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Directional hearing in the grass frog (*Rana temporaria* L.): I. Mechanical vibrations of tympanic membrane

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The vibration characteristics (amplitude and phase as a function of frequency) of the tympanic membrane in the grass frog were measured using a laser-doppler velocity meter. It was tested to what extent the frog's acoustic system behaves as a pressure gradient receiver. This might clarify how the frog localizes sound. Using a closed sound system the membrane was stimulated at three different entrances: in front of the membrane, at the contralateral ear and from inside the mouth. A combination of these can describe the motion of the membrane under free field conditions. It is found that the sound entrance from inside the mouth will give almost identical vibration characteristics as stimulation in front of the membrane. This can yield a perfect gradient receiver mechanism, when the frog opens its mouth. It is doubted however whether the frog in nature needs to open its mouth for localization of sound. With mouth closed the effectiveness of the gradient receiver will be determined by the transmission characteristics of sound across the tissues of the mouth. The entrance of sound via the contralateral ear is only effective at frequencies between 800 and 1600 Hz. At those frequencies crosstalk between the membranes is however not more than -4 to -8 dB. This is subject to changes in the acoustic properties of the mouth cavity and can possibly be altered by the frog in free nature.

directional hearing, pressure gradient receiver, vibration of tympanic membrane, frog ear

Introduction

Recent investigations, both neurophysiological and behavioral, gave good evidence for the directional hearing capabilities of the frog [5,6,8,11]. The mechanism of directional hearing is still a matter of discussion. Classical cues such as interaural physical differences in intensity and time are not likely to be used due to the small interaural distance (1–2 cm), whereas the sensitivity of the frog's auditory system is limited in general to frequencies below 3 kHz, which correspond to wavelengths of more than 10 cm. Localization based on interaural intensity differences resulting from acoustical shadowing effects of the head, generally requires sound wavelengths which are at most ten times the dimensions of the head, but

preferably much shorter. Differences in time of arrival of the sound waves at each tympanic membrane are also not likely to be used as direct cues. For instance, the capability of phase locking of neural firing with stimulus seems to cease above 350 Hz at an ambient temperature around 15°C as found in torus semicircularis of the grass frog [9], indicating that the neural processing of time information is rather poor.

Several investigators [7,11], therefore proposed the idea that the frog's auditory system is not acting as a usual pressure receiver but instead or only for a certain frequency band [6] as a pressure gradient receiver, which is sensitive to direction in itself. Such a gradient receiver requires spatially separated sound pathways to both sides of the membrane. The membrane will vibrate accordingly to the differences in intensity and phase across the membrane. In the frog, the inside of the membrane is accessible for sound via the short and generally open Eustachian tube between tympana

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num and mouth cavity. Several possibilities exist for sound to enter into the mouth. Most obvious is the opening of the mouth, but this is not observed to be necessary during localization behavioral experiments. When closed, we can think of an acoustic coupling of both tympanic membranes via the Eustachian tubes and mouth cavity. The coupled tympana will act as a special type of gradient receiver, provided the coupling is sufficiently tight. Another possibility is the transmission of sound through the mouth itself or the nares. The tissues of the mouth are probably quite transparent for sound of low frequencies [1].

Whether a gradient receiver mechanism is feasible and how it is used by the frog needs a more profound investigation. In the present paper the problem is tackled by studying the vibrations of the tympanic membrane under several conditions of stimulation. The results obtained will help to gain insight into the function of the frog's auditory system. Several investigators have already contributed in different ways: Chung et al. [3,4] in *free field* conditions observed the displacement of the tympanic membrane of *Rana temporaria* using laser speckle interferometry. The membrane was virtually unresponsive when the mouth was kept open. When the mouth was closed, the membrane became responsive for frequencies of between 1000 and 4000 Hz. They found a resonance in the membrane displacement around 1750 Hz. At this resonance they also measured the transmission from one ear to the other showing an attenuation of only 6 dB. This indicates the possible existence of a weak gradient receiver mechanism.

In contrast with those findings, Moffat and Capranica [10] using laser scattering spectroscopy concluded for *Bufo americanus* and *Hyla cinerea* an essential low pass characteristic for tympanic membrane displacement. At frequencies between 250 and 1250 Hz they found, using a *closed sound system* and sound pressure of 94 dB, a relatively constant displacement peak amplitude of 50–100 nm at the centre of the membrane with stimulation at the same (ipsilateral) ear. This appears to be nearly an order of magnitude larger than the maximal value of 16 nm (same pressure and 1800 Hz) which Chung et al. arrived at. In addition Moffat and Capranica could not find any appreciable effect of an open or closed mouth on the ipsi-

lateral tympanic membrane.

Faced with these seemingly conflicting findings it was decided to investigate in more detail the mechanical and acoustical properties of the auditory periphery in *Rana temporaria*. For that purpose we measured tympanic membrane displacement by means of a laser-doppler velocity meter as described by Buunen and Vlaming [2]. For acoustical stimulation a closed sound system is applied. By such a closed sound system either the ipsilateral, the contralateral tympanic membrane (with respect to the recording site of the vibrations) or the inside of the closed mouth can be stimulated independently. The results obtained for those entrances will be used to construct an analog model which can describe the acoustical and mechanical properties of the auditory system including directional sensitivity. This model will be presented in another paper, together with additional free field acoustical experiments [1].

