

Echolocation signal structure in the Megachiropteran bat *Rousettus aegyptiacus* Geoffroy 1810

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Accepted 20 September 2004

Summary

Rousettus aegyptiacus Geoffroy 1810 is a member of the only genus of Megachiropteran bats to use vocal echolocation, but the structure of its brief, click-like signal is poorly described. Although thought to have a simple echolocation system compared to that of Microchiroptera, *R. aegyptiacus* is capable of good obstacle avoidance using its impulse sonar. The energy content of the signal was at least an order of magnitude smaller than in Microchiropteran bats and dolphins (approximately $4 \times 10^{-8} \text{ J m}^{-2}$). Measurement of the duration, amplitude and peak frequency demonstrate that the signals of this animal are broadly similar in structure and duration to those of dolphins. Gabor functions were used to model signals and to estimate signal parameters, and the quality

of the Gabor function fit to the early part of the signal demonstrates that the echolocation signals of *R. aegyptiacus* match the minimum spectral spread for their duration and amplitude and are thus well matched to its best hearing sensitivity. However, the low energy content of the signals and short duration should make returning echoes difficult to detect. The performance of *R. aegyptiacus* in obstacle avoidance experiments using echolocation therefore remains something of a conundrum.

Key words: echolocation, click, Megachiroptera, bat, *Rousettus aegyptiacus*, intensity.

Introduction

Microchiropteran bats possess sophisticated echolocation systems, which are well matched to their ecological niche (Fenton, 1995). They employ a range of call types, consisting of frequency modulated and/or constant frequency portions that have durations from as short as 1 ms to >50 ms (Neuweiler, 1983). Other echolocating animals including cetaceans (Au, 1993), oilbirds and cave swiftlets (Griffin, 1953; Suthers and Hector, 1985; Fullard et al., 1993) use short duration impulsive clicks as echolocation signals (Fenton, 1984). From a theoretical basis, a signal of infinite amplitude and infinitesimally small duration is ideal for precise location of an echo in time, and thus a short duration, intense click stimulus that approximates this should make a good system for echolocation (Connor, 1982). In the terrestrial environment, however, the difference in impedance between the animal (which acoustically behaves effectively as water) and the transmission medium (air) results in large transmission losses both when the signal is produced and when the echo is received (Cracknell, 1980). Such a system requires the animal to produce a click signal with very high amplitude if the signal is to contain enough energy to produce a detectable echo. In the aquatic environment, by contrast, these clicks are ideally suited to the sound transmission medium as there is a good match in acoustic impedance between the dolphin and the water. Therefore sonar pulses

can be transferred much more efficiently to the water, resulting in high output levels (Norris and Harvey, 1974). Echolocating dolphins show impressive capabilities in target ranging and spatial resolution, thus demonstrating the effectiveness of impulse biosonar if the transmission problems are not an issue (Au, 1993). Given the constraints on impulse biosonar in air, click stimuli used by terrestrial animals for echolocation have been thought of as comparatively simple or rudimentary (Griffin et al., 1958), and little consideration has been given to the fine temporal or spectral structure of their signals.

Among the Megachiropteran bats, only the genus *Rousettus* has developed vocal echolocation, producing signals by clicks of the tongue (Möhres and Kulzer, 1956). The clicks of *Rousettus aegyptiacus* Geoffroy 1810 are emitted in pairs and have been reported to be in the region of 0.6–1 ms duration, with a frequency range of 12–70 kHz and peak frequency at 20–40 kHz (von Herbert, 1985). Despite the apparently rudimentary nature of its echolocation system, *R. aegyptiacus* appears to have spatial resolution comparable to Microchiropterans in some tasks, such as wire avoidance (Griffin et al., 1958; Waters and Vollrath, 2003). This leads to a conundrum if, as discussed earlier, the echoes of impulse clicks are difficult to detect in the terrestrial environment. However, to date, no measurement of amplitude or energy

content of impulse clicks produced by terrestrial echolocating animals has been made.

A recent study (Waters and Vollrath, 2003) recorded click durations in *R. aegyptiacus* that were shorter than in previous studies (Möhres and Kulzer, 1956; Novick, 1958; von Herbert, 1985), and are closer in duration to those of dolphins than other terrestrial animals using similar signals, such as oil birds and cave swiftlets (Griffin, 1953; Suthers and Hector, 1982).

