REVIEW

Click-based echolocation in bats: not so primitive after all

Yossi Yovel · Maya Geva-Sagiv · Nachum Ulanovsky

Abstract Echolocating bats of the genus *Rousettus* produce click sonar signals, using their tongue (lingual echolocation). These signals are often considered rudimentary and are believed to enable only crude performance. However, the main argument supporting this belief, namely the click's reported long duration, was recently shown to be an artifact. In fact, the sonar clicks of *Rousettus* bats are extremely short, $\sim$50–100 μs, similar to dolphin vocalizations. Here, we present a comparison between the sonar systems of the 'model species' of laryngeal echolocation, the big brown bat (*Eptesicus fuscus*), and that of lingual echolocation, the Egyptian fruit bat (*Rousettus aegyptiacus*). We show experimentally that in tasks, such as accurate landing or detection of medium-sized objects, click-based echolocation enables performance similar to laryngeal echolocators. Further, we describe a sophisticated behavioral strategy for biosonar beam steering in clicking bats. Finally, theoretical analyses of the signal design—focusing on their autocorrelations and wideband ambiguity functions—predict that in some aspects, such as target ranging and Doppler-tolerance, click-based echolocation might outperform laryngeal echolocation. Therefore, we suggest that click-based echolocation in bats should be regarded as a viable echolocation strategy, which is in fact similar to the biosonar used by most echolocating animals, including whales and dolphins.

Abbreviations

FM	Frequency modulated
CF–FM	Constant frequency–frequency modulated
ACRF	Auto-correlation function
WBAF	Wideband ambiguity function
SPL	Sound pressure level
SNR	Signal-to-noise ratio

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Introduction

Bats from the genus *Rousettus* are the only members of the Pteropodidae family (also known as Megachiropteran bats, or Megabats) that use echolocation. In contrast to all other genera of echolocating bats (Microbats), which emit laryngeal, or vocal-chord based biosonar vocalizations, *Rousettus* bats use their tongue to emit very brief wideband echolocation clicks (Holland et al. 2004). This click-based (lingual) echolocation was historically considered to be rudimentary, providing only crude biosonar information and low performance. The main reason for this belief was the seemingly-long duration of the clicks, which were reported by several researchers to be >1 ms or even several milliseconds long (Möhres and Kulzer 1956; Griffin et al. 1958; Herbert 1985): such a long duration for a signal that has no frequency modulation would result in a much lower

ranging accuracy of *Rousettus* echolocation compared to the frequency-modulated sonar signals of most microbats (Simmons and Stein 1980). An additional reason for this historic notion of "primitive click-based echolocation" was the bats' lack of ability to flexibly change signal parameters (e.g., duration or frequency modulation).

However, recent work has revealed that the biosonar click duration in the Egyptian fruit bat, *Rousettus aegyptiacus,* is much shorter than previously thought, with individual clicks being approximately ∼50–100 μs in duration (Holland et al. 2004; Waters and Vollrath 2003). This is an order of magnitude shorter than the shortest known laryngeal echolocation calls (Moss et al. 2006; Melcón et al. 2007), and similar to the duration of dolphin clicks (Ibsen et al. 2009). In fact, some dolphins, such as the false killer whale (*Pseudorca crassidens*) can emit clicks that are similar to the click of the Egyptian fruit bat (Fig. 1).

The previous over-estimated measurements of click duration (Möhres and Kulzer 1956; Griffin et al. 1958; Herbert 1985) were due to two reasons: (a) Poor recording conditions, without any acoustic foam to reduce reverberations, which resulted in the inclusion of long echo trains in the measurement of click duration—thus prolonging the

apparent click duration to >1 ms. In contrast, the new measurements (Holland et al. 2004; Waters and Vollrath 2003) were done in an environment surrounded by acoustic foam, which eliminated the echoes and revealed the extremely short duration of the sonar click itself. (b) Previous duration measurements were based on the spectrogram: this is a measurement method that is inappropriate for ultra-short biphasic clicks (where the click duration is on the order of one cycle of the carrier frequency), because the spectrogram tends to spread the energy in time and thus smear the apparent click duration. For such short signals, measurements of duration must be done in the time domain. Our own recordings have now confirmed that the duration of sonar clicks of *R. aegyptiacus* is ∼50–100 μs, both in the lab and in the field (Fig. 1).

To date, there are relatively little behavioral data available on the sonar performance of *Rousettus* bats, but these data indicate that these bats exhibit spatial acuity comparable to that of laryngeal echolocators—consistent with what would be expected from their ultra-short sonar click duration. For example, in a wire-avoidance experiment, *R. aegyptiacus* bats were able to detect wires with a diameter as small as 0.31 mm (Summers 1983), which is
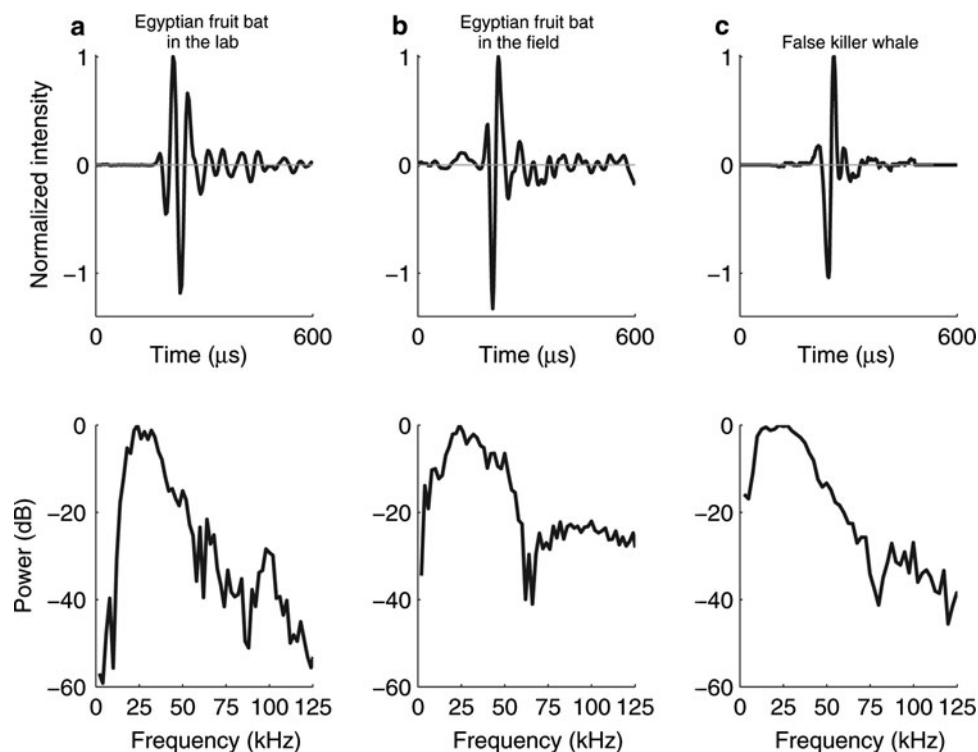

Fig. 1 Typical sonar clicks (*top row*) and spectra (*bottom row*) of the Egyptian fruit bat (*Rousettus aegyptiacus*) and the sonar click of the false killer whale (*Pseudorca crassidens*). **a** Sonar click of Egyptian fruit bat recorded in the lab under the same conditions as Yovel et al. (2010). **b** Sonar click of Egyptian fruit bat recorded in the field from a bat that exited a cave (microphone was pointing away from the cave entrance); courtesy of A. Tsoar. **c** Sonar click of a female false killer whale named "Kool", recorded in Kamogawa Sea World, Japan (remeasured from Nakamura and Akamatsu 2003; the click was zero-padded on both sides because the authors only provided a 0.4-ms recording): This dolphin's click is very similar to the sonar click of the Egyptian fruit bat. Click spectra were calculated with a 0.5-ms rectangular window for the bats and 0.4-ms window for the false killer whale

similar to the performance observed in laryngeal echolocators (Curtis 1952).

In light of these new data, we set out to re-examine the common notion regarding the 'primitiveness' of lingual echolocation. By 'primitive', we refer to its functionality and not its evolutionary origin. We compare the theoretically predicted and empirically observed echolocation performance of the most-studied lingual echolocator—the cave dwelling Egyptian fruit bat (*Rousettus aegyptiacus*)—to that of the best described laryngeal echolocator, the big brown bat (*Eptesicus fuscus*). Comparisons are presented both graphically (Figs. 2, 3, 4) and in the form of summary tables (Tables 1, 2).