Materials and Methods

Four adult grass frogs (*Rana temporaria* L.) from Ireland were anaesthetised using a 0.05% solution of MS-222. Temperature was kept near 18°C, ensuring that skin respiration was sufficient to maintain good oxygen supply to the animal. After disappearance of the cornea reflex the skull

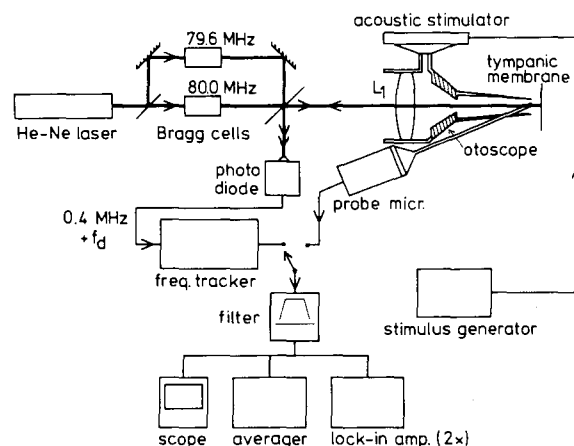


Fig. 1. Schematic diagram of the experimental setup. Position of lens L1 is adjustable over 25 mm in order to focus the laser beam on the tympanic membrane. The membrane is illuminated by a built-in lamp and light-conductor.

was fixed, and stimulating and recording equipment were attached.

The displacement of the tympanic membrane was measured by means of a laser doppler velocity meter (LDV). The instrument is described in detail elsewhere [2]. A brief description including some improvements will be given here. The basic principle is as follows: light when scattered or reflected by an object moving at a velocity v , will undergo a (doppler) shift f_d in frequency equal to $2v/\lambda$ where λ is the wavelength of light. Measurement of f_d will yield the vibration velocity of the object. In the set-up of Fig. 1, coherent light from a HeNe laser is split into a target beam and a reference beam. Each beam will pass through a Bragg cell that shifts the frequency of light by 80.0 MHz for the target beam and 79.6 MHz for the reference beam. The target beam is thereupon focussed by lens L1 on the object. At the surface of the photodiode, laser-light scattered by the object will interfere with the reference beam. When the object is at rest the photodiode will give a beat frequency of 0.4 MHz. For a moving object this output becomes $0.4 \text{ MHz} + f_d$, corresponding to a frequency modulated signal with modulation f_d . This signal is demodulated by a frequency tracker and its output is directly proportional to the velocity v of the object. Displacement is calculated by integration. For an object which vibrates at frequency f_s and displacement amplitude A_d , the relation between velocity A_v and A_d is simply $A_v = 2\pi f_s A_d$. In this paper all results are converted to displacement although velocity is actually measured.

For acoustic stimulation, closed sound systems were applied. In order to stimulate and measure the displacement simultaneously at the same ear, an adapted otoscope was used (Fig. 1). This stimulator permitted focussing of the laser beam on the tympanic membrane under visual inspection. Sound was applied by a Beyer DT 48 headphone and measured by a calibrated probe microphone (Brüel and Kjaer) in front of the membrane. The connection between otoscope and skin was sealed by silicone grease and was measured to be soundproof within 40 dB. For the measurement and stimulation of sound inside the mouth cavity, a calibrated probe microphone and probe sound stimulator were inserted. Both probes had a length of 30 mm and an inside diameter of 2 mm. They

were connected to a 1/2-inch Brüel and Kjaer microphone and Beyer headphone, respectively. The mouth was made soundproof within 40 dB by grease. The insertion of the probes had some influence on the acoustics of the mouth cavity. Its effect was estimated in the contralateral experiments.

The output of the laser-doppler velocity meter and sound-probes was analyzed by means of two lock-in amplifiers (PAR 124A and 128A) arranged in quadrature. For the velocity measurements the time constant of the lock-in amplifiers was set to correspond to a noise bandwidth of 0.01 Hz. Routinely 25 different pure tones were applied with frequency between 100 and 4000 Hz at a sound intensity of 80 dB SPL. The experiment was fully controlled by a PDP LAB 8 computer. Results are presented by amplitude and phase spectra and are corrected for the amplitude and phase characteristics of the probe microphones. Results are thus relative to the sound pressure (amplitude + phase) at the tip of the probe microphone. In some experiments acoustic clicks were used at a rate of 50/s. Click intensity is about 90 dB peak equivalent SPL. In order to reduce noise, 5000 responses were averaged by a PAR 4202 averager. Results were fed into the computer and spectra were computed with correction (amplitude and phase) for sound stimulus and probe-microphone. Both pure tone and click methods gave identical results within 2 dB and 10° for frequencies between 150 and 3000 Hz. Above 3000 Hz the click responses became corrupted by noise.

Results

The tympanic membrane was stimulated in three different ways: (1) ipsilateral, (2) contralateral, and (3) from inside the closed mouth cavity.

The vibration characteristics of the tympanic membrane for all three cases will be presented here.

Ipsilateral stimulation

In Fig. 2 displacement amplitude and phase of the centre of the tympanic membrane are shown as a function of frequency for four animals with mouth closed. Sound level is 80 dB SPL. All curves essentially show a low-pass shape with a roll-off

