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No correlation of body size and high-frequency hearing sensitivity in neotropical phaneropterine katydids

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Abstract

We investigated the relationship between body size (weight) and hearing sensitivity in response to a high-frequency, bat-like stimulus in a number of phaneropterine katydids on BCI, Panama. These phaneropterines are nocturnal flying species and thus potential prey of various insectivorous bats on the island. We tested the prediction that larger species compensate for the disadvantage — of producing stronger echoes for searching bats — by being more sensitive to bat calls, thereby increasing safety margins towards this predator. Contrary to this prediction, larger katydids were not more sensitive. This was corroborated in neurophysiological experiments in the nocturnal rainforest, where simultaneous recordings of the T-fibre activity in response to searching bats revealed no substantial difference between small and large katydids. We offer three explanations for the lack of correlation between body size and high-frequency sensitivity in these species.

Key words

katydid, Phaneropterinae, body size, hearing sensitivity, bat predation

Introduction

Organisms differ tremendously in their size, and many physiological variables and functional characters are related to body size (Schmidt-Nielsen 1984). "Scaling effects" are among the most important quantitative patterns in biology. Size and scale effects as constraints for sound communication are especially evident for insects (Michelsen & Nocke 1974, Bennet-Clark 1998) or other small animals (Ryan & Kime 2003). Since the mass (size) of the sound-producing structures is a major determinant of the carrier frequency of a sound signal, and larger structures can produce low-frequency signals more efficiently than small ones, small insects are usually bound to the production of higher frequencies. The relationship between size and carrier frequency often exists in a comparison between species, but also among individuals of the same species (Simmons & Ritchie 1996).

Whereas the importance of body size for efficient sound emission is evident, the relationship between body size and functional parameters of hearing appears much less clear. Studies on sexual selection and sexual dimorphisms are mainly concerned with male traits (Andersson 1994), but Bailey (1998) and Gwynne and Bailey (1999) provide evidence for sexual selection on females for increased sensitivity to the male signal. In their study on two species of Australian katydids, females with larger spiracular openings were more sensitive, which gives them a pairing advantage when attracted to a calling male. Since body size and spiracle size were correlated in both sexes, and spiracles and associated tracheal systems amplify high-frequency sound at the position of the hearing organ (Stumpner & Heller 1992, Michelsen 1998, Römer & Bailey 1998), the receivers´ hearing sensitivity is thus also affected by body size in katydids.

In addition to sexual selection, a major driving force for the evolution of the auditory system of insects is natural selection through predation. For example, there is a long history of research dealing with the co-evolution of insectivorous bats and moth hearing (review Fullard 1998). In this context, the relationship between body size of moth prey and their hearing sensitivity was investigated by Surlykke and Filskov (1999). The rationale behind the study was that large targets should produce stronger echoes, and therefore bats should be able to detect large moths at greater distances compared to smaller moths. The authors hypothesized that the advantage on the side of the predator to detect their prey earlier should be compensated, in an evolutionary arms race, by changes towards a higher sensitivity of larger moths for bat-like sound. Indeed, they found a correlation between wing/body size and the sensitivity and frequency tuning of ears, with larger moths being more sensitive (Surlykke & Filskov 1999).

A number of other insect taxa share behavioral and physiological properties with noctuid moths: they are also sensitive to frequencies far into the ultrasonic range, up to 100 kHz, and exhibit bat avoidance behavior during flight when stimulated with bat-like sound (reviews in Hoy 1992, Fullard 1998, Yager 1999). Many katydids are nocturnal flyers and subject to predation by bats. These katydids come in rather different sizes and, as in the case of nocturnal moths, katydids with large body size would be at a disadvantage when confronted with hunting bats, since they produce stronger echoes and would be detected at greater distances.

However, we also consider possible reasons why such a relationship between hearing sensitivity and body size may not exist. These include 1) the fact that, in contrast to most moths, the hearing system in katydids also serves the basic function of intraspecific communication, 2) that the absolute hearing sensitivity of katydids is already at a maximum and cannot be improved without a trade-off in masking by background noise, and 3) that size discrepancy discourages any predator-prey relationship. We therefore investigated the relationship between body size and hearing sensitivity in a number of species of phaneropterine katydids in the Panamanian tropical rainforest.

