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Echolocation performance and call structure in the megachiropteran fruit-bat *Rousettus aegyptiacus*

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The structure of the calls made by the echolocating fruit bat *Rousettus aegyptiacus* while flying within a flight tunnel were investigated. Calls are impulsive clicks lasting around 250 μs, with most energy occurring during the first 100 μs. Such a call duration is much shorter than that previously reported for this species. The ability of *R. aegyptiacus* to detect and avoid obstacles was tested in both the light and total darkness. Bats were able to detect and avoid 6 mm diameter wires significantly more often than 1.3 mm diameter wires when tested in the light. In the dark, the same relationship held, with no decrease in the ability to detect and avoid the obstacles. Bats used echolocation in both the light and the dark conditions. The simple impulsive clicks used in echolocation by this species are thus able to detect wires of at least 6 mm in diameter and probably smaller. The detection problems associated with very short duration signals is discussed. The possession of both a good visual system, and a good echolocation system in this species has implications for the evolution of echolocation in bats.

Key words: echolocation, *Rousettus*, bat evolution

INTRODUCTION

Echolocation has evolved a number of times, with performance of the different biosonar systems ranging widely. The echolocation systems of microchiropteran bats and dolphins are capable of impressive spatial and ranging resolution (Simmons *et al.*, 1995; Au, 1993), while the systems of oilbirds and cave swiftlets may augment the visual sense or just allow them to orientate within their dark roosting caves (Suthers and Hector, 1985; Fullard *et al.*, 1993). Within the Chiroptera, echolocation appears to have evolved twice; once to produce the sophisticated system found in the Microchiroptera, and again to produce the system

found in the megachiropteran genus *Rousettus*. Such a scheme does however remain controversial given the uncertainty regarding the monophyletic origins of bats (Pettigrew, 1991*a*, 1991*b*; Baker *et al.*, 1991; Simmons and Geisler, 1998; Springer *et al.*, 2001). Within the Microchiroptera, a range of call types exist which are matched to the ecological niche of each bat species (Neuweiler, 1983). These calls are characterised by frequency modulated and/or constant frequency segments ranging in duration from under 1 ms to over 50 ms. Unlike the Microchiroptera, the calls of *Rousettus* are similar to those produced by dolphins, consisting of impulsive clicks which are short in duration and have a wide bandwidth

(Au, 1993). Echolocation was first described in *R. aegyptiacus* by Möhres and Kulzer (1956), and it was subsequently discovered that the clicks are produced by the bat's tongue (Kulzer, 1956) and show the same characteristics as a shock wave resonator (Roberts, 1975). Pye and Pye (1988) report that similar signals are produced by *R. amplexicaudatus*, *R. lechenaulti* and *Rousettus* (*Stenonycteris*) *lanosus*. Herbert (1985) describes the calls of *R. aegyptiacus* as pairs of impulsive clicks of 0.6–1 ms duration, produced in a 1:1 relationship with the wingbeat cycle. The clicks have a peak frequency of 20–40 kHz, with a range of 10–60 kHz, and are produced by the bats only when flying in the dark. It is believed that echolocation evolved in this genus as they use caves for roosting where the complete darkness would make their sensitive visual systems redundant (Henson and Schnitzler, 1980). Early work by Griffin *et al.* (1958) suggested that the echolocation system of *Rousettus* showed similar performance to that of the Microchiroptera in obstacle avoidance experiments. Despite this suggestion, the echolocation system of *Rousettus* has often been described as 'rudimentary' or 'simple' (Koay *et al.*, 1998; Heffner *et al.*, 1999).

The echolocation system of *Rousettus* is not only of intrinsic interest as an independently evolved biosonar system, but may shed light on the controversies surrounding the evolution of both flight and echolocation in bats. Two possible schemes suggest that either flight evolved first with echolocation later, or vice versa (Arita and Fenton, 1997). However, the evolution of flight first would also have required a well-developed visual system to allow the avoidance of obstacles and the detection of landing sites. Once a fully formed visual system had evolved, the evolution of an echolocation system may be more difficult since the enlargement of the visual cortex is often at the expense of other areas of the brain (Harvey and Krebs, 1990; Speakman, 1993). Switching from a visual sensory modality to an echolocating one may involve a transitional state with both systems at a disadvantage — although Simmons and Geisler (1998) argues that this may not necessarily have been the case in the early echolocating niche. A bat which demonstrates both a good visual and biosonar system would thus demonstrate that such transitions can occur.