We start with comparing in detail the signal-design characteristics of the biosonar vocalizations of Egyptian fruit bats and big brown bats, using theoretical analyses of the autocorrelation function and the wideband ambiguity function of their sonar signals. These theoretical analyses are used to make experimental predictions about the sonar performance of these two bats, with the surprising result that—on some parameters—the Egyptian fruit bat may be as good as, or even better than the big brown bat; these predictions are in part confirmed by available empirical data. We then go on to compare in detail the echolocation behavior of the two species in a similar behavioral task: namely, an approach to a target in complete darkness.
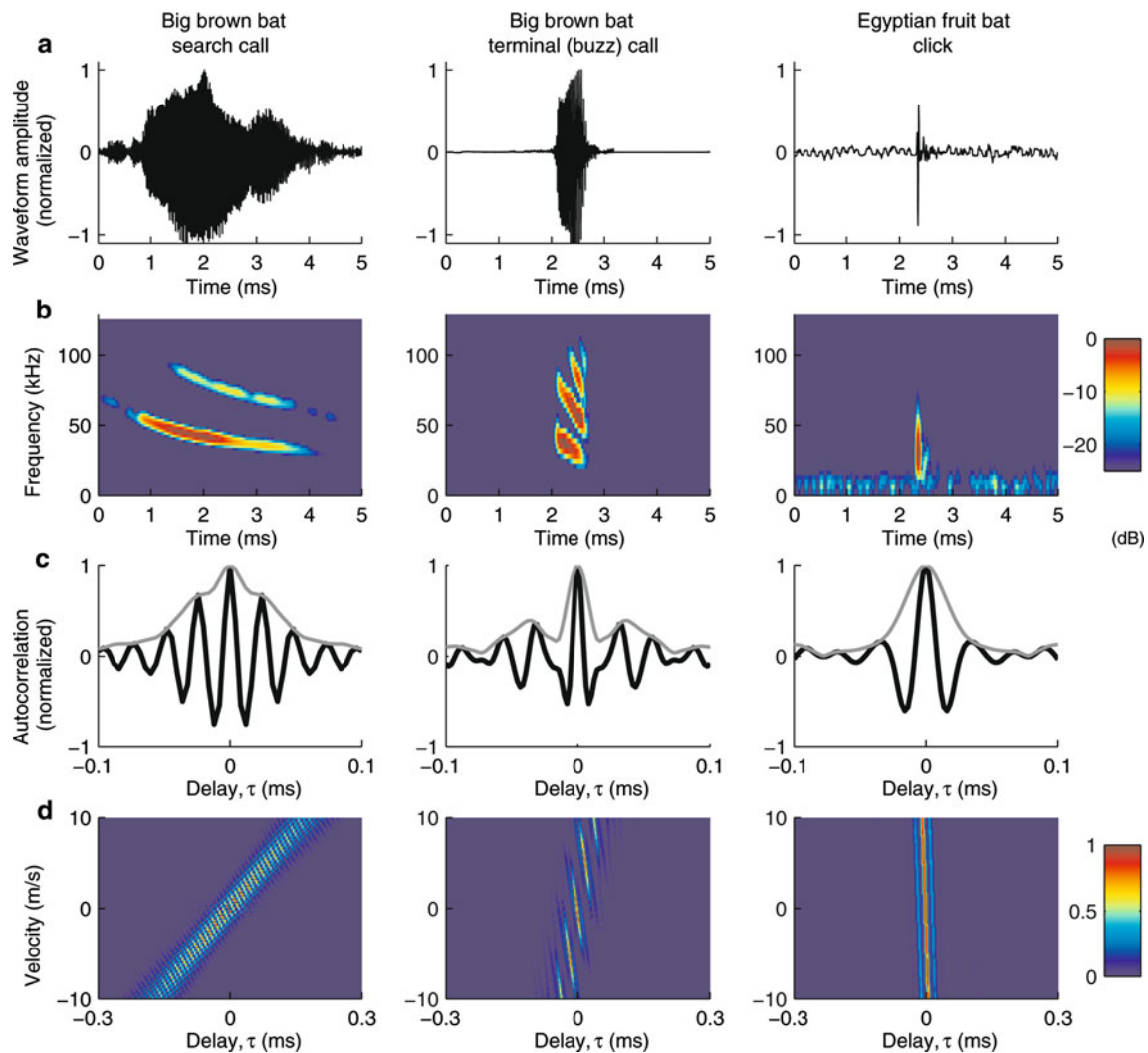
Fig. 2 Signal design of the biosonar clicks of Egyptian fruit bats versus FM-calls of big brown bats. **a** Call waveforms (normalized units). *Left* big brown bat search call (courtesy of B. Falk and C. Moss). *Middle* big brown bat terminal-phase (buzz) call (courtesy of M. Melcón). *Right* Egyptian fruit bat click, recorded in the field in Israel (courtesy of A. Tsoar). **b** Spectrogram representation (frequency × time) of the three echolocation vocalizations from *a*. All spectrograms were computed with the same settings; color-scale, normalized intensity (dB). **c** Autocorrelation function (ACRF) for the three calls (*black line*) and the ACRF envelope (computed via the Hilbert transform, gray). **d** Wide band ambiguity functions (WBAF). The WBAF was computed in the same way for all three signals; color-scale, normalized WBAF (red, maximum value of WBAF)
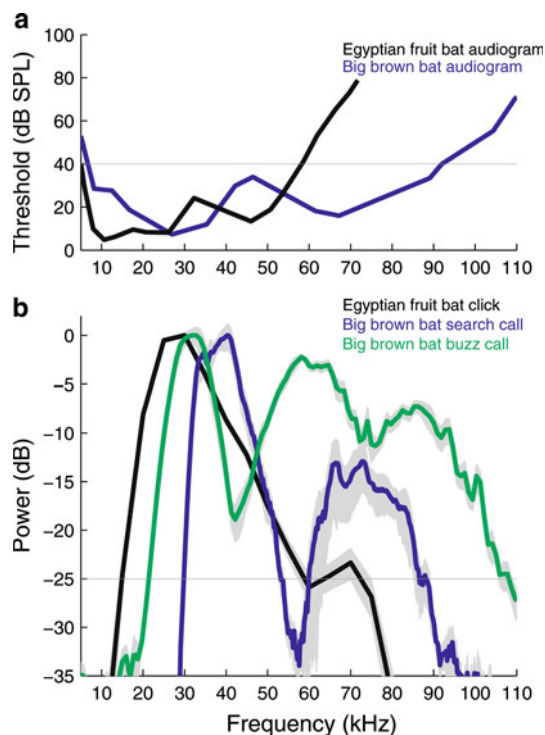
Fig. 3 a Audiograms of Big brown bat and Egyptian fruit bat (remeasured from Koay et al. 1997; Koay et al. 1998); note that the audible range of the Egyptian fruit bat spans both its echolocation calls frequency range (see **b**) and its communication calls range (5–13 kHz; Suthers and Summers 1980). *SPL* sound pressure level. **b** Average signal spectrum of Egyptian fruit bat click (*black*, averaged over $N = 70$ clicks) versus spectrums of FM calls taken from two phases of the big brown bat pursuit sequence: Search calls (*blue*, $N = 10$) and terminal phase (buzz) calls (*green*, $N = 10$). *Gray area*, mean ± sem (the sem is asymmetrical because it was computed on a linear *y*-scale and then transformed to a dB scale). Line at –25 dB denotes the level at which we computed the bandwidth of the sonar vocalizations (Table 1, row 4)

Signal design of the sonar vocalizations of Egyptian fruit bat versus big brown bat

The frequency-modulated (FM) biosonar signals of the big brown bat exhibit dynamic changes over time, getting shorter in duration and broader in bandwidth as the bat approaches a target (Hartley 1992; Surlykke and Moss 2000)—while the attributes of the Egyptian fruit bat's clicks remain relatively constant (see below). Hence, for the detailed comparison of signal design, we chose to compare the Egyptian fruit bat's click to *two* types of FM calls produced by the big brown bat during two stages of echolocation behavior. These three sonar signals are shown in Fig. 2 and summarized in Table 1: (a) A big brown bat sonar call from the "search phase", in which the FM-signal is relatively long, ~4 ms in duration (Fig. 2a, b, left column and Table 1, left column); (b) Big brown bat call from the very end of the "terminal (buzz) phase", where the call is shortest, ~0.7 ms in duration (Fig. 2, middle column;

Table 1, middle column); (c) Egyptian fruit bat biosonar click (Fig. 2, right column; Table 1, right column).

