

THE LUNG–EARDRUM PATHWAY IN THREE TREEFROG AND FOUR DENDROBATID FROG SPECIES: SOME PROPERTIES OF SOUND TRANSMISSION

GÜNTER EHRET, ELKE KEILWERTH

Abteilung Vergleichende Neurobiologie, Universität Ulm, D-89069 Ulm, Germany

AND TSUTOMU KAMADA

*Department of Oral Physiology, School of Dentistry, Hokkaido University,
Sapporo 060, Japan*

Accepted 23 June 1994

Summary

Frequency–response curves of the tympanum and lateral body wall (lung area) were measured by laser Doppler vibrometry in three treefrog (*Smilisca baudini*, *Hyla cinerea*, *Osteopilus septentrionalis*) and four dendrobatid frog (*Dendrobates tinctorius*, *D. histrionicus*, *Epipedobates tricolor*, *E. azureiventris*) species. The high-frequency cut-off of the body wall response was always lower than that of the tympanum. The best response frequencies of the lateral body wall were lower than those of the tympanum in some species (*S. baudini*, *O. septentrionalis*, *D. tinctorius*), while in the others they were rather similar. Best tympanic frequencies and best body wall response frequencies tended to differ more with increasing body size.

Stimulation of the tympanum by sound transfer through 3.14 mm² areas of the lateral body wall showed that the lung–eardrum pathway can be in two states, depending on breathing activity within the lungs: 44% (in *Smilisca*), 39% (in *Hyla*) and 31% (in *Osteopilus*) of the eardrum vibrations were 2.5–8 times (8–18 dB) larger when the frogs were breathing with the lungs compared with non-breathing conditions.

The vibration amplitudes of the tympanum and lateral body wall of the treefrogs followed the same dependence on sound intensity, only absolute amplitudes differed between species.

Our results suggest that the lung–eardrum pathway attenuates high-frequency components of species-specific calls and enhances low-frequency components. In addition, an amplitude modulation is imposed on the low frequencies during the rhythm of breathing.

Introduction

The lateral body wall overlying the lung of several species of frogs has been shown to vibrate in response to sound at frequencies similar to, or lower than, those to which the eardrum is sensitive (Narins *et al.* 1988; Jørgensen, 1991; Hetherington, 1992). The

Key words: amphibian hearing, auditory periphery, lung–eardrum pathway, tympanum vibration, frogs.

sound that enters the lungs passes through an internal pathway *via* the glottis, mouth cavity and Eustachian tubes to the inner surface of the tympanum, where a vibrational response occurs (Ehret *et al.* 1990; Jørgensen *et al.* 1991). This sound transmission from the lung is one component of the pressure gradient established between the outer and inner surfaces of the tympanum. Sounds directly impinging on the eardrum from outside and from other internal sources, such as a pathway from the contralateral tympanum, also contribute to the pressure gradient, so that the amplitude and phase of the tympanic vibration is the result of a complex interaction of waves reaching the eardrum by various routes (Chung *et al.* 1981; Feng and Shofner, 1981; Vlaming *et al.* 1984; Michelsen *et al.* 1986). Since pressure-gradient systems are inherently directionally sensitive, the vibrational amplitude of the tympanum also depends on the angle of incidence of the sound (Michelsen *et al.* 1986; Jørgensen, 1991; Jørgensen and Gerhardt, 1991; Jørgensen *et al.* 1991). Thus, it has been suggested that the biological function of the multi-input system to the frog tympanum is to provide the basis for the localization of sound, which is remarkably accurate despite the tiny heads of some hylid and dendrobatid frogs (Feng *et al.* 1976; Gerhardt and Rheinlaender, 1980; Rheinlaender *et al.* 1981; Klump and Gerhardt, 1989).

Many questions remain concerning the actual contribution to the tympanic response of each of the routes the sound can take before reaching the eardrum. In our present study, we report eardrum and lateral body wall vibrations of seven frog species and thus broaden the comparative basis for a discussion of the significance of this input to the ear. Furthermore, we present data on the modulation of the effectiveness of sound transmission *via* the lung and mouth cavity when the glottis is closed or open, and finally measure the intensity-dependence of vibration amplitudes of the tympanum and body wall, in order to estimate the relative influence of the lung on the tympanum at various sound intensities.

Materials and methods

Animals

Six American treefrogs, two *Hyla cinerea* (body lengths 51 and 46 mm), three *Osteopilus septentrionalis* (72, 72 and 65 mm) and one *Smilisca baudini* (59 mm), and ten dendrobatid frogs, three *Dendrobates tinctorius* (37, 40 and 42 mm), three *Dendrobates histrionicus* (25, 28 and 32 mm), two *Epipedobates azureiventris*, (23 and 27 mm) and two *Epipedobates tricolor* (20 and 22 mm), were used. All frogs were adult males captured at their natural habitats. The animals were kept in terraria (23.5 cm × 24 cm × 34.5 cm) with plants and water basins in an air-conditioned room at the University of Konstanz, Germany. Lights were on from 08:00 h to 20:00 h. Room temperature was 22–24 °C during the day and 18–20 °C at night, humidity was 80–90 %.

All experiments were performed with fully awake, unrestrained animals between 09:00 h and 21:00 h. Prior to the measurements, the treefrogs were exercised by letting them leap in the terrarium for several minutes. This tiring of the frogs markedly reduced their tendency to move during data recording and increased the ventilation of the lungs. Several procedures were attempted to keep the dendrobatid frogs sitting motionless for at

least the several minutes necessary to obtain reproducible measurements. By leaving the frogs as undisturbed as possible, we finally managed to obtain data under free-field sound conditions. Stimulation with a closed-sound system, as carried out with the treefrogs, was impossible for the dendrobatids.

Laser measurements

The apparatus and procedures have previously been described (Narins *et al.* 1988; Ehret *et al.* 1990). A frog was placed on a vertical post (10 cm in diameter) in the centre of a vibration-damped terrarium. A 5 mW He/Ne laser beam could be focused onto the tympanum or any part of the frog's body on the side directly exposed to the free-field sound. Vibrations were recorded in the Doppler vibrometer mode of the laser (Disa 55x). The analog signals of the laser output were bandpass-filtered (0.1–10 kHz, Kemo VBF/8, 48 dB per octave), amplified (Hewlett-Packard 465A) and stored either on channel 1 of a four-channel tape recorder (Teac A-2340SX), for off-line analysis, or Fourier-transformed (Nicolet spectrum analyzer 446A) and velocity or displacement spectra were viewed on-line. Channel 2 of the tape recorder was used for storage of the sound signal, channel 3 for stimulus synchronous trigger signals and channel 4 for vocal comment. The precise spots of measurements on the frog's body were recorded photographically (Kodak Ektachrom 400ASA). During the laser measurements, breathing activity was observed and movements of the body flank were noted on channel 4 of the tape recorder.

