Directional hearing in the gray tree frog *Hyla versicolor*: Eardrum vibrations and phonotaxis

Morten Buhl Jørgensen[1]* and H. Carl Gerhardt[2]

[1] Biological Institute, Odense University, DK-5230 Odense M, Denmark;
[2] Division of Biological Sciences, University of Missouri, Columbia, MO 65211, USA

Summary. 1. We used laser vibrometry to study the vibrational frequency response of the eardrum of female gray tree frogs for different positions of the sound source in three-dimensional space. Furthermore, we studied the accuracy of 3-D phonotaxis in the same species for sounds with different frequency contents.

2. The directionality of the eardrum was most pronounced in a narrow frequency range between 1.3 and 1.8 kHz.

3. The average 3-D, horizontal and vertical jump error angles for phonotactic approaches with a sound similar to the natural advertisement call (1.1 and 2.2 kHz frequency components) were 23°, 19° and 12°, respectively.

4. 3-D jump error angle distributions for the 1.4 + 2.2 kHz, 1.0 kHz and 2.0 kHz sounds were not significantly different from that for the 1.1 + 2.2 kHz sound.

5. The average 3-D jump error angle for the 1.4 kHz sound was 36°, and the distribution was significantly different from that for the 1.1 + 2.2 kHz sound. Hence, phonotactic accuracy was poorer in the frequency range of maximum eardrum directionality.

6. Head scanning was not observed and is apparently unnecessary for accurate sound localization in three-dimensional space.

7. Changes in overall sound pressure level experienced by the frog during phonotactic approaches are not an important cue for sound localization.

Key words: Hyla versicolor – Directional hearing – Eardrum vibrations – Frequency response – Phonotaxis

Introduction

Sound localization plays an important role in mating and territorial behaviors of many anurans, and several

Abbreviations: IVAD interaural vibration amplitude difference; *VA* vibration amplitude

* To whom offprint requests should be sent

species have been shown to perform phonotaxis with considerable accuracy. For example, female green tree frogs, *Hyla cinerea*, showed an average jump error angle of 16.1° during phonotactic approaches toward a loudspeaker emitting a synthetic call similar to the conspecific advertisement call (Rheinlaender et al. 1979). Removing the high frequency components (2.7 and 3.0 kHz) in the call leaving only a 0.9 kHz component, did not affect the accuracy of localization. In experiments performed in their natural, acoustically complex environment, males of the tiny dendrobatid *Colostethus nubicola* showed an average jump error angle of 23° (Gerhardt and Rheinlaender 1980). Furthermore, open-loop experiments with barking tree frogs, *Hyla gratiosa*, showed that they can disriminate between different angles of sound incidence and not just lateralize the sound source (Klump and Gerhardt 1989).

The above studies were concerned only with the ability of frogs to localize a sound source in the horizontal plane. However, males of many frog species call from elevated positions in the vegetation, and the females thus face the task of localizing the males in three-dimensional space. Female green tree frogs readily localized an elevated loudspeaker that they could approach through a three-dimensional grid (Gerhardt and Rheinlaender 1982). Passmore et al. (1984) used a similar grid and quantified the localization accuracy of the painted reed frog, *Hyperolius marmoratus*, in terms of three-dimensional jump error angles. They found that the average 3-D jump error angle (43°) was much greater than the average jump error angle (22°) in a two-dimensional grid. The authors concluded that the resolution of sound source elevation although effective was poorer than the resolution in azimuth.

The mechanisms behind the ability of frogs to localize elevated sound sources are not understood. In mammals and owls the determination of sound source elevation is thought to depend on cues produced by external auditory structures (e.g. Kuhn 1987; Knudsen and Konishi 1979). However, no such structures are present in tree frogs, in which the eardrums are symmetrical and flush

with the surface of the head. Rheinlaender et al. (1979) noted that green tree frogs often made lateral head scanning movements during phonotactic approaches and found that this behavior improved the accuracy of subsequent jumps. Gerhardt and Rheinlaender (1982) suggested that changes in binaural differences during lateral head scanning would be smaller if the sound source was elevated than if it was in the horizontal plane. Hence, the head scanning behavior could also provide cues for determination of sound source elevation.

