

Acoustic Communication in the Grass Frog (*Rana t. temporaria* L.): Calls, Auditory Thresholds and Behavioral Responses

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Summary. 1. The grass frog's vocal repertoire includes mating and territorial calls, as well as release and warning calls. These may be distinguished by differences in spectral composition, in number of pulses, and in pulse repetition rate.

2. Recording of the responses of neurons in the torus semicircularis has revealed no effects of season or sexual state upon auditory ability (Figs. 3, 4, 5). The shape of the auditory thresholds vs. frequency curve is related to body size (Fig. 7).

3. Behavioral response thresholds to tones determined by the electrodermal response (i.e., the galvanic skin response; Figs. 8, 9) and the neural audiograms demonstrate that the grass frog is sensitive to its various types of calls.

4. The sensitivity of the electrodermal response differs in a characteristic way from the audiograms obtained at the neuronal level (Fig. 10). The largest differences occur at the mating call frequencies. The relevance of the call frequency spectrum in intraspecific communication among grass frogs is discussed.

A. Introduction

In recent years several studies of Central European anurans have been made regarding the types of calls produced and the effects of internal and external factors on calling (Schneider, 1966, 1967, 1973; Lörcher, 1969; Wahl, 1969; Heinzmann, 1970; Lörcher and Schneider, 1973). But the auditory ability of these animals has not yet been analyzed in this way. Volkmer (1959) used the optomotor reflex of *Rana temporaria* and *Rana esculenta* that had been treated with gamma-hexachlorocyclohexane to determine an auditory threshold curve in the range 40–5000 Hz. Vassilyew et al. (1969), in recording evoked potentials from the nucleus dorsalis and the superior olive, measured responses to sound at frequencies from 200 to 3000 Hz. The response characteristics of auditory neurons of *Bufo bufo* and *Rana ridibunda* have been described by Ewert and Borchers (1971) and by Bibikov (1971, 1974).

A close match between the spectra of conspecific calls and the auditory characteristics of the American species *Rana catesbeiana*, *Acris crepitans* and *Eleutherodactylus coqui* has been demonstrated by Frishkopf et al. (1968), Capranica et al. (1973) and Narins and Capranica (1976). Similar results were obtained by Loftus-Hills and Johnstone (1970) and Loftus-Hills (1971, 1973a, b) in a number of Australian species.

In our studies of intraspecific communication in Central European species, we have made electrophysiological measurements in the auditory system of the grass frog *Rana t. temporaria*, which is widely distributed in this region. Since only the mating call and the male release call of this species have been described (Schneider, 1973; Weber, 1975), we began by studying the extent of its repertoire of calls and their frequency composition. Neural audiograms (plots of threshold intensity vs. frequency of the sound stimulus) were obtained separately from females and from males both during the mating season and a few months after the spawning period, so that differences in auditory performance based on sexual or seasonal influences could be sought.

Auditory thresholds were compared with behavioral responses to acoustic stimuli. Since frogs seldom show motor reactions to pure tones and since it is difficult to train frogs to acoustic stimuli (Brzoska, unpublished), we decided to record the electrodermal response, namely the galvanic skin response (Veraguth, 1909; Fowles, 1974; Wilcott, 1967). Strother (1962) successfully used this method to measure responses of the bullfrog to tones over the entire audible range.

Finally, the auditory thresholds measured at the neuronal and behavioral levels were compared with the frequency composition of the various calls.

B. Materials and Methods

1. Recording and Frequency-Analysis of the Calls

The calls of the grass frog were recorded between the end of February and the end of March, 1976, unless otherwise mentioned, at ponds in the vicinity of Bonn; the apparatus comprised two microphones, a Beyer M 101N and a Sennheiser MKH 415T, and two portable tape recorders (Grundig Type TK 3200 and Uher Type 4200 Report Stereo IC) operated at a tape speed of 9.5 cm/s. The air temperature was 15–20°C and that of the water, 11–15°C. A sonagraph (Kay Electric Co., Type 7029A) was used to obtain frequency spectrograms of the calls. Their temporal properties were analyzed on a storage oscilloscope (Tektronix Type 564B).

2. Neurophysiological Experiments

Auditory thresholds were measured for 12 female and 5 male grass frogs during the mating season, and for 12 males a few months after the spawning period (i.e., in summer), by recording multi-unit activity of neurons in the torus semicircularis. In addition, we studied the neural sensitivity of this auditory center in a number of other frogs for which the behavioral-response threshold had been measured – 10 females and 9 males, tested during the mating season. The body temperature of the animals was 23°C in summer and 20°C during the mating season.