Acoustic stimulation

Continuous white noise was presented free-field in 20 s long bursts to all frog species. In addition, the treefrogs were stimulated with bursts of two alternating tones, either free-field or through a closed sound system. Tones of known frequency (Kontron counter 400B) were produced in two generators (Wavetek 130 and 132) and each was passed through attenuators (Hewlett-Packard 350D) into one channel of a two-channel electronic switch, where they were formed into bursts (300 ms duration, 5 ms rise and fall times, 300 ms inter-burst interval) and added to give an alternating series. The output of the switch was amplified (Hewlett-Packard 467A) and passed to a dynamic loudspeaker (Transco HTF 80/5), for free-field stimulation, or to an electrostatic speaker (Machmerth *et al.* 1975) in a closed sound system consisting of a metal headpiece with a 9.2 cm long metal tube (inside diameter 2 mm, outside diameter 3 mm at its tip) screwed onto the speaker as a sound outlet. At the base of the tube, a calibrated 6.35 mm condenser microphone (Bruel and Kjaer 4135) connected to a measuring amplifier (Bruel and Kjaer 2606) was fitted into the sound pathway to monitor the sound pressure level on-line (dB SPL re 20 μ Pa) in the tube. During stimulation, the open end of the tube gently touched the frog's skin and was sealed to it with a film of silicone grease. With this arrangement, 3.14 mm² areas of the frog's body could be stimulated with tone bursts of known sound pressure level (SPL).

Noise was produced in a generator (Wavetek 132) and passed through a filter (Kemo VBF/8, bandpass 0.1–10 kHz, 48 dB per octave), attenuator (Hewlett-Packard 350D) and amplifier (Hewlett-Packard 467A) to the free-field speaker. The spectral response of this speaker was flat to within ± 6 dB between 0.9 and 8.7 kHz (Fig. 1) measured at the position of the experimental frog. Thus, the speaker characteristics reflect the response of

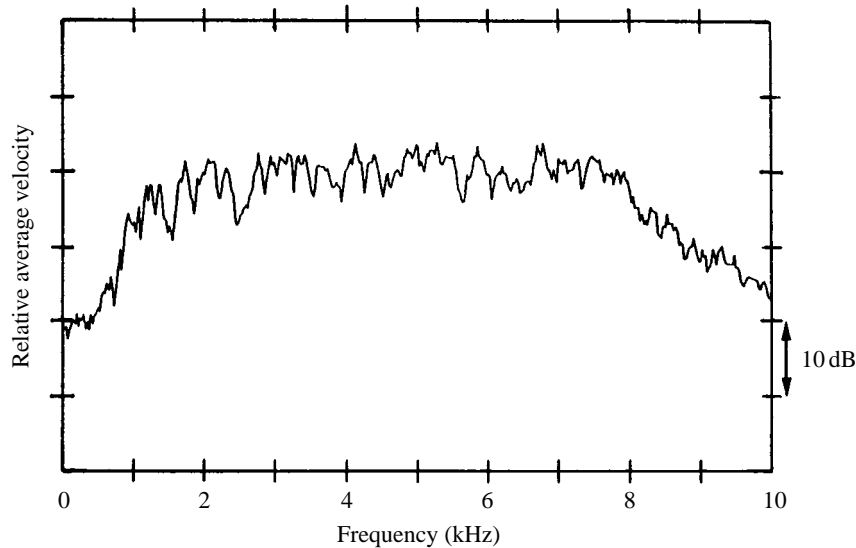


Fig. 1. Frequency characteristics of the free-field loudspeaker in response to white noise (bandpass 0.1–10 kHz) measured at the position of the experimental frog.

the sound-generating system and the acoustics of the apparatus. This speaker was mechanically decoupled from the terrarium so that possible stimulation of the frog *via* vibrations from the speaker was excluded. The distance between speaker and frog was 70 cm; the angle to the frog's long axis was 90° .

SPLs of the tone bursts and the free-field noise bursts were calibrated at the position of the frog after every experiment with the condenser microphone and measuring amplifier described above. The tone frequencies for stimulation of the treefrogs were selected according to the frequency content of their calls. *Hyla cinerea* was stimulated at 0.9 and 2.7 kHz (Gerhardt, 1974; Oldham and Gerhardt, 1975), *Smilisca baudini* at 0.96 and 2 kHz (Duellmann, 1970) and *Osteopilus septentrionalis* at 1 and 2 kHz. These are the main frequencies of calls of *Osteopilus* from a disc supplied with Rivero (1978); they were analyzed with a sonograph (Uniscan II).

Data analysis

The equipment for data recording and analysis was calibrated so that the vibration measured by the laser and stored on tape could be calculated as absolute values for velocity or displacement. The stored laser signal was Fourier-transformed by the spectrum analyser (Nicolet 446A) and plotted (Nicolet 136a). Average velocity or displacement spectra of the sound response at a given spot on a frog's body were calculated ($N=128$). The average background spectrum without sound stimulation taken at the same spot on the frog's body ($N=128$) was subtracted from the average values in response to sound. Single spectra of tone responses were also measured.

Before quantitative data were recorded, the body of each frog was scanned with the laser to determine the area of the body wall with the largest vibrational amplitude. Fig. 2

shows a typical example of the distribution of vibrational amplitudes at various points on the body in comparison with those on the tympanum. It is evident that, besides the eardrum, the lung area is most sensitive to sound and shows the best vibrational responses. This was true for all species in our study.

Results

Frequency response ranges

Responses to free-field stimulation with the bandpassed white noise (total level 90 dB SPL) were measured at the tympanum and the lateral body wall area (lung area), where the highest vibrational amplitudes were recorded. Fig. 3 shows an average velocity spectrum from one of each treefrog species; the spectra for the dendrobatid species are given in Fig. 4. Frequency response ranges can be estimated as the bandpass between the lowest and highest frequencies at which a vibration above the average background noise becomes noticeable. Table 1 presents the maximum extensions of the frequency response ranges combined from all the animals of each species used in this study. Frequency response ranges of individual frogs can be smaller (compare Figs 3 and 4).