Egyptian fruit bats emit very brief clicks, predicting good ranging accuracy

Our recordings of Egyptian fruit bat biosonar signals corroborate recent studies (Holland et al. 2004; Waters and Vollrath 2003) which showed that Egyptian fruit bat clicks are ultra-short, having a duration of ~50–100 µs (Fig. 1). This duration is one order of magnitude shorter than the shortest calls of the terminal buzz phase emitted by the big brown bat, and two orders of magnitude shorter than typical big brown bat search calls (Table 1, row 1) (Hartley 1992). In general, such ultra-short pulse duration in the Egyptian fruit bat predicts a good ranging accuracy, as will be analyzed in detail below.

Egyptian fruit bats exhibit good performance in detection tasks, despite the low total energy of their biosonar clicks—which might suggest special adaptations of their auditory system

The extremely short duration of Egyptian fruit bat clicks means that these signals have relatively low total energy. The total energy measure we used to compare the sonar signals ('energy flux density', Au 1993; see Appendix A) takes into account the peak intensity, but also the signal duration and the attenuation due to the impedance of the medium (which is similar in these two airborne echolocators; see Appendix A). This measure showed that, when compared to 'search mode' of laryngeal echolocation, the total energy of Egyptian fruit bat clicks is four orders of magnitude lower than in the big brown bat's strongest search calls: Egyptian fruit bat click energy was calculated to be 3–6×10^{-8} J/m^2 (Holland et al. 2004), whereas big brown bat search calls have total energy of $\sim 10^{-4}$ J/m^2 (Hartley 1992). However, during the 'terminal buzz' mode of echolocation, the total energy of big brown bat calls drops dramatically, to $\sim 10^{-9}$–10^{-8} J/m^2—very similar to the total energy of Egyptian fruit bat clicks. Thus, because the total energy of Egyptian fruit bat clicks is much lower than in FM search calls, we might expect a limited detection range for the sonar system of the Egyptian fruit bat—while, in contrast, the fact that the total energy is very similar between these two species during the terminal buzz, suggests that Egyptian fruit bats should have adequate energy output to perform well at short ranges.

Indeed, Egyptian fruit bats show very good performance in detection of nearby small objects. This was shown in wire-avoidance experiments in which these megabats were able to detect 0.31-mm diameter wires, in complete darkness (Summers 1983), similar to the abilities of microbats
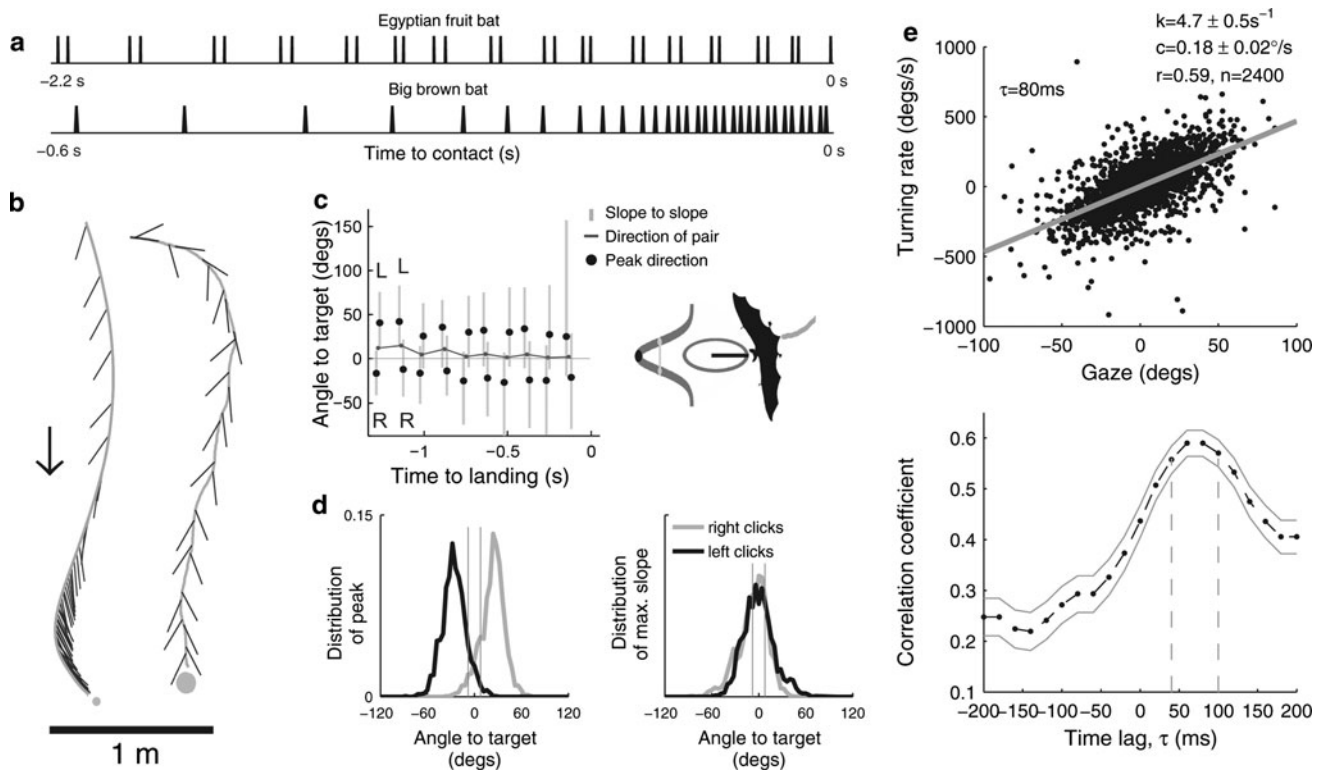
Fig. 4 Echolocation and flight behavior of Egyptian fruit bats versus big brown bats approaching an object. **a** Temporal emission pattern of an Egyptian fruit bat landing on a target (*top* data re-measured from Herbert 1985) and a big brown bat attacking a mealworm (*bottom* data re-measured from Ghose and Moss 2006). **b** Examples of flight trajectories of a big brown bat attacking a mealworm (*left* modified from Ghose and Moss 2006, with open-access permission from *PLoS*) and an Egyptian fruit bat landing on a 10-cm sphere (*right*). Flight direction is marked by an *arrow*; *short black lines* represent the beam-aim for each sonar vocalization. *Scale bar* 1-m, is identical for both trajectories. Note the left–right alternation of the beam aim of the Egyptian fruit bat (*right*). **c** Maximum-slope strategy used by the Egyptian fruit bat (Yovel et al. 2010): *Left* example of one behavioral trial; each vertical line corresponds to the angular extent of the beam between its left- and right-maximum-slope, *black dots* direction of peak. *Right* illustration of the vertical-line and black-dot notations in a schematic showing a single emission curve (note especially the plot in Cartesian coordinates). The experimental data from the Egyptian fruit bat (*left plot*) exhibit a clear left–right alternation of the beam aim;

note also that the maximum-slope locks onto the target (top and bottom of the vertical lines are around Direction 0°). Shown are the last 10 click-pairs before landing. **d** Distribution of the directions of the sonar beam's peak (*left*) and of the maximum slope (*right*) for all the locked clicks in six Egyptian fruit bats. **e** Egyptian fruit bats use a similar control law to that of big brown bats (compare to Ghose and Moss 2006). Top, linear relation between the Egyptian fruit bat's "sonar gaze" (angle between flight direction and click-pair direction) and its turning rate, shown here at a time-delay of $\tau = 80$ ms between gaze and turning-rate; indicated also are the fitted parameters of the control-law (see text and Table 2). The regression line is shown overlaid in gray. The slope is denoted by k, and the offset (intercept, c) is negligible. Bottom, correlation coefficient of the fit versus the time-lag, showing that the time lag between the gaze and the turning rate is ~ 80 ms (peak value of the correlation); gray lines, s.t.d. of the correlation coefficient, computed as in Ghose and Moss (2006). Data taken from unlocked click-pairs only (i.e., search phase), pooled over 256 behavioral trials in six bats

(Curtis 1952). This detection performance implies that there might be additional aspects that compensate for the low total energy and enable Egyptian fruit bats to perform well in tasks relevant to their lifestyle.

One important feature that could facilitate sonar performance is the high *peak intensity* of the sonar click. The peak intensity of Egyptian fruit bat clicks, when measured at 10 cm from the mouth, is 105–115 dB SPL (Holland et al. 2004). This value, which was measured in the laboratory, is comparable to measurements from laryngeal echolocators recorded in the laboratory (75–125 dB SPL at 10 cm; Hartley 1992): See Table 1 (row 2). Currently, no field measurements exist of the absolute signal intensity for

either of the two species, big brown bats or Egyptian fruit bats; however, it is likely that in the field, big brown bats can further increase their peak intensity (Holderied et al. 2005), whereas it is reasonable to assume that tongue-clicks are more limited physiologically in how much further their peak intensity could be increased (although preliminary data indicate that Egyptian fruit bats *can* increase their click energy; Y.Y. and N.U., unpublished observations).

