effect and trials and individual bat were random effects. AIC, Akaike's information criterion; BIC, Bayesian information criterion.
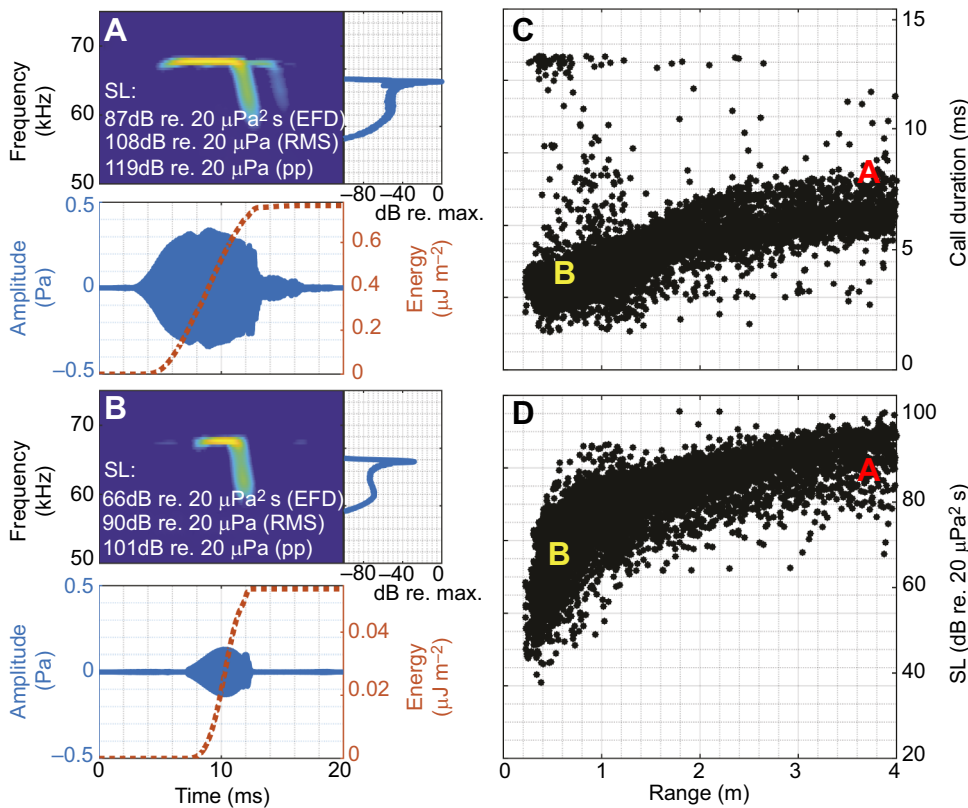
Fig. 3. Output changes during approach. (A,B) Time and frequency domain representation of a long (A) and a short (B) *Hipposideros armiger* call. The spectrogram of the calls was made by using a fast Fourier transform (FFT) length of 512 with a window length of 512 and an overlap of 500 samples at a sampling rate of 187.5 kHz and a dynamic range of 40 dB. SLs of both calls using peak–peak (pp), root mean square (RMS) or energy flux density (EFD) units over a −6 dB window are shown for comparison. (C) Call duration and (D) SL reduction during an approach from 4 m distance, pooled for all bats. The long (red A) and short (yellow B) calls that are detailed in the left-hand panels are indicated in both right-hand plots.

comparison with previous studies, we first fitted SLs to logarithmic curves over the last 2 m of the approaches (Fig. 3, Table 1). When approaching the targets, all bats decreased the SL (Fig. 3D) and duration (Fig. 3C) of their vocalizations. In the last 2 m before landing, the three bats showed energy compensation of 5–11 dB per distance halved with an average of 9 dB per distance halved ($29\log_{10}R$; Table 1) but with considerable variation (16–41$\log_{10}R$; Table 1). Absorption over this 2 m interval did not cause a strong deviation from a logarithmic model. Thus, to test whether there was a non-logarithmic SL adjustment consistent with the greater absorption at longer ranges, we performed fits of measured SL within logarithmically spaced bins from 0.6 to 4 m. The rate of

energy compensation increased as the bats approached the targets from approximately 0–20$\log_{10}R$ at 2–4 m to approximately 40$\log_{10}R$ close to the target, but with large individual differences (Fig. 5).