In all individuals tested, the high-frequency cut-off of the frequency response range of the lung area was always lower than that of the tympanum. The low-frequency cut-off of the lung area response was either lower or similar to that of the tympanum. There was no common trend with regard to the best response range of the tympanum compared with that of the lung area. In *Smilisca baudini*, there was no overlap of best response ranges. The lung area maximum responsiveness was at much lower frequencies than that of the tympanum (Table 1; Fig. 3A). In *Osteopilus septentrionalis* and *Dendrobates tinctorius*, the lung area responded best at frequencies just lower than those leading to the best responses of the tympanum (Table 1, Figs 3C, 4B). In the other four species (*Hyla cinerea*, *Dendrobates histrionicus*, *Epipedobates tricolor*, *Epipedobates azureiventris*), the best frequency response range of the lung largely overlapped with or lay within the best response range of the tympanum (Table 1; Figs 3B, 4A,C,D).

Selective stimulation of the lung area

While recording vibrations of the tympanum in response to selective stimulation of a spot of the lung area with the closed sound system, we noted that the frogs did not breathe regularly with the lungs. Bouts of breathing activity were separated by periods during which we did not see any movement of the body flank. We found that the amplitudes of tympanic responses to a single tone burst (single spectra) were either large or small (Fig. 5), but rarely intermediate, when the frog was breathing with the lungs, but only small when the frog was not breathing. During breathing activity, large amplitudes were found in 44% ($N=85$) of all observations of *Smilisca*, 39% ($N=139$) of *Hyla* and 31% ($N=237$) of *Osteopilus*. The difference between large and small amplitudes was between 8 and 18 dB (2.5–8.0 times; see Fig. 5). A statistical analysis of the distributions of amplitude values during breathing activity in all treefrogs at all sound intensities used showed that 19 out of 22 distributions were not normally distributed (χ^2 -test; Sachs, 1974). Response amplitudes measured in single spectra (as shown in Fig. 5) were divided

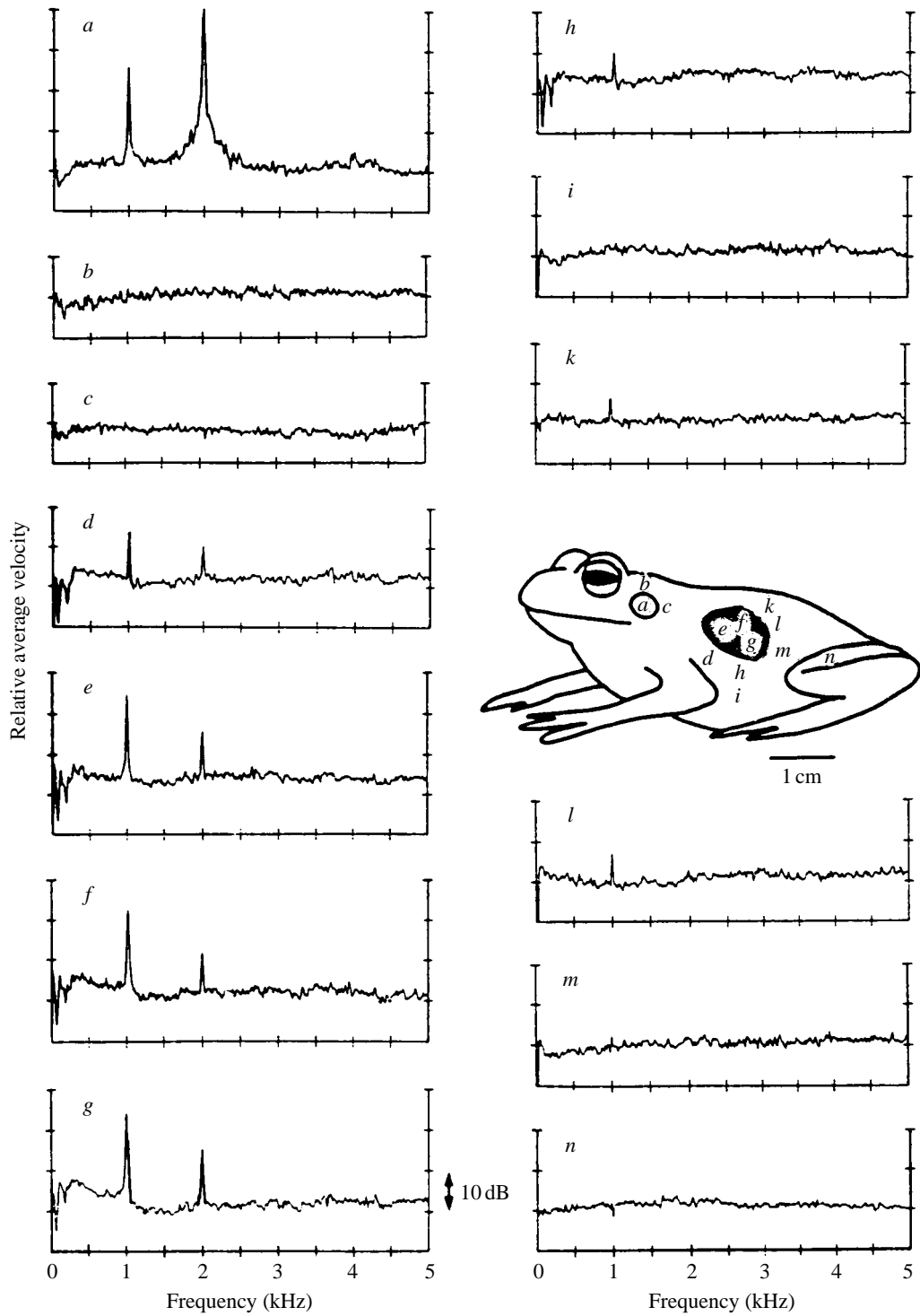


Fig. 2

Fig. 2. Average relative velocity in response to 1 and 2 kHz tones measured at the eardrum (a) and various spots on the body wall (b–n) of an alert *Osteopilus septentrionalis*. The response amplitudes are largest in the lung area (e–g, shown shaded).

into classes of equal width using the algorithm: $(\max - \min)/\sqrt{N}$ = class width, where max or min are the maximum or minimum measured amplitudes, N is the number of measured amplitudes and \sqrt{N} is the number of classes (Sachs, 1974; Ramm and Hofmann, 1987). The results are bimodal distributions such as those shown in Fig. 6, i.e. small (class 1) and large (class 4) amplitudes dominated. These bimodal distributions of vibrational amplitudes of the tympanum show that the pathway from the lung to the tympanum can be in two functional states while the frog is breathing with the lungs.

