

Listening for bats: the hearing range of the bushcricket *Phaneroptera falcata* for bat echolocation calls measured in the field

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The hearing range of the tettigoniid *Phaneroptera falcata* for the echolocation calls of freely flying mouse-eared bats (*Myotis myotis*) was determined in the field. The hearing of the insect was monitored using hook electrode recordings from an auditory interneuron, which is as sensitive as the hearing organ for frequencies above 16 kHz. The flight path of the bat relative to the insect's position was tracked by recording the echolocation calls with two microphone arrays, and calculating the bat's position from the arrival time differences of the calls at each microphone. The hearing distances ranged from 13 to 30 m. The large variability appeared both between different insects and between different bat approaches to an individual insect. The escape time of the bushcricket, calculated from the detection distance of the insect and the instantaneous flight speed of the bat, ranged from 1.5 to more than 4 s. The hearing ranges of bushcrickets suggest that the insect hears the approaching bat long before the bat can detect an echo from the flying insect.

Keywords: bat–insect interaction; predator avoidance; hearing; detection distance; sensory ecology; echolocation

1. INTRODUCTION

Certain insects that possess hearing organs are able to evade the attacks of insectivorous bats by monitoring the echolocation calls emitted by the bats as they hunt (e.g. Roeder 1967; Miller & Olesen 1979). In several insect groups, ears seem to have evolved primarily for this purpose (Lepidoptera (several times), Neuroptera, Dictyoptera, Coleoptera; review in Hoy 1992). In ensiferans (Tettigoniidae and Gryllidae) hearing functions in rather complex intraspecific communication systems, which probably evolved long before the appearance of bats (Alexander 1962). Nevertheless, these groups exhibit bat-evasive behaviours resembling those of moths and lacewings (Popov & Shuvalov 1977; Moiseff *et al.* 1978; Libersat & Hoy 1991). Bat avoidance in ensiferans thus seems to be a secondary function of the hearing system, in contrast to the groups mentioned above.

In crickets, the communication signals are normally limited to low frequencies (below 12–15 kHz) and crickets react bimodally to sound stimulation: positive phonotaxis occurs at low frequencies, negative phonotaxis is elicited by ultrasonic frequencies (reviewed in Hoy 1992). In bushcrickets, however, the evolution of bat-evasive behaviour was shaped by other constraints imposed by the communication system: their communication signals extend well into, or are limited to the ultrasonic range (Heller 1988). This prevents bushcrickets from discriminating between conspecific and predator signals based solely on spectral characteristics of the signals. On the other hand, the sensitivity of bushcrickets to ultrasound is in general higher than in crickets, giving bushcrickets the potential to evolve more sophisticated bat-evasive behaviours.

To judge the ecological significance of such bat-evasive behaviours of insects, knowledge about the insects' sensory abilities, especially the hearing range for the echolocation signals, is crucial. Following the pioneering approach of Roeder (1966), we measure here the hearing range of the bushcricket *Phaneroptera falcata* for echolocation calls of the mouse-eared bat (*Myotis myotis*) in the field. We reconstructed the flight path of the bats from the echolocation calls recorded by two microphone arrays, using the method of Aubauer (1996), while simultaneously recording the hearing responses of the bushcricket to these echolocation calls neurophysiologically. By synchronously measuring both the neuronal activity of the bushcricket auditory system and the position of the bat when it produced its echolocation calls we determined the maximum distance at which the bushcricket detected the bat.

The long-winged bushcricket *P. falcata* (subfamily Phaneropterinae) has a duetting communication system: the calling song of the males elicits a response song from receptive females. The male then phonotactically approaches the responding female. The communication signals have a broadband spectral composition centred around 28 kHz (Heller 1988). Communication takes place at night, and males often call from exposed perches on the vegetation. Males frequently fly during phonotaxis or to change calling perches, and are therefore exposed to predation by aerial-hawking bats during flight, and also by gleaning bats, which also localize their prey passively by sounds produced by the prey.

The foraging behaviour of the mouse-eared bat *M. myotis* and its sibling species *M. blythii* (body weight 20–25 g) is highly flexible, including gleaning as well as aerial hawking using echolocation (Arlettaz *et al.* 1990). Prey items of the mouse-eared bat include tettigoniids of a size range that includes *P. falcata* (Arlettaz 1996). Echolocation calls in free airspace are frequency modulated

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(fundamental frequency *ca.* 80 to 27 kHz) with strongest amplitudes in the range around 30 kHz, and have durations of 5–10 ms. In free airspace, the echolocation calls of *M. myotis* are comparable in intensity, duration and frequency range with other aerial-hawking bats large enough to prey on tettigoniids (Weid & Helversen 1987). When the bat is hunting near obstacles (e.g. vegetation) call duration and probably call intensity are reduced and frequency modulation is steeper (Habersetzer & Vögler 1983).