Jørgensen et al. (1991) and Jørgensen (unpublished) described the directionality of eardrum vibrations in the horizontal plane in several species of frogs. The eardrum directionality is especially pronounced in a narrow frequency range, the exact location of which depends on the species. Sound transmitted across the lateral body wall into the lungs and further on to the internal side of the eardrum via the glottis, mouth cavity and Eustachian tubes is involved in the generation of this strong directionality (see also Ehret et al. 1990). Surprisingly, the major frequency components of the advertisement calls of the species are not found in the narrow frequency range where the strongest directionality is seen.

We used laser vibrometry to study the vibrational frequency response of the eardrum of female gray tree frogs for different positions of the sound source in three-dimensional space. Encouraged by the results of these experiments, we studied the accuracy of 3-D phonotaxis in the same species for sounds with different frequency contents.

Materials and methods

Laser measurements

Three female gray tree frogs (two *Hyla versicolor* and one *Hyla chrysoscelis*) were used for the experiments. These two cryptic species are morphologically indistinguishable and produce advertisement calls with very similar spectral contents (Gerhardt 1982). The animals weighed 8.8–10.0 g and had snout-vent lengths of 5.2–5.6 cm.

The frogs were anaesthetized by immersion in a 0.2% solution of tricaine methanesulphonate (MS222) before an experiment. Next, the Eustachian tubes were cleaned and if the lungs had been deflated they were reinflated via a thin glass tube inserted through the glottis. This procedure ensured that the eardrum vibrations were similar to those of awake animals (Jørgensen, unpublished).

The frog was then placed in a natural sitting posture on a small platform in the center of a roundabout carrying a loudspeaker (KEF C35) at a distance of approximately 55 cm from the frog. The frog's head was supported by a thin steelwire (1 mm diameter) under the rim of its lower jaw. The platform was made of similar thin steelwires in order to minimize its effect on the sound field around the frog. The loudspeaker could be moved all around the frog in the horizontal plane except within an arc of ±30° from the ipsilateral direction where the laser vibrometer was located. Furthermore, it could be moved from 60° below the horizontal plane to 90° above it.

The sound stimulation and vibration measurement procedures are described elsewhere (Jørgensen et al. 1991). Briefly, a short frequency sweep (80 Hz–5 kHz, 20 ms) generated in a computer and clocked out at 50 kHz (Data Translation DT2821-F 12 bit D/A converter) was fed to the loudspeaker. A probe microphone (B&K 4170) was used to record the sound stimulus 1–2 mm from the frog's left eardrum. The amplitude variations in the sound stimulus was within 12 dB between 500 Hz and 5 kHz. A Dantec

laser Doppler vibrometer was used to measure the vibration velocity of the center of the frog's left eardrum (see Michelsen and Larsen 1978 for details). A small reflecting sphere (Scotchlite, 30–50 μm diameter) was placed on the eardrum in order to ensure a good reflection of the laser light. The laser vibrometer was located on the line connecting the two eardrums at a distance of approximately 70 cm. The measured sound and vibration signals were fed to the two channels of a dual-channel FFT-analyzer (HP3582A), which also calculated the transfer function between the two inputs. The transfer functions were corrected for the frequency response of the probe microphone, converted to displacement (dividing by $2\pi f$, where f is the frequency) and scaled to 90 dB SPL.

The direction that the frog was facing is referred to as 0°. Angles on the left (ipsilateral) side are referred to using positive numbers (0° to 180°) and angles on the right (contralateral) side using negative numbers (0° to −180°).

Behavioral experiments

Sixteen amplectic pairs of gray tree frogs (*Hyla versicolor*) collected from breeding ponds near Columbia, Missouri were used for the experiments. The pairs were kept on ice until the next day when the females were separated from the males shortly before they were tested.

We constructed a three-dimensional grid by mounting 36 wooden dowel sticks (10 mm diameter) vertically in a plywood plate (1 m × 1 m). The sticks were arranged in a rectangular array with 6 rows each containing 6 sticks (see Fig. 4). The distance between neighbouring sticks was 20 cm. The sticks were 110 cm high and marked with 10 cm intervals. The plywood plate was covered with a sound absorbing material (Sonex) to reduce echos.

A release platform (10 cm × 5 cm) was mounted with it's front edge approximately 10 cm in front of the grid and 50 cm above the floor. A small loudspeaker (Hecomp KC52) was mounted 10 cm behind the grid and 100 cm above the floor (see Fig. 4). The loudspeaker pointed directly toward the release platform.