Table 1. Frequency ranges of vibrational responsiveness measured at the tympanum and lung area of the lateral body wall and main frequencies of advertisement calls of seven frog species

	Frequency range (kHz)		Call frequencies (kHz)
	Tympanum	Lung	
<i>Smilisca baudini</i>			$\approx 0.1+2^1$
Range	0.7–4.5	0.7–2.1	
Best response	2.0–2.8	0.7–0.9	
<i>Hyla cinerea</i>			$0.9+2.7+3.0^2$
Range	0.2–5.3	0.2–3.2	
Best response	1.2–3.5	1.4–2.2	
<i>Osteopilus septentrionalis</i>			$\approx 1+2$
Range	0.3–4.6	0.3–3.0	
Best response	1.0–3.2	0.7–1.4	
<i>Dendrobates histrionicus</i>			$2.7-3.9^3$
Range	1.0–4.4	1.0–3.5	
Best response	1.7–3.4	1.7–2.6	
<i>Dendrobates tinctorius</i>			$3-4^4$
Range	1.7–5.5	1.0–3.1	
Best response	2.0–3.4	1.6–2.1	
<i>Epipedobates tricolor</i>			$3.5-4.7^3$
Range	0.3–8.2	0.1–6.8	
Best response	3.0–6.0	3.3–4.6	
<i>Epipedobates azureiventris</i>			$2.8-5.0^5$
Range	0.2–8.0	0.2–3.7	
Best response	2.0–5.2	1.8–2.8	

The ranges given are the maximum extensions of the frequency response ranges combined from all animals of each species.

The best response indicates the frequency range in which the peaks of the response curves of all animals of a given species are located (compare Figs 3 and 4).

¹Duellmann (1970); ²Oldham and Gerhardt (1975); Gerhardt (1974); ³Zimmermann and Rahmann (1987); Zimmermann (1990); ⁴Zimmermann and Zimmermann (1988); ⁵Myers and Daly (1976).

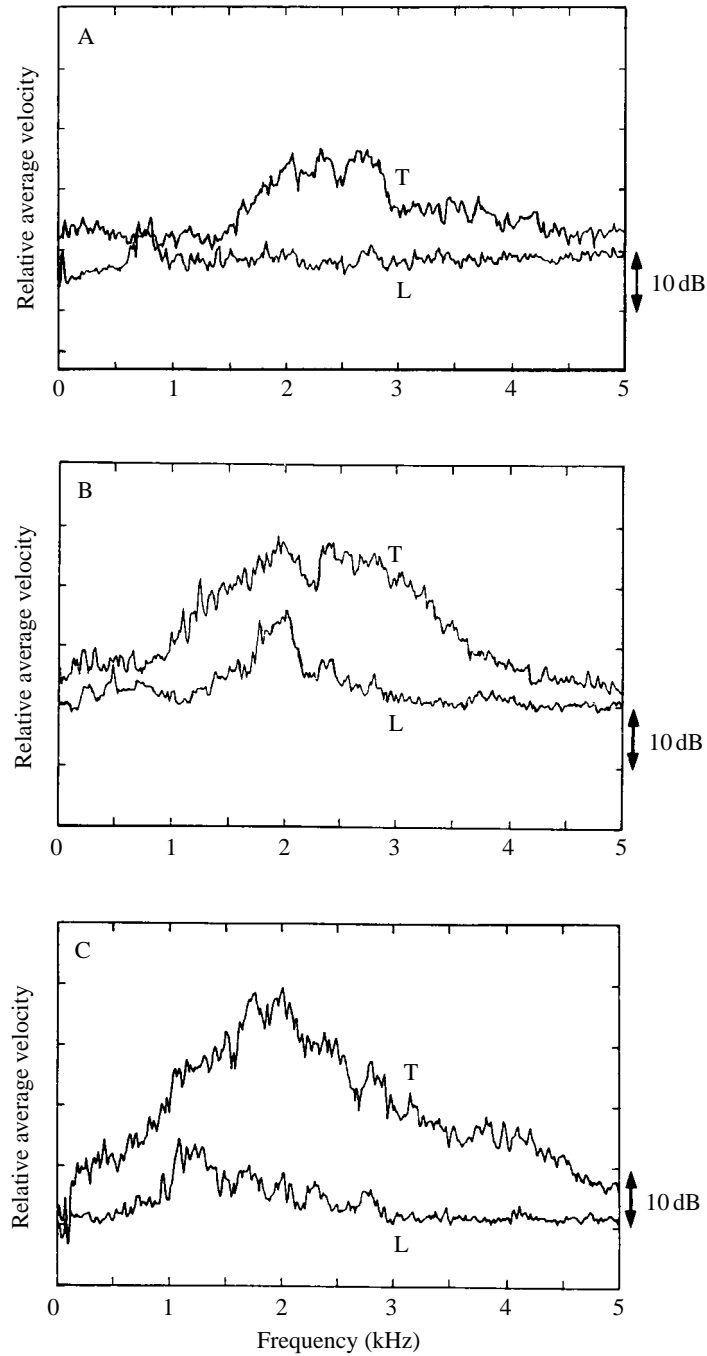


Fig. 3. Frequency response characteristics of the tympanum (T) and the best response area of the lateral body wall (L) of one individual each of (A) *Smilisca baudini*, (B) *Hyla cinerea* and (C) *Osteopilus septentrionalis*.