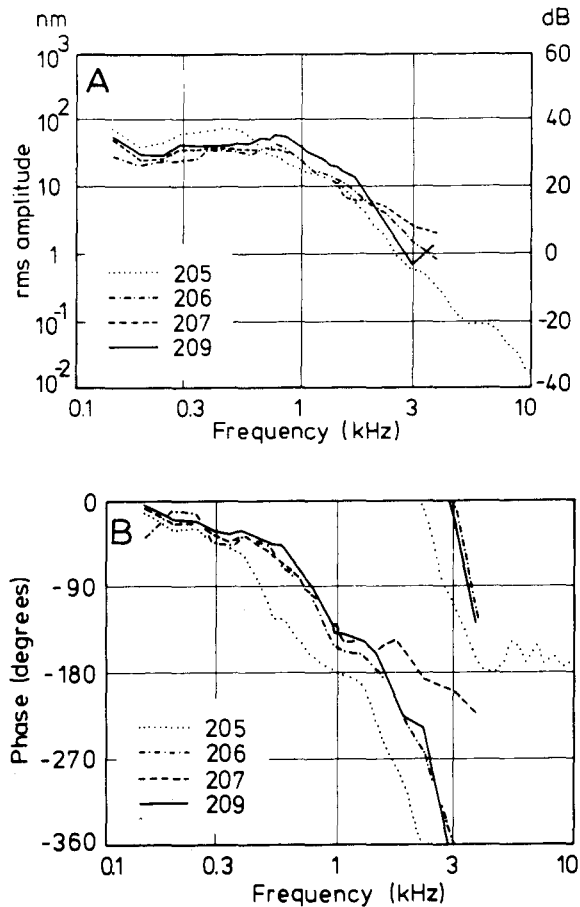


Fig. 2. Displacement amplitude (A) and phase (B) of the centre of the tympanum as a function of frequency. Sound level is 80 dB SPL. Mouth is kept closed.

above 800 Hz between 12 and 18 dB/octave. In the low frequency region amplitude values are between 25 and 60 nm. Phase lag (relative to acoustic stimulus before the tympanic membrane) increases from 0 to 540°. The frequency at 90° lag corresponds well with an amplitude resonance. The rather large increase of phase lag, indicates that the motion of the centre of the membrane above some 1–1.5 kHz, cannot be described by a simple mass-compliance mechanical model. This is caused most probably by the mechanical loading of the columella complex. The effect of opening the mouth is shown in Fig. 3. Differences between open and closed mouth in general amount to values between +5 and -5 dB. Phase characteris-

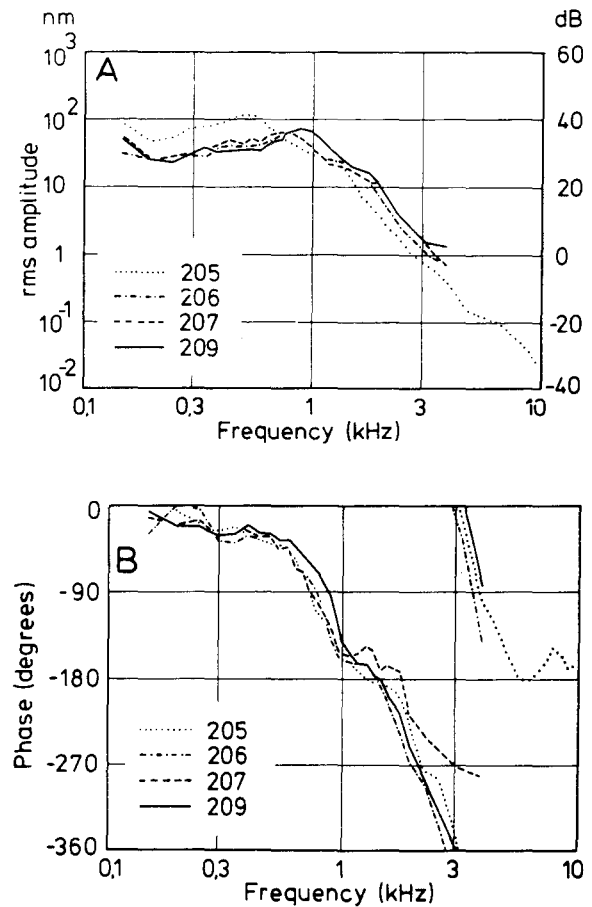


Fig. 3. Displacement amplitude (A) and phase (B) of the centre of tympanum. Sound level is 80 dB SPL. Mouth is kept open.

tics for the open mouth in general differ less than 40° for frequencies below 2000 Hz. From those marginal changes it can be concluded that the acoustics of the mouth (volume) are of little influence for the ipsilateral displacement characteristics.

When discussing the mechanics and acoustics of the auditory periphery of the grass frog it is of importance to check the linearity over the normal range of operation. This is verified by continuation of the above ipsilateral measurements for three frequencies at several sound intensities. Fig. 4 gives the measured relation between displacement and sound intensity between 35 and 100 dB SPL for animal 205 with mouth closed. This relation

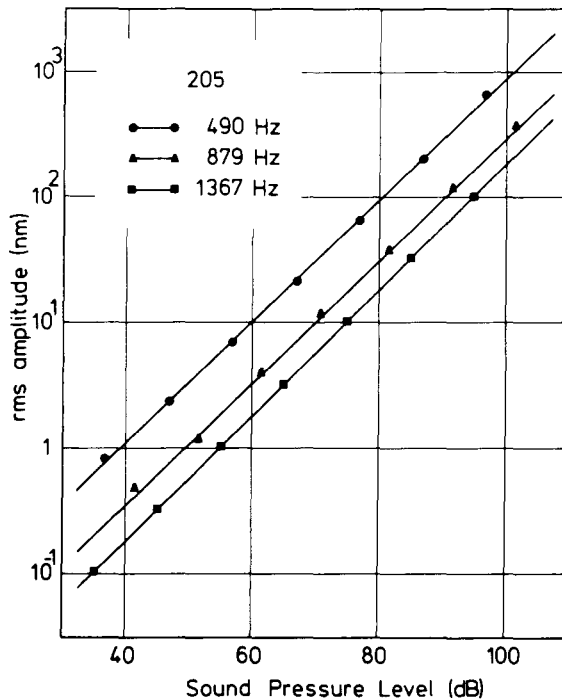


Fig. 4. Displacement of the centre of tympanum for one animal at several frequencies as function of sound intensity.

proves to be linear within 2 dB, which corresponds with the errors of measurement. Results are similar for the other animals.