The grid was placed in a semi-anechoic chamber. A red light bulb provided a dim illumination. A dim flashlight was also used occasionally in most experiments to verify some locations of the frog in the grid. All experiments were conducted at approximately 20 °C.

Five digitally synthesized artificial advertisement calls were used as acoustic stimuli. All calls had the same gross temporal structure (Fig. 1) but different carrier frequencies. Three calls had single-frequency carriers (1.0 kHz, 1.4 kHz, 2.0 kHz) and two calls had two-frequency carriers (1.1 + 2.2 kHz, 1.4 + 2.2 kHz). Figure 1 also shows frequency spectra of the 5 calls.

The calls were clocked out from a Dell 316LT computer using a commercial 8-bit D/A-board (Supersound, engineering version), amplified and fed to the loudspeaker. They were repeated every 4 s.

Another computer (AT&T 6300) controlled an attenuator used to adjust the sound pressure level (1.5 dB steps) and a switch that could turn the sound off completely. We wrote a computer program that allowed us to easily and quickly track the position of the frog on a graphical display of the 3-D grid on the computer screen. Hence, the new position of the frog was immediately input to the computer, which then adjusted the attenuation to a position-specific value. In some experiments this value was simply a constant, i.e. the sound power delivered by the loudspeaker was independent of the position of the frog. However, in most experiments the attenuation was continually adjusted to provide a constant sound pressure level (85 dB SPL) at the frog's position. The grid was calibrated by placing a 1″ random-incidence microphone of a General Radio 1933 sound level meter at 12 different positions on each stick in the grid (0–110 cm, 10 cm intervals) and then saving the attenuation values nescessary to keep the sound pressure level constant. Separate calibrations were done for each of the 5 calls used. The sound pressure level was also 85 dB SPL at the release platform at the start of an experiment.
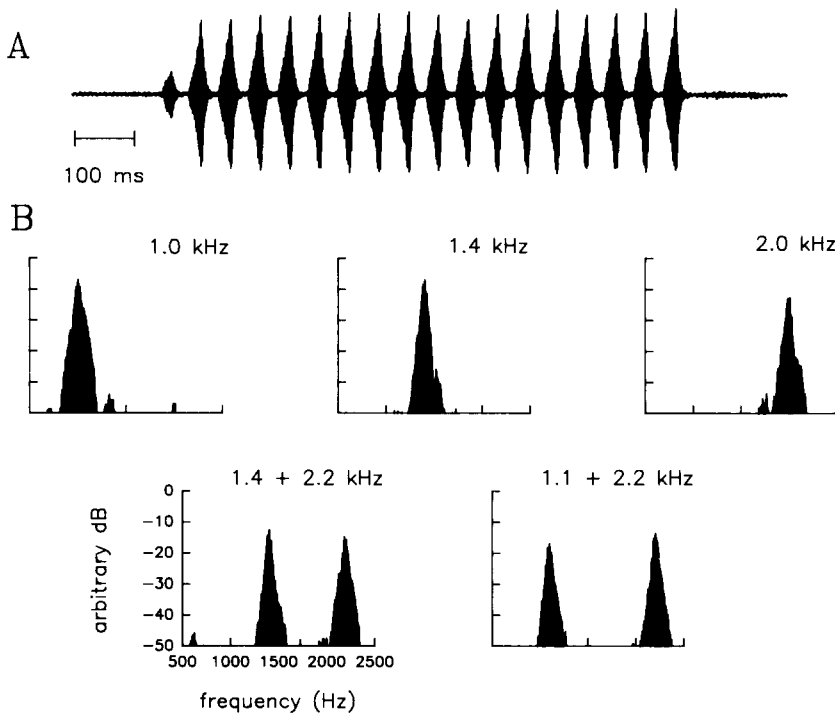
A

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|———|
100 ms
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B

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1.0 kHz            1.4 kHz            2.0 kHz




1.4 + 2.2 kHz      1.1 + 2.2 kHz

  0
-10
-20
-30
-40
-50
   500 1000 1500 2000 2500

   frequency (Hz)
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arbitrary dB

Fig. 1. A Gross temporal structure of the synthetic calls used in the phonotaxis experiments. **B** Frequency spectra of the five calls