After immobilizing the frogs by injection of a 2% Succinyl-Asta® solution (0.15 ml per 100 g body weight) into the caudal dorsal lymph sac, we removed the skin of the head from the posterior margin of the eyes to the insertion of the neck musculature. A hole 2 mm in diameter was drilled in the skull over the midbrain, the meninges were cut open, and the recording electrode, a tungsten wire

insulated with glass and having a tip diameter of about 50 μm (impedance ca. 40 K Ohm), was inserted into the torus semicircularis. A few drops of liquid paraffin prevented drying. During the operation and the subsequent measurements the frog was covered with a layer of moist cellulose to maintain respiration through the skin.

The measured responses, representing the summed activity of many cells, were amplified (Tektronix Type 122 Low-Level Preamplifier), band-pass filtered (400–6000 Hz, Krohn-Hite Model 3323), and displayed on the storage oscilloscope.

The experiments were done in a sound-attenuating Faraday cage from which light was excluded. The stimulus used to measure threshold curves was a 30 ms tone presented once per second. The rise and fall times, each 5 ms, were controlled by a pulse generator (Hewlett Packard 8010A) which modulated the output of a sine-wave generator (Wavetek Model 136 VCG/VCA). The stimulus frequencies were monitored throughout the experiments by a frequency counter (Eldorado Model 1608), and varied in steps of 100 and 200 Hz. To determine the threshold at each frequency, we reduced the intensity of the tone by adjusting an amplifier (Kenwood Solid State Stereo Amplifier KA-2500) so that regularly recurring activity were just detectable on the oscilloscope screen. These measurements were repeated several times. The voltage input to the loudspeaker was used as a measure of intensity, and calibrated for the corresponding sound pressure level (re. 2×10^{-4} dyne/cm²) at each frequency. Sound pressure level was measured with a condenser microphone (Brüel & Kjaer Type 4133, with amplifier Brüel & Kjaer Type 2606) in the position occupied by the animal during the experiment.

3. Measurement of the Electrodermal Response

The threshold of the electrodermal response to acoustic stimuli was studied in 19 males and 19 females during the mating season. The results from ten of these females and nine of the males were compared with the subsequently measured neuronal auditory thresholds. A dose of 0.05 ml per 100 g body weight of the immobilizing drug (2% solution of Succinyl-Asta®) ensured that the frogs made no spontaneous movements.

For measurement of the skin potential response we used the same experimental setup described above. Two miniature alligator clips were used as electrodes, one being attached to the neck of the animal and the other to the back 1 cm anterior to the anus. The recorded signals were low-pass filtered (cut-off at 0.5 Hz). Initial experiments showed that a series of tones lasting 15 s was a suitable acoustical stimulus. The amplitude-modulated pulses of which this series was composed were 50 ms in duration, separated by intervals of 50 ms. Each stimulus was followed by a pause of at least one minute before the next was presented. Since the electrodermal response habituates rapidly during repetition of identical stimuli (cf. Buytendijk and Eerelman, 1930), the frequencies presented in successive series differed by at least 300 Hz. Sound pressure was varied in steps of 3–5 dB SPL. Changes in skin potential recorded up to 20 s following the stimulus onset were counted as responses.

C. The Calls of the Grass Frog

1. The Mating Call

The mating call is the most common of those observed. In giving this call the males may remain in one spot or swim slowly about. A single call is composed of ca. 20 brief, sharp pulses with a pulse repetition rate of ca. 29/s (Fig. 1 a, b). The intensity of subsequent pulses gradually increases to a maximum which is then maintained up to the last 1–3 pulses. The fundamental frequency band extends from 300 to 900 Hz, with a distinct maximum between 350 and 500 Hz. Often the call includes two higher frequency bands, the higher of the two having the greater amplitude (Figs. 1 a, 2 a). The frequencies in the first band are distributed in the range 1000–1400 Hz, with a maximum at 1200 Hz. Components with frequencies