It is also of interest to know whether the vibration of the center of the membrane is representative for the whole membrane. For a homogeneous membrane at frequencies below the excitation of higher order modes, vibration will gradually decrease towards the suspending ring. Phase characteristics will be identical over the membrane. Excitation of higher order vibration modes can only be expected when they are symmetrical. The second symmetrical mode will be excited at frequencies between two and three times the fundamental resonance frequency (about 800 Hz), but will couple rather inefficiently to the sound waves [7]. However, the frog's membrane is loaded by the columella structures. These structures are attached to the membrane from the upper part towards the centre. These will give a non-symmetrical load, facilitating the excitation of non-symmetrical vibration modes. Consequently, at some frequen-

cies the membrane may vibrate non-uniformly, which will show up as differences in amplitude and phase over the membrane. The actual extent of this is measured for three animals at nine different locations as presented in Fig. 5. For the focusing of the laser beam at different locations, no significant adjustments which might influence the results were necessary. From the results it can be seen that amplitude and phase are similar over the membrane for frequencies below 1000–1400 Hz. At higher frequencies deviations become more apparent. At several locations, differences in phase of more than 180° with respect to the centre are seen (locations 4, 5, 6, 8 and 9). Amplitude responses sometimes show dips (locations 3, 4 and 6). In general, locations along the columella (locations 1, 2, 3 and also 7) show phase lags increasing to more than 360° . At locations close to the tympanic ring (locations 5, 6 and 9) phase lag remains below 180° . From these data it can be concluded that for frequencies below 1000–1400 Hz, tympanic vibration is quite uniform.

Vibration of the centre thus will be representative for the whole membrane. This means that adequate models should be able to describe the curves found till about 1400 Hz. At higher frequencies discrepancies may turn up. These discrepancies could possibly be accounted for when the mechanics of the columella complex and its interaction with the tympanic membrane are also incorporated into the model.

Contralateral stimulation

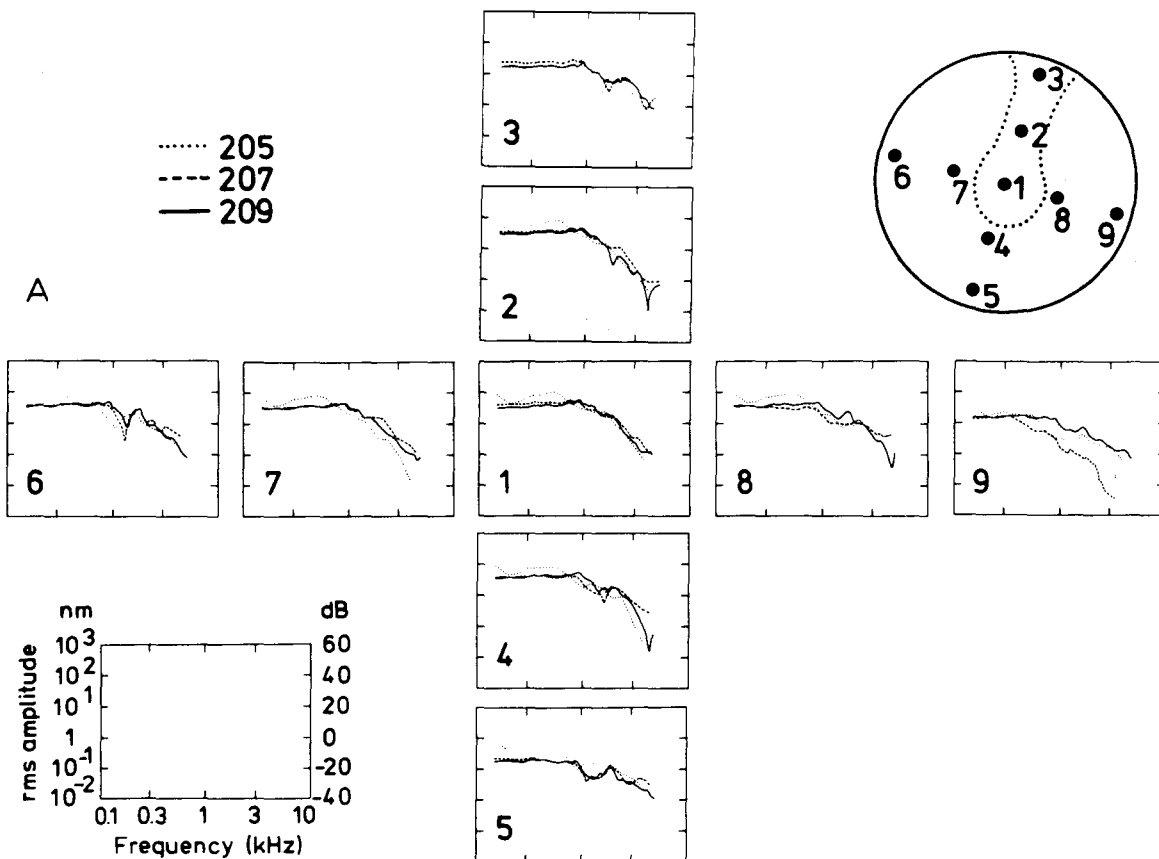
In Fig. 6 displacement amplitude and phase responses are shown for four animals while stimulating at the contralateral ear, by means of the otoscope stimulator system which acts now only as an acoustic stimulator. The laser beam is focussed at the open ipsilateral tympanic membrane by a simple lens. Sound reaches the inside of the membrane via the Eustachian tubes and mouth cavity. Except for one animal all cases show a typical bandpass character, with a maximum response of 20 nm around 900 Hz. This resonance is at the same frequency as the cut-off point from ipsilateral stimulation studies shown in Figs. 2 and 3; the response is about 6 dB down. A second maximum or plateau is found between 1600 and 2000 Hz. Its amplitude is about 10–20 dB less than the

first maximum. The low-frequency slope amounts from 12 to 18 dB/octave, and the high frequency slope amounts from 18 to 30 dB/octave. The response of animal 205 is very much different from the other ones. Its amplitude is reduced by 20–40 dB. This result is most likely caused by an obstruction in the sound pathway between the ears, probably the contralateral Eustachian tube. This type of result was also found for the other animals when the mouth was opened (results not shown). Opening of the mouth will prohibit sound reaching the other membrane.