2. MATERIAL AND METHODS

Recordings were conducted in Ettenheim (Baden Württemberg, Germany) in mid-September, at ambient conditions of 9–13 °C and 70–90% relative humidity. A roosting colony of *M. myotis* lived in a former furniture factory. At dusk, the bats left the colony for their hunting grounds. One of their main routes crossed a creek and then over an open field, which was surrounded by trees. For about 1 h each evening, a large number of bats crossed this field alone or in small groups. Although the bats were commuting to their foraging grounds, their in-transit echolocation calls represent relevant signals for the insect since these calls are similar to search-phase calls, and bats will prey on insects they detect during commuting flight (Kalko & Schnitzler 1989).

(a) Tracking of the bat flight path

The method of tracking the bat flight path is described in detail by Aubauer (1995, 1996). The flight paths of the bats were reconstructed from recordings of their calls. The calls were recorded with two microphone arrays, each consisting of four microphones (Knowles BT 1759, Knowles, Burgess Hill, UK), one in each corner of an equilateral triangle with 1 m sides, and one in its centre. By measuring the arrival time of the calls at the four microphones it is possible to calculate the angle of incidence of the bat call with high accuracy ($< 0.5^\circ$). Since we used two arrays, we could calculate the bat's position by triangulation with an error for distance between 0.2 and 2%.

The signals of all eight microphones were recorded on magnetic tape (Racal 4DS, Racal, Irvina, CA, USA) and later digitized (sampling rate 320 kHz). The time-delays between the signals recorded by different microphones were calculated using the polarity cross-correlation function with a time-resolution of 3.1 μ s. The maximum location range of the system for *M. myotis* was 20–25 m.

The microphone arrays were 8 m apart with the microphones facing towards the approaching bats. The distance to the nearest trees was about 35 m in this direction. The insect preparation was placed 3–7 m behind the arrays. The insect preparation (see §2(b)) was placed either on the ground *ca.* 10 cm above the vegetation, or on a tripod at a height of 1.5 m. We did not find a statistically relevant difference between hearing ranges of the insects for the two heights of the preparation.

We used only approaches of bats that crossed the field alone. We identified the first bat call to which the auditory interneuron (T fibre) responded, and also the first call after which all additional calls elicited at least one spike. The distances corresponding to these calls were calculated not as distances on the ground, but included the bats' elevation. The escape time of the insect was calculated from this distance and the instantaneous flight speed at the time of the corresponding echolocation call.

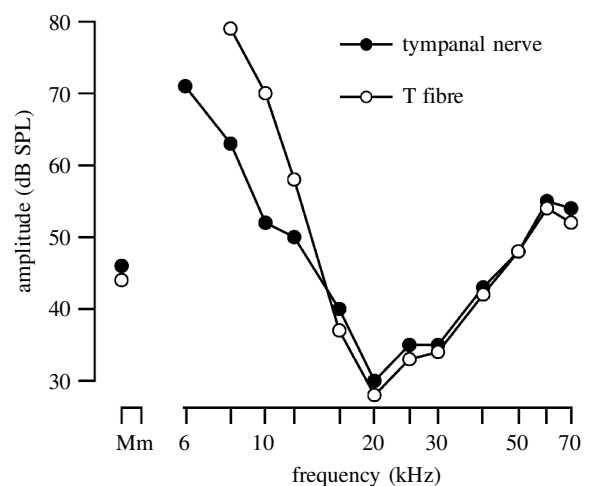


Figure 1. Example of the hearing threshold of a male of *P. falcata* determined from hook recordings of the leg nerve (containing the auditory receptor fibres, filled symbols) and the cervical connective (containing the T fibre, open symbols). The thresholds were determined audiovisually as the lowest stimulus amplitude that elicited a neuronal response. Stimulation with sine waves (duration 20 ms + 1 ms rise and fall time) or artificial echolocation calls of *M. myotis* (Mm, frequency sweep 70–30 kHz, duration 10 ms). Above 16 kHz and for the bat call, both methods result in almost identical threshold values.

In some cases, the insect heard bat calls at a distance for which the signal-to-noise ratio for one or more microphones was too low to calculate the bat's position. Because the bats were flying in a straight course across the field we extrapolated the flight path beyond the range of our system for up to three calls, using the timing of the recorded calls and flight speed and direction at the point when the flight paths became measurable. Approaches of bats were only used when their flight direction was towards the arrays at the detection range of the insect.