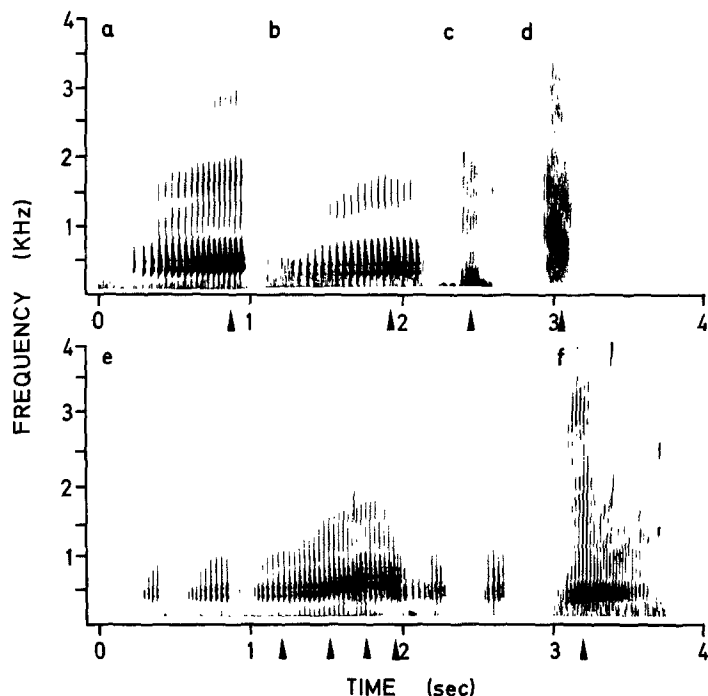


Fig. 1 a-f. Typical frequency spectrograms of grass-frog calls (effective filter bandwidth 150 Hz). **a** mating call with two higher frequency bands; **b** mating call with one band of overtones; **c** male's release call; **d** female's release call; **e** territorial call; **f** warning call. (The distance from the animal to the microphone in **a-d** was 10–30 cm; in **f** 1 m; in **e** 3 m.) The arrows mark the points in the calls at which amplitude spectrograms were made

between 1400 and 1900 Hz form the second band; its maximum is near 1600 Hz. However there are other males which produce mating calls that contain only one band with overtones, covering frequencies from 1200 to 1800 Hz, with maximum amplitude near 1400–1500 Hz (Figs. 1 b, 2 b).

2. The Territorial Call

If one male swims directly toward another calling frog, the latter gives one or more “territorial” calls. Should the intruder not withdraw, the two frogs fight until one is forced to retreat. Territorial calls may also be uttered between two mating calls, even though no intruder approaches the calling frog. When giving territorial calls the animals may stay in one spot, as with the mating call, or they may swim in short spurts within a radius of ca. 30 cm.

The territorial call is made up of several individual calls (Fig. 1 e); a series of 2–7 calls, each composed of 4–14 pulses, is followed by one with 23–48 pulses, which in turn is followed by further brief calls. The regularity with which this pattern of short calls preceeding and following a long call occurs suggest that the

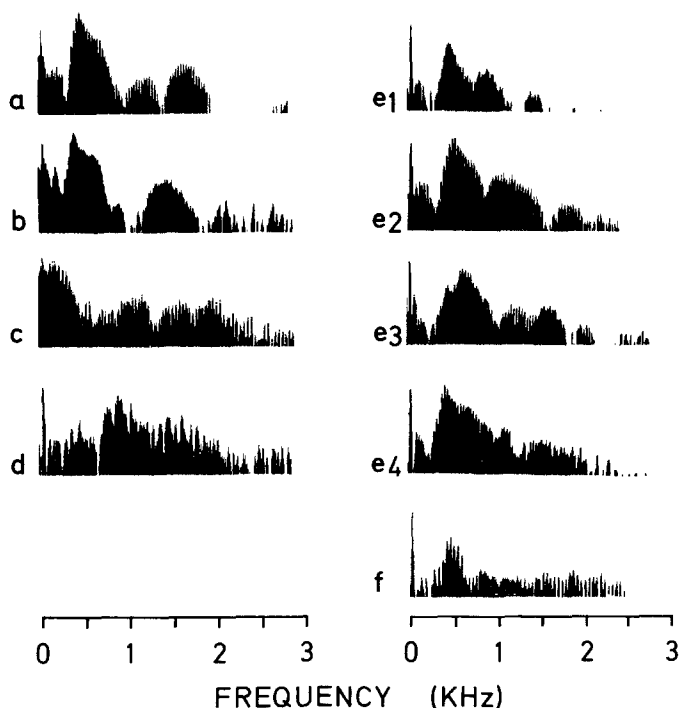


Fig. 2a–f. Typical amplitude spectrograms of grass-frog calls (effective filter bandwidth 22.5 Hz). **a** mating call with two higher frequency bands; **b** mating call with one band of overtones; **c** male's release call; **d** female's release call; **e_{1–4}** territorial call (analyzed at four different points); **f** warning call