We proposed to test the performance of the echolocation system of the Egyptian fruit bat *Rousettus aegyptiacus* (E. Geoffroy) through an obstacle avoidance experiment using two different diameters of wires (6 mm and 1.3 mm) in light conditions and in total darkness. We hypothesised that in the light, with the bats using their visual system, the large wires should be detected and therefore avoided more effectively than the small wires (or demonstrate the same effect but for motivational reasons — small wires being less harmful to collide with). If the bats are using an effective biosonar system, then this relationship should also hold in the dark. While we may expect an overall reduction in performance of the biosonar system with respect to the visual system, there should be no interaction between the factor of light condition and wire diameter unless one sensory modality was superior to the other.

MATERIALS AND METHODS

Seven adult *R. aegyptiacus* were loaned from a local zoo (5 ♀♀ and 2 ♂♂). Bats were maintained in a 10 m × 5 m × 2.5 m room at 25°C on a 12 h light 12 h dark reversed photoperiod and provided with fruit and water at all times.

All experiments were performed in a 14 m × 2.5 m × 1.5 m corridor with wire mesh roosting sites suspended from the ceiling at either end. A horizontal pole was placed close to the ceiling spanning the corridor at 6.5 m from the bat's start position. From the pole were suspended a series of wires which formed the obstacles. There were three wire treatments 1. No

wires (pole only); 2. Wide diameter wires (6 mm diameter plastic coated copper wire); 3. Small diameter wires (1.3 mm diameter plastic coated copper wire). Both wires were light grey in colour. For each of the wire treatments, the wires could have one of two configurations: a central wire and two flanking wires 53 cm from the central one, or two wires, 48.5 cm from the sides of the corridor with a 53 cm gap in the centre. To eliminate other cues to the bats, such as the weights tied to the bottom of the wires, the bottom of the wires were hidden by a cardboard screen which was always present. The order of presentation of the wire types was randomised, as was the configuration of the wires. Thus, although the bat would be aware that a treatment would occur at the same position along the corridor, it would not be aware which of the three wire treatments it would receive, nor which configuration the wires would be in. Experiments were performed under fluorescent light and in total darkness. Light levels were measured using a Tektronix J16 Digital Photometer and were 0.211 W/m^2 in the light treatment, and less than 1×10^{-6} W/m^2 in the dark treatment (below the sensitivity of the device). Each bat received ten treatments of each wire type (five of each wire configuration) in the light and also in the dark (sixty presentations in total). Light and dark experimental runs were performed on consecutive nights for each bat, the order of presentation to each bat being reversed. During an experimental run, the bat would be persuaded to fly from a roosting site at one end of the corridor through the wires to the roost at the far end by the experimenter clicking their fingers. Echolocation calls produced by the bat were recorded using an Ultrasound Advice U-30 bat detector ($\pm$ 3 dB 10–120 kHz) situated at the far end of the corridor, sampled at 450 kHz by an Ultrasound Advice Portable Ultrasound Processor (PUSP) and stored at 10x time expansion onto audio-tape (Marantz CP-230 recorder: $\pm$ 3dB 20 Hz–18 kHz). Calls were later analysed on a PC using custom routines written in MATLAB. In order to monitor collisions with the obstacles, small bells were attached to the bottom of each wire which would ring if the bat touched it. To ensure that all collisions were recorded, each experimental run was filmed by a digital infra-red video (Sony DCR-TRV110) illuminated by an HVL-IRW infra-red lamp (approximately 580 nm peak illuminance). Where collisions were ambiguous, these could be later verified with reference to the video recording. Wing dimensions were taken from each bat with the wing held flat and photographed by digital camera (Olympus C-830L). Data obtained were the number of collisions of each bat with each treatment, and the mean inter-pulse interval between the click pairs during each treatment. All seven bats

were used, completing a total of 420 experimental runs. Since each bat was exposed to all treatments, repeated measures analysis of variance could be used.