(b) Recording of the insect hearing activity

Males of *P. falcata* were collected as adults in the field within one week of the experiments. To record the hearing activity, we used a portable recording unit similar to the one described by Rheinlaender & Römer (1986). The insect was mounted ventral side up with the forelegs (bearing the hearing organs) fixed perpendicular to its body. The cuticle covering the cervical connectives (between prothoracic and suboesophageal ganglion) was removed to allow access with electrolytically sharpened tungsten hook electrodes. The indifferent electrode was inserted into the abdomen. The base of the recording unit contained a preamplifier ($\times 400$) and a band-pass filter (300–3000 Hz). The neuronal activity was transmitted through a 12 m cable from the recording unit to an eight-channel digital audio tape (DAT) recorder (Sony PC208A, Sony, Tokyo, Japan). The preparation was orientated with its longitudinal axis perpendicular to the assumed flight direction of the bats. Recordings were made from the connective facing the approaching bats.

Large spikes of a T fibre can reliably be detected (see figure 2a) in the summed activity of the cervical connective. The sensitivity of the T fibre (Suga & Katsuki 1961) in the frequency range above 16 kHz represents the absolute hearing threshold of the insect: subsequent determination of hearing threshold from the T fibre and the tympanal nerve resulted in almost identical values within each preparation (figure 1).

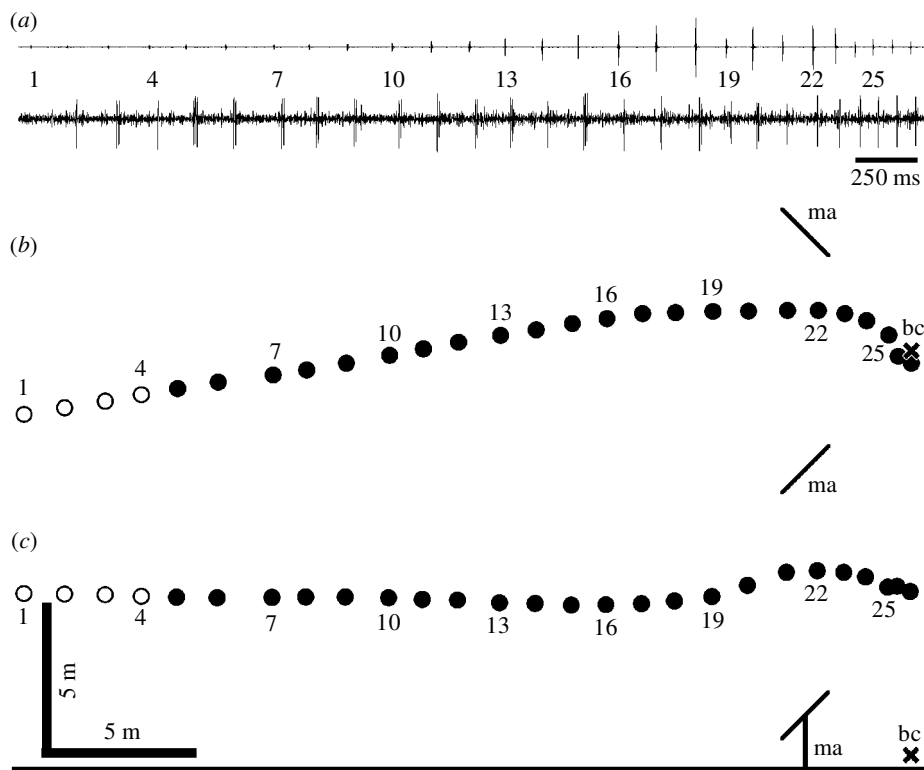


Figure 2. Example of a flight path of *M. myotis* as calculated from its echolocation calls (*b,c*) and the hearing responses of *P. falcata* recorded from the cervical connectives (*a*). (*a*) Top trace: echolocation calls of the bat as recorded by a microphone placed at the insect's position. Bottom trace: hook recording from the cervical connective. The large spikes stem from the T fibre. The microphone signal was transformed by the heterodyning system of a bat detector. (*b*) Top and (*c*) side view of the bat's flight path. The filled circles mark the calculated positions of the bat when emitting the corresponding echolocation call, the open circles denote extrapolated positions (see §2). The positions of the bushcricket (bc) and of the microphone arrays (ma) are indicated. The numbers indicate the corresponding signals in (*a*) and positions in (*b*) and (*c*).