The efficiency of the peak intensity could be further enhanced by auditory processing within the central nervous system. The hearing threshold at best frequency is similar in both species: 7 dB SPL for big brown bats and 4 dB SPL

Table 1 Summary of signal design comparisons for Egyptian fruit bat versus big brown bat

Signal design criterion	Big brown bat (Laryngeal FM signal)		Egyptian fruit bat (Lingual click signal)
	Search signal	Terminal buzz signal	
1 Duration of sonar pulse	4.1 ± 0.75 ms[a] ($N = 10$ pulses)	0.68 ± 0.085 ms[b] ($N = 10$)	0.076 ± 0.004 ms[c] ($N = 70$)
2 Peak power of sonar vocalizations	75–125 dB SPL at 10 cm from mouth[d] (measured in the lab)		105–115 dB SPL at 10 cm from mouth[e] (measured in the lab)
3 Hearing threshold	7 dB SPL[f]		4 dB SPL[f]
4 Bandwidth	$BW_{-25dB} = 58$ kHz[a] ($N = 10$ pulses)	$BW_{-25dB} = 86$ kHz[b] ($N = 10$)	$BW_{-25dB} = 57$ kHz[c] ($N = 70$)
5 Ranging errors due to sidelobes in the autocorrelation function (ACRF) of the sonar call	Main lobe/side lobe Ratio = 1.5 • *Theoretically*: High sidelobes. Bat is expected to make many ranging errors at $\sim\pm30$ μs, due to sidelobes at $\sim\pm30$ μs (assuming bats use a coherent matched filter) • This prediction fits ranging performance reported in some behavioral experiments[g]	Main lobe/side lobe Ratio = 2.5	Main lobe/side lobe Ratio = 6 *Theoretically*: Low sidelobes Bat is expected *not* to make sidelobe-induced ranging errors
6 Ranging accuracy assuming coherent receiver: Depends on ACRF period	The ACRF period (corresponding to 360° phase) is: 25.2 μs ($N = 10$) Range jitter experiments from several labs[h] showed that bats can discriminate range-jitter of 0.4 μs. Hence we assume that bats can discriminate a phase difference of: 360°/(30 μs/ 0.4 μs) $\sim$ 5°	ACRF period : 31.9 μs ($N = 10$) (similar to value reported before[g])	ACRF period: ~ 34 μs[c] (Fig. 2c, right, black line) Because ACRF period is similar between the two bat species, assumption of a coherent receiver leads to the prediction that ranging accuracy should be similar between the clicks of Egyptian fruit bats and the FM-calls of big brown bats
7 Ranging accuracy assuming a semi-coherent receiver: Depends on ACRF envelope width	Envelope width at half height: 71 μs[a]	Envelope width at half height: 19 μs[b]	Envelope width at half height: 39 μs[c] (Fig. 2c, gray line) Egyptian fruit bats are expected to have *better* ranging accuracy in search phase than the big brown bat— but be worse than the FM-bat during the terminal approach phase
8 Ranging errors due to Doppler shift: Based on Wideband Ambiguity Function (WBAF) Analysis	*Theoretically*: Large ranging errors. For a speed of 10 m/s, the WBAF shows a ranging error of 160 μs, which corresponds to a distance error of 57.6 mm[a]	*Theoretically*: Medium ranging errors. For a speed of 10 m/s, the WBAF shows a ranging error of 34 μs, which corresponds to a distance error of 11.6 mm[b]	*Theoretically*: The smallest ranging errors. For a speed of 10 m/s, the WBAF shows a ranging error of only 9 μs, which corresponds to a distance error of 3.1 mm[c]. Thus, the clicks of Egyptian fruit bats are more Doppler-tolerant than even the shortest "buzz" calls of the big brown bat (Fig. 2d)
9 Beam-width (at –3 dB of the peak intensity)	• Mean beamwidth value for big brown bats is 70°[i] • Smaller values of 40° were measured for another FM laryngeal echolocator, *Myotis daubentonii*[j]		Mean beamwidth value for Egyptian fruit bats is $50° \pm 2°$[k]

Signal duration (*row 1*) in both species is based on measurements in the lab: duration was measured in the time-domain, and was defined as the duration of the envelope of the time signal which exceeded 10% of the peak amplitude. The bandwidth (*row 4*) was defined as the spectral width at –25 dB below the peak of the power spectrum (BW_{-25dB}). Average values denote the mean $\pm$ SD, throughout this table

[a] Our measurements, using big brown bat search signals recorded courtesy of B. Falk and C. Moss

[b] Our measurements, using terminal (buzz) signals of big brown bats recorded courtesy of M. Melcón

[c] Data recorded by Y. Yovel

[d] Hartley (1992)

[e] Holland et al. (2004)

[f] Koay et al. (1998)

[g] Simmons (1979); Simmons et al. (1990)

[h] Menne et al. (1989); Simmons (1979); Simmons et al. (1990)

[i] Ghose and Moss (2003)

[j] Surlykke et al. (2009a)

[k] Yovel et al. (2010)

Table 2 Echolocation behavior during approach to a target: comparison between laryngeal versus lingual (click-based) echolocating bats

Parameter	Laryngeal echolocating bats	Lingual (click-based) echolocating bats
Pulse repetition	• Is increased in a stereotypic manner during the approach: can increase more than 15-fold, up to ~ 200 pulses/s[a,b,c]	• Can increase threefold, up to a limit of ~ 25 click-pairs/s; probably restricted by the maximum tongue speed[d,e]
	• Pulses are arranged in groups during the approach phase. Group size increases as the bat gets closer to the target[b,c]	• Pulses are always arranged in pairs[f]
Synchronization of echolocation calls and ear movements with the wing-beat cycle	Ear movements are generally not synchronized with the wing-beat cycle (except in horseshoe bats whose ears move in anti-phase with each other[g])	Ear movements are synchronized with wing-beat. Ears move in-phase with each other[e,h,i]
Information flow	Large: $\sim 22 \pm 3$ calls/m	Low: $\sim 7 \pm 2$ clicks/m
Beam-steering	During approach, the peak of the emission beam becomes locked on the target at the end of the approach[j,k]	• Peak of emission beam alternates Left→Right→Right→Left (one click-pair points Left→Right and the next pair Right→Left)[f]
		• During approach, the peak is directed sideways from the target ($30 \pm 5°$ to the left or to the right) but the maximum *slope* of the emission beam is directed towards the target[f]
		• At the very end of the approach, the average of a click-pair points precisely towards the target[f]
Echolocation-flight control law	$\dot{\theta}_{\text{flight}}(t+\tau) = k\theta_{\text{gaze}}$	$\dot{\theta}_{\text{flight}}(t+\tau) = k\theta_{\text{gaze}}$
	$\dot{\theta}_{\text{flight}}$—Turn rate	$\dot{\theta}_{\text{flight}}$—Turn rate
	θ_{gaze}—Gaze direction	θ_{gaze}—Gaze direction
	$3 < k < 7$	$k \sim = 5$
	90 ms $< \tau < 150$ ms[k]	60 ms $< \tau < 100$ ms (see Fig. 4e)

[a] Melcón et al. (2007)

[b] Moss et al. (2006)

[c] Moss and Surlykke (2001)

[d] Summers (1983)

[e] Herbert (1985)

[f] Yovel et al. (2010)

[h] Holland and Waters (2005)

[i] Möhres and Kulzer (1956)

[j] Ghose and Moss (2003)

[k] Ghose and Moss (2006)

for Egyptian fruit bats (Table 1, row 3); however, the click's design may concentrate the energy content in order to enable stronger response of the auditory system to returning echoes. Holland et al. (2004) showed that Egyptian fruit bat clicks fit well to a Gabor function. Using a Gabor-like signal, in which the carrier frequency is modulated by a Gaussian envelope, ensures that the energy within the returning echo is most concentrated in frequency, which implies that the energy can be focused into fewer critical auditory bands within the animal's region of highest hearing sensitivity.