Fig. 7A shows the ratio of tympanic membrane displacement between contralateral and ipsilateral stimulation (cf. Figs. 6A and 2A). When only one membrane is stimulated, the contralateral membrane will vibrate at a level given by this figure, relative to the motion of the membrane stimulated.

This coupling of vibration is caused by the internal acoustic pathway. From this figure it is seen that coupling is maximal around 1100 Hz with a value between -4 and -8 dB. At higher frequencies till 2500 Hz the coupling is still considerable but varies between -4 and -20 dB. Fig. 7B shows the difference in phase between contralateral and ipsilateral stimulation (cf. Figs. 6B and 2B). It is seen that contributions to tympanic vibration of contralateral and ipsilateral stimulation are opposite in direction (difference = -180°) for frequencies around 1000 Hz. This coincides quite well with the frequency region of maximal coupling (Fig. 7A) and to the resonance frequencies found in Figs. 6 and 2.

When stimulating one ear, sound will be conducted via the mouth to the contralateral ear. This results in a build up of sound pressure inside the



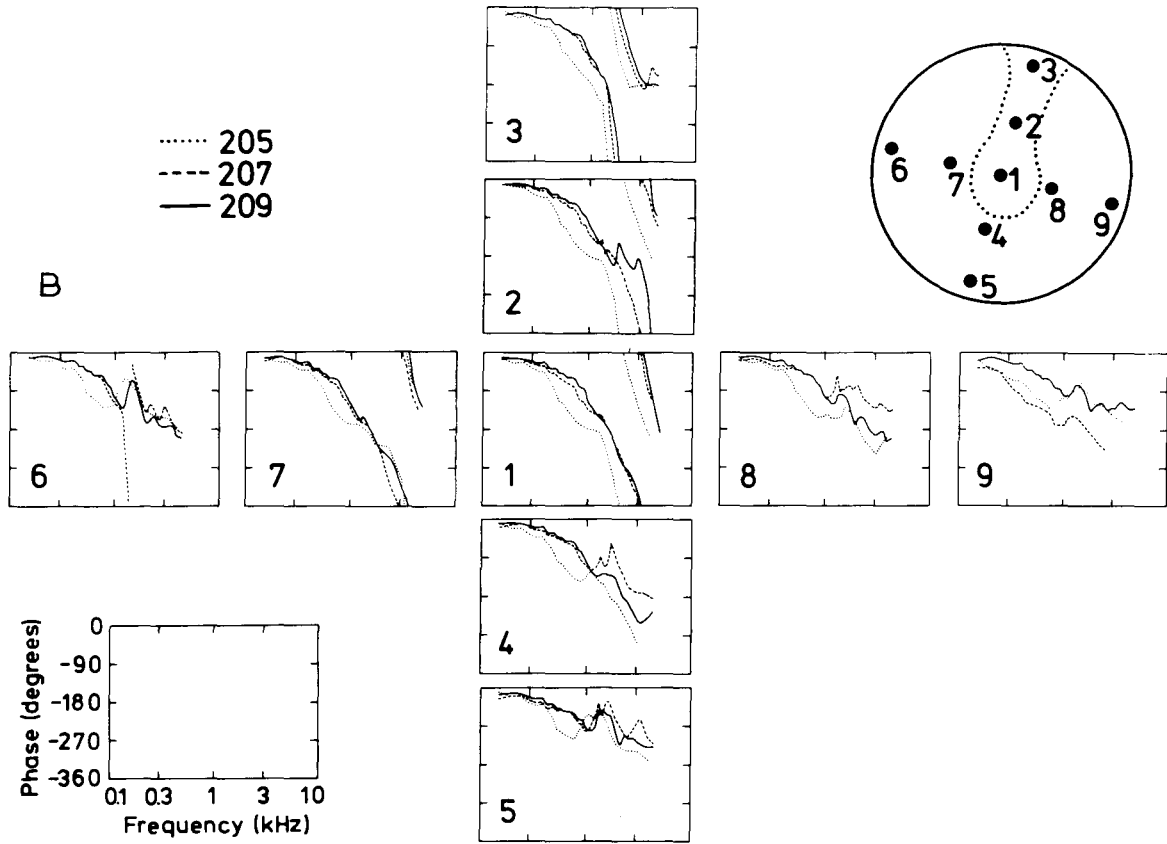


Fig. 5. Displacement amplitude (A) and phase (B) at 80 dB SPL for three animals at 9 different locations on the tympanum. Stimulation is at the ipsilateral ear using a closed sound stimulator. Acoustic clicks are used for animals 207 and 209 and pure sinusoids for animal 205. Location 9 is at the posterior side of the membrane.