An experiment was initiated by placing a frog on the release platform and immediately starting to play one of the 5 calls. Usually, the frog faced the loudspeaker when it was released. In a few initial experiments the frog was released at floor level. However, it would then often traverse most of the grid on the Sonex material and not jump onto any sticks. By releasing the frog on the release platform, we avoided any underestimation of its localization accuracy caused by this tendency to stay on the floor. After the frog leaped from the platform into the grid and after any subsequent movements within the grid (either leaps from stick to stick or vertical climbs on one stick) the sound was turned off. Then the animal's new position was recorded on the computer, which adjusted the attenuation accordingly and restarted the playback. This procedure was continued until the frog jumped onto the loudspeaker, jumped out of the grid or did neither within an imposed time limit of 10 min. Our data are based on 62 successful phonotactic approaches. Each frog made 1–12 approaches but never more than 3 with the same stimulus.

The accuracy of phonotaxis was quantified in terms of 3-D jump error angles (θ) calculated using the following formula:

$$\cos \theta = \frac{d_t^2 + d_1^2 - d_2^2}{2 d_1 d_t}$$

where d_1 is the distance from the old to the new position of the frog, d_2 is the distance from the new position of the frog to the loudspeaker and d_1 is the distance from the old position of the frog to the loudspeaker. The same formula was used by Passmore et al. (1984), and readers are referred to their paper for the derivation. We also calculated horizontal and vertical error angles by projecting the frog's and the loudspeaker's positions onto a horizontal or vertical plane before using the above formula.

The Mann-Whitney U-test (MW U-test) was used for pairwise comparison of the jump error angle distributions.

Results

Laser measurements

The frequency response of the eardrum changed with the position of the sound source in three-dimensional

space (Fig. 2). The directionality was especially pronounced in a narrow frequency range between approximately 1.3 and 1.8 kHz. Here a deep dip in the transfer function occurred when the loudspeaker was located in the horizontal plane at an azimuthal angle of $-30°$ or $-60°$ (i.e. on the contralateral side). When the loudspeaker was moved away from this position in either a horizontal or vertical direction, the dip became shallower or even disappeared.