The experiments were designed to test the following predictions:

1. The large wire should be more detectable in both the light and dark conditions, therefore a difference should be expected in the response to the factor 'wire diameter'. However, it is not possible to differentiate this response from a motivational one;

2. Obstacles should be more easily detected in the light using vision, than in the dark using echolocation, therefore a difference should be expected in the response to the factor 'light treatment';

3. Detection of the small wire in the dark should be proportionally more difficult in the dark than the light compared to the large wire, therefore a significant interaction term should be expected between 'wire diameter' and 'light treatment'. As there appeared to be a great deal of call to call variation which was possibly due to multiple echoes from the flight tunnel walls, 50 calls from the same bat were extracted, the start position of each call was aligned, and the calls averaged. As the calls were sudden impulsive clicks on a relatively quiet baseline, the sudden start of the call was used as a marker for alignment and averaging. This would have the effect of removing all out of phase components such as echoes, and enhancing all in-phase components from the actual call.

To investigate the effect of the corridor on the propagation of the calls from the bat, simulated *Rousettus* calls were generated and played back in the flight tunnel. The calls were generated using 200 μs duration square wave pulse gating a 20 kHz sine wave produced from a signal generator (Thandar TG501) and broadcast from an Ultra Sound Advice ultrasonic amplifier and electrostatic loudspeaker. Simulated calls were broadcast at one end of the tunnel and recorded at the other using the U-30 bat detector and PUSP as previously described.

RESULTS

Call Structure

Bats echolocated in both the dark and the light conditions. Calls consisted of double pulses (Fig. 1) with a mean interpulse interval between pulse pairs of 86 ± 3.0 ms ($\bar{x}$ ± SD, $n = 7$) and 22.9 ± 2.17 ms within double pulse pairs. The peak frequency of the calls was 19 kHz with a -3 dB bandwidth of 11 kHz, with a second peak in the
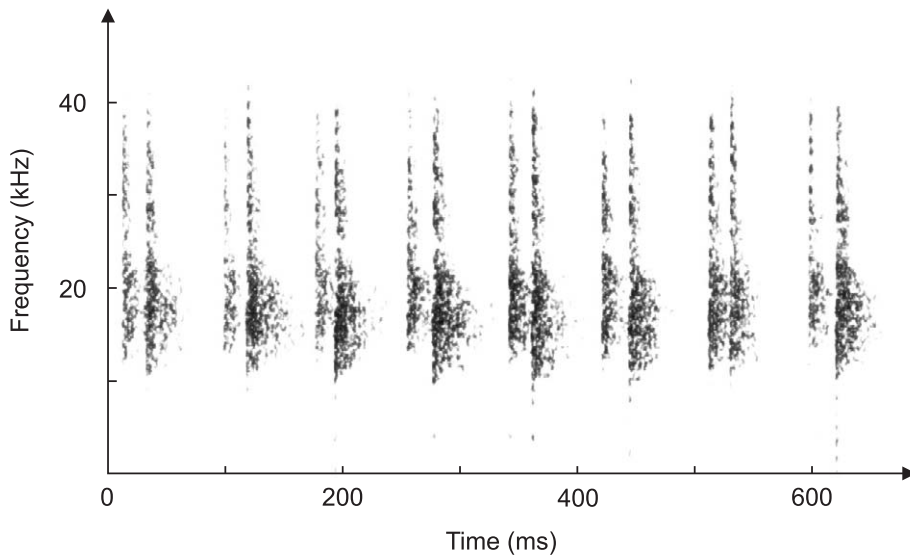
FIG. 1. Sonogram of a sequence of echolocation calls from *R. aegyptiacus* showing the production of double pulses (512 point FFT, Hamming window)

power spectrum 6 dB below the first at around 30 kHz. The power spectrum of 14 calls from two bats was averaged to determine the peak frequency of the call (Fig. 2). Examination of the calls in detail suggested that the apparently long duration of ca. 5 ms for each may have been due to multiple overlapping echoes reflected from the flight tunnel walls. The time base on a single click

was expanded to show the detailed structure of the start of the call (Fig. 3). A short duration single click can be seen, lasting around 250 μs.