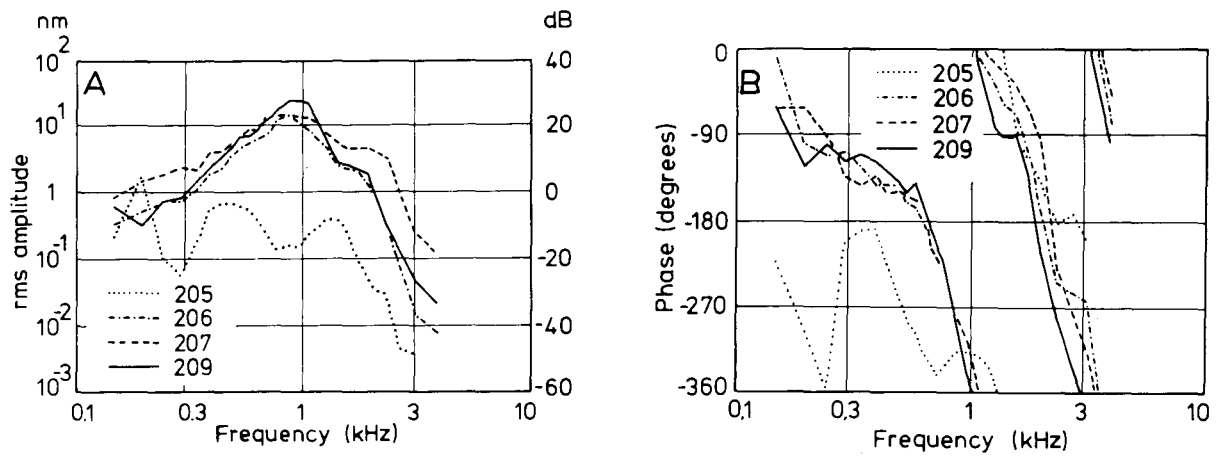


Fig. 6. Displacement amplitude (A) and phase (B) of the centre of tympanum for stimulation at the contralateral ear. Mouth is closed and sound intensity is 80 dB SPL.

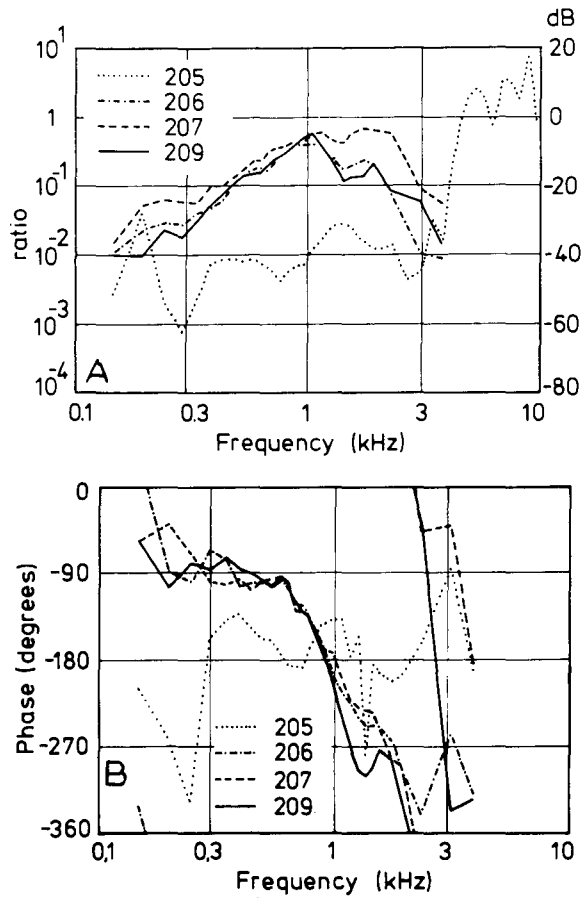


Fig. 7. Ratio of displacement amplitude (A) for ipsilateral and contralateral stimulation (division of Fig. 2A by Fig. 6A) and (B) difference in phase (subtraction of Fig. 2B from Fig. 6B).

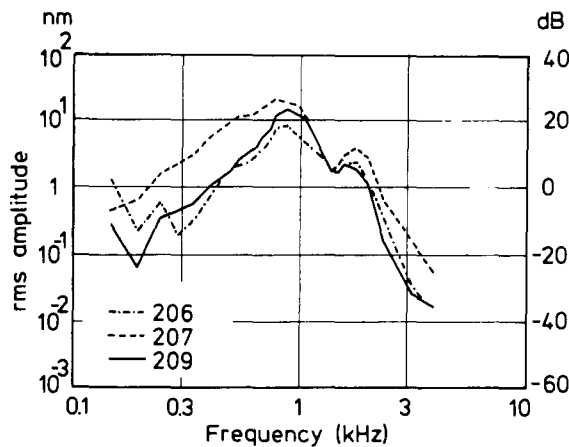


Fig. 8. Displacement amplitude of the centre of the membrane as in Fig. 6, now with probe microphone and probe stimulator inserted into the closed mouth; phase is similar to Fig. 6B within 20° .