Auditory processing has a major effect on the signal-to-noise ratio (SNR) at which the bat can operate, and thus on its detection abilities. The processing in the inner-ear is generally modeled as a filter-bank, meaning that the analysis of a stimulus is performed in separate frequency bands. Concentrating the signal's energy at a relatively narrow frequency band, as achieved by using the Gabor-like signal of *Rousettus*, should therefore increase SNR at this band and increase detection performance. Another key parameter that will influence the SNR is the integration time of the auditory system. The integration time of *Rousettus* is currently unknown, but previous studies in some species of laryngeal echolocators have estimated the integration time to be as low as ~ 100–200 μs (Weissenbacher et al. 2002)—longer than Rosette clicks but certainly shorter than big brown bats calls—which would imply that analysis of total energy does not necessarily reflect the correct

inter-species comparison, and that in fact, the correct comparison, from the standpoint of the auditory system, should use a measure that is somewhere between the total energy and the peak energy. Further, this reported measurement of a ~100–200 μs integration time (Weissenbacher et al. 2002) was, to our knowledge, the only measurement of integration time in bats that was done using ultra-short stimuli which were as short as *Rousettus* clicks (50 μs). Finally, we note that the auditory processing of ultra-short transient signals, such as the clicks of Rosette bats, is non-linear and poorly understood (Beyer, 1990); therefore, more work needs to be done in order to elucidate the effective echo energy available to the auditory system of clicking bats.

The Egyptian fruit bat's click has relatively large bandwidth with peak energy at 30 kHz

Fourier spectral analysis shows that the clicks of Egyptian fruit bats have a bandwidth of ~57 kHz at –25 dB (Fig. 3b, black; Table 1, row 4)—very similar to that of search calls of the big brown bat, which have a bandwidth of ~58 kHz (Fig. 3b, blue), but narrower than the terminal (buzz) calls of the big brown bat (~86 kHz, Fig. 3b, green; Table 1, row 4). We found the peak energy of the Egyptian fruit bat clicks to be around 30 kHz (Fig. 3b, black), which is consistent with previous measurements (Herbert 1985). The Gabor-like shape of the signal predicts that the spectral energy will be symmetrically concentrated around the same peak frequency as the FFT (Holland et al. 2004; see above), but this does not seem to be the case when using a Fourier spectral analysis (Fig. 3b, black). However, note that Fourier analysis of such ultra-short clicks needs to be taken cautiously, as it does not capture the brief-signal characteristics of the biphasic clicks. Nevertheless, despite this methodological caveat, it is noteworthy that the spectral analysis of the Egyptian fruit bat clicks does fit well with the audiogram for this species (Fig. 3a), which shows a high auditory sensitivity (threshold < 40 dB SPL) spanning frequencies between ~5 and 58 kHz (Koay et al. 1998). The total extent of the Egyptian fruit bat's audiogram, at 60 dB SPL, is between ~2 and 65 kHz—which allows good hearing of communication calls on the lower-frequency end, and good hearing of the biosonar clicks' and echoes on the high-frequency end (Koay et al. 1998).

Autocorrelation function (ACRF) of Egyptian fruit bat sonar signals predicts that the ranging acuity of the Egyptian fruit bat should be similar to the big brown bat

There is an ongoing debate regarding bats' receiver model: Several ranging experiments (Simmons 1979;

Simmons et al. 1990) have consistently reported a dip in the big brown bat's ranging performance around an echo-delay of 30 μs, which is the time delay of the first positive peak of the ACRF (Fig. 2c, left)—and these findings have been used as the critical argument in proposing the existence of a receiver in bats that is equivalent to a coherent matched-filter, i.e., a receiver that cross-correlates the emitted signal with the returning echo and has access to phase information (Simmons 1979; Simmons et al. 1990; Simmons and Stein 1980; Levanon and Mozeson 2004). This type of receiver can be shown to be an 'ideal receiver', in the sense that it maximizes the SNR of analyzed echoes.

An alternative commonly suggested receiver for bat sonar is an equivalent of the semi-coherent matched filter, i.e. a receiver that is not sensitive to phase. This model predicts that bats' ranging performance will behave like the *envelope* of the cross-correlation between outgoing pulse and returning echo (Hackbarth 1986; Menne and Hackbarth 1986). Conducting a cross-correlation analysis is therefore valuable for both of these commonly assumed receivers. In addition, the performance predicted by classical auditory models usually correlates to that predicted by the ACRF (Hewitt and Meddis 1991; Boonman et al. 2003). A matched filter—either the coherent or the semi-coherent type—takes the delay of the central peak of the cross-correlation of signal and echo to be its estimated echo delay (and hence the estimated target range). Therefore, two important parameters of the ACRF are: (a) the side-peaks' amplitude (also known as sidelobes): Prominent sidelobes could be confused with the main peak, thus confounding the estimate of echo-delay, and reducing the accuracy of target ranging. Therefore, a "good" signal, which marks reliably the time-of-arrival of the echo, should have an ACRF with a single narrow central peak and with the lowest possible sidelobes (Levanon and Mozeson 2004). (b) The width of the main-lobe (which is proportional to the ACRF period) can be used to predict the accuracy of a matched filter. These two parameters are especially important for a coherent receiver, but they also influence the range estimates for a semi-coherent receiver (see below).

To compare the predicted sonar performance under the assumption of a coherent (phase-sensitive) matched-filter receiver, we computed the ratio of the ACRF main peak to its first sidelobe, and compared this ratio in Egyptian fruit bats versus big brown bats. Our analysis showed that the peak/sidelobe ratio (height of ACRF main peak divided by height of ACRF first sidelobe) equals 6 in the ACRF of Egyptian fruit bat clicks, 2.5 in a terminal buzz call of the big brown bat, and only 1.5 in its search call (Fig. 2c; Table 1, row 5). Thus, if one assumes that echolocating bats use a coherent receiver—which is certainly not a

universally accepted assumption (Menne et al. 1989; Saillant et al. 1993; Matsuo et al. 2004; Peremans and Hallam 1998; Wiegrebe 2008; Boonman and Ostwald 2007)—then we predict that, unlike the reported dip in performance in the big brown bats, Egyptian fruit bats should *not* have a decrease in range-detection performance at delays fitting the ACRF first sidelobe. In other words, under the coherent-receiver assumption, the click-based signal design of Egyptian fruit bats is *superior* to that of big brown bats in terms of its sensitivity to sidelobe-induced ranging errors (Table 1, row 5). Moreover, the lower sidelobes in the ACRF of Egyptian fruit bats would imply a more reliable performance at lower SNR conditions than is possible for big brown bats. Lower sidelobes might be important for the cave-dwelling Egyptian fruit bats, in whose caves the echoes returning from the walls mask the echoes from objects of interest, such as protruding landing-points.

As explained earlier, the second relevant descriptor of the ACRF is its *period* (i.e. the location of the first sidelobe peak) can be used to predict the accuracy of a cross-correlation ideal receiver. Experiments that used a jittering virtual target (Simmons 1979; Menne et al. 1989; Simmons et al. 1990) have shown that big brown bats can discriminate range-jitter of ∼0.4 μs. Since the ACRF period of the Egyptian fruit bat click (∼34 μs) is similar to that measured for big brown bats terminal approach calls (∼32 μs: Table 1, row 6), we predict that—if the bats use a coherent (phase-sensitive) receiver—the range-accuracy capabilities of the clicking Egyptian fruit bat should be similar to that of the big brown bat. No such experimental data currently exists for Egyptian fruit bats, but this is a clear prediction from the coherent-receiver model.

To compare performance under the assumption of a semi-coherent (envelope-based) receiver, we analyzed the envelope of the ACRF (Fig. 2c, gray line). We have used the width of the envelope at half-height as a measure of predicted ranging acuity in both species, under the assumption of a semi-coherent receiver. The Big brown bat's ACRF envelope had a width of 71 μs for search signal and 19 μs for the terminal buzz signal. For the Egyptian fruit bat, the click's ACRF envelope had a width of 39 μs, which is in-between the two cases of the FM signals of the big brown bat (Table 1, row 7; Fig. 2c).

To conclude, we propose that—*regardless* of whether one assumes that echolocating bats use a fully coherent-like receiver or a semi-coherent-like receiver in order to estimate target range—the ACRF analysis presented here (Fig. 2c; Table 1, rows 6–7) gives the *same* prediction: namely, that click-producing Egyptian fruit bats should have a similar ranging acuity to that of the most-studied FM bat species, the big brown bat. This prediction remains to be tested experimentally.