The recording of the simulated *R. aegyptiacus* call taken from directly in front of the speaker and compared to the re-recorded signal after transmission along the flight tunnel shows that the recorded signal
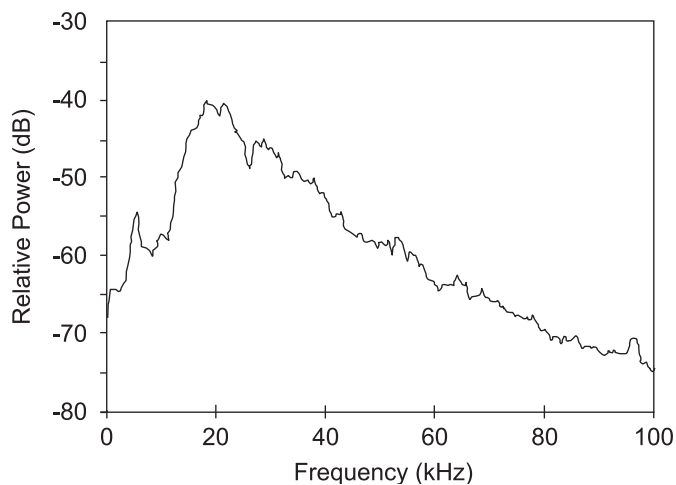

FIG. 2. Averaged power spectrum of a 14 echolocation pulses from *R. aegyptiacus* (256 point FFT, Hamming window)
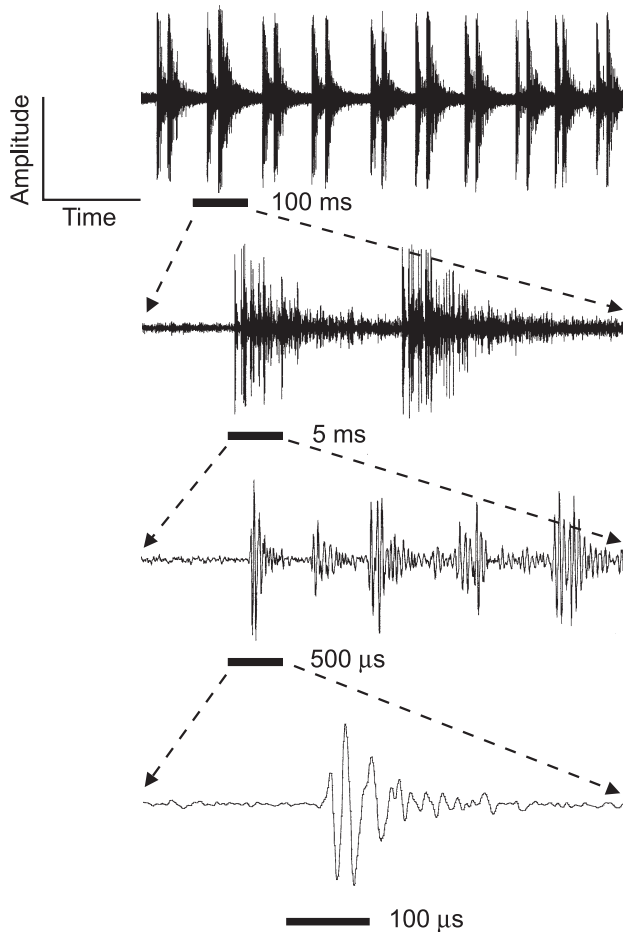
FIG. 3. Waveforms of a sequence of echolocation calls from *R. aegyptiacus* with a successively expanded time-base. The scale bar represents the approximate extent of the waveform represented in the figure beneath it. Amplitude is on an arbitrary scale

appears to be a series of superimposed copies of the original signal which are displaced in time (Fig. 4). This would be expected with multiple echoes from the walls of the flight tunnel.

The averaged waveform of fifty calls has removed out of phase overlapping echoes, and the initial click is revealed to be a very rapid transient click of a few hundred microseconds in duration (Fig. 5).