When analysed by conventional sonographic methods based on Fourier decomposition, short-duration impulsive clicks appear to contain a wide range of frequencies, some of which may lie outside the animal's range of sensitivity. Since the total energy content of the click is limited, this spreading of energy into inaudible frequencies would further degrade the detectability of the echo. However, Fourier methods are not well suited to the analysis of brief time-limited signals, because the technique confounds frequency components of the emitted carrier frequency with frequency decomposition of an amplitude envelope, and the apparent wide bandwidth may be artefactual. Fourier methods can be extended to be applied to time-limited signals by employing a range of windowing functions (e.g. short-term Fourier transform; Vetterli and Kovacevic, 1995); one of the more appropriate windows is the Gaussian, but others are available. However, as with all Fourier methods, the resolution of the carrier frequencies is constrained by the sampling frequency; short-duration signals may not contain sufficient samples to allow the spectral information of carrier frequencies to be determined reliably, and amplitude transients can dominate the frequency spectrum of short-duration signals. An alternative to Fourier methods is wavelet decomposition, in which case the Gaussian-envelope Morlet–Gabor wavelet (Vetterli and Kovacevic, 1995) could be used. The initial choice of basis function in wavelet analysis is usually arbitrary unless there are *a priori* reasons to select a specific basis function type. Different basis functions may be tried until the required level of resolution and/or signal characteristics are revealed. As an alternative approach to both fast Fourier transform (FFT) analysis and wavelet decomposition, we adopt here a related technique that has previously been applied to the very short duration clicks of dolphins: this is to fit a Gabor function of arbitrary frequency and other parameters to the sampled signals (Lanen and Kamminga, 1988; Kamminga and Beitsima, 1990). In this analysis, we fit a specific function to the captured signals, as there are good *a priori* reasons for so doing related to the inverse relationship between the duration of a signal and its bandwidth. A Gabor function consists of a constant-frequency carrier enveloped by a Gaussian amplitude term. An appropriate choice of carrier frequency and Gaussian width can represent a signal containing few pressure amplitude peaks, as is the case in dolphins and in *R. aegyptiacus*. Uniquely this signal has a power spectrum that is also modulated by a Gaussian envelope, centred on the carrier frequency, and has a minimum time-bandwidth product that conveys advantages for sonar detection (Wiersma, 1988). If *R. aegyptiacus* signals can realistically be approximated in this way, then the

technique should give more meaningful estimates of signal properties in the frequency domain than can Fourier methods.

The expectation that a Gabor function might approximate the signals is not based solely on a perceived similarity in waveform. Signals with a Gaussian envelope are potentially of great importance to animals using short-duration impulsive clicks since they have the minimum bandwidth for any given duration, they minimize frequencies transmitted in unfavourable bands away from the carrier frequency, and they also minimize detection ambiguity of signals in space and time (Vetterli and Kovacevic, 1995). By reducing the energy in signals and echoes outside the animal's best frequency of hearing, and concentrating energy into the most sensitive range, a bat using a signal of this type should improve the chances of detection. It is also more likely to be able to measure the start time of the returning echo, and thus should have a more accurate ranging ability. Additionally, focussing the energy into a limited bandwidth will increase the energy per unit frequency, with a subsequent increase in the signal-to-noise ratio within each critical band, further enhancing detection (Zwicker et al., 1957).

Experiments that have measured the total energy content of Microchiropteran signals have shown that the energy is distributed across the duration of the signal (Waters and Jones, 1995). It should be predicted, therefore, that for click sonar to be effective with comparable distances and targets, each click should be comparable in energy content with that of a Microchiropteran, but the short duration of a click signal would necessitate much higher peak amplitude to maintain energy content. Given the previous lack of accurate data on the waveform structure of *R. aegyptiacus* clicks it is crucial that measurements of amplitude, energy, duration and peak frequency are made, to determine whether *R. aegyptiacus* signals are like those of other terrestrial animals using broadband clicks or are more similar to those of dolphins. Accurate measurements will also allow the modelling of signals by Gabor functions, to determine whether, like dolphins, *R. aegyptiacus* clicks minimise bandwidth for any given duration.

Materials and methods

Experimental subjects

Five adult *Rousettus aegyptiacus* (4 males, 1 female), on loan from Tropical World Zoo, Leeds, UK, were housed in a 4 m×2 m×1 m cage in a room at 25°C and subjected to a 12 h:12 h light:dark reversed photoperiod. They were fed 150 g of fruit each per day and had access to water at all times. Bats were marked with animal marker spray on their backs for identification. Whilst bats were obtained from a captive colony, they were actively able to fly within their large home cage and echolocation calls were heard freely when the room was dark. Previous experience from bats in the same colony has shown that their echolocation system is fully functioning and allows them to detect and avoid obstacles in complete darkness (Waters and Vollrath, 2003).

Waveform structure and signal intensity

Measurements were made using $\frac{1}{4}$ " microphones (Larson Davis 2520; Provo, UT, USA) with the protective grid removed (± 4 dB 20–100 kHz). The signals were recorded in a flight corridor (length 25 m, height 2.59 m, width 1.45 m) that was unfamiliar to the bats upon their first release. Signals were recorded using a symmetrical star array of four microphones oriented perpendicular to the flight path. The array resembled a letter Y with each arm 42.5 cm long and separated by an angle of 120° with one microphone in the centre. The bats were released facing directly towards the array at a distance 7 m from it, and recording was triggered simultaneously. The signals were recorded with all lights in the corridor off and light levels were measured at 0.0002 mW m^{-2} using a Tektronix J16 Digital Photometer (Beaverton, OR, USA) (effectively complete darkness). Data were captured at 12 bits at a rate of 300 kHz on a Keithley Metrabyte kPCI 3110 A/D board (Cleveland, OH, USA) mounted in a PC. The microphone was calibrated using a 1411E calibrator (Dawe Instruments, London, UK). At least five signal trains from separate runs were recorded for each bat. Data files collected were converted to WAV format and analysed using Cool Edit Pro[®] software (Syntrillium Software; San Jose, CA, USA). For signal duration, ten signals were analysed for each bat. Mean click duration was measured as the point at which amplitude had reduced to less than 10% of its maximum intensity, as this provided the most consistent estimate of signal duration before the amplitude of the signal became indistinguishable from fluctuations in the noise floor. Inter-click pair interval was measured, and frequency at the peak amplitude was estimated by a 512 point FFT with Hanning window.