entire sequence should be considered the territorial call. In the long call the pulse repetition rate is ca. 33/s, whereas that of the short calls varies between the repetition rate of the mating call and that of the long call. A striking aspect of the long call is the frequency modulation of both the fundamental and the overtones. The frequency spectra of the first pulses resemble those of mating calls (Fig. 2e₁). In the subsequent pulses the frequencies are shifted upward (Fig. 2e_{2,3}). The energy maximum of the fundamental then is at 600–650 Hz, with that of the first harmonic at 1100–1200 Hz. There is but a trace of a second harmonic at 1800–2000 Hz. Toward the end of the call the frequencies may be shifted down again (Fig. 2e₄).

3. The Release Call

If a male tries to clasp another male, then the latter utters release calls. A non receptive female also gives a series of release calls if she is clasped by a male.

Since the weak release calls are difficult to record in the natural environment, they were evoked artificially in the laboratory at temperatures of 12–15°C.

Release calls of males and females differ in spectral composition, in number of pulses, and in their interpulse intervals. The frequency spectrum of the male release calls shows amplitude maxima near 200–300 Hz, 1100–1300 Hz and 1700–2000 Hz (Figs. 1c, 2c). The low frequency peak is absent in the female release call (Figs. 1d, 2d). The male release call consists of ca. 5 pulses with a pulse repetition rate of 45/s. The number of the female's release call has a mean value of 18, which is considerably greater than in the male's call. The interpulse intervals of the first few and of the last few pulses sometimes vary between 6 and 32 ms, whereas the pulse repetition rate in the middle of the call is much higher, of the order of 220 pulses/s.

4. The Warning Call

If a grass frog is startled it dives away, sometimes giving a warning call as it does so. This call is quieter than the mating or territorial calls. The lowest frequency band extends not higher than 600 Hz (Figs. 1f, 2f). At the onset of the call the distribution of spectral energy shows a broad band extending to higher frequencies.

D. The Auditory Threshold of the Grass Frog

The shape of the tuning curves does not depend on the electrode position in the torus semicircularis. The results were reproducible throughout a recording session lasting several hours, at which time the animal began to recover (Fig. 3).

Many neurons of the torus semicircularis give on-responses to auditory stimuli. The latencies of the action potentials amount in some cases to less than 10 ms, though in the threshold region measured latency can be as much as 25 ms. With 700–1200 Hz tones at high intensity a second maximum of neuronal activity appears after 20–25 ms.

About half of the animals examined responded to tones in the range 100–3600 Hz; one male responded even at 4600 Hz. Thresholds were lowest for tones between 400 and 1800 Hz, the best frequencies being between 700 and 1400 Hz. One female, conspicuous by her unusually large tympanum, had a best frequency of 400 Hz. The greatest sensitivity was measured in a female stimulated at 700 Hz; in this case, a sound pressure level of 29 dB elicited a response.

Differences between the average auditory thresholds of summer frogs (Fig. 4) and those studied during the mating season (Fig. 5) are small. The two curves diverge at 400 Hz and at 1100 Hz. The high average threshold (70 dB) at 400 Hz in the audiograms obtained in summer is misleading, however, in that 75% of the males had thresholds at 47–53 dB. This range is consistent with that of the data obtained at this frequency during the mating season. From 900–1300 Hz the two curves differ, with a maximum difference of 10 dB at 1100 Hz. We do not consider this to be an evidence of a dependence of auditory performance upon season of the year.

No significant differences between the audiograms of the males studied during the mating season (Fig. 5) and those of females (Fig. 6) could be demonstrated.