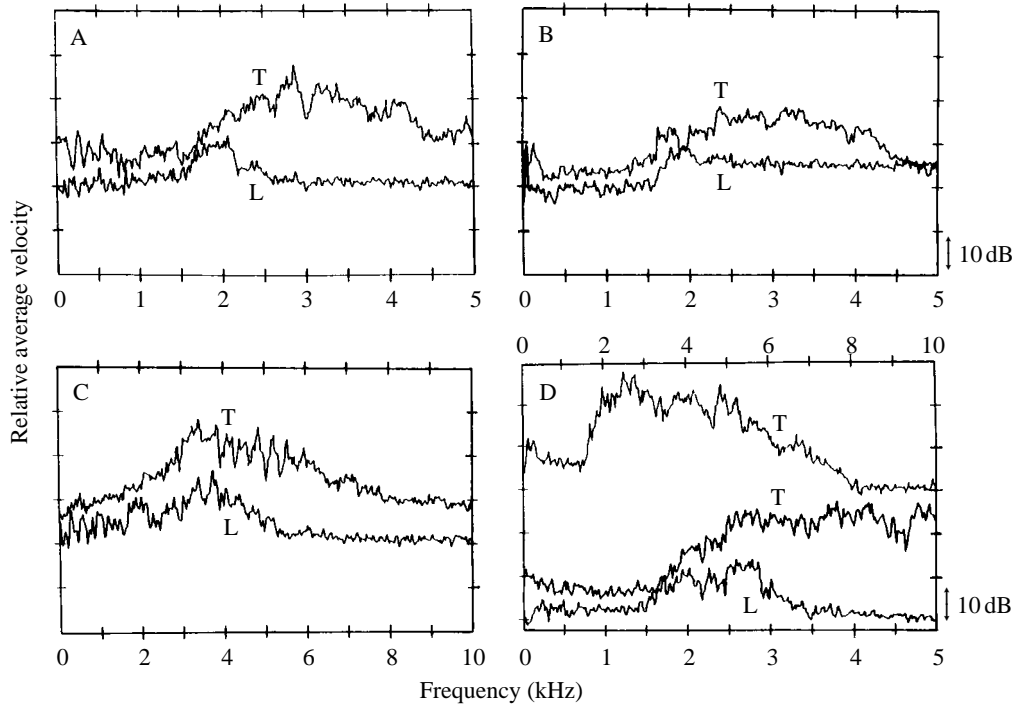


Fig. 4. Frequency response characteristics of the tympanum (T) and the best response area of the lateral body wall (L) of one individual each of (A) *Dendrobates histrionicus*, (B) *D. tinctorius*, (C) *Epipedobates tricolor* and (D) *E. azureiventris*. In D, the upper x -axis scale is related to the upper tympanum curve, which shows the whole frequency response range of the tympanum; the lower x -axis scale is related to the lower tympanum and body wall curves showing the tympanum and lung response with higher resolution.

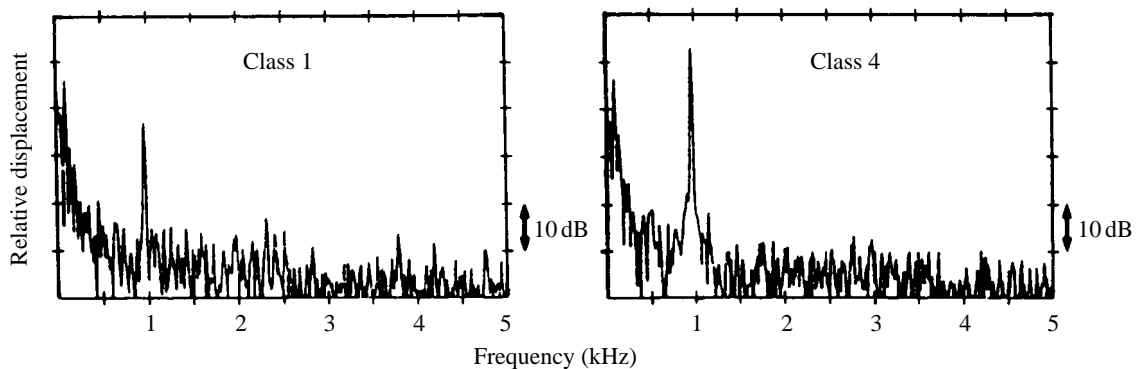


Fig. 5. An example showing a small (class 1) and large (class 4) response of the tympanum of *Smilisca baudini* to selective stimulation via the lung area of the body wall.

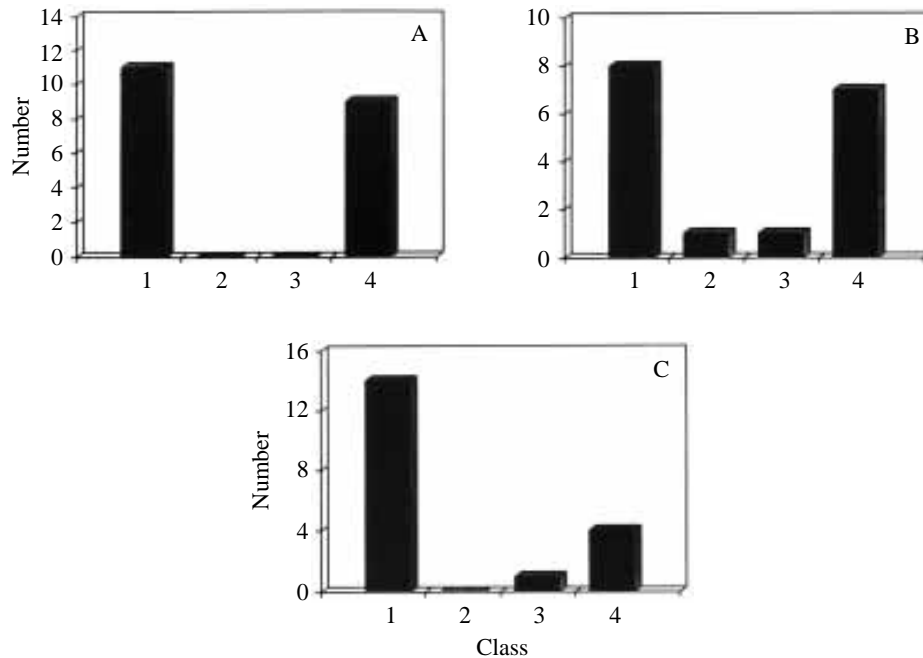


Fig. 6. Division of displacement amplitudes of the tympanum into four classes (see Results); class 1, small; class 4, large; classes 2, 3, intermediate. The tympanic displacements were caused by selective tone stimulation *via* the lung area of the body wall while the frog was breathing. Example distributions are shown for (A) *Smilisca baudini*, ($N=20$), (B) *Hyla cinerea* ($N=17$) and (C) *Osteopilus septentrionalis* ($N=19$). Number, number of values in each sample.

Intensity-dependence of vibration amplitudes

The intensity-dependencies of the displacement amplitudes at the tympanum to free-field and selective lung area stimulation and at the lung area to free-field stimulation are presented in Fig. 7 for the three treefrog species. Of 36 investigated functions, 31 (those shown in Fig. 7) showed a linear (in the double logarithmic plots) and statistically significant relationship between displacement amplitude and sound pressure level ($0.001 < P < 0.05$). Since the slopes of all significant correlations do not differ much (range 0.038–0.056), the relationship between displacement amplitude and sound intensity is comparable among species and across conditions of stimulation and measurement. Only the absolute amplitude of vibration of the tympanum and the lung area may be different. The relationship between sound intensity and displacement amplitude was not significant for the remaining five functions. These functions concerned some measurements of free-field and selective lung area stimulation in both individuals of *Hyla* and two individuals of *Osteopilus*.