If bats adjust their SL so as to stabilize ELs, they risk losing information about target size. To test whether EL varied with target size, the ELs from each on-axis call were extracted from the tag recordings (Fig. 4) in the overlap-free zone between 0.6 and 1.5 m distance (Fig. 6). Because of the length of the calls, echoes were masked by the bats' own vocalizations at target ranges closer than 0.6 m, while at distances further than 1.5 m, the echoes were embedded in clutter even though the flight room was covered in
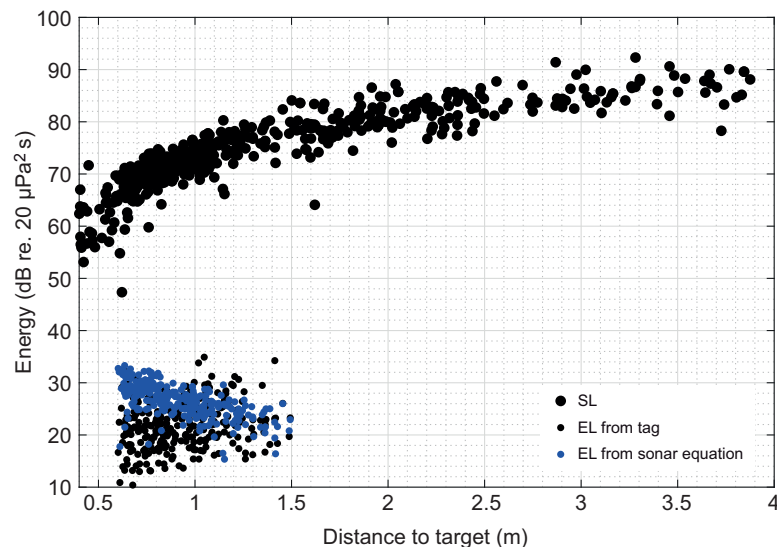
Fig. 4. Example of energy compensation during approach. SL (large black circles) adjustment during approach of the largest target. The returning ELs recorded by the tag (small black circles) are mostly lower than, but roughly comparable to, the calculated ELs based on the sonar equation (blue circles) in the range interval over which they could be measured (0.6–1.5 m).
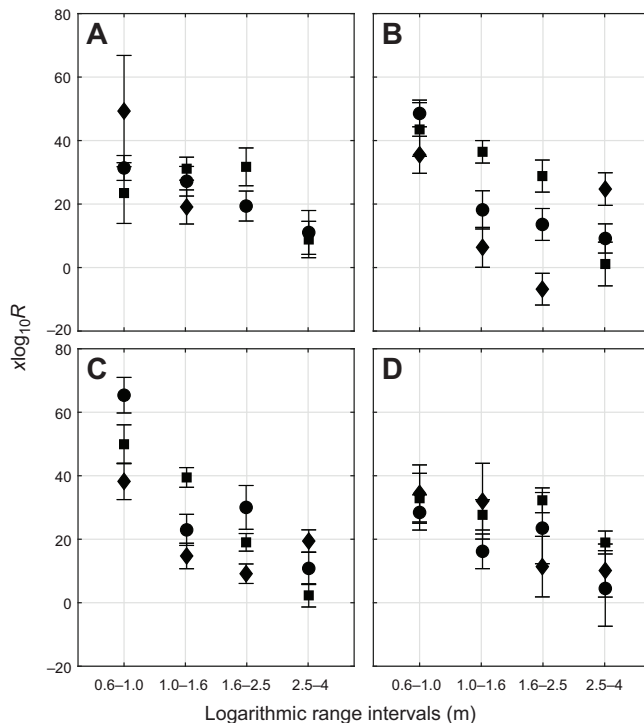
Fig. 5. Energy compensation in logarithmically spaced bins for four different-sized targets. Slopes of the $x\log_{10}R$ curves in logarithmically spaced intervals (0.6–1, 1–1.6, 1.6–2.5 and 2.5–4 m) for each target (A, 30 cm; B, 20 cm; C, 12 cm; D, 7 cm). The slopes are based on SL measured in EFD. Because of the high number of replications, a mean of 97 data points is included in each logarithmically spaced bin per target size. Two sessions included fewer than 25 points and were excluded from this figure. Diamonds and squares: *Hipposideros pratti*, circles: *H. armiger*.