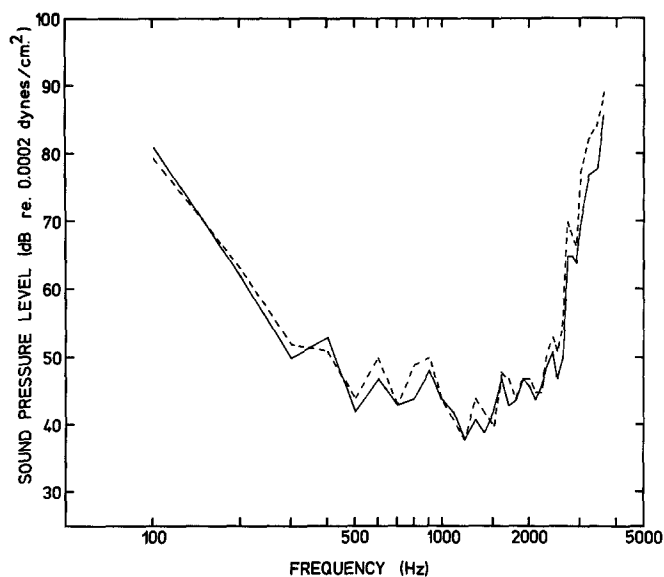


Fig. 3. Typical audiogram of a single male *Rana temporaria*. Thresholds were determined twice: — 1st measurement; ---- 2nd measurement (5 h later, electrode position 300 μ m anterior to the first position)

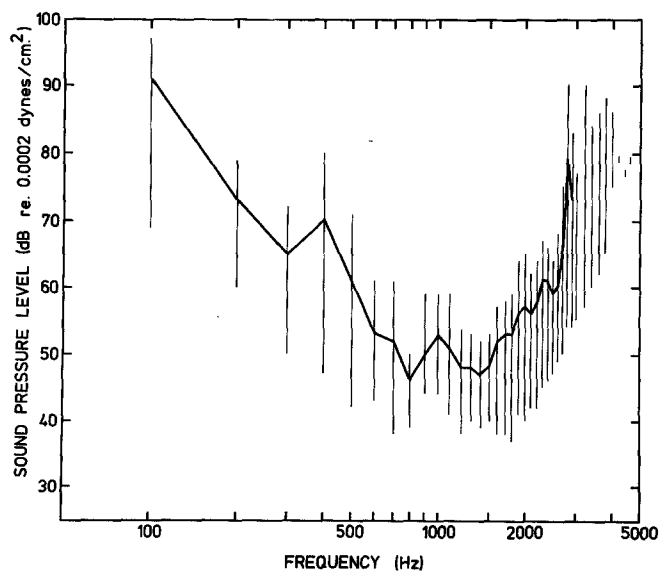


Fig. 4. Audiogram of male *Rana temporaria*, summer frogs ($n = 12$); the mean threshold intensities are joined by a line, and the ranges of variation are indicated by vertical bars

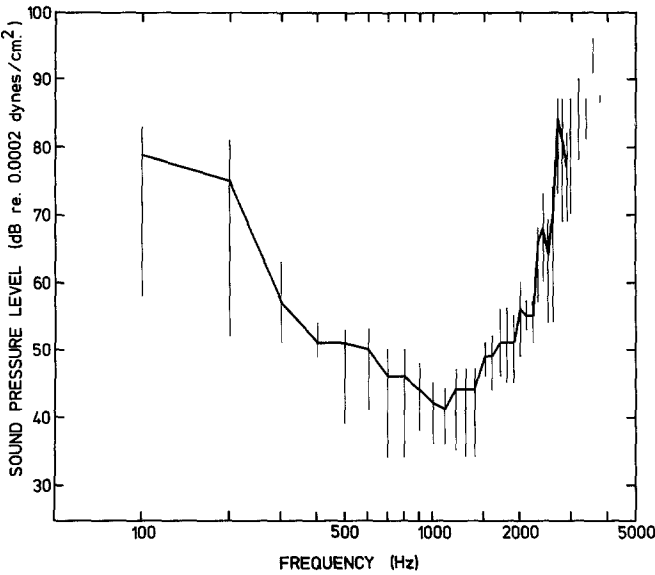


Fig. 5. Audiogram of male *Rana temporaria*, ($n = 5$) measured during the mating season

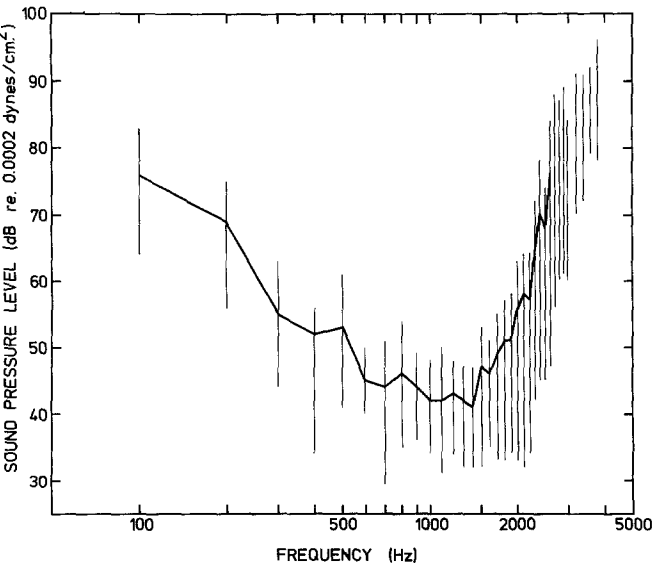


Fig. 6. Audiogram of female *Rana temporaria* ($n = 12$)