At the stimulation frequencies examined, the tympanum always showed the largest displacement amplitudes when stimulated free-field. The displacement values in response to the lower frequencies tested for each species (0.96, 0.9, 1.0 kHz) were between 1.5 and 2 times larger than those of the lung area. The differences were even larger (between 20

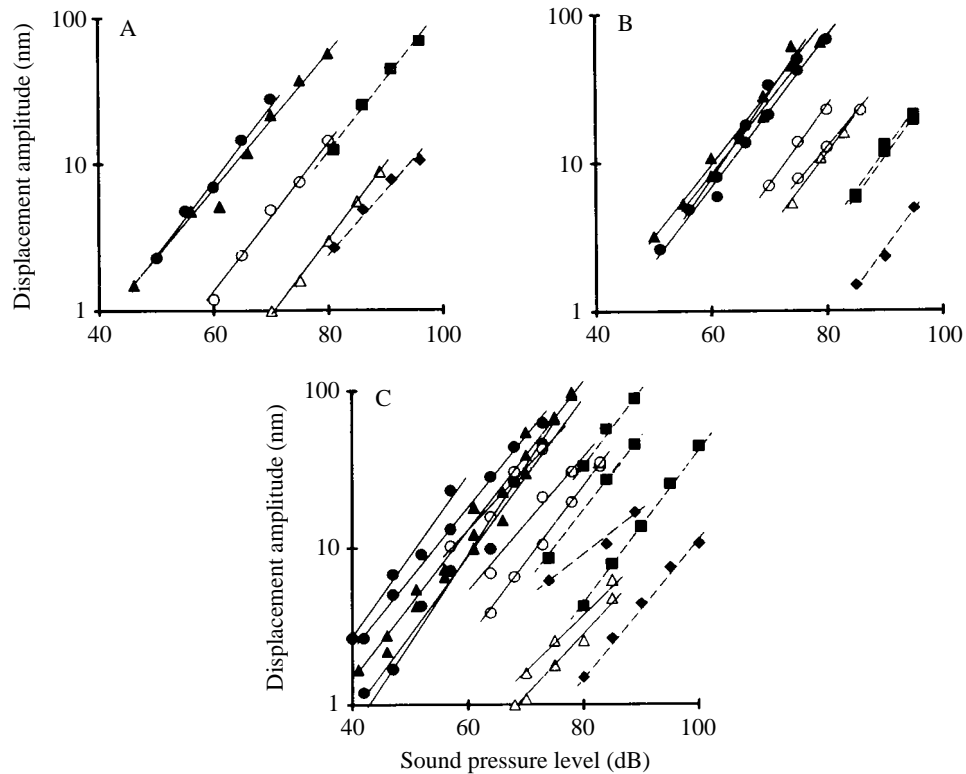


Fig. 7. Intensity-dependence of average displacement amplitudes for (A) *Smilisca baudini*, (B) *Hyla cinerea* and (C) *Osteopilus septentrionalis*. Measurements from all individual treefrogs are shown. Regression lines indicate statistically significant correlations. Tympanum (filled circles) and lateral body wall (open circles) by free-field stimulation at 0.96 kHz (*Smilisca*), 0.9 kHz (*Hyla*) or 1 kHz (*Osteopilus*). Tympanum (filled triangles) and lateral body wall (open triangles) by free-field stimulation at 2 kHz (*Smilisca*, *Osteopilus*) or 2.7 kHz (*Hyla*). Class 4 response (filled squares) and class 1 response (filled diamonds) of the tympanum by selective stimulation at the respective lower frequencies mentioned above are also given (see also Results and Fig. 5).

and 53 times) for the higher frequencies tested (2.0 and 2.7 kHz). In *Smilisca* and two individuals of *Osteopilus*, the vibrational amplitudes of the lung area in response to free-field stimulation with the lower frequencies were comparable to the displacements measured at the tympanum when the lung area was selectively stimulated with the closed sound system and the frog was breathing with the lungs. This indicates a very effective coupling between lung and tympanum vibrations.

Discussion

Frequency response characteristics

The general physics of sound receptor systems (Fletcher and Thwaites, 1979) predicts that the frequency response ranges and resonance frequencies of the lateral body wall

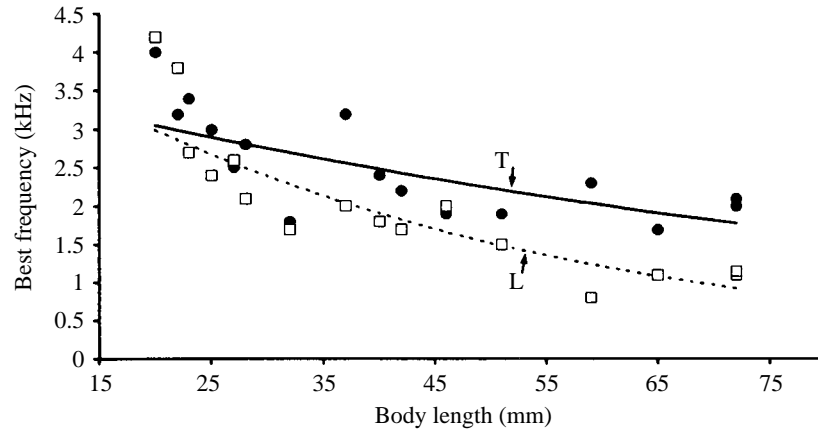


Fig. 8. Relationship between body length and the best response frequency of the tympanum T (filled circles) and lung area of the body wall L (open squares) of all 16 individual frogs investigated (for equations, see Discussion).

depend on the lung volume and the stiffness of the vibrating structures, mainly of the skin covering the lung area. The tympanic frequency response is determined by the size, mass and stiffness of the tympanic membrane and the middle ear ossicles and by the middle ear volume (Dallos, 1973). Thus, the frequency response of the tympanic membrane and body wall must not be the same. In harmony with previous studies on frogs and toads (Narins *et al.* 1988; Jørgensen, 1991; Jørgensen *et al.* 1991; Hetherington, 1992), the frequency response range of the lateral body wall always has the high-frequency cut-off at lower frequencies than the tympanum (Figs 3, 4; Table 1). The frequencies of the best body wall response, however, are not always lower than those of the best tympanic response. Fig. 8 shows the relationship between best frequencies and body size for the individuals in the present study. Best frequencies (BF) decreased significantly ($P < 0.005$) with increasing body length (S): $\ln BF = a - bS$. The slope (b) is about twice as large for the lung area of the body wall ($b = 0.023$) as for the tympanum ($b = 0.01$). The constants (a) in the equation are similar (tympanum, $a = 1.32$; lung area of body wall, $a = 1.56$). This indicates that the resonance frequency of the body wall vibration depends much more on the size of the frog, and thus on the area of the skin covering the lung, than does the best frequency of the eardrum. The best frequency response ranges of the tympanum and lateral body wall may be similar only when the frogs are small, like the small dendrobatids, or have a smooth and rather stiff skin covering the lungs, like hylid and some ranid frogs (Figs 3, 4, 8; Table 1; see also Jørgensen, 1991). In this context, the very low best frequency of the body wall of the *Smilisca* (Fig. 3A) can be explained by the structure of its skin, which is rather coriaceous and covered with little warty swellings.