acoustic foam (Fig. 6). EL predictions based on the sonar equation using SL, range and TS agreed well with the actual ELs recorded by the tag for the largest target (Fig. 4). The calculated ELs were therefore used for further analysis to avoid interference and clutter and to allow the same method to be used for all targets. The calculated ELs were overall between 0 and 40 dB re. 20 µPa² s (Fig. 7; 95% distribution of ELs between 7 and 36 dB re. 20 µPa² s), but varied widely with individual and target size (95% distribution

of ELs for each individual: 11–34, 6–29 and 6–40 dB re. 20 µPa² s). A two-way ANOVA using bat ID and target size as explanatory variables revealed that ELs differed significantly for each bat [F=183, P<0.0001, population means of 19 and 22 dB re. 20 µPa² s (*H. pratti*) and 25 dB re. 20 µPa² s (*H. armiger*)]. Target size was also a significant explanatory variable (F=120, P<0.0001). The four targets (30, 20, 12, 7 cm) reflected mean ELs of 22, 26, 25 and 20 dB re. 20 µPa² s, respectively.

DISCUSSION

Bats actively control the echo information available to them during navigation and prey acquisition by changing the time and frequency pattern of their calls to match the task at hand (Griffin et al., 1960). As part of this dynamic control over echo information, they have been reported to reduce their output levels logarithmically as they approach targets, presumably to maintain ELs in a dynamic range suited for their hearing system and to reduce forward masking of the echoes received milliseconds after emission of calls (Hartley, 1992b; Koblitz et al., 2011). This transmission-level control is joined by a receiving sensitivity control in which the hearing threshold is gradually increased during target approach by contraction of the stapedial muscles. In concert, these two mechanisms have been proposed to render stable perceived ELs for FM bats (Hartley, 1992b) by compensating for the decreasing TL as bats approach targets. However, the TL is the sum of a geometric spreading component which is logarithmic with range and an absorption component that is linear with range (Fig. 2). The contribution of absorption is minor for bats using low frequencies, but the effect is substantial for species such as the hipposiderid bats studied here (Fig. 3A,B). With the inherent limitations of the low sample size in this study, we sought to understand how bats facing high absorption adjust their sonar emissions during active approaches to point targets. We hypothesized that because of the increasing effect of absorption at greater distances, CF bats using higher frequency vocalizations would adjust their SLs less at large distances to ensure a sufficiently high echo-to-noise ratio (ENR), and more at shorter distances where the absorption is less significant.