The range of the bat was determined using the methodology of Aubauer (1995) as modified by Au and Herzing (2003), by measuring the time of arrival difference between the centre and the other three microphones. If the difference in arrival time is denoted as τ_{0i} , where the three microphones are represented as $i=1, 2$ and 3 , then the range R can be expressed as:

$$R = \frac{3A^2 - c^2(\tau_{01}^2 + \tau_{02}^2 + \tau_{03}^2)}{2c(\tau_{01} + \tau_{02} + \tau_{03})}, \quad (1)$$

where c is the velocity of sound in air and A is the length of each arm of the array (Au and Herzing, 2003). Any signal in which the amplitude at the centre of the array was either not the highest or was within 3 dB of the highest was rejected. This technique has been used successfully by Aubauer (1995), Au and Herzing (2003) and Holderied and von Helversen (2003). The device was calibrated using a 95 dB 10 kHz sine wave with a square envelope 0.02 ms in duration synthesised by a SD5 stimulator (Grass Instruments, West Warwick, RI, USA) gating a 5 MHz function generator (Thandar TG501, Huntingdon, UK) and played back through a speaker (Ultrasound Advice, London, UK) positioned at a set distance from the microphone. At each distance, ten measurements were taken from the array. The distance error between actual distance and distance calculated from the arrival times at the

array microphones corresponds to a maximum error of 1.94 dB at 7 m and 0.97 dB at 6 m.

All sound pressure levels are expressed as peak-equivalent (dB peSPL) values after Stapells et al. (1982).

To calculate intensity at 1 m (source level) a regression of distance on intensity was performed from the data. As many signals as were available for each of the five bats and conformed to the criterion defined above were included in the intensity regression. Intensity I at range R is given by the power P per unit area. The area over which the power is distributed is expected to conform to the spherical spreading law for transmission loss so that

$$I = P / \pi r^2, \quad (2)$$

where r is the radius of the circular area over which the power is distributed at range R . Since r is proportional to R ,

$$I \propto 1 / R^2. \quad (3)$$

Sound level S is expressed on a decibel scale as 10 times the logarithm of sound intensity at distance R (m) compared to intensity at distance 1 m, and following Equation 3 can be evaluated as:

$$S = 20 \log R. \quad (4)$$

The measured relationship between sound level and intensity was tested against the predicted values derived from this equation (though there would be additional extra losses through excess atmospheric attenuation that may be frequency-dependent).

Energy flux density

The energy flux density E is a measure of the energy content of a sound pulse at 1 m from the source, assuming the source is isotropic. Au (1993) defined E in a form compensated for the density of the medium as:

$$E = \frac{1}{\rho c} \int_0^T P^2(t) dt, \quad (5)$$

where E is energy flux density in J m^{-2} , $P(t)$ is the time varying sound pressure, T is the duration of the signal, ρ is the density of the medium (kg m^{-3}) and c is the velocity of sound in the medium. This form makes it possible to compare intensities in terrestrial and aquatic environments. Since $P(t)$ is effectively the amplitude of a signal at a given time a program was written using Testpoint[®] (Capital Equipment Corporation, Bedford, NH, USA) to extract these values from a given click waveform and to calculate the integral using the trapezoid rule. Ten energy values were obtained from clicks from each bat and standardised to a distance of 1 m, assuming spherical spreading.

Modelling a Gabor function

Preliminary analysis suggests that the echolocation signals of *R. aegyptiacus* are brief and intensely amplitude-modulated, with either a uniform frequency or a slow frequency sweep.

Such signals are not amenable to conventional Fourier or sonographic analysis because of the relatively poor frequency information available owing to the brevity of the signals (and correspondingly low number of samples), and potential cross talk between frequency information in the signal envelope and the signal frequency itself. Typically, sonographic analysis resolves the signals simply as broadband clicks with poorly determined frequency structure. To better understand the frequency content and duration of such signals, they are compared to an idealised Gabor function where frequency and temporal parameters can be extracted directly.

For any given signal duration, the minimum bandwidth is achieved using a Gabor function, in which the carrier frequency is modulated by a Gaussian envelope. The real zero-centred Gabor function $G(t)$ is written:

$$G(t) = ae^{-t^2/\sigma^2} \cos 2\pi(ft + \phi), \quad (6)$$

where a is the amplitude, σ the width of the modulating envelope, f is the frequency and ϕ the phase of the carrier wave. These four parameters are independent and mathematically unambiguous up to a multiple of 2π in the phase. The equivalent time-shifted Gabor function relative to time centre \bar{t} can be written:

$$G(t) = ae^{-(t-\bar{t})^2/\sigma^2} \cos 2\pi[f(t-\bar{t}) + \phi]. \quad (7)$$

The first harmonic can also be added to the calculation, represented by the equation:

$$G_2(t) = e^{-(t-\bar{t})^2/\sigma^2} \{a_1 \cos 2\pi[f_1(t-\bar{t}) + \phi_1] + a_2 \cos 2\pi[2f(t-\bar{t}) + \phi_2]\}. \quad (8)$$

Suppose that an experimental signal has been digitized at sampling frequency f_s as:

$$S_i = S(t_i), \quad 1 \leq i \leq N \quad (9)$$

at time points

$$t_i = \bar{t} + f_s i, \quad (10)$$

where \bar{t} is an arbitrary base time. Then in principle the signal parameters a , f , σ and ϕ (as well as the Gabor centre \bar{t} and the base time \bar{t} , which are arbitrary and not significant to the shape or information content of a single signal) can be determined by minimizing the mean-square error:

$$s_e^2 = \sum_{i=1}^N [S_i - G(t_i)]^2, \quad (11)$$

Gabor functions modelling the real data were generated by determining the values of a , f , σ and ϕ that minimize s_e^2 with the solver function in Microsoft Excel, using the Generalized Reduced Gradient (GRG2) method. Starting estimates of the parameters a , f , σ and ϕ were extracted from real signals using custom functions written within Testpoint.