In general, Fig. 8 shows that a coincidence of best frequency responses of the tympanum and lateral body wall is more likely in small than in larger frogs. This suggests that during postmetamorphic growth the best frequency response of the eardrum and lateral body wall may change from being similar to being different, which means that the

contribution of the lung pathway to the frequency response pattern of the tympanum may vary with age.

The magnitude of the influence of the lung on tympanic vibration

A 15–20 dB enhancement of the sound from the lung to the eardrum by an open glottis has been reported in the Puerto-Rican treefrog *Eleutherodactylus coqui* by Jørgensen *et al.* (1991). It has also been shown that the greater is the degree of inflation of the lungs, the larger is the effect of the lung pathway on the eardrum (Jørgensen, 1991). Our present results suggest a similar influence of the lung on the eardrum response. If the lungs are ventilated by breathing (through an open glottis), the sound propagates up to eight times (18 dB) better from the lung to the tympanum than when the frog is not breathing (possibly with its glottis closed). Thus, the sound propagation from the lung to the eardrums is highly variable and depends on breathing activity. An actively moving or calling frog with high energetic demands will be more likely to ventilate its lungs than a resting one, so that the lung pathway is expected to make the greatest contribution to hearing in frogs when they are active, e.g. in male–male or female–male interactions during the breeding season.

When the frogs were breathing with their lungs, we recorded about 30–40% of the large response amplitudes at the tympanum, while the lung was stimulated with tone bursts. If large amplitudes are related to a glottis-open condition, this suggests that the glottis in our frogs may have been open for 30–40% of the breathing cycle, which is comparable to about 25% in the resting treefrog *Eleutherodactylus coqui* (Narins *et al.* 1988). Thus, the lung input seems to be a source of amplitude modulation, by 15–20 dB, of tympanic vibrations in the rhythm of breathing.

Furthermore, a change in the angle of incidence of a sound wave can attenuate the tympanic response at certain frequencies by up to 40 dB if the glottis is open (Jørgensen *et al.* 1991; Jørgensen, 1991). This induction of a highly directional frequency response of the tympanum, by coupling it with the lung, suggests that the lung pathway of sound may play a role in the sound localization of frogs. Behavioural tests of directional hearing in the grey treefrog (*Hyla versicolor*), however, do not support this suggestion, because this species locates a sound source less well when the sound contains frequencies to which the eardrum response shows its maximum directionality (Jørgensen and Gerhardt, 1991). Instead of having a positive influence on the ability to localize sound, the lung pathway seems to have a deleterious effect. Whether this result can be generalized has yet to be evaluated in further studies.

Relationship of the frequency response range of the lungs to frequency spectra of calls

In Table 1, the best frequency response ranges of the tympanum and lateral body wall over the lungs are shown together with the main frequency components of the advertisement calls of the species investigated. With the exceptions of *Osteopilus* and *Epipedobates tricolor*, the best response range of the lung area does not overlap with the major frequencies of the calls. The frequencies leading to the maximum displacement of the lateral body wall lie either between (*Smilisca*, *Hyla*) or below (*D. histrionicus*, *D. tinctorius*, *E. azureiventris*) the main call frequencies. A similar incongruity between call frequencies

and best frequency response ranges of the body wall has been found in other treefrogs, such as *Eleutherodactylus coqui* (Narins *et al.* 1988), *Hyla gratiosa* and *Hyla versicolor* (Jørgensen, 1991; Gerhardt, 1981, 1982), in which the maximum body wall response always occurs between low and high call frequencies. This mismatching of frequency ranges, however, does not necessarily mean that the sound pathway *via* the lung is of little importance to call perception in frogs. The available data on *E. coqui*, *H. versicolor*, *H. gratiosa* and *Rana temporaria* (Jørgensen, 1991; Jørgensen *et al.* 1991) indicate that the lung input to the eardrum contributes to the maximum directional response by attenuation of the eardrum vibration *at* or *above* the frequency of maximum displacement of the lateral body wall. For *Hyla cinerea*, the frequency range of attenuation may lie between 1.5 and 2.5 kHz (see Fig. 3). However, the lung input also leads to a maximum amplification of eardrum vibrations *below* the frequency of the maximum body wall response. Thus, eardrum vibrations in response to the low-frequency components of the advertisement calls of *H. cinerea* (0.9 kHz), *H. gratiosa*, *H. versicolor* and *E. coqui* may be optimally amplified by the sound pathway through the lungs. At the same time, higher-frequency components are attenuated by the lung pathway, the magnitude of attenuation depending on the angle of incidence of the sound. The lowpass filter of the lung pathway could lead to considerable attenuation of high-frequency call components or even entire advertisement calls for some species in addition to an attenuation of high-frequency noise from the environment. In conclusion, the few data available suggest that the major functional contribution of the lung input to the hearing of treefrogs, at least, is the enhancement of the perception of low-frequency components of advertisement calls. This hypothesis could be tested by measuring the ability of animals in the presence of various background noises to detect a conspecific caller against the noise, with and without a contribution of the lung pathway to the eardrums. When the lungs are involved, the detection of a calling frog should require a smaller signal-to-noise ratio than when there is no input from the lung.

In the dendrobatids, such as *D. histrionicus*, where the frequency range of the advertisement calls is above the best response range of the lateral body wall (Table 1), the lungs may play a role in detecting conspecific territorial (aggressive), courtship and release calls, all of which may have a spectrum with more low-frequency components (1.2–4 kHz in *D. histrionicus*) than the advertisement call (Zimmermann, 1990; Zimmermann and Zimmermann, 1982). Hence, the comparison of species characteristics suggests that the sound pathway through the lungs may contribute to auditory behaviour in different ways depending on the frequency response patterns of the tympanum and lateral body wall and the main frequencies of the species' calls.