Previous target approach studies of some species of CF bats have shown that they reduce SLs logarithmically with target range by between 6 and 9 dB per distance halved when approaching large targets (Hiryu et al., 2008; Kobler et al., 1985; Tian and Schnitzler,
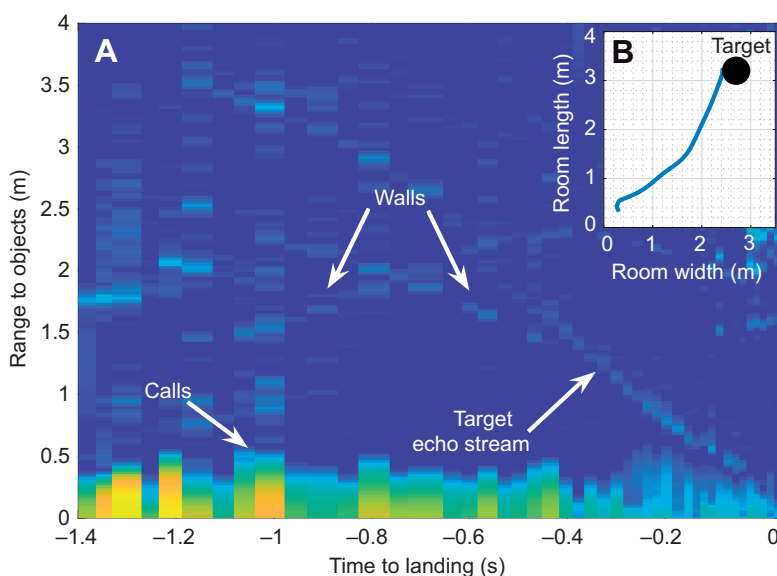
Fig. 6. Echoic scene during target approach. (A) Echogram illustrating the echoic scene during a typical target approach to the large sphere. Sound envelopes corresponding to each outgoing call and the returning echoes are represented by vertical coloured bars and displayed in the horizontal axis at the production time of the call (Johnson, 2004). The y-axis represents the time delay converted into distance between emission of a call and return of the echoes; the y-axis distance resolution is enhanced by using the FM downward sweep of the call as a matched filter to process the echoes. As this echogram is based only on the FM part of the calls, in order to visualize the echoic scene, the CF part of the calls is not visualized. Within the last 0.6 m before landing, the outgoing calls overlap in time with the target echoes because of the long duration of these CF calls used to estimate the Doppler shift of the echoes. At a target range >1.5 m, clutter echoes from the walls and ceiling either mask the target echoes or return to the bat before the target echo of interest. (B) Dead-reckoning track of the approach laid on top of the flight room dimensions for comparison with the echogram.
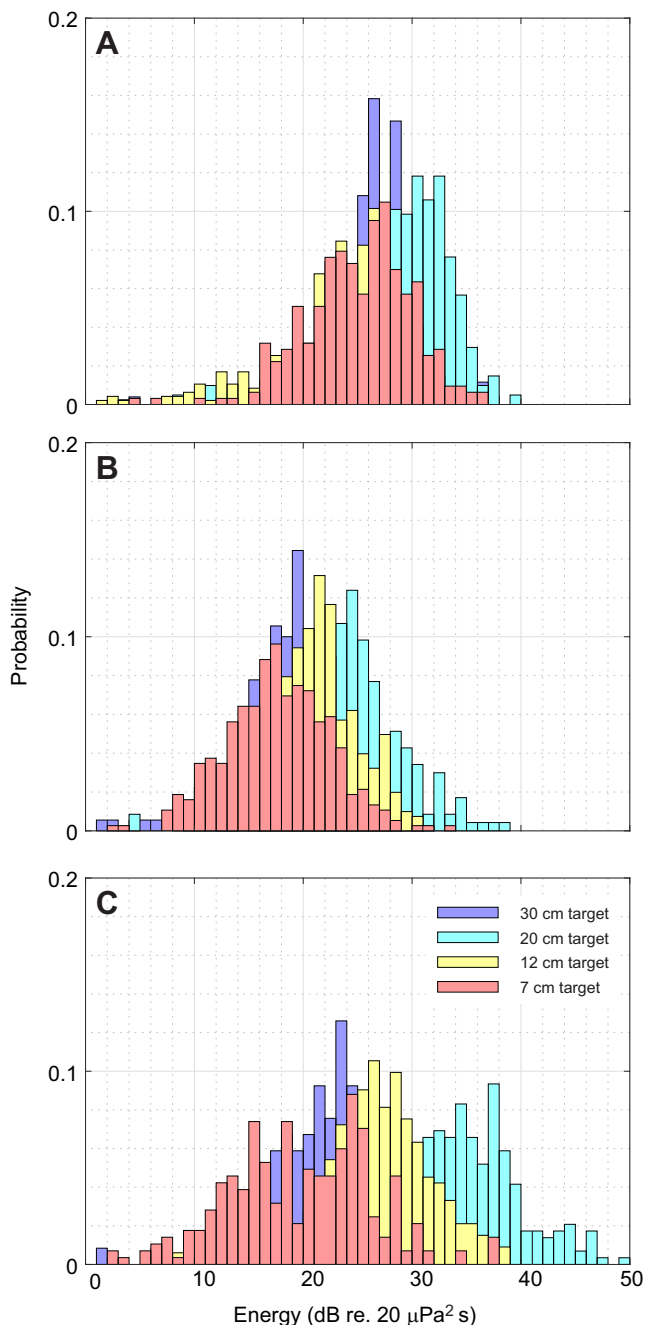
Fig. 7. Dynamic range of returned estimated ELs. Each panel (A–C) represents an individual bat. The ELs were calculated based on the sonar equation in the range interval of 0.6–1.5 m before landing and are colour coded according to the target size. The 95% distribution of ELs for each panel is 11–34 dB re. 20 μPa^2 s (A), 6–29 dB re. 20 μPa^2 s (B) and 6–40 dB re. 20 μPa^2 s (C).