Ten signals from each bat were analysed and the fit between the sampled signal and the estimated Gabor function was then tested by cross-correlation. The frequency f of the carrier wave extracted by the Gabor model should be equivalent to the

frequency at peak amplitude of the click; the duration t_c of the Gabor modelled click, determined by the times at which the envelope amplitude exceeds 10% of its maximum, satisfies $e^{-t_c^2/4\sigma^2} = 0.1$ and can be calculated as:

$$t_c = 2\sigma\sqrt{\ln 10} = 3.04\sigma. \quad (12)$$

The parameters f and t_c were extracted and compared with the values calculated by Fourier methods from the recordings. The Gabor phase parameter ϕ has no direct equivalent among sonograph outputs.

The Fourier transform

$$F(\omega) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} G(t) e^{-i\omega t} dt \quad (13)$$

of the real Gabor function $G(t)$ can be evaluated as:

$$F(\omega) = \frac{a\sigma e^{-i\omega\bar{t}}}{2\sqrt{2}} \left[e^{2\pi i \phi - \frac{1}{4}(\omega - 2\pi f)^2 \sigma^2} + e^{-2\pi i \phi - \frac{1}{4}(\omega + 2\pi f)^2 \sigma^2} \right]; \quad (14)$$

each branch of the transform has a Gaussian envelope of bandwidth $\omega_c/2\pi$ estimated from the 10% amplitude of the envelope as:

$$\frac{\omega_c}{2\pi} = \frac{2}{\pi\sigma} \sqrt{\ln 10} = \frac{0.966}{\sigma}. \quad (15)$$

An Excel spreadsheet was written to calculate a 64 point FFT for the signal and the Gabor function model.

By substituting $G(t)$ from Equation 7 into Equation 5 the signal energy flux density E for a Gabor model can be evaluated as:

$$E = \frac{a^2 \sigma \sqrt{\pi}}{2\sqrt{2} \rho c} \left(1 + e^{-2\pi^2 f^2 \sigma^2} \cos 2\phi \right). \quad (16)$$

In principle energy is maximized for Gabor phase $\phi=0$ or π , but since typically $f\sigma$ is in the range 0.75–1.25 the effect of varying phase is predicted to be small.

Results

Signal structure

Signals emitted by *Rousettus aegyptiacus* are short duration impulsive clicks that are emitted in pairs. Fig. 1 shows representative waveform structures of single clicks from three of the bats and Table 1 shows the signal parameters for each bat. The mean duration of clicks using the 10% amplitude criterion was $138.1 \pm 26.78 \mu\text{s}$. This compares with a mean of $289.02 \pm 124.77 \mu\text{s}$ for a selection of signals that show the best signal-to-noise ratio.

Signal intensity and energy

Fig. 2 shows a logarithmic regression of signal sound level $S=10\log I$ against distance from the target. The regression line $S=-24.27\log R+89.92$ ($r^2=0.717$) is not significantly different ($t_{200}=0.12$, $P>0.05$) from the predicted line $S=-20\log R+88.05$ (in which 20 is the theoretical slope for spherical spreading

Table 1. Summary of selected signal parameters for the five subjects

Bat ($N=10$)	Measured click duration (μs)	Gabor model duration (μs)	FFT peak frequency (kHz)	Gabor carrier wave peak frequency (kHz)	Inter-click pair interval (ms)
1	142.00 \pm 26.30	50.99 \pm 3.62	34.08 \pm 0.58	34.09 \pm 0.98	12.31 \pm 2.91
2	141.00 \pm 19.10	47.74 \pm 3.15	35.83 \pm 2.07	38.40 \pm 2.38	16.21 \pm 2.38
3	141.00 \pm 19.12	47.74 \pm 3.15	35.83 \pm 2.07	38.40 \pm 2.38	21.44 \pm 1.49
4	165.67 \pm 24.70	43.83 \pm 10.89	34.14 \pm 3.01	38.99 \pm 5.87	22.2 \pm 1.83
5	165.67 \pm 24.70	43.83 \pm 10.89	34.14 \pm 3.01	38.99 \pm 5.87	19.28 \pm 2.89

Values are means \pm s.d.

Click duration is measured from waveform amplitude, including low-amplitude oscillations following the main pulse, and peak frequency is estimated by Fourier methods (see text). Gabor carrier frequency estimated from Gabor model and duration calculated from estimated bandwidth by Equation 12.