Results and Discussion

We tested the hypothesis using an approach with an identified interneuron, which is considered to be homologous in various species of katydid. The neuron was the so-called T-fiber, originally described by Suga & Katsuki (1961), and later studied with respect

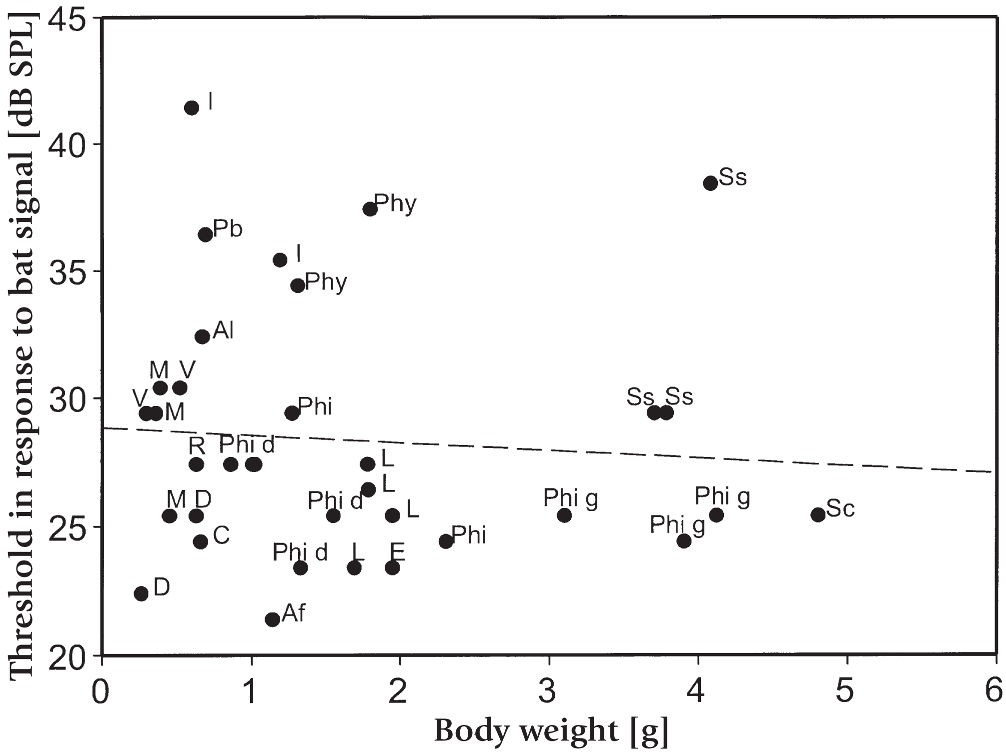

Fig. 1. Threshold values of the T-fiber in response to a bat-like stimulus in 17 species of phaneropterine katydids. (ρ: -0.17, p > 0.05, N = 36, Spearman Rank Order correlation). Af = *Anaulacomera furcata*; Al = *Anaulacomera laticauda*; C = *Ceraia* sp.; Dl = *Dolichocercus latipennis*; E = *Euceraia atrix*; I = *Itarissa* sp.; L = *Lamprophylum* sp.; M = *Montezumina bradleyi*; Phi = *Philophyllia* sp.; Phi d = *Philophyllia diminuata*; Phi g = *Philophyllia guttulata*; Phy = *Phylloperta panamae*; Pb = *Pycnopalpa bicordata*; R = *Rossophyllum colosseum*; Sc = *Steirodon careovirgulatum*; Ss = *Steirodon stalii*; V = *Viadana* sp.

to morphology, directionality, frequency tuning, left-right symmetry, and response to bat-like sound (Rheinlaender & Römer 1980; Römer *et al.* 1988; Faure & Hoy 2000a, b; Schul *et al.* 2000; Schul & Sheridan 2006). Several properties of the cell are consistent with the assumption that it is involved in the ultrasound-triggered startle response during flight, in particular the large axon diameter and presumed monosynaptic connection to receptor fibres (Römer *et al.*,1988), favoring a fast behavioral response away from predators. Further, the physiology of the cell appears to be biased towards responses to bat-like sounds, rather than conspecific mating calls (Faure & Hoy 2000b, Schul *et al.* 2000, Schul & Sheridan 2006).

Extracellular recordings with hook-electrodes were made from the neck connectives, and the sensitivity of the cell in response to a standard bat-like sound stimulus was determined for all species investigated (for details of the preparation see Rheinlaender & Römer 1980). The stimulus was a series of 10-ms sound pulses repeated at 10 Hz for 1 s. Each pulse was modulated in frequency from 60 kHz down to 20 kHz within 10 ms. All threshold measurements were carried out in an acoustically isolated chamber (size 1×1×1m), where background noise at frequencies > 5 kHz was < 25 dB SPL. Threshold was determined as the SPL where the cell just responded to the pulse rate of the stimulus, when listening to the action potential activity through headphones. Prior to each experiment, the weight of the insect was measured to the nearest 0.01 g.