Figure 3 shows the vibration amplitude of the left eardrum at 3 frequencies plotted as a function of the position of the loudspeaker in elevation and azimuth. The 3 frequencies are in the range of the major components of the advertisement call of *H. versicolor* (1 and 2 kHz; Gerhardt 1982) and in the range where the dip occurs in the frequency response of the eardrum (1.4 kHz). The interaural vibration amplitude difference
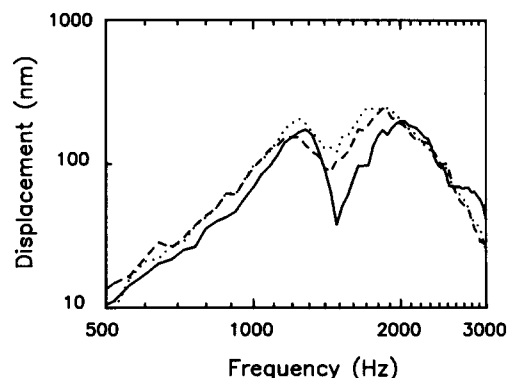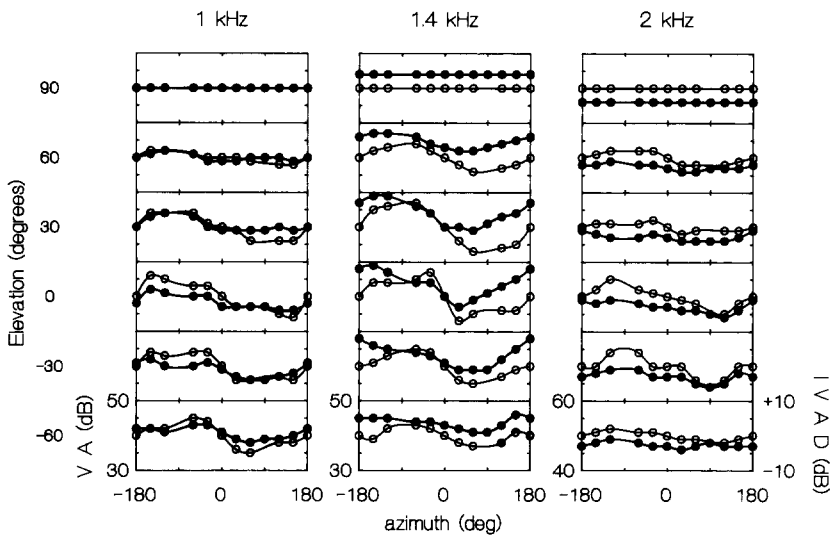
```
1000




 100




  10
   500      1000        2000  3000
        Frequency (Hz)
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Displacement (nm)

Fig. 2. Frequency responses of the left eardrum of a gray tree frog (*H. versicolor*). The loudspeaker was located at $-60°$ in azimuth and at elevations of 0° (———), 30° (- - - -) and 60° (·····). The sound pressure level at the eardrum was 90 dB

Fig. 3. Vibration amplitude (VA) of the left eardrum of a gray tree frog (*H. versicolor*) at 3 frequencies plotted as a function of the position of the sound source in azimuth and elevation (*filled circles*). The VA is given in dB re 1 nm. The interaural vibration amplitude difference (IVAD, see text) is also shown (*open circles*). The datapoints are connected with a cubic spline curve for better visualization
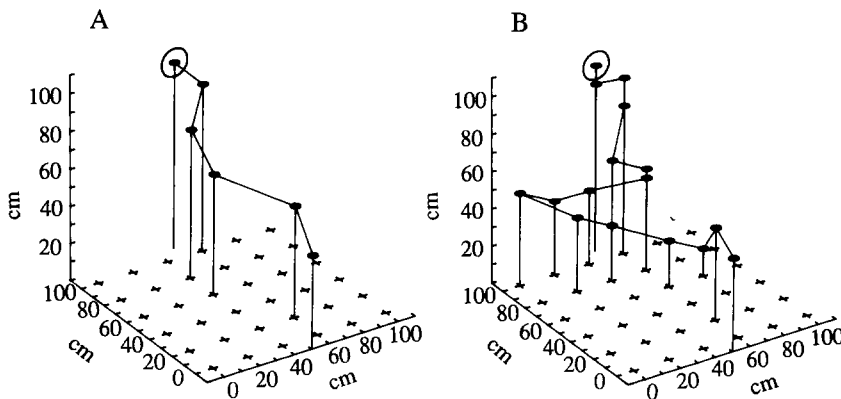
Fig. 4. Examples of one of the best (**A**) and one of the poorest (**B**) phonotactic approaches. The diagrams show the route followed by the female from the release platform (not shown) to the loudspeaker (circle). The vertical lines show the elevation at each position. The crosses indicate the positions of the vertical sticks in the grid

(IVAD, the vibration amplitude of the left eardrum minus that of the right eardrum) is also plotted. It was calculated assuming that the auditory periphery of the frog is symmetrical and that the directionality pattern of the right eardrum therefore is a mirror image of that of the left ear. Clearly, the eardrum is most directional in both azimuth and elevation at 1.4 kHz. For example, moving the sound source from 30° to −30° in the horizontal plane produces an effective change in the IVAD of 14 dB at this frequency.

Behavioral experiments

A motivated female usually responded quickly to the sound stimulus by performing one or several orientation movements on the platform before jumping into the grid. The movements nearly always consisted of whole-body turns that occurred right after a call was heard. Successive orientation movements seemed independent, and the alignment of the body axis with the target axis did not appear to improve during a series of such movements. Lateral head scanning movements like those performed by *H. cinerea* (Rheinlaender et al. 1979) and *H. marmoratus* (Passmore et al. 1984) were not observed in the gray tree frog.

After orienting on the release platform the female leaped onto a stick in the grid. She first assumed a vertical posture on the stick, but usually she quickly rotated her body into a posture where her head was held almost horizontally and she was ready for the next jump. This behavior was similar to that of *H. marmoratus* (see Fig. 4 in Passmore et al. 1984). The female often performed one or more orientation movements on the stick before proceeding toward the loudspeaker. These movements were similar to those performed on the release platform. In addition to jumping from stick to stick the female often climbed vertically on one stick.