Wideband ambiguity function (WBAF) analysis predicts that the click signals of Egyptian fruit bats are more Doppler-tolerant than the FM calls of big brown bats

The relative velocity of a bat compared to the target introduces a Doppler shift to the returning echoes of the bat's signals; for a typical bat flight speed of between 3 and 8 m/s, the echoes from the bat calls will be perceived with Doppler shifts of 1.8–4.8% in frequency (Boonman et al. 2003). Here, we employed another commonly used tool in radar signal design and analysis—the ambiguity function (Skolnik 2001; Levanon and Mozeson 2004)—as an additional quantitative measure of comparing pulse characteristics, especially the pulse's sensitivity to Doppler shifts. We employed here the full version of this function, known as the wideband ambiguity function (WBAF): the WBAF is described in detail in Appendix B, and it is the correct form of the ambiguity function that must be used if one wishes to analyze the wideband calls of fast-flying bats (Cahlander 1962; Altes and Titlebaum 1970; Simmons and Stein 1980; Holderied et al. 2008). In brief, the WBAF is helpful for analyzing the sensitivity of an ideal receiver (matched filter) to Doppler shifts: specifically, how the Doppler-shift affects range estimation. For example, in FM bats, the Doppler shifts due to the bat's motion are expected to cause a substantial bias in range-estimation, due to the time–frequency coupling in the FM signal (Cahlander 1962; Simmons and Stein 1980; Holderied et al. 2008). In the WBAF computation, the sonar signal is delayed, to simulate all possible delays to targets, and Doppler-shifted, to simulate the effect of the bat's speed relative to the target. The color-code of the function at a given point on the plot (Fig. 2d) represents the strength of the receiver output at a particular delay τ and speed v. Note that "cutting" the WBAF diagram horizontally at zero velocity yields the ACRF of the signal (Levanon and Mozeson 2004).

Examining the inverse steepness of the WBAF is a measure of the sensitivity of range-estimation to Doppler shifts, because the theoretical ranging offset can be found by calculating the shift of each cross-correlation maximum from the maximum at zero velocity (Skolnik 2001); this is under the assumption that the bat employs a coherent matched-filter for range estimation (see previous section for alternative bat receiver models).

We compared the inverse steepness of the WBAF for the click-signal of Egyptian fruit bats versus the FM signal of the big brown bat, separately for the big brown bat's search- and terminal-phase calls (Fig. 2d; Table 1, row 8). Our analysis showed that the Egyptian fruit bat's click is more tolerant to Doppler shifts than the most-tolerant call of the big brown bat (the terminal-phase call). Measuring the ranging error for a relative speed of 10 m/s, the WBAF

of the big brown bat search call shows a ranging error of 160 μs, which corresponds to a distance error of 57.6 mm. The WBAF of the terminal phase (buzz) call shows a smaller ranging error of 34 μs, which corresponds to a distance error of 11.6 mm. The WBAF of the Egyptian fruit bat click is almost "vertical" to the time-delay axis (Fig. 2d, right), and measuring its steepness shows an even smaller ranging error, of 9 μs, which corresponds to a distance error of only 3.1 mm. Thus, the sonar clicks of Egyptian fruit bats are 17 times more Doppler-tolerant than big brown bat's search calls and 4 times more Doppler-tolerant than the shortest terminal (buzz) calls of the big brown bat.

Angular beam-width of the sonar emission beam is comparable between Egyptian fruit bats and FM bats such as the big brown bat

By using an array of microphones to measure signal intensity, Yovel et al. (2010) calculated the angular width of the Egyptian fruit bat's beam in the lab to be $50° ± 2°$ (Table 1, row 9). The width was determined by finding the half-power point of the beam, where intensity falls to –3 dB below the peak. Using a similar experimental procedure, Ghose and Moss (2003), reported big brown bats to have a beam-width of 70°. A later study in another FM laryngeal echolocator, *Myotis daubentonii*, reported a beam-width of 40° in the field (Surlykke et al. 2009a). Thus, clicking bats and FM laryngeal echolocators have a rather similar ability to focus the transmitted energy into a restricted direction in space (Table 1, row 9). However, as will be discussed below, recent studies show that the *behavioral strategy* used by clicking bats to steer their sonar-beam in space differs in interesting ways compared to that of the big brown bat.

Echolocation behavior of Egyptian fruit bats versus big brown bats when approaching an object

The echolocation behavior of laryngeal echolocating bats during approach to objects has been studied extensively over many years (Simmons et al. 1979; Schnitzler et al. 2003; Melcón et al. 2007; Ulanovsky and Moss 2008; Melcón et al. 2009). Here, we have set out to examine the approach behavior of free-flying Egyptian fruit bats, and to compare it to that of the big brown bat and other FM bats. To this end, we trained six Egyptian fruit bats to detect, localize, approach and land on a relatively large (10-cm diameter) sphere that was mounted on a vertical pole positioned inside a large empty flight-room. We used several steps to ensure that the bats were relying solely on echolocation to perform the task: (a) the target was painted black and the room was completely dark (illuminance $< 10^{-4}$ lux), to exclude visual cues. (b) The bats were food-rewarded only after landing, to prevent use of olfactory cues. (c) After every trial, the target was randomly re-positioned inside the room, both in the horizontal and in the vertical directions. (d) The walls of the room and the pole on which the target was mounted were covered with sound-attenuating materials; in contrast, the large target sphere was made of a highly-reflective material (polystyrene), hence the target was the most salient acoustically-reflective object in the room. The flight of the bats was videotaped with two high-speed infrared cameras, which enabled a 3-D reconstruction of the flight trajectory, and the echolocation behavior was recorded with a 20-microphone planar array, which allowed us to reconstruct the shape of the emitted sonar beam. For full details on these experiments, see Yovel et al. (2010).

Behavioral adaptation of click intensity is similar in lingual and laryngeal echolocators

In contrast to what was previously believed, we found that Egyptian fruit bats decreased the emitted intensity of their clicks while approaching a landing target (results were recently submitted elsewhere). This behavior is similar to the well-documented decreases in call intensity observed in laryngeal echolocating bats during target approach (Schnitzler et al. 2003).

Pulse repetition rate follows very different dynamics in lingual versus laryngeal echolocating bats

Laryngeal echolocating bats increase pulse rate when approaching a target. In the big brown bat, the repetition rate increases from ∼10 Hz before the beginning of the approach to ∼150 Hz during its final phase (Ghose and Moss 2006). Pulse repetition rate is increased in a stereotypical manner that allows defining the onset of the approach and dividing the entire behavioral sequence into clear phases (Moss et al. 2006; Melcón et al. 2007, 2009). Laryngeal echolocators sometimes arrange their approach calls in groups with a short and relatively constant time interval between the calls: these are referred to as 'strobe groups' (Moss and Surlykke 2001; Moss et al. 2006).

Egyptian fruit bats, as well as other studied Rosette species (Grinnell and Hagiwara 1972), emit clicks in pairs with a short time interval within pairs (20–25 ms) and a longer time interval between pairs (60–150 ms): They always emit clicks in pairs, and they never emit groups with more than two clicks (Fig. 4a, top; Table 2). Similar to laryngeal echolocators (Speakman and Racey 1991), Egyptian fruit bats also synchronize their pulse emissions with the wing-beat, emitting both clicks of the pair during

the down-stroke phase of the wing-beat cycle (Möhres and Kulzer 1956; Herbert 1985; Holland and Waters 2005). Interestingly, unlike the big brown bats (and most other laryngeal echolocators), Egyptian fruit bats also synchronize their ear movements to the wing-beat: They move both of their ears in-phase, back and forth, in synchronization with the wing-beat cycle, and tend to emit the click-pair during the forward movement of the ears. Holland and Waters (2005) showed that in the forward position, the auditory sensitivity of the bats increases, which might suggest that the purpose of the forward ear movements is to improve auditory sensitivity when echoes are expected to arrive.

Among laryngeal echolocators, horseshoe bats (Rhinolophidae) were shown to move their ears in anti-phase to each other and in synchronization to the calls (Pye et al. 1962)—unlike the in-phase ear movements of Egyptian fruit bats (Table 2). The ear movements of horseshoe bats were shown to assist vertical target localization, which differs from the proposed function of increasing auditory sensitivity in Egyptian fruit bats (Holland et al. 2004).

Egyptian fruit bats almost do not increase their pulse repetition rate when approaching an object in complete darkness (Yovel et al. 2010)—and even when they do exhibit an increase in pulse-rate during approach (Fig 4a, top) (Summers 1983), this increase is typically less than threefold, i.e. much smaller than the dramatic increase in pulse-rate exhibited by big brown bats approaching an object (Fig. 4a, bottom). The reason for the minor increases that we observed in pulse repetition rate (Yovel et al. 2010) is probably that under the extremely low illumination levels that we used ($<10^{-4}$ lux), the bats were continuously operating at the maximum rate allowed by the physiologically limited speed of tongue motion. Indeed, there is evidence that at higher light levels, Egyptian fruit bats tend to use lower pulse-rates most of the time, and to increase the pulse-rate during landing from ~ 8 to ~ 13 click-pairs per second (Herbert 1985). However, some obstacle-avoidance tests in complete darkness have indicated that even in complete darkness the Egyptian fruit bats sometimes increase their pulse rate threefold, from ~ 7 to ~ 20 click-pairs per second (Summers 1983).