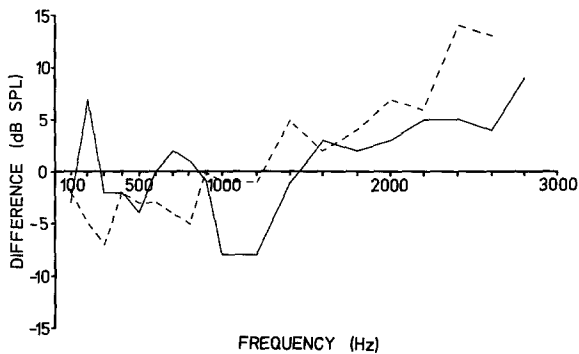


Fig. 7. Effect of body size upon auditory threshold in the grass-frog, expressed as the ratio of the threshold sound pressure levels in larger-than-average and smaller-than-average frogs; — male frogs, - - - female frogs

Whereas neither season nor sex have an appreciable effect upon hearing, sensitivity to sound is correlated with body size. To illustrate this relationship we have averaged the audiograms of frogs larger than the average¹ and of those smaller than the average (treating males and females separately), and calculated the differences between these two average curves. This difference (in dB) between sound pressure levels (in dB SPL) corresponds to a ratio of the mean sound pressures. The results of these calculations are presented in Figure 7.

As the frequency is raised above 1000 Hz the curves take on increasingly positive values. In the curve for the females this tendency is pronounced at frequencies from 100 Hz upward. That is, small frogs are more sensitive to high-frequency sounds than large frogs, and the difference is greater the higher the frequency.

E. Electrodermal Response

The skin potential responses had durations of 5–15 s and appeared with latencies ranging from 2 to more than 20 s. Responses to stimuli at a given frequency and intensity differed in both amplitude and shape. Sometimes stimuli which once had elicited a clear response were ineffective in a later presentation. Three of the males studied did not respond to sound; in one female the skin response adapted so rapidly that it was impossible to obtain a threshold measurement.

With most of the animals, the frequency range in which a skin response could be elicited extended from 100 to 2200 Hz. However, some frogs failed to respond to frequencies below 200 Hz and above 2000 Hz at the intensities available. The averages and ranges presented in Figures 8 and 9 include only data for animals responding over the entire frequency range 100–2200 Hz. The considerable variance in the data reflects the fact that the skin response, as a general autonomic reflex, is a much higher-level reaction—a form of behavior. Differences in

¹ The average size of males was 7.2 cm, and the average size of females was 7.7 cm

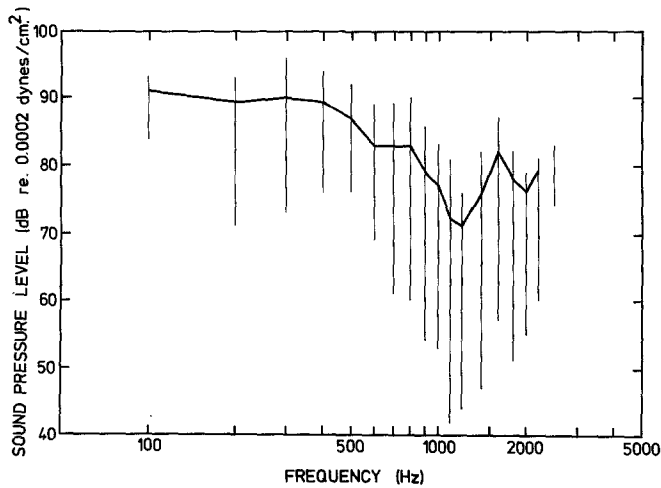


Fig. 8. Threshold curve of the skin potential response to tones in male *Rana temporaria* ($n = 12$); the solid line indicates the average, and the vertical bars indicate the ranges of variation