In addition to the neuronal activity, we recorded one of the microphone signals of the arrays onto the DAT recorder. We also recorded the microphone signal of an ultrasound microphone (Knowles BT 1759), which was placed at the insect's position, on the same tape. These two microphone signals, which were transformed by the heterodyning system of two bat detectors to match the frequency response of the DAT, allowed us to correlate the neuronal responses of the insect to the flight activity of the bats.

3. RESULTS

The bats flew across the field in fairly straight flight paths at elevations of typically 5–8 m above the ground (figure 2). The flight speed of the bats at the detection range of the bushcrickets varied from 6.5 to 8.5 m s⁻¹ (mean ± s.d., 7.64 ± 0.53 m s⁻¹, *n* = 33). A typical recording is shown in figure 2. It was possible to calculate the bat's position from the microphone array recordings from a distance of approximately 20 m (filled dots in figure 2*b,c*). Because of the constant speed of the bat and the straight flight direction, we could extrapolate the flight path for another three to five bat calls for which we could not directly calculate the position (open dots in figure 2*b,c*). The bats often responded to the presence of the

microphone arrays by increasing their call rate and by flying to higher elevations as they approached the arrays (19–25 in figure 2).

In the example shown in figure 2, the T fibre of the bushcricket responded to all echolocation calls, starting with the second one shown, until the bat passed the insect's position. The timing of the spikes faithfully reflected the echolocation call pattern. In some bats, the echolocation calls alternated between high and low amplitudes, as seen in calls 18–22 in figure 2*a*. For this reason, in several recordings the T fibre did not respond to all bat calls after it detected the first one, but skipped low-amplitude calls at greater distances.

We recorded the neuronal responses to 31 bat approaches in eight bushcricket preparations (figure 3). The bat calls were neurally detected at distances ranging from 13 to 30 m (figure 3*a*, filled symbols). The distance after which consistent responses to every bat call occurred was always greater than 12 m (figure 3*a*, open symbols). The large variation in the detection distances is probably due to variability both of the sensory abilities of the bushcrickets and of the call intensities of the bats: some preparations had consistently short or long detection distances (e.g. no. 3-1 and no. 5, respectively), while for others these distances varied considerably (no. 1, no. 2, no. 4-1).

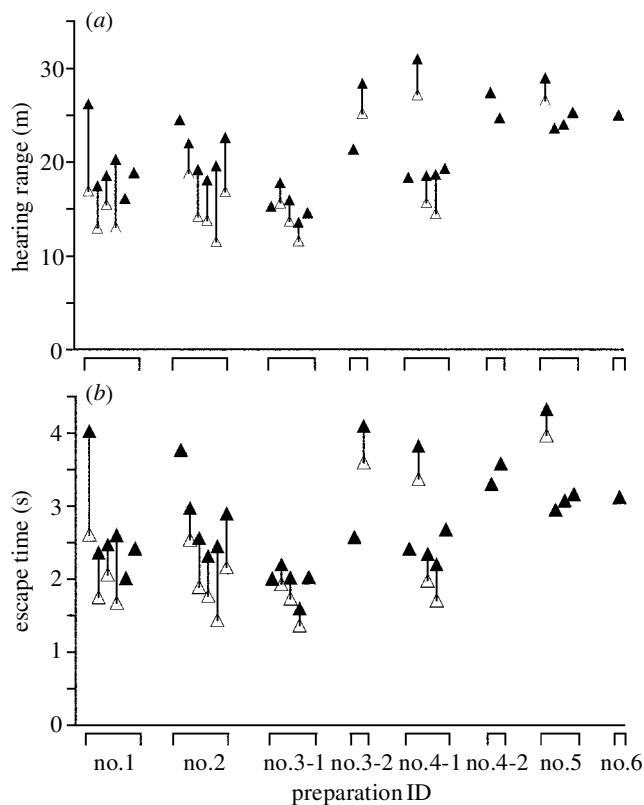


Figure 3. Hearing range (a) and escape time (b) of *P. falcata* for the echolocation calls of *M. myotis*, as determined from recordings of the T fibre. Each symbol denotes the result of a single bat approach to one insect. Filled symbols indicate the first response to a bat call, open symbols the bat call after which all calls elicited neuronal responses. For two preparations (no. 3 and no. 4), recordings from both left and right connectives were obtained sequentially (i.e. the preparation was turned by 180°). The data are given separately for each hemisphere facing the approaching bat.