1997) and on average 6 dB per distance halved when approaching a meal worm close to the ground (Hartley et al., 1989). Mantani and co-workers (2012) recorded the reduction in the intensity of vocalizations of *Rhinolophus ferrumequinum nippon* catching fluttering moths using a telemike. A reduction of 35 dB was found during an approach spanning 2.5 s. However, the range to the target and absolute on-axis SL were not measured in that study. Here, we show that three individuals from two species of CF bats (*H. armiger* and *H. pratti*) reduce both call duration (Fig. 3C) and SL (Figs 3D and 4) when approaching target spheres. The CF bats

used in this study on average halved the duration of their emitted signals during the approach (Fig. 3). For the same amplitude, a halving of the pulse length will result in the same peak–peak and RMS levels for the two pulse lengths. In contrast, the energy level (EL) would decrease by 3 dB, which explains the slightly larger values of EFD adjustment compared with RMS (Table 1). The difference in SL adjustment estimates using RMS pressure versus energy will be larger for some FM species in which call duration may change by an order of magnitude during approach, leading to a 10 dB reduction in energy (but not RMS) from just the change in duration. This assumes that bats are using all the available energy in their calls even if the duration of these exceeds the integration time (Surlykke and Bojesen, 1996). The integration time has been measured in only a few studies, with values of 200–400 μs (Simmons et al., 1989; Wiegrebe and Schmidt, 1996), 2.4 ms (Surlykke and Bojesen, 1996) and 60 ms (Schmidt and Thaller, 1994) for FM bats, suggesting an adaptable integration time matched to the task (Surlykke et al., 2016). To our knowledge, integration time has not been measured in either *Hipposideros armiger* or *H. pratti.* However, as these bats exert an impressive dynamic control of the duration of their calls in relation to different tasks, it appears parsimonious to assume a dynamic integration time in keeping with those changes in call duration and hence report levels in energy.