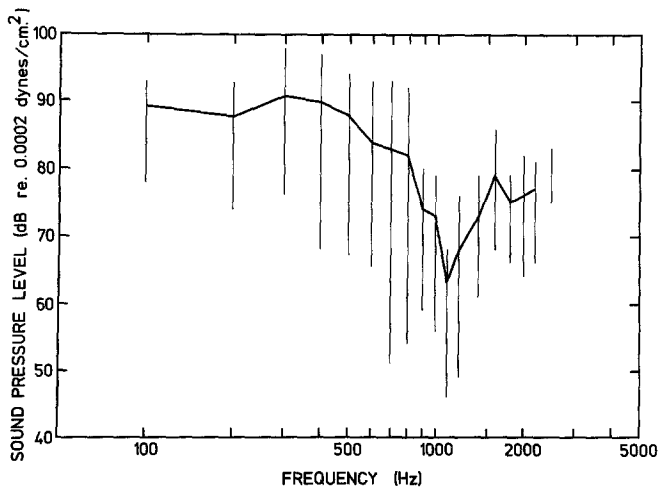


Fig. 9. Threshold curve of the skin potential response to tones in female *Rana temporaria* ($n = 17$)

threshold are determined not only by individual differences in auditory ability, but also by the general state of the frog, by its readiness to respond.

The threshold curves of males and females do not differ significantly from one another. Frequencies up to 900 Hz elicit responses only at high intensities, as do the frequencies 1400 and 1600 Hz. But responses to 1100 and 1200 Hz tones appear at lower intensities. There is a slight reduction in threshold at frequencies above 1600 Hz (1800 and 2000 Hz). The lowest effective intensity in a male was 42 dB SPL at 1100 Hz; at the same frequency a female responded to intensities as low as 46 dB SPL.