This study was supported by grants of the Deutsche Forschungsgemeinschaft. We thank Dr T. Breithaupt, Dr B. Schmitz and Dr J. Tautz for their support during the course of this study.

References

- CHUNG, S. H., PETTIGREW, A. G. AND ANSON, M. (1981). Hearing in the frog: dynamics of the middle ear. *Proc. R. Soc. Lond. B* **212**, 459–485.
- DALLOS, P. (1973). *The Auditory Periphery*. New York: Academic Press.

- DUPELLMANN, W. E. (1970). *The Hylid Frogs of Middle America*, vol. III. Lawrence, Kansas: Mus. Nat. His. Univ. Kansas Monograph.
- EHRET, G., TAUTZ, J., SCHMITZ, B. AND NARINS, P. M. (1990). Hearing through the lungs: lung–eardrum transmission of sound in the frog *Eleutherodactylus coqui*. *Naturwissenschaften* **77**, 192–194.
- FENG, A. S., GERHARDT, H. C. AND CAPRANICA, R. R. (1976). Sound localization behavior of the green treefrog (*Hyla cinerea*) and the barking treefrog (*H. gratiosa*). *J. comp. Physiol.* **107**, 241–252.
- FENG, A. S. AND SHOFNER, W. P. (1981). Peripheral basis of sound localization in anurans. Acoustic properties of the frog's ear. *Hearing Res.* **5**, 201–216.
- FLETCHER, N. H. AND THWAITES, S. (1979). Physical models for the analysis of acoustical systems in biology. *Q. Rev. Biophys.* **12**, 25–65.
- GERHARDT, H. C. (1974). The significance of some spectral features in mating call recognition in the green treefrog (*Hyla cinerea*). *J. exp. Biol.* **61**, 229–241.
- GERHARDT, H. C. (1981). Mating call recognition in the barking treefrog (*Hyla gratiosa*): responses to synthetic calls and comparisons with the green treefrog (*Hyla cinerea*). *J. comp. Physiol.* **144**, 17–25.
- GERHARDT, H. C. (1982). Sound pattern recognition in some North American treefrogs (*Anura: Hylidae*): implications for male choice. *Am. Zool.* **22**, 581–595.
- GERHARDT, H. C. AND RHEINLAENDER, J. (1980). Accuracy of sound localization in a miniature dendrobatid frog. *Naturwissenschaften* **67**, 362–363.
- HETHERINGTON, T. E. (1992). The effects of body size on functional properties of middle ear systems in anuran amphibians. *Brain Behav. Evol.* **39**, 133–142.
- JØRGENSEN, M. B. (1991). Comparative studies of the biophysics of directional hearing in anurans. *J. comp. Physiol. A* **169**, 591–598.
- JØRGENSEN, M. B. AND GERHARDT, H. C. (1991). Directional hearing in the gray treefrog *Hyla versicolor*: eardrum vibrations and phonotaxis. *J. comp. Physiol. A* **169**, 177–183.
- JØRGENSEN, M. B., SCHMITZ, B. AND CHRISTENSEN-DALSGAARD, J. (1991). Biophysics of directional hearing in the frog *Eleutherodactylus coqui*. *J. comp. Physiol. A* **168**, 223–232.
- KLUMP, G. M. AND GERHARDT, H. C. (1989). Sound localization in the barking treefrog. *Naturwissenschaften* **76**, 35–37.
- MACHMERTH, H., TEIB, D. AND SCHNITZLER, H. U. (1975). Konstruktion eines Luftschallgebers mit konstantem Frequenzgang im Bereich von 15 kHz bis 130 kHz. *Acustica* **34**, 81–85.
- MICHELSSEN, A., JØRGENSEN, M., CHRISTENSEN-DALSGAARD, J. AND CAPRANICA, R. R. (1986). Directional hearing of awake, unrestrained treefrogs. *Naturwissenschaften* **73**, 682–683.
- MYERS, C. W. AND DALY, J. W. (1976). Preliminary evaluation of skin toxins and vocalizations in taxonomic and evolutionary studies of poison-dart frogs (Dendrobatidae). *Bull. Am. Mus. nat. His.* **157**, 173–262.
- NARINS, P. M., EHRET, G. AND TAUTZ, J. (1988). Accessory pathway for sound transfer in a neotropical frog. *Proc. natn. Acad. Sci. U.S.A.* **85**, 1508–1512.
- OLDHAM, R. S. AND GERHARDT, H. C. (1975). Behavioral isolating mechanisms of the treefrogs *Hyla cinerea* and *H. gratiosa*. *Copeia* **1975**, 223–231.
- RAMM, B. AND HOFMANN, G. (1987). *Biometeorologie*, 3rd edn. Stuttgart: Enke-Verlag.
- RHEINLAENDER, J., WALKOWIAK, W. AND GERHARDT, H. C. (1981). Directional hearing in the green treefrog: a variable mechanism? *Naturwissenschaften* **68**, 430–431.
- RIVERO, J. A. (1978). *The Amphibians and Reptiles of Puerto Rico*. Departamento Biología, Universidad de Puerto Rico, Mayaguez: Editorial Universitaria.
- SACHS, L. (1974). *Angewandte Statistik*, 4th edn. Berlin: Springer-Verlag.
- VLAMING, M. S. M. G., AERTSEN, A. M. H. J. AND EPPING, W. J. M. (1984). Directional hearing in the grassfrog (*Rana temporaria*). I. Mechanical vibrations of tympanic membrane. *Hearing Res.* **14**, 191–201.
- ZIMMERMANN, E. (1990). Behavioral signals and reproduction modes in the neotropical frog family Dendrobatidae. *Fortschr. Zool.* **38**, 61–73.
- ZIMMERMANN, E. AND RAHMANN, H. (1987). Acoustic communication in the poison-arrow frog *Phyllobates tricolor*: advertisement calls and their effects on behavior and metabolic brain activity of recipients. *J. comp. Physiol.* **160**, 693–762.
- ZIMMERMANN, E. AND ZIMMERMANN, H. (1982). Soziale Interaktionen, Brutpflege und Zucht des Pfeilgiftfrosches *Dendrobates histrionicus*. *Salamandra* **18**, 150–167.
- ZIMMERMANN, H. AND ZIMMERMANN, E. (1988). Etho-Taxonomie und zoogeographische Artengruppenbildung bei Pfeilgiftfröschen. *Salamandra* **24**, 125–160.