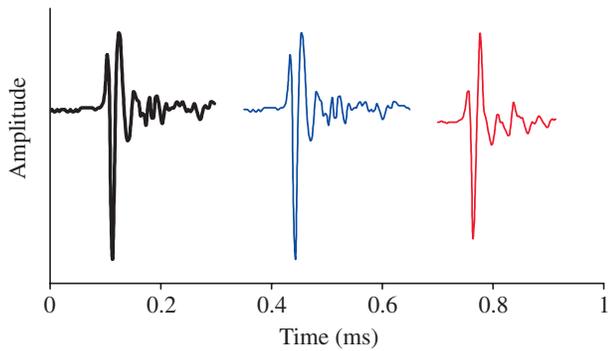


Fig. 1. Representative waveforms of single clicks. Amplitude is scaled to a maximum of ± 1 .

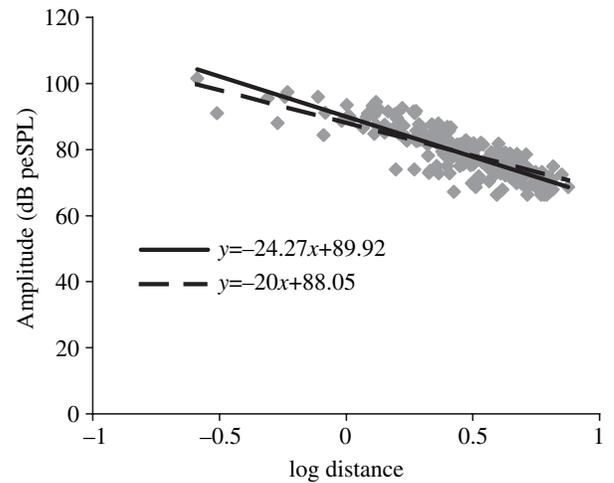


Fig. 2. Regression of distance on intensity. The line represents the equation $S = -24.27 \log R + 89.92$ and is not significantly different to the broken line plotted from the predicted values obtained from the equation $S = -20 \log R + 88.05$.

from Equation 4) and 88.05 dB peSPL is the intensity at 1 m generated from the idealised fit of the data equivalent to 108.05 dB peSPL at 10 cm). Fig. 3 shows a scatter plot of source level 1 m from the bat plotted as a function of the range from the microphone array. If the bats are signalling at a source level that is constant regardless of the distance from the target, a level response would be expected, i.e. $S = 0 \cdot \log R + C$ for constant intensity $C = 88.05$. The fitted regression $S = -4.27 \log R + 89.92$ ($r^2 = 0.073$) shows no significant difference from this prediction ($t_{200} = 0.12$, $P > 0.05$). Table 2 shows measured amplitude and estimated energy for each bat.

Gabor function

Representative Gabor function models compared with the sampled waveform, together with the error between the two, are shown in Fig. 4. A good fit to the earlier portion of the bat signal is obtained in each case, although there may be as few

Table 2. Measured intensity, regression of intensity against distance from target, and estimated energy flux density for the five subjects

Bat	N	Intensity at 1 m (dB peSPL)	Slope	r^2	P	Energy at 1 m (J m^{-2})	Gabor energy at 1 m (J m^{-2})
1	34	87.70	-16.75	0.73	<0.001	6.12 \pm 6.92 $\times 10^{-8}$	3.7 \pm 2.27 $\times 10^{-8}$
2	36	88.50	-23.93	0.61	<0.001	3.72 \pm 2.14 $\times 10^{-8}$	1.53 \pm 0.783 $\times 10^{-8}$
3	42	95.91	-31.28	0.83	<0.001	3.79 \pm 2.29 $\times 10^{-8}$	5.35 \pm 4.30 $\times 10^{-8}$
4	38	91.48	-26.1	0.94	<0.001	2.49 \pm 2.55 $\times 10^{-8}$	1.40 \pm 0.898 $\times 10^{-8}$
5	50	86.98	-23.06	0.52	<0.001	3.48 \pm 2.20 $\times 10^{-8}$	5.30 \pm 4.37 $\times 10^{-8}$

Values are means \pm s.d. For energy flux density values, $N=10$ per bat.

Intensity at 1 m is taken from the regression equation for that bat.

Energy flux density derived from the integral of the waveform is estimated from Equation 5 and Gabor energy flux density is estimated from Equation 16.

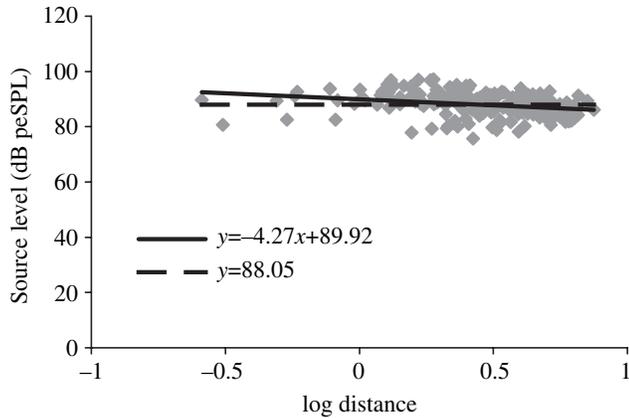


Fig. 3. Scatter plot of sound source level as a function of the range between the bat and the microphone. The line represents the equation $S = -4.27 \log R + 89.92$ and is not significantly different to the broken line plotted from the predicted values obtained from the line $S = 88.05$.