Obstacle detection

The wingspan ($\bar{x} \pm$ SD) of the bats was 61 ± 4.4 cm, compared to the 53 cm gap in the wires. For the collision data, the count data of the number of collisions per treatment was square-root transformed prior to the analysis. A repeated measures analysis of variance was performed using SPSS on the number of collisions of each bat with light condition and wire diameter as factors. There was a significant effect of wire diameter on the number of collisions ($F_{1, 6} = 13.14$, $P < 0.05$; Fig. 6) with bats colliding more often with the smaller wires. There was no effect of the light condition on the number of collisions ($F_{1, 6} = 0.80$, $P = $ ns), nor was there any interaction

Direct Recording
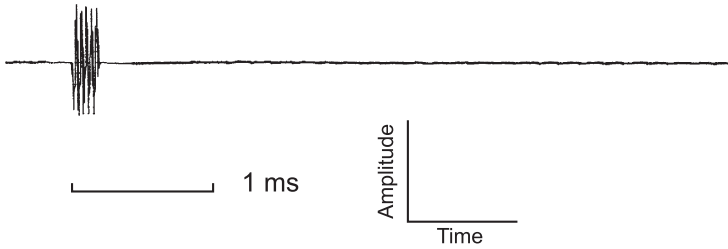
Re-recorded Signal

FIG. 4. Simulated call of *R. aegyptiacus* recorded from directly in front of the loudspeaker (above) and the call after being broadcast from one end of the flight tunnel, and re-recorded at the other (below). Amplitude is on an arbitrary scale

term ($F_{1, 6}$ = 0.47, P = ns). These results indicate that while the performance of the bat at avoiding the wires depends on the diameter of the wire, overall performance is not affected by whether the runs are performed in the light or the dark. The absence of a significant interaction term indicates that the relative performance of avoiding the large wires compared to the small wires is unaffected by the light conditions.
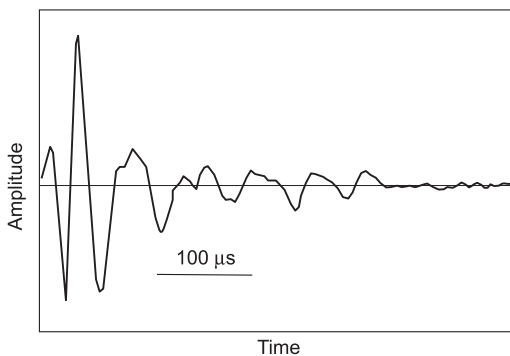

FIG. 5. Averaged waveform from 50 calls of one representative individual of *Rousettus aegyptiacus*. Amplitude is on an arbitrary scale

For the data on the repetition rate of the click pairs, there was a significant effect of light on the repetition rate ($F_{1, 6}$ = 64.47, $P < 0.001$; Fig. 7), with a marginally higher repetition rate in the dark (11.8 ± 0.46 Hz) compared with the light (10.1 ± 0.86 Hz). There was also a significant effect of the wire diameter on repetition rate ($F_{2, 5}$ = 4.33, $P < 0.05$) though post-hoc analysis using Bonferroni-corrected paired *t*-tests could not reveal between which wire treatments differences occurred. There was no significant interaction term ($F_{2, 5}$ = 0.78, P = ns). Thus, bats echolocated in both light and dark conditions, with a slight reduction in repetition rate in the light condition.

DISCUSSION

The call structure used by *Rousettus* is fundamentally different from that used by microchiropteran bats. In the latter, calls are usually longer than 1 ms, and contain many cycles of the wavelengths used. The calls of *Rousettus* are impulsive, similar to those used by oilbirds and cave swiftlets in aerial
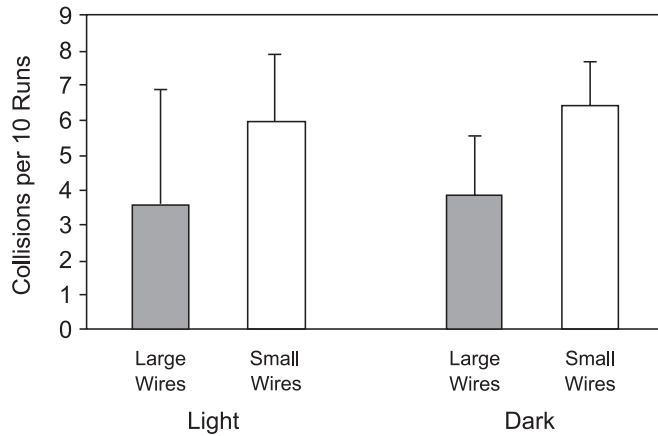
FIG. 6. Mean (+SD) number of collisions per bat per treatment (*n* = 7) for the large and small diameter wires in the light and dark conditions