Since both pronotum width and length of wings are highly correlated with body weight (pronotum width *vs* weight: ρ = 0.84, N = 72, p < 0.001 and wing length *vs* weight: ρ = 0.84, N = 37, p < 0.001, Spearman Rank Order correlation) the quick measure of body weight was a reliable indicator of size.

The following species of Phaneropterine katydid were used for threshold measurements: *Steirodon stalii*, *Steirodon careovirgulatum*, *Viadana* sp., *Euceraia atrix, Ceraia* sp., *Rossophyllum colosseum*, *Dolichocercus latipennis*, *Anaulacomera furcata*, *Anaulacomera laticauda*, *Itarissa* sp., *Lamprophyllum* sp., *Montezumina bradleyi*, *Phylloptera panamae*, *Pycnopalpa bicordata*, *Philophyllia guttulata*, *Philophyllia diminuata*, and *Philophyllia* sp.

The results of these threshold measurements are summarized in Fig. 1. The thresholds in response to the bat-like stimulus vary from 21 to 41 dB SPL, and body weight from 0.26 to 4.8 g. There is no correlation with body weight, and thus the size of katydids (ρ: -0.172, p > 0.05, N = 36, Spearman Rank Order correlation). Even after removal of the one potential outlier at a body weight of about 4g and a threshold of 38.4 dB SPL, the correlation is not significant.

We also used the "biological microphone-approach" (Rheinlaender & Römer 1986) to test the hypothesis that larger katydids are more sensitive. Portable preparations with extracellular recordings of the action potential activity of the T-fiber were placed at the edge of rainforest gaps on Barro Colorado Island (Panama), where insectivorous bats were active after sunset. Next to the preparations a bat detector recorded the echolocation pulses of free-flying bats, which approached the setup to varying degrees.

Figure 2A demonstrates the activity of the T-fiber of a medium-sized katydid species (*Philophyllia* sp.; body weight 1.27g) in response to free-flying bats. The neuron responds to both the search phase and final buzzes of echolocation calls in an almost phase-locked manner to each short sound pulse. (Note however, that this may not always be the case, because the directionality of the bat detector and of the katydid ear may differ considerably; in general, the directionality of the bat detector is much more selective compared to that of katydid ears).

In a series of similar experiments, two such preparations with a small and a large katydid respectively, were positioned simultaneously next to each other (distance less than 10 cm), so that they perceived the same stimulation from echolocating bats. Figure 2B shows a typical example with a recording of the T-fiber of *Steirodon careovirgulatum* (body weight 3.9 g), and the homologous neuron in *Montezumina bradlei* (body weight 0.39 g, lower trace). The T-fiber of the latter species, a species with a ten-times reduced body weight, responds to the bat calls in a rather similar manner, with an only slightly reduced number of action potentials. Moreover, this degree of variation in the overall activity to the very same stimulus