as three pressure peaks present, and cross correlations between the sample waveform and the Gabor function is greatest at time offset=0 in all signals analyzed. The Gabor function does not capture the quasi-regular low amplitude oscillations that follow the main portion of the signal, however. Comparison of the error between signal and Gabor function suggests that including the first harmonic gives a better fit using the mean square error estimate, and the FFT of the Gabor signal more closely matches the FFT of the actual signal when the first harmonic is included with amplitude of 12% of the carrier amplitude (Fig. 4C). Fig. 5 shows representative signals from bat 1 and their associated Gabor functions including the first harmonic. Comparison of the duration and peak frequency estimated by Fourier-based sonograph methods with duration and carried frequency estimated by the Gabor model shows that there is a significant difference in both cases (REML Variance Components Analysis; duration: response = duration; treatment = FFT vs Gabor; random term = individual; Wald statistic $\chi^2 = 574.31$, d.f.=1, $P < 0.001$; Frequency: response = frequency; treatment = FFT vs Gabor; random term = individual; Wald statistic $\chi^2 = 12.13$, d.f.=1, $P < 0.001$). The energy of the Gabor function was estimated from Equation 16 and is reported in Table 2. Comparison of the energy derived from the integral of the waveform and that derived from the Gabor fit showed no significant difference (REML Variance Component Analysis: response = log energy; treatment = FFT vs Gabor; random term = individual; Wald statistic $\chi^2 = 1.46$, d.f.=1, $P > 0.05$).

Discussion

Click durations in *R. aegyptiacus* in the range 75–534 μs derived from the waveform, or 35–80 μs estimated by the fit of a Gabor function, are shorter than those previously recorded by von Herbert (1985) (0.6–1 ms), and substantially shorter than those recorded by other authors (3.5–5.6 ms; Novick, 1958; Möhres and Kulzer, 1956). Studies have

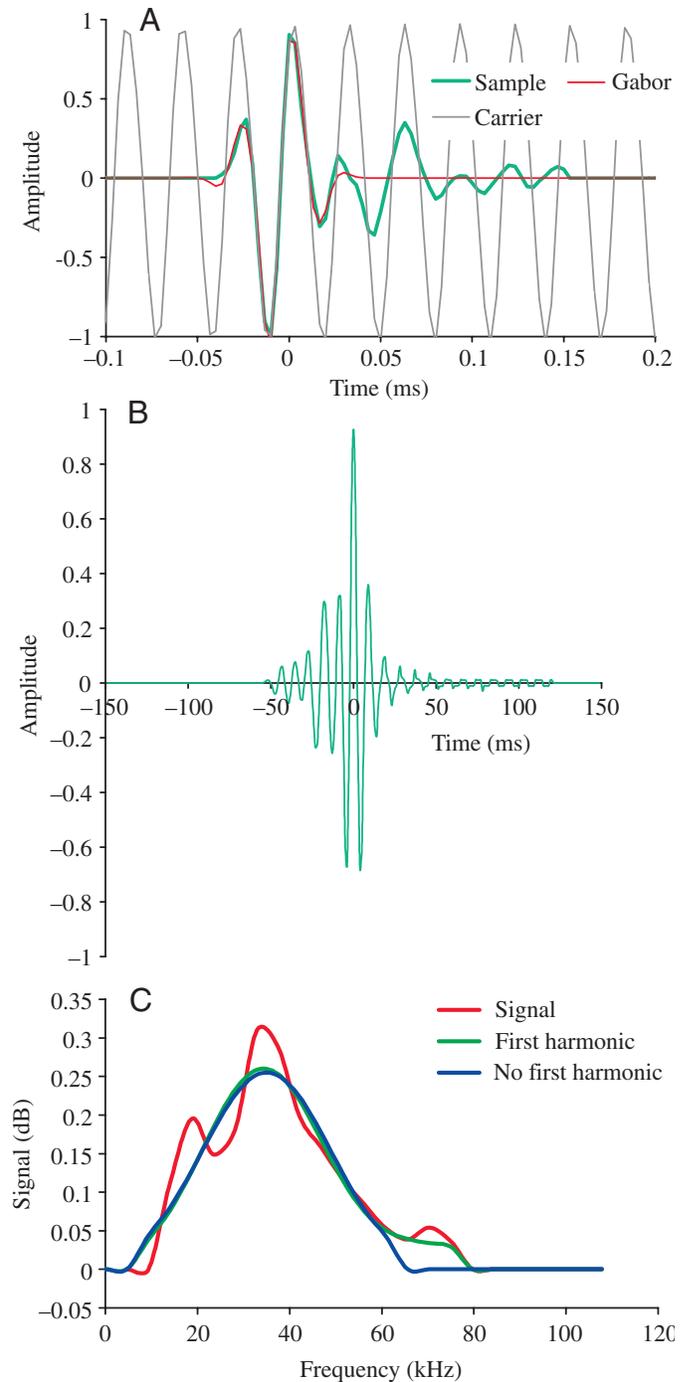


Fig. 4. (A) Sample waveform and best-fit Gabor function from bat 1. Amplitude has been scaled to a maximum of ± 1 . (B) Cross correlation between sample waveform and Gabor function. (C) FFT analysis of the Gabor model as compared to the signal with and without a first harmonic for bat 1.

shown that Microchiroptera flown in the laboratory show reduced call duration and changes in peak frequency and bandwidth compared to the same species in the wild (Surlykke and Moss, 2000). The durations recorded from our experiments may not, therefore, be representative of those produced by *R. aegyptiacus* in free flight in open