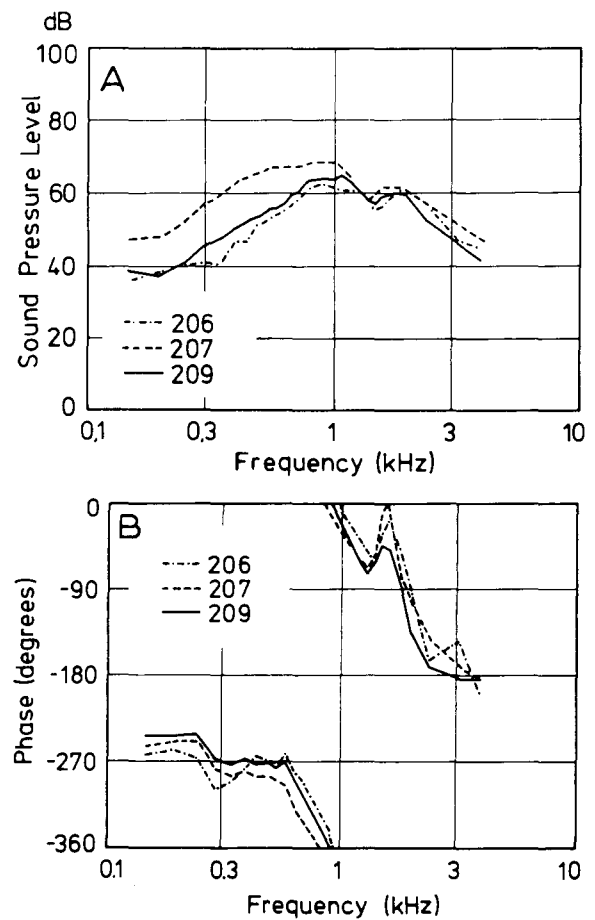


Fig. 9. Amplitude (A) and phase (B) of sound pressure inside mouth while stimulating one ear at 80 dB SPL.

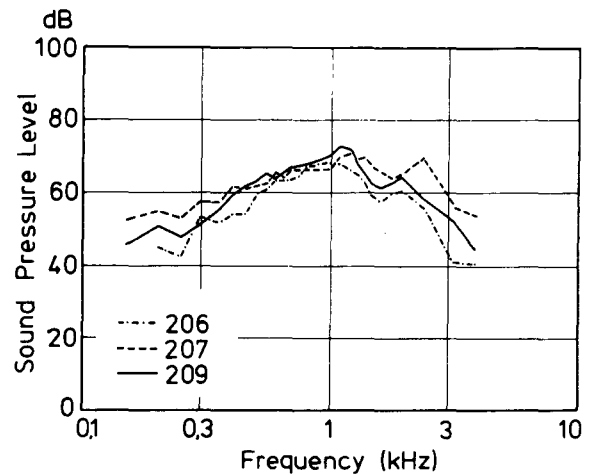


Fig. 10. Amplitude of sound pressure inside the mouth, corrected for the effect of inserting the probe microphone and probe stimulator into the mouth.

mouth cavity. This pressure can be recorded by the insertion of a probe-microphone (including also a probe sound stimulator) as described under Materials and Methods. Due to the small but unavoidable change of mouth cavity acoustics, the contralateral results of Fig. 6 will be altered as shown in Fig. 8. Changes in phase are less than 25° and are not presented here. In general, the amplitude response below 1400 Hz is lowered by about 4–6 dB for animals 206 and 209. At higher frequencies only marginal changes are seen. For animal 207 the changes are less than 4 dB for all frequencies. In Fig. 9 sound pressure inside the mouth is measured while stimulating at one ear at a level of 80 dB SPL. Around 1000 Hz a maximum sound level is found at 68 dB SPL. A second maximum of 60 dB is found at about 2000 Hz. Slopes amount to about 12 dB/octave for both high and low frequencies. Fig. 9 can be corrected for the effect of the insertion of the probe microphone and probe stimulator into the mouth as given by the difference between Figs. 6 and 8. This correction seems justified, assuming that the insertion does not affect the Eustachian tubes and that coupling of the membranes is solely determined by the sound level existing in the mouth cavity, provided no other parallel coupling mechanisms are present. The result of this correction is given in Fig. 10. Maxima are shifted a bit to the right, the first maximum around 1000 Hz now reaches a value between 68 and 73 dB SPL, whereas the second maximum around 2000 Hz is between 60 and 69 dB SPL. High and low frequency slopes remain about 12 dB/octave.

Stimulation from inside the mouth

In the next experiment sound is applied from inside the closed mouth (see Materials and Methods). This type of stimulation is of interest to simulate the situation when the frog opens its mouth, or when sound from outside can pass the tissues of the closed mouth easily [1]. In the experiment, sound is applied inside the closed mouth in order not to stimulate the ears from outside. Displacement amplitude and phase of the left ear are shown in Fig. 11. Results are almost identical to the ipsilateral experiments with mouth open (Fig. 3). Differences between both curves are in general less than 2 dB. Phase curves are identical within

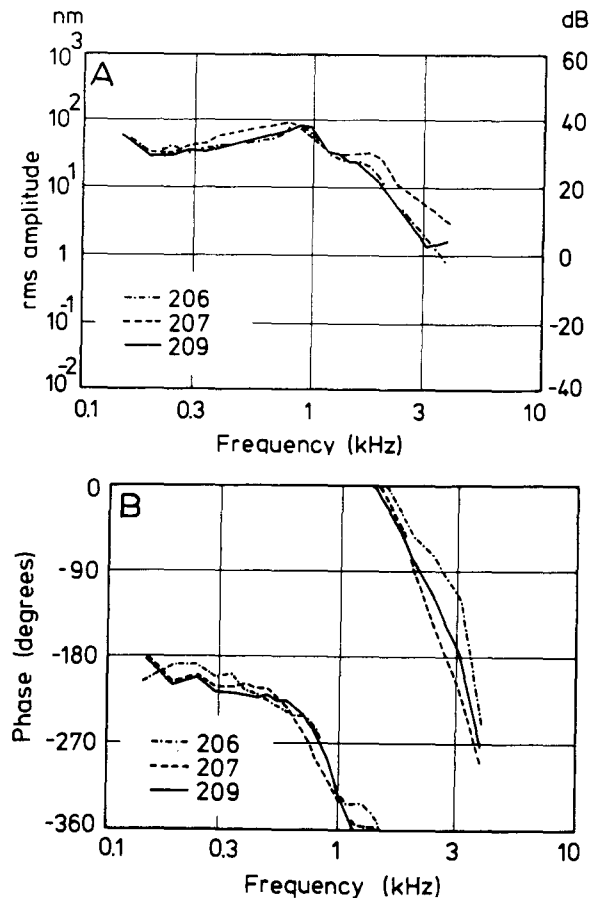


Fig. 11. Displacement amplitude (A) and phase (B) of the centre of tympanum at one side for acoustic stimulation from inside the closed mouth at a level of 80 dB SPL.