The accuracy of phonotaxis varied considerably from trial to trial. In Fig. 4 we show one of the best and one of the poorest approaches. The number of jumps and vertical climbs used to reach the loudspeaker varied between 5 and 15. The average number of jumps used to reach the loudspeaker was 6.2 for trials with the 1.4 kHz call and varied between 4.9 and 5.1 for trials with the other four calls. The average proportion of climbs varied from 25% for the 1.4+2.2 kHz trials to 35% for the 1.0 kHz trials.

The 1.1+2.2 kHz synthetic call was very similar to, and as attractive as, the natural advertisement call of *H. versicolor* (Gerhardt, unpublished). In Fig. 5 we show the distribution of 3-D jump error angles in trials with
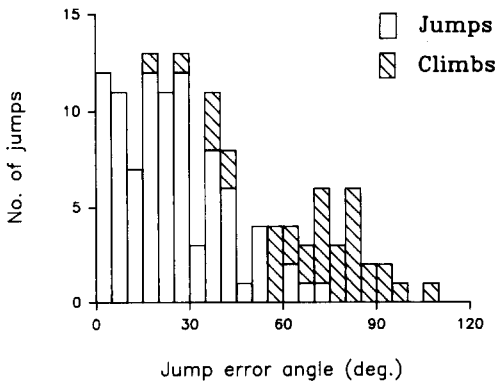
Fig. 5. Distributions of 3-D jump and climb error angles for all phonotactic approaches with the 1.1+2.2 kHz synthetic call
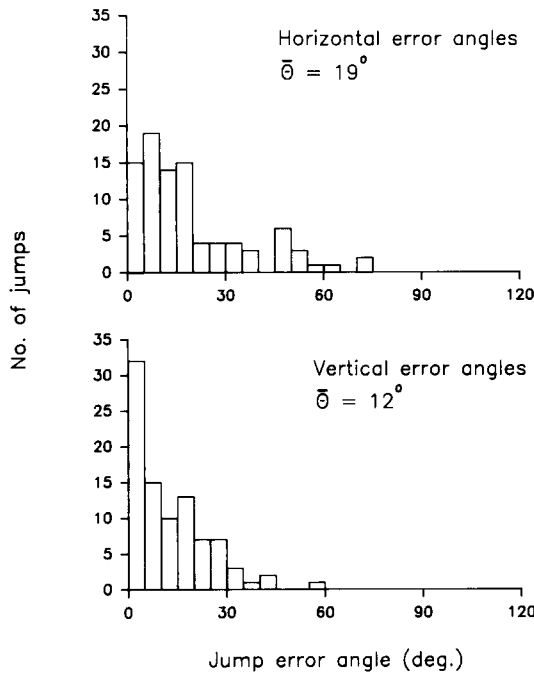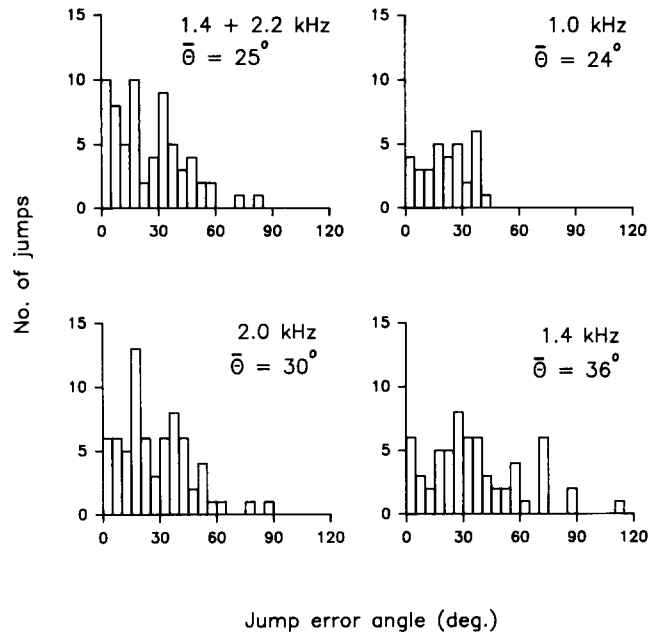

Fig. 6. Distributions of horizontal and vertical jump error angles for all phonotactic approaches with the 1.1+2.2 kHz synthetic call

Fig. 7. Distributions of 3-D jump error angles for phototactic approaches with the 1.4+2.2 kHz, 1.0 kHz, 2.0 kHz and 1.4 kHz synthetic calls

this call. Also, the error angles of vertical climbs are shown. The average jump error angle ($\bar{\theta}$) was 23°. When climbs were included $\bar{\theta}$ was 36°. The distributions of error angles with and without climbs were significantly different (MW U-test, $p=0.002$). In order not to underestimate the localization ability of gray tree frogs we excluded climbs in the following analyses although they were part of the phonotactic approaches.

The distributions of horizontal and vertical jump error angles for trials with the 1.1+2.2 kHz call are shown in Fig. 6. The average vertical error angle was smaller than the average horizontal error angle for trials with this call as well as for trials with the other four synthetic calls. However, the distributions of vertical and horizontal error angles were not significantly different.

The distributions of 3-D jump error angles for trials with the 1.4+2.2 kHz, 1 kHz, 2 kHz and 1.4 kHz calls

are shown in Fig. 7. The 1.4+2.2 kHz and 1 kHz distributions were not significantly different from the 1.1+2.2 kHz distribution. Also, the average error angles were very similar for trials with these 3 calls. The average error angle for the 2 kHz trials was somewhat higher, but the 2 kHz and 1.1+2.2 kHz distributions were not significantly different. The 1.4 kHz trials had an even higher average error angle, and this distribution was significantly different from the 1.1+2.2 kHz distribution (MW U-test, $p=0.001$).

In most of the above trials the sound energy emitted by the loudspeaker was continually adjusted to provide a constant sound pressure level at the frog's position. However, in 9 trials with the 1.1+2.2 kHz and 1.4+2.2 kHz calls the sound output was kept constant. Hence, in these trials the sound pressure level perceived by the frog increased as it moved toward the loudspeaker. The average error angle of these 9 trials was 26°. The average error angle of the rest of the 1.1+2.2 kHz and 1.4+2.2 kHz trials, in which the sound pressure level was kept constant at the frog's position was 23°. The two distributions were not significantly different.

Discussion

The eardrum of the gray tree frog was most directional in a narrow frequency range between the two major frequency components of the advertisement call. A similar mismatch between the frequency of maximum eardrum directionality and the frequency contents of conspecific advertisement calls is also seen in several other species (Jørgensen et al. 1991; Jørgensen, unpublished). This observation is surprising because females use the advertisement call to localize conspecific males.