For the bats studied here, the SL reduction resulted in an energy compensation between 5 and 11 dB/dh during the last 2 m before landing (Table 1) with an average of 9 dB/dh, when computed from the RMS. The rates are slightly higher for SL calculated in energy rather than RMS (Table 1), but the effect is most pronounced for the $x\log_{10}R$ values (Table 1). We further show that the energy reduction rate was not constant during the approach (Fig. 5). At more than 2.5 m target range, the bats on average adjusted their SL little to changing range. As the bats closed in on the target, the energy compensation gradually increased to on average around $40\log_{10}R$ at close distances, but with large variations (Fig. 5). These results are consistent with data from eight FM species (*Artibeus jamaicensis, Macrophyllum macrophyllum, Myotis daubentonii, Phyllostomus hastatus, Phyllonycteris poeyi, Saccopteryx bilineata, Saccopteryx leptura* and *Rhynchonycteris naso*) showing variable reduction rates far above the established $20\log_{10}R$ relationship with a maximum of $99\log_{10}R$ in one extreme case (i.e. 30 dB/dh), spanning both laboratory settings and in the wild (Jakobsen et al., 2015; Norum et al., 2012). However, the reported reduction rates vary widely between studies from 3 to $99\log_{10}R$, leading us to posit that logarithmic fitting of SL to target range is not biologically relevant, as also suggested by Norum and colleagues (2012). In contrast to exponential fitting suggested by these authors, we argue that the search for a general control law for SL operable over all target ranges may mask the finer details of how bats adjust their transmitting energy.

Instead, we propose for long target ranges that these bats produce high-intensity calls with little range adjustment to match the high absorption at greater ranges to improve poor ENRs after initial detection. This notion is supported by a weak mean EL of 2 dB re. 20 μPa^2 s (23 dB re. 20 μPa RMS for a 7 ms echo) for all targets at a distance between 3 and 4 m. This must be assumed to be close to the hearing threshold of bats (Stilz and Schnitzler, 2012), which supports the hypothesis that absorption is an important limiting factor for these species at greater ranges. In contrast, at closer ranges, the relative effect of absorption on the total TL is much lower, which in concert with a greatly reduced geometric spreading loss means that the increase in EL of a point target during a decrease of bat–target range will increase rapidly if no SL adjustment is used.

Thus, these bats are reducing their outgoing call levels a lot at close ranges, resulting in received ELs of all targets in a dynamic range between 6 and 40 dB re. 20 µPa^2 s (Fig. 7).

We initially hypothesized that target size would not affect the output adjustments, meaning that the relative EL differences between targets would correspond to the differences in the actual TS. The four targets (largest to smallest TS: −3, −6, −10, −15 dB) resulted in mean ELs of 22, 26, 25 and 20 dB re. 20 µPa^2 s, but with large variation. As the differences in mean received ELs are smaller than the relative differences in TS between the spheres and do not even vary monotonically with the TS, the bats must have been partially adjusting for target size, but not in a 1 dB:1 dB fashion. As the largest target did not result in the largest mean EL (22 dB re. 20 µPa^2 s), estimation of target size by the bats is apparently not informed solely by relative differences in EL distribution between targets during approaches, but rather perhaps by the relationship between the loudness of the outgoing call and the EL for a given echo delay (Denzinger and Schnitzler, 1998). Alternatively, bats might use only the first few call–echo pairs after detection to estimate the size of the target rather than the entire EL distribution of approach calls. Either way, it means that the studied bats do not seek to stabilize perceived ELs. When bats approach targets, they can also use other cues to distinguish the targets, e.g. the angular range in which the echoes return (Heinrich and Wiegrebe, 2013). It may also be that the bats were adjusting SL more steeply in the approach as the target size increases. This notion is supported by the literature showing that bats decrease their output levels at a distance of 2 m before landing on platforms and walls representing large targets (Kobler et al., 1985; Koblitz et al., 2011), whereas smaller target interceptions cause a delayed reduction beginning within the last 1 m of approach (Boonman and Jones, 2002; Hartley, 1992b; Melcón et al., 2007; Saillant et al., 2007). Hence, it seems as if these CF bats defend a fairly narrow received EL dynamic range for all target sizes, which span 6–40 dB re. 20 µPa^2 s, matching the preferred dynamic range of some 40 dB of non-echolocating mammals, such as humans for speech (Rhebergen et al., 2009). The dynamics of the perceived EL would be further narrowed if the stapedial reflex affects the sensitivity to echoes received just after sound emission, as seen for FM bats (Hartley, 1992b). But, there is no clear evidence of a stapedial reflex affecting perceived echo intensities in CF bats, perhaps because of the Doppler-induced spectral decoupling between outgoing calls and returning echoes by which outgoing calls and incoming echoes will excite different populations of auditory neurons given the sharp tuning curves of CF bats (Tian and Schnitzler, 1997).