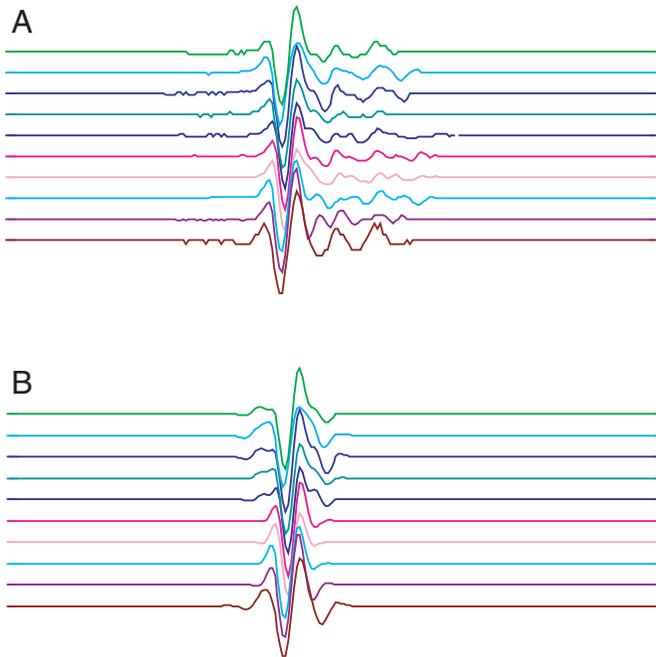


Fig. 5. Representative clicks and the associated Gabor functions generated. The colour matches the click to the associated Gabor function. (A) Bat 1 click signals; (B) bat 1 Gabor functions.

environments. However, the flight corridor is probably a good mimic of the natural cave conditions in which these bats are known to echolocate. The Gabor model duration estimates are much shorter than the durations derived purely from the signal waveform because they exclude the quasi-regular low amplitude oscillations that follow the main portion of the signal; this component of the signal is variable in length and contains relatively little energy, although the oscillations apparently retain the same carrier frequency as the earlier part of the signal. Most of the energy is contained in the first 100 μs , as indicated by the lack of a significant difference between the energy of the Gabor function and the integral of the waveform which includes these oscillations. The signals we have measured are much shorter than those of cave swiftlets (1.5 ms; Coles et al., 1987) and oilbirds (50 ms; Suthers and Hector, 1985), but the waveforms appear to be broadly similar; a Gabor model may be equally successful for these impulse echolocators. *R. aegyptiacus* signals have a structure and duration that are similar to those of dolphins (Au, 1980). The structure of *R. aegyptiacus* signals has previously been compared to a shock-excited resonator (Roberts, 1975). von Herbert (1985) notes a steep transient amplitude rise at the start of signals, but we see a more regular rise and a symmetric fall in envelope.

Dolphin signals have been modelled successfully using a Gabor function (Kamminga, 1988; Wiersma, 1988). This theoretical model for signal structure is expected to be realistic for short-duration signals since it provides the minimum spread of frequencies, thus minimising energy outside the animals audiogram of best frequencies, focuses energy into fewer

critical bands (Vetterli and Kovacevic, 1995), and has the minimum time-bandwidth product, which has implications for the sonar detection model used (Urkovitz, 1967). Here we make the assumption that the signals we record are optimised for echolocation alone and do not also serve a secondary function such as communication. The Gabor model applied to *R. aegyptiacus* signals provides an excellent match with the part of the signal that contains the majority of the energy, and most of the error occurs in the smaller oscillations seen afterwards. It is unclear whether these are a significant part of the signal that is in some way employed in signal detection, or is a function of constraints on the signal production method. The signal durations calculated from the Gabor models are significantly shorter than those of the actual signal, due to the fact that the Gabor model does not capture these oscillations. There is also a significant difference in the peak frequency of the Gabor model when compared to Fourier estimates. This is not unexpected, since Fourier techniques are not good models of spectral information for short-duration signals (see Introduction). Cross-correlation shows that there is good agreement between signal and model, so it seems that the echolocation signals of *R. aegyptiacus* conform well to a Gabor model and are thus well designed to contain the minimum bandwidth for the given duration. Such a structure will ensure that most energy within the returning echo is focussed within the animal's region of highest hearing sensitivity, and additionally is focussed into fewer critical bands, with a subsequent increase in signal-to-noise ratio and an increased chance of signal detection. An audiogram by Koay et al. (1998) reported this region of high sensitivity to be between 8 and 45 kHz. The peak frequencies reported here fall within this region. Audiograms of bats may, however, show sensitivity to other frequency ranges that are not used for echolocation, such as social calls (Bohn et al., 2004) and passive prey localisation (Heffner et al., 2003). However, in *R. aegyptiacus* maximising detection through a good match between signal and hearing may be especially important due to the very brief nature of the signals and their low energy content.