The gray tree frogs performed phonotaxis significantly more poorly with a sound containing energy in the frequency range of maximum eardrum directionality (the 1.4 kHz sound) than with a sound similar to the natural advertisement call (the 1.1 + 2.2 kHz sound). They also required more jumps to reach the loudspeaker in trials with the 1.4 kHz sound. Apparently, the frogs are not able to use the strong eardrum directionality near 1.4 kHz to improve their localization accuracy. The strong directionality is generated by sound reaching the inner surface of the eardrum via the lungs, the glottis and the Eustachian tubes (Jørgensen, unpublished). It has been suggested that this 'lung input' may affect sound localization (Narins et al. 1988). However, our results suggest that, although the lung input increases the eardrum directionality, it does not improve sound localization. Jørgensen (unpublished) showed that the eardrum directionality in the frequency range near 1.4 kHz is strongly dependent on the amount of air in the lungs. At 1.1 and 2.2 kHz this is not the case. Hence, a likely explanation of the frogs' poorer performance at 1.4 kHz is that the cues provided by the auditory periphery in this frequency range – although large – are also so variable that the localization ability actually deteriorates.

It could be argued that the poorer performance in locating the 1.4 kHz sound might have been caused by the lower sensitivity (and hence, motivation) of females responding to this frequency compared to frequencies of 1.0–1.1 and 2.0–2.2 kHz, which occur in the natural advertisement call. Indeed, two-choice experiments have shown that a call of 1.4 kHz is less attractive to *H. versicolor* females than 1.9–2.2 kHz calls; however, a call of 1.1 kHz is even less attractive (Gerhardt and Doherty 1988; see also Lombard and Straughan 1974 for an audiogram). Thus, because our females performed as well in response to the 1.0 kHz sound as to the 1.1 + 2.2 kHz sound, it is unlikely that the relative preferences revealed by choice experiments have any influence on the localization performance in phonotaxis experiments where only one stimulus is presented at a time.

One might also argue that the 1.1 + 2.2 kHz sound provides more directional information than the 1.4 kHz sound simply because it contains two frequency components. However, the frogs' performance with the 1 kHz sound, which also contains only one frequency component, was not poorer than that with the 1.1 + 2.2 kHz sound. A similar result was obtained with *H. cinerea* which localized a call with only one 0.9 kHz component as accurately as a call containing additional components at 2.7 and 3.0 kHz (Rheinlaender et al. 1979). In the present study the gray tree frogs performed as well when a 2.2 kHz tone was added to the 1.4 kHz carrier as they did with the 1.1 + 2.2 kHz sound.

The gray tree frogs localized the sound source in three-dimensional space with considerable accuracy. The mean 3-D jump error angle with the 'standard' advertisement call (1.1 + 2.2 kHz) was 23°. In comparison, *H. marmoratus* showed a mean 3-D jump error angle of 43° (Passmore et al. 1984). Hence, 3-D phonotaxis was considerably more accurate in the gray tree frogs.

Indeed, the mean 3-D error angle was similar to the mean 2-D error angle in *H. marmoratus* (22°). Passmore et al. (1984) included climb error angles in their analyses but also noted that the mean error angle was similar if climbs were excluded. We excluded climbs because their inclusion significantly changed the distributions of error angles. The proportion of climbs was somewhat higher in the experiments with the gray tree frogs (25–35%) than in the experiments with *H. marmoratus* (10%). However, the comparison is difficult because the loudspeaker was at the same height above the ground as the release platform in the experiments of Passmore et al. (1984). In addition, many of the recorded climbs in our experiments occurred in series of 2 to 3 climbs with only a few seconds in between, and such series may have been recorded as a single climb by Passmore et al. (1984).