The consequence of this difference in the dynamics of pulse-rate is that Egyptian fruit bats are able to perform a landing task with similar success to laryngeal echolocators while using a substantially lower rate of information flow: in our experiments, along the last 2 m before landing, Egyptian fruit bats acquired information with a rate of 7 ± 2 clicks/meter (this should be halved if each pair is regarded as a single information unit)—whereas landing experiments in big brown bats have indicated that these bats acquire information with a much higher rate of 22 ± 3 pulses/m (Table 2; M. Melcón, personal communication).

Thus, the example of the Egyptian fruit bat shows that large increases in pulse-rate are *not* a necessary prerequisite for successful landing maneuvers in echolocating bats.

Beam-steering follows two different behavioral optimization strategies

When approaching a target object, big brown bats point the peak of their sonar emission beam towards the target, thus maximizing the signal-to-noise ratio (SNR) (Ghose and Moss 2003, 2006); an example of this is shown in Fig. 4b (left). Egyptian fruit bats, on the other hand, direct the peak of their sonar beam *off-axis* relative to the target, pointing the beam repetitively Left→Right→Right→Left (Fig. 4b, right). The result of this is that the point of the maximum *slope* of the emission curve is being directed towards the target (Fig. 4c, d). The center of the click-pair (the mean direction of both clicks) is directed towards the target at the final part of the approach with an accuracy of $\sim 15°$ (Table 2)—with some trials showing locking accuracy of $\sim 5°$ (Yovel et al. 2010).

What is the advantage of such a Left→Right beam steering strategy? When the maximum-slope of the beam is directed towards an object, any azimuthal motion of the object relative to the bat (or vice versa) will result in the largest possible change in echo intensity. The sign of the change in intensity (positive or negative) corresponds to the direction of motion. We therefore hypothesized that Egyptian fruit bats lock the maximum-slope of their beam on target as a strategy that maximizes their sensitivity to *changes* in target azimuth—in order to better localize the target. Using a standard theoretical measure, the Fisher information, we were able to show that this strategy is mathematically optimal for localizing a target based on changes in the reflected energy (Yovel et al. 2010).

When pointing the maximum slope of the emission-curve towards an object, rather than its peak, less energy (6 dB) is reflected back from the object, reducing object detectability—and calculations based on the sonar equation show that this reduction decreases the maximal detection range of the target by $\sim 16\%$ (Yovel et al. 2010). We hypothesize, therefore, that the part of the beam between the peak and the maximum-slope of the emission curve can be used by bats to trade-off between detection and localization: the beam's peak provides optimal detection (optimal SNR), while the maximum-slope provides optimal localization. This leads to the prediction that, when facing easy detection conditions (as in our experiments with a large highly reflective object in an empty room), the bats should use the maximum-slope strategy—as indeed our bats did—but when confronted with difficult detection conditions, the bats should point their peak towards the

target, in order to optimize SNR. And indeed, in a control experiment, when we created a difficult detection problem by placing a masker behind the target, the Egyptian fruit bats switched strategy and directed towards the target a point close to the peak of their sonar beam (Yovel et al. 2010).

Can laryngeal echolocating bats also use a slope-based localization strategy? It is noteworthy that the Left→Right alternating double clicks of Egyptian fruit bats are advantageous for localization because comparing *two* different slopes within a short time interval doubles the intensity-difference. However, a double-pulse emission pattern is *not* a prerequisite for using a slope-based localization strategy: laryngeal echolocators, for example, might (in principle) also use a slope-based strategy, by always placing *one* of their beam's slopes on-target (e.g. Right → Right → Right…) and analyzing echo-amplitude changes between successive calls. Why has not a slope-based strategy been described to date in laryngeal echolocating bats? We believe that the reason is as follows: to date, all studies that tested beam-steering in laryngeal echolocators (Ghose and Moss 2003, 2006; Surlykke et al. 2009b) did so in the context of very small targets, which created a detection problem. We predict that, when localization is paramount and detection is not challenged—for example, when confronting big brown bats with a landing task onto a relatively large target—these laryngeal echolocators might also employ a slope-based localization strategy, and would place *one* of their beam's slopes on-target, e.g. Right → Right → Right.

The Left→Right steering of the sonar clicks in space probably underlies previous reports on differences in the intensity, duration or spectral content of the two clicks within a pair (Summers 1983). In our recordings, we did not find any systematic differences in these parameters between the two clicks within a click-pair. Therefore, we propose that the Left→Right spatial steering of the clicks, which we found (Yovel et al. 2010), underlies the reported differences in click intensity. The differences in previously-reported durations (Summers 1983) have been, most likely, a result of erroneous inclusion of echoes into the click-duration analysis—and indeed we expect to see different numbers of echoes from the two clicks coming from the left versus the right side, because of differences in object layout and geometry of reflecting surfaces on the left versus the right.

Finally, it is interesting to note that the Left→Right beam steering in Egyptian fruit bats is very similar to a well known Left→Right beam steering strategy in tracking radars, known as 'sequential lobing' (Skolnik 2001). Thus, as is often the case in studies of biosonar, the natural world and the world of engineering seem to have converged on a similar solution.

Echolocation motor control follows very similar control laws in the Egyptian fruit bat and the big brown bat

Big brown bats were previously reported to follow an adaptive control law that links locomotion dynamics to gaze direction (the angle of the sonar beam relative to the flight direction) (Ghose and Moss 2006). According to this law, the bat's turn-rate (the rate at which flight-direction changes) at time $t + \tau$ is linearly related to the echolocation gaze direction at time t (Table 2). The gain of this relation, k, and the lag τ depends on the bat's behavioral state (search, approach, attack).

We found that the exact same form of a control law described the echolocation and flight behavior of the Egyptian fruit bat (Fig. 4e; compare to Ghose and Moss 2006). Here, we calculated the sonar gaze as the angle of the average direction of a click-*pair* relative to the flight direction (i.e., each pair of clicks was treated as a single entity). Further, the parameters of the control equation, k and τ, were numerically almost identical between the Egyptian fruit bat and the big brown bat (Table 2)—suggesting that the same fundamental control law operates in the case of both laryngeal and lingual echolocating bats.

Landing performance is similar in lingual and laryngeal echolocating bats

Finally, we aimed to assess whether the echolocation behavior of Egyptian fruit bats enables them a comparable landing performance to that of laryngeal echolocators. We examined two performance measures (a) percentage of successful landings: Once trained to perform the landing task, Egyptian fruit bats easily learned to detect the target, approach it and smoothly land on it with virtually no errors (i.e. no misses of the target). Qualitative observations of videos of these landings compared to videos of landing greater mouse-eared bats (Melcón et al. 2007), another well-studied laryngeal echolocator, suggested that Egyptian fruit bats landed just as smoothly and efficiently on their target, in complete darkness, as did the greater mouse-eared bats. (b) Target size: the 10-cm diameter of the target that we used (Yovel et al. 2010) was approximately 2/3 of the body-length of the Egyptian fruit bats. Furthermore, in preliminary training of our bats, they successfully landed in complete darkness on even smaller targets ($\sim$5 cm diameter), that were 1/3 of their body length. Since the target was mounted on a pole, the bats had to land on it from the top (belly down). Although to our knowledge this was never tested systematically, it is difficult to imagine a big brown bat or a greater mouse-eared bat landing successfully belly-down on a sphere whose diameter is much smaller than 1/3 of their own body length. Thus, we conclude that the landing performance of the Egyptian fruit

bat, when guided by biosonar alone (in complete darkness), is at least as good as the landing performance of the big brown bat.

Discussion

The lingual (click-based) echolocation of bats from the genus *Rousettus,* with the Egyptian fruit bat as their most-studied representative, is to date still considered 'primitive' by many scientists working on echolocation, i.e. it is thought that the performance allowed by click-based echolocation is strongly inferior to laryngeal echolocation. This 'stereotype' of "primitive click-based echolocation" can be traced back to the first studies of *Rousettus* in the 1950s, and, as detailed in the introduction, this view was primarily due to erroneous measurements of the sonar click duration of these bats. Recent studies, however, have shown that these bats have remarkably brief sonar clicks ($\sim$50–100 μs, Holland et al. 2004; Fig. 1)—but the view that echolocating clicks are 'primitive' still persists. In this review, we therefore sought to examine this 'primitiveness' notion—and we did this by comparing in detail the theoretically expected and empirically observed echolocation performance of the most studied lingual echolocator, the Egyptian fruit bat, to the most studied laryngeal FM-echolocator, the big brown bat. We found that both theoretically and experimentally (behaviorally), the echolocation performance of Egyptian fruits bats is not inferior to that of the big brown bat. Furthermore, when examining the signal design of these two bat species and analyzing their theoretically expected performance based on sonar theory, we predict that the click-based echolocation signals emitted by Egyptian fruit bats are in some respects *better* than those of the big brown bat—better both in terms of ranging errors and in Doppler-shift tolerance (Table 1, rows 5–8).