The peak amplitude of signals is comparable to measurements of Microchiropteran bats recorded in the laboratory, but the energy flux density of *R. aegyptiacus* clicks in the range $2\text{--}7 \times 10^{-8} \text{ J m}^{-2}$ is an order of magnitude smaller than that of laboratory-based microbat echolocation signals in most cases (in the region of 10^{-7} J m^{-2} ; Waters and Jones, 1995). Cetacean echolocation signals have amplitudes in the region of 200 dB SPL (Au, 1993). Energy flux density is a more meaningful comparison, however, since this allows for the impedance of the medium and the duration of the signal. Au (1993) reports that *Tursiops truncatus* has an energy flux density in the region of $8 \times 10^{-3} \text{ J m}^{-2}$ but that all other cetacean species studied have similar energy flux density to microbats, of the order of 10^{-7} J m^{-2} . The low energy flux density of *R. aegyptiacus* clicks is due to their much shorter duration when compared to microbat signals. The recordings were made under laboratory conditions and some studies have shown that Microchiropteran bats use much higher intensity calls in the field (Surlykke and Moss,

2000; Holderied and Helversen, 2003). However, the energy flux density measurements comparing *R. aegyptiacus* and microchiropterans are all laboratory based studies so it seems likely that the signals of *R. aegyptiacus* do indeed contain relatively little energy. The lower energy content should make echoes of *R. aegyptiacus* clicks harder to detect than echoes of microbat echolocation signals.

In addition to the relatively low energy content of the signals, the detection of impulsive echoes may be compounded by the relatively long duration of mammalian integrating time constants (ITC). The integration time of an auditory system is the duration over which acoustic energy is summed (Plomp and Bouman, 1959). The ITC is the duration at which a pure tone pulse is detected or the duration at which two click stimuli can be discriminated (Zwislocki, 1960). The length of the time constant depends on the method used. If a pure tone is used then the ITC is relatively long compared to a method in which the separation of two click stimuli is detected. Using the tone pulse paradigm, Suthers and Summers (1980) demonstrated a time constant of 15 ms in *R. aegyptiacus*. In microbats and dolphins, if the double click paradigm is used, then a shorter constant is obtained (220 μ s in *Megaderma lyra*, Wiegrebe and Schmidt, 1996; 264 μ s in *Tursiops truncatus*; Au et al., 1988). However, it remains to be seen whether *R. aegyptiacus* has a shorter integrating time constant with this method. Nevertheless, the short duration of click stimuli produced by *R. aegyptiacus* is below the ITC values so far recorded, and unless it is markedly shorter for a signal of the type now measured the echo of such a stimulus is likely to be difficult to detect. Even if the ITC values of bats and dolphins are comparable, dolphins still have an advantage in echo detection over bats by virtue of their impedance matching to their environment.

The source level of the signals remains constant with decreasing distance. Although we cannot be entirely certain that the bats were ensonifying the microphone array, it presented a large target that the bats had to avoid, and on some occasions would collide with. There was no modulation of source level with distance when the array was placed at the end of the corridor right against the entrance doors (R. A. Holland, D. A. Waters and J. M. V. Rayner, unpublished). Thus these bats are unlike dolphins and Microchiroptera, which modulate signal amplitude, decreasing it with decreasing distance to the target (Au and Benolt-Bird, 2003; Hartley, 1992). This is thought to have the effect of achieving automatic gain control to optimise signal-to-noise ratio over all target distances. The Microchiropteran bat *Eptesicus fuscus* has also been shown to have an additional automatic gain control mechanism: it increases the sensitivity of its hearing as a function of time from emission of the echolocation signal, rather than by modulating signal amplitude (Simmons et al., 1992). Given that the signals are similar in amplitude to those of Microchiropterans, *R. aegyptiacus* might be predicted to have some mechanism to achieve automatic gain control, as this would allow them to signal at high amplitude at further distances, while reducing the amplitude at nearer distances to

optimise signal to noise ratio. This effectively increases the dynamic range of the sonar system. Although *R. aegyptiacus* does not have specialised ear muscles to achieve self-deafening, they do have highly mobile pinnae, and preliminary high-speed video analysis suggests that these move in a highly regulated fashion that corresponds with click emission (R. A. Holland and D. A. Waters, unpublished). Further analysis is required to discover whether these ear movements function to self deafen and/or control gain. If *R. aegyptiacus* do not use automatic gain control then they would be forced to compromise. They could signal at the highest amplitude at which no signal distortion or forward masking would occur at short distance to the target, but this would reduce the range of the echolocation system. Alternatively, they could signal at the maximum amplitude available, which would reduce accuracy at short distance due to distortion and forward masking of early returning echoes. Given the relatively low energy content of these impulses, if they chose the former, this would add further constraints on the effective range of the echolocation system of *R. aegyptiacus*.

The results of this study indicate that the impulse clicks of *R. aegyptiacus* are very short in duration and similar in length to the clicks of cetacean bio-sonar than to those of other terrestrial vertebrates using comparable mechanisms. As for cetaceans, a Gabor function, which contains the minimum bandwidth for the frequencies present and therefore avoids spreading energy into bands outside the frequencies of best hearing, is a good model for the signal. However, the relatively low energy content of the signals, coupled with the mismatch between the integrating time constant and the click stimulus of these animals, may make the echoes of these clicks hard to detect. Impulse bio-sonar remains a difficult system to use in air and the performance of this animal in obstacle avoidance experiments using echolocation continues to provide something of a conundrum.

List of symbols

a	amplitude
A	length
c	velocity of sound in the medium
E	energy flux density
f	frequency
f_s	sampling frequency
I	intensity
P	power per unit area
$P(t)$	time varying sound pressure
r	radius
R	range
S	sound level
\hat{t}	arbitrary base time
t	duration of the signal
t_c	click duration
ϕ	phase of the carrier wave
ρ	density of the medium
σ	width of the modulating envelope

This research was supported by BBSRC grant S15544. We would like to thank Tropical World Zoo, Leeds, for the loan of the fruit bats and Scott for animal husbandry.

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