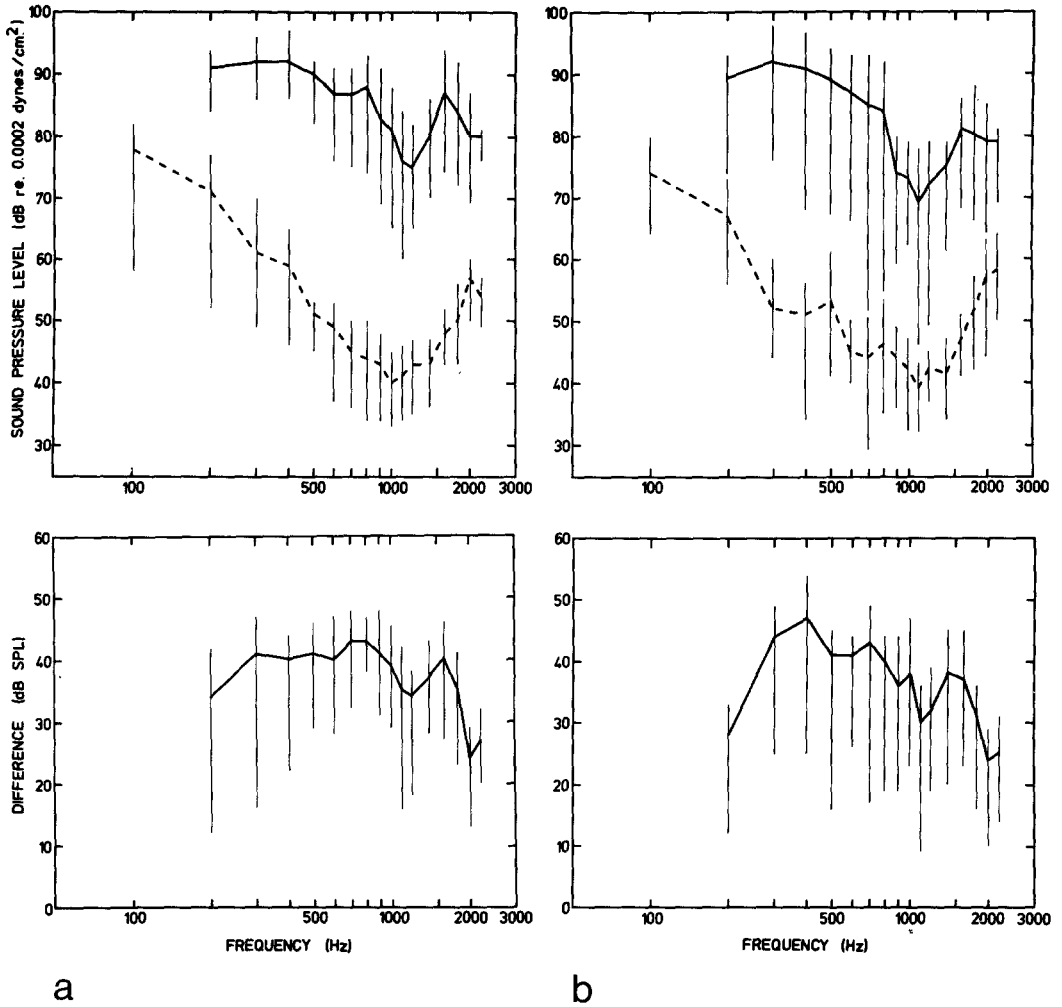


Fig. 10 a and b. Comparison of audiograms with the threshold curves for the skin potential response in male (a; $n = 9$) and female (b; $n = 10$) frogs. Above: — threshold curves of the skin response, ---- neuronal threshold curves; below: difference between the skin-response and neuronal thresholds

F. Comparison of the Electrodermal Response and the Neuronal Thresholds

The differences between the thresholds of the skin response and those measured at the neuronal level were computed individually for each animal. The extreme values of the individual difference curves extend over a range of at least 14 dB and up to 38 dB. Figure 10 shows the required average increase in sound pressure level, above the neuronal threshold, in order that a skin response be elicited.

The smallest difference was found with a female stimulated at 1100 Hz. The

threshold of the skin response in this case was just 9 dB above the neuronal threshold. The largest difference was also obtained with a female, 54 dB at 400 Hz.

The threshold curves measured at the skin and at the neuronal level have different shapes; the differences are more pronounced at certain frequencies than at others. The thresholds for the skin response to 300–1000 Hz tones exceed the neuronal threshold by a greater amount than do those to tones at frequencies below 300 Hz and above 1600 Hz. At frequencies of 1100 and 1200 Hz, relatively low intensities suffice to elicit both types of response.

G. Discussion

Our studies of auditory thresholds in the torus semicircularis imply that the grass frog's auditory system is sensitive to all of the calls in its vocal repertoire.

It is evident that tones at the frequencies contained in the mating call must be presented at relatively high intensities to elicit skin responses. But at frequencies, which are more strongly emphasized in the territorial, release and warning calls than in the mating call, the thresholds for the skin response are only slightly higher than those for neuronal responses. This finding suggests that the different spectra in the various types of call are significant in intraspecific communication. Capranica (1965) showed that tones at frequencies near 500 Hz—those with the greatest amplitude in the territorial and warning calls of *Rana catesbeiana*—inhibit the evoked vocal response of frogs of this species. A threshold curve measured by Strother (1962), for the skin response of a male bullfrog, had a minimum at 500 Hz, whereas in the two frequency ranges effective in eliciting the mating call threshold was relatively high. The shapes of threshold curves of this kind depart considerably from those measured electrophysiologically at the torus semicircularis (personal observation). The differences between the thresholds of the skin potential response and the auditory neurons, found in both the bullfrog and the grass frog, imply that the skin response appears as a reaction to stimuli that cause the animals to flee or prepare for flight. A similar inference has been drawn by Kohlrausch and Schilf (1922) and Buytendijk and Eerelman (1930), who used stimuli of various modalities to produce the skin response in anurans.

The short latency and phasic nature of the neuronal response is suitable for transduction of signals composed of brief pulses, as are the calls of grass frogs (cf. Schneider's (1973) description of the mating call). Thus the pulse pattern is likely to be an information parameter at least as important as the frequency spectrum of a call.

Our findings, that the electrode position does not influence the shape of the tuning curves, coincides well with Potter's results (1965). He recorded from single units in the various nuclei of the torus semicircularis of the bullfrog and concluded that there was no tonotopic organization in the midbrain.

Loftus-Hills (1973b) noted an inter-specific correlation between the auditory thresholds of different Australian anurans and the size of their tympanum and their head width.

Intra-specific correlations of body size (or the size of the middle-ear structures) with anuran hearing performance have previously been considered

negligible or non-existent (Frishkopf et al., 1968). Our experiments, however, show that audition in the grass frog is decidedly dependent upon body size. Because the size of structures in the middle ear is closely correlated with body size, this effect probably arises from size differences within the sound-conducting apparatus. Presumably there is no biological significance to this dependence, for the differences in sensitivity of different-sized animals tend to be slight at those frequencies which play a role in intraspecific communication.

Finally, our comparison of the neuronal audiogram with those for the "higher-level" skin responses, showing characteristic frequency-dependent differences, suggest further investigation of the intervening neural processing of these auditory signals.

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