15° , except of course for a 180° overall shift. Measurements at the right ear resembled the results shown within 2 dB, as expected from symmetry between the ears. The result of this experiment (Fig. 11) can be combined with the measured sound level inside the mouth (Fig. 9). This will yield a reconstruction of the contralateral response of Fig. 6. Results are not shown but resemble Fig. 6 within 4 dB for frequencies below 2500 Hz. This reconstruction demonstrates that the results of Fig. 6 (contralateral stimulation), Fig. 11 (stimulation from inside the mouth) and Fig. 9 (sound level inside the mouth) are very consistent with each other, validating to a great extent the correctness of measurement methods.

Discussion

Our results concerning ipsilateral stimulation (Fig. 2) do support the results found by Moffat and Capranica [10] for *Bufo americanus*. Amplitude characteristics are both essential low-pass with a response amplitude of equal order and a high frequency cut-off at 900 Hz found by us, as compared to 2000 Hz found by them, this difference being connected with the different species used. Like the results of Moffat and Capranica, our results also differ from those of Chung et al. [3,4], concerning mainly the order of vibration amplitude and effect of opening the mouth. This discrepancy needs clarification.

In our experiments and those of Moffat and Capranica [10], a closed system acoustic stimulation was used as opposed to free field stimulation used by Chung et al. The free field type of stimulation however will stimulate all entrances to the membrane, i.e. directly in front of the membrane and at the back via the mouth and contralateral ear. Suppose the mouth is kept open, sound level in front of the membrane and inside the mouth is a function of incident sound angle. Here this will be almost equal (within 1 dB [13]), due to the small animal size and low frequencies used. From our experiments (Figs. 3 and 11) it is seen that both stimulation from inside the mouth or in front of the membrane gives almost identical contributions to the vibration of the membrane. Phase of vibration is, however, opposite, so those contributions will cancel each other to a great extent, depending on the incident angle of sound. From this we can conclude that vibration response is minimal when the mouth is kept open under free field stimulation conditions. This indeed was found by Chung et al. [3,4]. While stimulating with mouth forced open, they found a reduction of response by at least 15–20 dB (in fact responses dropped below their noise level), relative to experiments with mouth kept closed. Unfortunately Chung et al. did not specify their free field incident angle of sound. Variation of this angle in the open mouth condition would be of even more interest. As expected from our results (Figs. 3 and 11) a pure pressure gradient receiver might be expected for the open mouth condition. Direct verification of this is not attainable since our LDV instrumenta-

tion prevents the establishment of an accurate free sound field. Feng and Shofner [6], however, did obtain directivity patterns for the open mouth from eighth nerve auditory fibers in *Rana pipiens*. Both for low and high frequencies they found figure-8 patterns which are characteristic for pure pressure gradient receivers. This opening of the frog's mouth in order to localize sound is not yet observed to be necessary in behavioral experiments.

If the mouth is closed, free field response will be different. Transmission of sound across the tissues of the closed mouth will determine sound level inside the mouth cavity and hence its contribution to vibration of the membrane. In a forthcoming paper [1] we will report on experiments where this transmission was actually determined and from which it can be concluded that the tissues of the mouth are quite transparent to sound for frequencies below some 2000 Hz. The actual free field response and directionality will be a function of this transmission characteristic. A third sound entrance which is relevant in free field stimulation is the transport of sound from the contralateral ear via the Eustachian tubes and mouth cavity. This coupling between ipsi- and contralateral ears is shown in Figs. 6 and 7. Maximal coupling is about -4 to -8 dB for frequencies between 900 and 1600 Hz. This is sufficient to provide some very weak directionality. When the impedance of the mouth is changed, the coupling of the membranes will change accordingly. This is shown by the differences between Figs. 6 and 8, in which the impedance of the mouth is lowered due to the insertion of sound recording and stimulation probes. Improvement of coupling can be obtained when the acoustic impedance of the mouth is raised, for instance by reducing the volume of the mouth. This is supported by the experiments from Rheinlaender et al. [12], in which they interconnected the Eustachian tubes by moulds of various diameter and volume. Monaural directionality at 1 kHz measured in the torus semicircularis of green tree frog increased when volume and diameter of mould were decreased. On the basis of those results it was suggested that the animal is probably capable of changing its directional sensitivity by variation of the configuration of the internal sound pathway. This active variation is not yet verified in

behavioral studies. At low frequencies the coupling of membranes will, considering the coupling between the ears as shown in Fig. 7, almost certainly be insufficient for directional hearing. This is also confirmed by the directionality patterns found in *Rana pipiens* by Feng and his colleagues [5,6]. When the contralateral membrane is blocked the good directionality pattern found around 300 Hz remained unchanged. This also indicates that not the contralateral ear but the entrance via the mouth is used for localization at low frequencies. At moderate and high frequencies both the entrance via the contralateral ear and the mouth are good candidates for establishing a possible pressure gradient receiver. In both situations the acoustics of the mouth cavity will play an important role. Reduction of sound entrance and leakage via the mouth will help the input from the contralateral ear, but will also alter the transmission of sound across the tissues of the mouth. These effects can be studied further by means of a theoretical model enabling variation of parameters. Results of this theoretical approach will be presented elsewhere [1].

Acknowledgements

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