Passmore et al. (1984) concluded from their experiments with *H. marmoratus* that the resolution of sound source elevation was poorer than the resolution in azimuth. In contrast, the vertical jump error angles shown by the gray tree frogs were smaller than the horizontal error angles for all 5 synthetic calls. We note, however, that because our grid consisted of vertical sticks, the possible jump directions were restricted in the horizontal plane but not in the vertical plane. It is therefore likely that the localization ability in azimuth is somewhat underestimated by the horizontal error angles reported here. On the other hand, the average horizontal error angle was only slightly higher than that found for *H. cinerea* in 2-D experiments (19° vs 16.1°, Rheinlaender et al. 1979). We conclude, that gray tree frogs can determine sound source elevation with similar or maybe even higher accuracy than they can determine the direction in azimuth.

H. cinerea (Rheinlaender et al. 1979) and *H. marmoratus* (Passmore et al. 1984) performed lateral head scanning movements during phonotactic approaches. This scanning behavior improved the localization accuracy in *H. cinerea*. Furthermore, Gerhardt and Rheinlaender (1982) suggested that lateral head scanning could provide cues for determination of sound source elevation. Our gray tree frogs performed seemingly independent whole-body orientation movements and head scanning, although observed sometimes during 2-D phonotactic approaches (Gerhardt, unpublished), either did not occur or was undetected in the present 3-D experiments. Hence, our results indicate that head scanning is unnecessary for accurate sound localization in three-dimensional space. Indeed, given the evidence that another tree frog (*H. gratiosa*) can discriminate between different angles of sound incidence in open loop experiments (Klump and Gerhardt 1989), even whole-body orientation movements may not be an absolute requirement for sound localization.

In most of our phonotaxis experiments the sound output from the loudspeaker was continually adjusted to provide a constant sound pressure level at the frog's position. Hence, no changes in sound pressure level with position, as would normally occur during a phonotactic approach, were available to the frogs. In some experi-

ments the sound output from the loudspeaker was kept constant, but the frogs did not perform any better under these conditions. Hence, changes in overall sound pressure level do not seem to be an important cue for sound localization.

The mechanisms behind the impressive ability of frogs to localize a sound source in three-dimensional space are not understood. Existing mathematical models of the frog auditory periphery do not simulate the measured eardrum directionality very well (Aertsen et al. 1986; Palmer and Pinder 1984; Jørgensen et al. 1991; Jørgensen, unpublished), and the models provide no mechanism for localization of elevated sound sources. The directional characteristics of the probable 'extratympanic' transmission of sound energy to the inner ear (Wilczynski et al. 1987) are unknown, and the processing of directional information in the nervous system is poorly understood. Hence, much more research is needed before a clear understanding of sound localization in frogs can be achieved.

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