environments (Griffin, 1953; Suthers and Hector, 1982), and by dolphins in aquatic environments (Au, 1993). Previous descriptions of the calls of *R. aegyptiacus* may have overestimated the duration of the call due to the multiple overlapping echoes received at the microphone. The calls are of the order of 250 μs, with most energy being produced during the first 100 μs. These calls are much shorter in duration that those used in similar circumstances by cave swiftlets (5 ms, with most energy produced in the first 1.5 ms — Coles *et al*., 1987) and oilbirds (ca. 50 ms — Suthers and Hector,

1985). Their structure and duration are comparable with those produced by dolphins (Au, 1980), which are suggested to be similar to Gabor functions (Au, 1993). The peak frequency of the call at 19 kHz corresponds well with audiograms for this species which are broadly tuned with a peak sensitivity between 10 and 45 kHz (Suthers and Summers, 1980; Pye and Pye, 1988; Koay *et al*., 1998).

It has been assumed that *Rousettus* uses its visual sense when flying and searching for food, and that the echolocation system is reserved for orientation within their cave
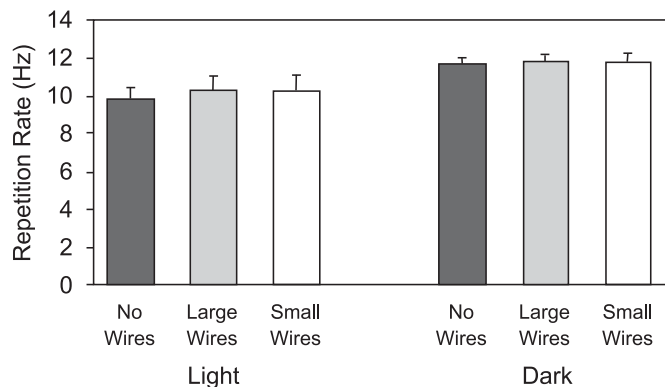

FIG. 7. Mean (+SD) repetition rates for the control and large and small diameter wires in the light and dark conditions (*n* = 7)

roosting sites (Herbert, 1985). Contrary to the finding by Herbert (1985), the bats in our experiments echolocated in both the light and dark conditions, although as the flight tunnel was a highly reverberating environment, this would mimic the situation in which these bats echolocated in caves.

Griffin *et al*. (1958) suggested that *Rousettus* could detect and avoid vertical wire obstacles down to about 1 mm in diameter, and showed a similar performance to a microchiropteran bat down to wires of 3 mm in diameter, though these experiments used only one bat. The results from our experiments looked at ability to avoid obstacles in both the light (where both echolocation and vision could be used), and in the dark (where echolocation alone could be used). The results show that *Rousettus* found it harder to detect and/or avoid small 1.3 mm diameter wires than larger 6 mm diameter wires. This suggests that either the bats visual/echolocation systems could not detect the smaller wires so easily, or that there was a motivational difference between the two treatments. One other possibility is that collision rate may be affected by flight speed if there was a difference in flight speed with light condition. Flight speed was not directly measured, but a close relationship between wingbeat cycle and pulse emission was found by Herbert (1985). As the pulse emission rate is higher in the dark than the light, it suggests that flight speed increases in the dark. As there is no loss of performance in the dark, we can only conclude that the echolocation system coupled to the visual system used in the light is no more efficient than the echolocation system alone being used in the dark. As the number of collisions is higher for the 1.3 mm wires than the 6 mm wires, we can conclude that by using echolocation, *Rousettus* is able to detect wires of at least 6 mm in diameter and probably much smaller, supporting the findings of Griffin *et al*. (1958). The video

recordings of the bats approaching the wires clearly showed that even in complete darkness the bats took evasive action when nearing the 1.3 mm wires, bringing the wings in closer to the body when within ca. 50 cm of the wires. This behaviour was not seen in control runs where the wires were absent.