The corresponding escape times, i.e. the time the insect would have after it detected the bat, before a bat flying at constant speed would reach it, are given in figure 3b. While for some bat approaches the escape times were as much as 4 s, most bats were detected neurally with escape times between 2.0 and 3.5 s. The minimum escape times encountered here were *ca.* 1.5 s.

4. DISCUSSION

In the field, bat–insect encounters normally take place unnoticed by human observers, because they occur at night and in the ultrasound. Studies of these interactions are therefore mostly conducted in the laboratory. Assumptions have to be made to transfer such results to the natural situation, reducing the strength of the conclusions. We, therefore, took a physiological experiment into the field: we determined the effective hearing range of a bushcricket for a predator in a ‘real world’ situation. The measured hearing ranges of 13–30 m, therefore, are realistic values for the sensory performance of *P. falcata*, without the inherent uncertainties of estimates. These

hearing ranges are similar to those described for noctuid moths: *Caenurgina erechtea* detected bat calls at distances of 32–40 m (Roeder 1966); Surlykke (1988) estimated a 15 m hearing range for the less-sensitive *Agrotis segetum*.

We directly measured the hearing distance of the bushcrickets for the bat calls, but we could calculate only an estimate for the escape time. This estimate (figure 3b) is conservative because bats often reduce flight speed within the approach phase, i.e. after the bat has detected the prey (Kalko 1995).

In ensiferans, hearing serves in both mate-finding and predator detection. This double function constitutes the need for a discrimination of conspecific songs and bat calls. In tettigoniids, discrimination between mates and bats cannot, as in crickets, be based on spectral properties alone, because communication signals extend well into the ultrasonic range, and are limited in many species (including *P. falcata*) to the frequency range 20–60 kHz (Heller 1988), which is also used by the majority of aerial-hawking bats (Fenton *et al.* 1998). Pattern recognition here might rely on temporal properties of the signals. One characteristic that could be used for discrimination is the call repetition rate, a parameter used by arctiid moths in recognition of bats (Fullard 1984). Temporal pattern recognition based on repetition rate takes time, however, because several repetitions of the signals are required to constitute the crucial parameter. The role of temporal pattern recognition in bat avoidance has not been investigated in tettigoniids, and has received only little attention in most other insect groups (e.g. Fullard 1984).

There are two avoidance strategies for a flying insect that detects a hunting bat: to perform some erratic flight manoeuvres when the bat is at very close range, so that the final attack misses the insect, or to perform early avoidance reactions such as steering away or stopping wing-beats, to escape from the echolocation search cone of the bat (reviewed in Hoy 1992). While the first strategy demands high manoeuvrability and flight performance of the insect, the latter strategy would work best when the insect can hear the bat before the bat can detect the echo. Because of their limited flight performance, tettigoniids appear unlikely to rely on close range manoeuvres alone but seem more likely to adopt the strategy of early avoidance. How does their hearing range compare with the detection ability of bats?

Only few data are available regarding the real detection ranges of bats for their prey. Kalko & Schnitzler (1989, 1993) measured distances of 1.2–2 m for several small bat species, but the prey size was much smaller than *P. falcata*. In training experiments, *Eptesicus fuscus* was able to detect spheres of 1.9 cm diameter (which cause echoes of amplitude similar to those of medium to large insects) at distances of up to 5 m (Kick 1982). Surlykke (1988) estimated detection distances in a similar range for medium-sized moths. Other estimates for maximum detection distances, assuming low hearing thresholds of bats and high intensities of the reflected echoes (= target strength), range from 10 to 15 m (e.g. Waters *et al.* 1995; Jensen & Miller 1999). Echo intensity depends largely on the wing position of the insect, with largest echoes occurring when the direction of the incident sound is perpendicular to the wing surface

(Kober & Schnitzler 1990). This ideal situation occurs only briefly during each wing-beat cycle, while for other wing positions the echo intensity is considerably smaller (Kober & Schnitzler 1990). Therefore, effective detection ranges are likely to be smaller than these estimates, and a detection distance for a medium-sized insect like *P. falcata* of ca. 5 m as found by Kick (1982) and estimated by Surlykke (1988) seems to be realistic.

Comparing the 5 m detection range of bats for their echolocation signals with the bushcricket's minimum hearing range of 13 m for bat echolocation calls (figure 3*a*), the insect has more than 1 s for recognition of the predator and an evasive response, before the bat will hear a returning echo. This sensory advantage should constitute the potential for the evolution of a recognition system that reliably detects bats while minimizing the number of false alarms. The hearing sensitivity also constitutes the sensory basis for the evolution of a behavioural repertoire for bat avoidance to give bushcrickets a considerable advantage in the 'arms race' with aerial-hawking bats.

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