Thus, while CF bats use a tight closed-loop echo feedback to provide spectral Doppler compensation, they do not show a closed-loop energy compensation even when they approach a point target. What then guides the onset of the energy compensation? This is an important question not only to help understand the way bats perceive their environment but also because SL adjustment is widely interpreted as marking the beginning of the acoustical approach phase (Griffin et al., 1960).

Previous studies have suggested that the transition into approach phase is guided by target detection (Griffin et al., 1960; Kalko and Schnitzler, 1989) or by a target EL threshold (Budenz et al., 2018). Budenz and co-workers (2018) proposed that the onset of energy reduction was triggered by a certain target EL, which in their study was around 41–42 dB re. 20 µPa^2 RMS (duration: ∼2 ms resulting in 15 dB re. 20 µPa^2 s) for *Myotis myotis* under cluttered conditions. Our bats performed energy compensation in response to echoes below this threshold in 13% of the calls emitted between 0.6 and 1.5 m ranges, which means that for CF bats this is not a valid threshold even under semi-cluttered conditions (Fig. 6). As the mean calculated ELs between 3 and 4 m were around 2 dB re. 20 µPa^2 s (or 23 dB re. 20 µPa^2 RMS for a call duration of 7 ms), which is slightly above the estimated hearing threshold of 20 dB re. 20 µPa^2 RMS (Stilz and Schnitzler, 2012), we argue that bats should just be able to detect the spheres at take-off and during their first few metres of flight, where they do not yet adjust, probably to maximize ENR. Thus, the onset of SL and inter-call interval adjustment to a target is probably not triggered by target detection, or by a specific EL, as the ELs around the time of adjustment vary over a 20 dB range. Our data therefore support the notion that acoustically and behaviourally defined approach phases may differ and that the detection distance cannot be reliably inferred from the acoustically defined approach phase (Boonman and Jones, 2002).

In conclusion, we found that three individuals of two species of *Hipposideros* reduce their emitted energy during target approach in a non-logarithmic fashion to maximize ENR at long ranges and to avoid high ELs when close to the targets. The effect of this adjustment is that target echoes are maintained in a dynamic range from 6 to 40 dB re. 20 µPa^2 s over the target distance, which gives non-overlapping target echoes. As the energy compensation is loosely controlled in contrast to the extremely well-regulated spectral Doppler-shift compensation, we posit that the energy compensation should not be seen as an automatic gain control but rather as a dynamic range compression strategy. This may be operated as a hysteretic control whereby bats reduce their emitted intensity gradually when the EL in a sequence of calls increases progressively closer to the presumed upper limit of the comfort zone of the receiving sonar system of approximately 40 dB re. 20 µPa^2 s (∼60 dB re. 20 µPa RMS for these calls). For species affected by high sound attenuation, and limited at long ranges by a maximum call energy, the rise in EL would begin closer to the target during active approaches compared with that for lower-frequency species for the same output level. Thus, we predict that CF bat species using even higher frequency (e.g. 100–200 kHz; Heller and Helversen, 1989) will start reducing biosonar output (and therefore transition into the acoustically defined approach phase) closer to a target in comparison to a low-frequency species performing the same task and using the same initial output level. To study further how bats perceive the auditory sensory stream from a target, it will be necessary to measure the integration time(s) in CF bats, to understand how the hearing sensitivity changes with varying SL, range and species, and to address how the energy compensation is modulated during capture of moving prey in the wild with natural masking noises and higher SLs.

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