If click-based echolocation signals are optimal,
why do not all echolocating animals use them?

They actually do. In fact, laryngeal echolocating bats are the *only* known animals which use tonal echolocation signals. Echolocation has probably evolved 4 or 5 times during the evolution of those vertebrate species that we currently know to echolocate. In all of these events, except perhaps one (see paragraph on evolution of bats below), a click-like echolocation system has evolved (Morisaka and Connor 2007). Thus, all dolphins and other toothed whales use click-like echolocation signals, which are often very similar to the clicks of *Rousettus* bats (Fig. 1). Some toothed whales (e.g., beaked whales) use signals that contain more than a single period per click, but their clicks, too, are much shorter ($\sim$100–200 μs) than any laryngeal

bat signals, and are much more click-like than any laryngeal bat echolocation calls (Nakamura and Akamatsu 2004; Johnson et al. 2004). Despite their use of click signals, no one would claim dolphins' echolocation performance as being functionally primitive. All other terrestrial echolocators (swiftlets and oil-birds) also use click-like echolocation signals (Konishi and Knudsen 1979; Thomassen et al. 2004). Bird clicks are longer in duration and lower in frequency in comparison to Egyptian fruit bat or odontocete clicks, and are therefore expected to provide inferior functional performance (Konishi and Knudsen 1979); this performance, however, is probably sufficient for their needs. Nevertheless, bird echolocation signals are still click-like in the sense that they are short transients with signal duration of a few periods of the carrier frequency.

Why, then, do laryngeal echolocators use tonal signals rather than ultra-short clicks? The reason is probably the very high total energy that is required in order to detect very small prey (such as insects) at large distances. The total energy that can be emitted in a short signal is limited by physiological constraints and by the very large difference between the impedances of tissue and air (a problem that is not relevant for marine echolocators). A simple way to bypass these constraints is to prolong the duration of the signal; such a solution, however, requires a counter-measure to deal with the decrease in ranging accuracy that results from a long sonar signal. Laryngeal echolocators have solved this problem by adding a frequency-modulated part to their signal, which couples frequency and time and thus enables to maintain a wide bandwidth, but to increase the energy at each frequency. Many RADARs use similar frequency-modulated signal designs to deal with the same problem (Simmons and Stein 1980; Skolnik 2001). Notably, our analysis (Fig. 2c; Table 1, rows 6–7) shows that Rosette bats are predicted to reach a similar ranging accuracy as FM echolocators, by using ultra-short clicks of 50–100 μs duration.

Functional uses of biosonar in click-based echolocating bats

The main limitation of the Egyptian fruits bat's click signals seems to be not ranging accuracy, but rather their low total energy—which is between 1 and 4 orders of magnitude smaller than in the big brown bat (see above). This low total energy is a direct result of the ultra-short duration of their sonar clicks. It was therefore commonly assumed that Rosette bats are limited to use their echolocation mainly for general orientation in their roosting caves—and that they possibly developed echolocation as a result of becoming cave dwellers. Numerous observations, however, show that Egyptian fruit bats use echolocation also when flying outside their caves—for example, during low-altitude

commuting flights, or while feeding at fruit trees (Y.Y. and N.U., personal observations). Thus, echolocation seems to play a much broader role in the lives of these bats than previously thought.

Behavioral studies of Egyptian fruit bats have shown that when the object of interest is close to the bat, such as in wire-avoidance experiments, the wire detection abilities of Egyptian fruit bats are quite comparable to those of big brown bats, as they are able to detect 0.31-mm diameter wires (Summers 1983). This may suggest that, for detection of small wires from a short distance, the *total* energy is not as important as the *peak* intensity—and the peak intensity is in fact more similar between Egyptian fruit bats and big brown bats (Table 1, row 2). This implies that, in the echolocation tasks which are relevant to the lifestyle of Egyptian fruit bats—namely, detection of large objects (cave walls, trees) and detection and localization of medium-sized stationary objects (such as fruits or branches)—these click-producing bats perform just as well as laryngeal echolocators.

Evolution

For many years, bats were divided into two sub-orders: echolocating Microchiroptera ('microbats') and non-echolocating Megachiroptera ('megabats'), with the *Rousettus* genus being the only echolocating bats within the Megachiroptera. Moreover, due to their non-specialized diet, Rosette bats were often considered to be evolutionarily primitive members of the Megachiroptera, and Donald Griffin even postulated that these bats may resemble the common ancestor of Megachiroptera and Microchiroptera (Griffin et al. 1958). Recent genetic evidence, however, completely revised the taxonomic tree of bats (Jones and Teeling 2006). One of the major results of this revision has been the new positioning of the Pteropodidae (previously known as Megachiroptera) as the closest family to the horseshoe bats (Rhinolophidae and Hipposideridae) (Jones and Teeling 2006; Jones and Holderied 2007). The horseshoe bats use constant frequency–frequency modulated (CF–FM) signals, which are considered by many researchers as the most sophisticated echolocation signals (Jones and Teeling 2006; Jones and Holderied 2007). There is an on-going debate whether laryngeal echolocation has evolved twice independently during bat evolution, or has been lost by old-world fruit bats (Veselka et al. 2010); in either case, in light of the new phylogenetic findings, it is clear that the notion of Rosette bats as evolutionarily 'primitive' is not supported by the data (Springer et al. 2004; Jones and Teeling 2006; Jones and Holderied 2007). Thus, Rosette bats cannot be regarded as 'primitive' in any way, neither in terms of evolution nor in terms of the performance subserved by their echolocation signals.

Summary and future outlook

We propose that click-based bat echolocation should no longer be termed 'primitive'—just as dolphin echolocation should not be regarded 'primitive' solely because it is based on clicks. Of course, much more work needs to be done on click-based bat echolocation, in order to understand its capabilities and limitations—and we are certain that this comparative approach to echolocation will fuel fruitful work in years to come. Nevertheless, we believe that the limited body of work reviewed here already clearly suggests that the click-based echolocation of Rosette bats is much more developed than formerly thought. True, click-based echolocation is different from laryngeal echolocation—but it is not so primitive, after all.

Appendix

Appendix A: Energy Flux Density

The term "Energy Flux Density", which is useful for measuring the energy content of a transient sound wave, was defined in order to allow comparisons of sonar signal intensities between terrestrial and aquatic environments (Au 1993). To do so, the classical Energy Flux definition is modified to take into account both the signal duration and the acoustic impedance of the medium:

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

where E is the energy flux density (in units of J/m^2), $P(t)$ is the time-varying sound pressure measured at 1-m from the source, T is the signal duration, ρ is the density of the medium (in units of kg/m^3) and c is the sound velocity in the medium.

Appendix B: Wide band ambiguity function

The Ambiguity Function is a common tool in radar and sonar signal-design, used for quantitative estimations of the system's sensitivity to Doppler shifts, and the effect of Doppler on range measurements. The wide-band ambiguity function (WBAF) considers the actual time-compression or

expansion of the signal modeled by the Doppler effect, rather than the frequency-shift approximation which can be used for narrow-band signals (which is sufficient for most radar applications) (Levanon and Mozeson 2004).

The first modifications of the conventional ambiguity-function from radar theory to the case of wideband signals were done by Kelly and Wishner (1965) and Cahlander (1962)—the latter study applied the new wideband theory to analyzing bat signal design. Later, WBAF analysis of bat signals was used by several other researchers (Altes and Titlebaum 1970; Simmons and Stein 1980; Holderied et al. 2008)—all of them used the WBAF to analyze FM signals of laryngeal echolocators. Here, we applied for the first time the WBAF analysis to the case of click-based biosonar, and compared the results to a classic FM call, that of the big brown bat.

The WBAF describes the response of a matched filter to a pure returning echo (with no added noise or attenuation) for a set of target distances and relative speeds: See Fig. 2d. Each horizontal slice through the WBAF is a cross-correlation function calculated between the transmitted signal and a Doppler-distorted version, for a particular relative speed. For our calculations, we used the following version of the WBAF (Kelly and Wishner 1965):

$$\chi(\tau, \eta) = \eta^{\frac{1}{2}} \int z(t) z^*(\eta(t - \tau)) dt$$

where $z(t)$ is the bat's call waveform at time t, * stands for complex conjugation, τ is the time delay to the target (which is proportional to the target's distance), and η is the Doppler scale factor:

$$\eta = \frac{1 + v/c}{1 - v/c}$$

where v is the relative flight speed of the bat compared to the target, and c is the speed of sound (we used $c = 343$ m/s for the speed of sound in air).

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