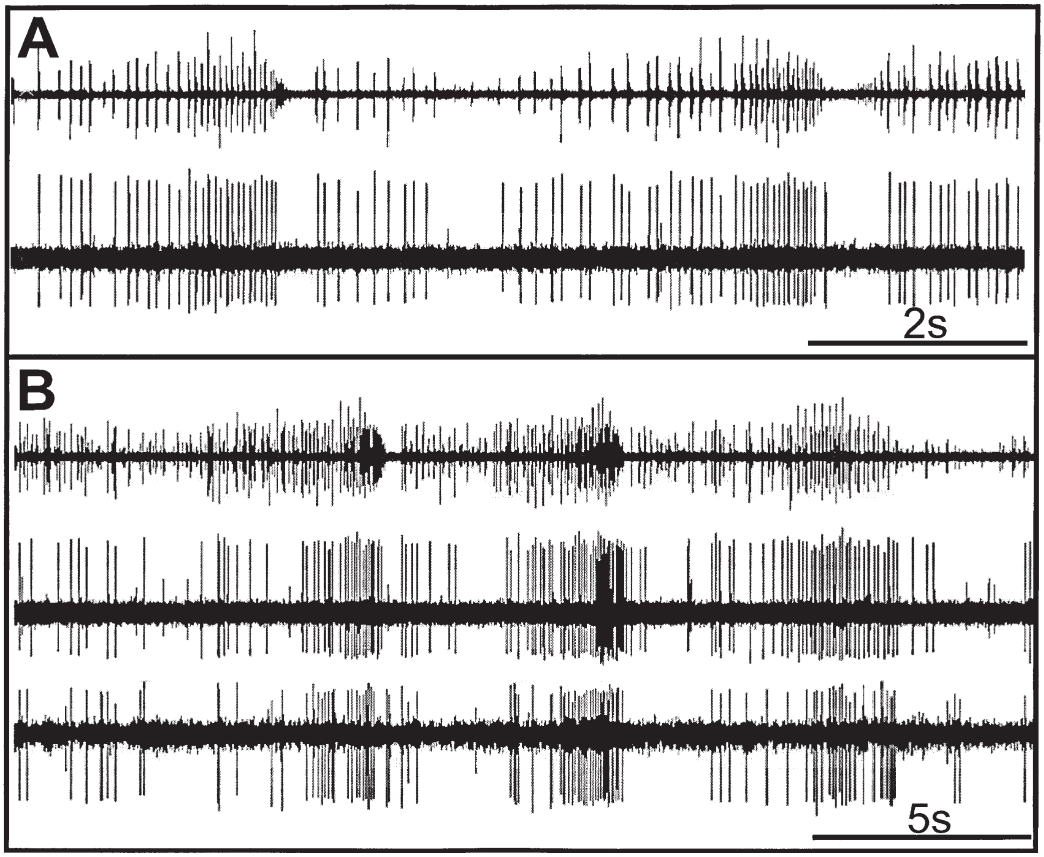

Fig. 2. A. Simultaneous recording of bat emissions (top), and activity of the T-fibre of *Philophyllia* sp. (bottom), positioned in a rainforest gap 2 h after sunset. The cell fires in response to echolocation calls of free-flying bats, both to HF- pulses in the search phase and in the final buzzes (upper trace) in an almost phase-locked manner. **B**. Simultaneously recorded bat output (top) and T-fiber responses of *Steirodon careovirgulatum* (body weight 3.9 g, middle trace), and *Montezumina bradleyi* (body weight 0.39 g, lower trace).

was also observed in experiments, where two preparations of the same species have been placed next to each other.

Thus, in both of our approaches there was no indication that larger phaneropterine katydids on BCI are significantly more sensitive to bat sound. How do we explain this lack of correlation, in contrast to the similar predator-prey relationship in moths observed by Surlykke & Filskov (1999)?

We would offer three possible explanations: the most obvious is the fact, that in katydids the hearing system also serves the basic function of intraspecific communication, which is in contrast to most moths (for exceptions see Connor 1999). Unlike the situation in crickets, where communication and predator avoidance are separated along the frequency dimension and the relevant stimuli are categorically perceived as attractive or repulsive (Wyttenbach *et al.* 1996), conspecific calling songs in katydids very often include ultrasonic frequencies and thus overlap in the frequency domain with aversive stimuli. Even if large katydids evolved a high sensitivity in the context of bat predation, small katydids may also be more sensitive at high frequencies as a result of sexual selection in the context of intraspecific communication, and therefore a positive correlation between body size and high frequency sensitivity does not exist.

The proximate mechanism by which high ultrasonic sensitivity is achieved is through a sophisticated anatomical arrangement of the hearing organ in the tibia of the foreleg, in conjunction with a tracheal tube which connects the inner surface of the ear drum with the lateral surface of the body wall through a spiracular opening. This trachea acts as a sound guide, and its specific geometry increases the sound pressure at the inner surface of the ear drum by more than 10 times compared to the external surface, particularly at high frequencies (Bailey 1991, Michelsen 1998, Römer & Bailey 1998).

The absolute hearing sensitivity of Orthoptera, and in particular katydids, is remarkably high and ranges between 25 to 40 dB SPL, compared to 40 to 70 dB SPL in other hearing-capable insect taxa without a function in intraspecific communication (Fullard 1998, Yager 1999, Gerhardt & Huber 2002). A further increase in sensitivity at ultrasonic frequencies would not improve the safety margin the katydids have over the bats, due to the high background noise in the nocturnal rainforest, even at frequencies beyond 20 kHz (Lang *et al.* 2005). Such background noise at ultrasonic frequencies would in turn produce strong bursting activity in afferent neurons and create false alarms both in the detection of bat-like sound and conspecific signals.

Finally, the size relationship between predator and potential prey may also explain why larger katydids are not more sensitive: some of the katydid species investigated in this study, such as *Steirodon* or some *Philophyllia* species, are so large that most of the small species of insectivorous bats may not include them in their prey repertoire. This reduces natural selection for higher ultrasound sensitivity in these large katydids.

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