For dolphins, impulse-like sonar pulses are capable of very high spatial resolution, while the resolutions for aerial use are predicted to be much lower. This is partly a function of the acoustic coupling between the sound producing organ and the environment, and also of the time-intensity trade-off in the integration time of the animal's auditory system. Since there is a good match in acoustic impedance between the dolphin and the water, sonar pulses can be transferred much more efficiently to the water, resulting in high output levels (Norris and Harvey, 1974). This can compensate for the reduced detectability of the returning echo due to the short duration compared to the animals integrating time constant. The detection of short duration impulsive echoes may be problematic due to the long duration of mammalian integrating time constants if assessed using time-intensity trade-off functions. Time constants from these experiments are often much longer than those based on the temporal separation of clicks, e.g. an integration time of 14–62 ms in *Tadarida brasiliensis* using time-intensity trade-off functions (Schmidt and Thaller, 1994), compared to 220 µs in *Megaderma lyra* using a double click paradigm (Wiegrebe and Schmidt, 1996). Suthers and Summers (1980) suggest a short integrating time constant for *Rousettus*, perhaps shorter than 15 ms, again using a time-intensity trade-off function, compared to the 150–225 ms often quoted for most mammals and birds using the same paradigm (Dooling, 1980). An integrating time constant of 15 ms is still far longer than the 100–250 µs duration of the call. If the

detection of short duration impulsive clicks is problematical to the bats due to integration time constraints, this further compromises the usefulness of impulse-based sonar in air.

The visual acuity of *Rousettus* has a value of three cycles per degree (Heffner *et al.*, 1999). This appears to be of similar performance to that of the non-echolocating megachiropteran *Pteropus giganteus* (Neuweiler, 1962), and generally superior to that of microchiropteran bats (Pettigrew *et al.*, 1988), though differences in experimental protocols make comparisons difficult (Bell and Fenton, 1986). At 1 m, the 6 mm wire would subtend an angle of 20', and the 1.3 mm wire, an angle of 4'30''. Thus, the 6 mm wire would predicted to be detectable optically at 1 m, while the 1.3 mm wire would not be detected until the bat was closer (ca. 22 cm). Contrary to the findings of Herbert (1985), *Rousettus* appear to echolocate in light as well as dark situations, although with a slightly reduced repetition rate. In the light therefore, *Rousettus* has both vision and echolocation available to it, but shows no performance loss when restricted to echolocation alone. In *Phyllostomus discolor*, visual cues appeared more important than echo-acoustical cues in orientation within an artificial roost (Holler and Schmidt, 1996), thus it seems probable that in the light *Rousettus* were using mainly visual cues, perhaps supplemented with echolocation. Interestingly, Eklöf *et al.* (2002) found that collision rate was higher in the light for the emballonurid bat *Balantiopteryx plicata*. They suggest that visual information takes precedence over echolocation when both cues are available.

If we assume that the bats were using both echolocation and vision to detect the wires in the light, then the performance when restricted to echolocation alone does not suffer. *Rousettus* appears to have a similar visual acuity to other Megachiroptera, which is generally superior to that found in the Microchiroptera (Heffner *et al.*, 1999), yet also demonstrates the ability to detect and avoid small obstacles using echolocation. The presence of a functioning echolocation system in *Rousettus aegyptiacus* may help in understanding the process of the evolution of echolocation in the Chiroptera. Recent molecular data suggests that bats are paraphyletic, with the echolocating Rhinolophidae and Megadermatidae being closely allied with the megabats (Teeling *et al.*, 2002). Such studies also suggest that echolocation evolved in the common ancestor of bats, and was subsequently lost in megabats, with the echolocation system in *Rousettus* being secondarily gained, rather than being in the process of being lost (Springer *et al.*, 2001). Additionally, Schnitzler *et al.* (2003) suggests that echolocation may have first developed for spatial orientation, only later becoming adapted for food acquisition. This would certainly appear to be the mechanism by which echolocation arose in *Rousettus*. While these experiments demonstrate that *Rousettus* is capable using echolocation effectively, further experiments will need to demonstrate the ranging accuracy of this echolocation system, and its ability to resolve complex spatial information, before true comparisons can be made with the microchiroptera.

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