DIRECTIONAL HEARING IN THE JAPANESE QUAIL (*COTURNIX COTURNIX JAPONICA*)

I. ACOUSTIC PROPERTIES OF THE AUDITORY SYSTEM

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SUMMARY

The auditory tympana in the quail, *Coturnix coturnix japonica* (L.) are internally coupled by an interaural air space. Unilaterally applied sound causing vibration of the ipsilateral tympanum is conducted through the interaural cavity to the inside surface of the contralateral tympanum. In a free sound field at frequencies up to 3150 Hz, sound pressure at the external surface of the tympanum contralateral to the source is within about 3 dB of the pressure exterior to the ipsilateral tympanum. Sound pressures developed at the inner surfaces of the tympana are of similar amplitude to the external pressures at several frequencies in the range 800-6300 Hz. In addition, pressure at each side of the tympanum ipsilateral to the source are generally out of phase, whereas pressures at each side of the contralateral tympanum are relatively close to the same phase. From measurements of amplitude and phase of the interacting pressures at the tympanum, the calculated driving pressure at the ipsilateral tympanum exceeds that at the contralateral tympanum by 10-20 dB over a range of frequencies. The auditory tympana in quail have considerable inherent directionality, therefore, due to their function as pressure-gradient receivers. Anatomical analogies with anurans and reptiles indicate that they derive directional hearing from the same acoustic mechanism that operates in the quail.

INTRODUCTION

To perceive sound the ears of most terrestrial animals utilize a light tympanic membrane which is exposed directly, or via a canal, to the exterior. An air cavity exists behind the tympanum so that it is sensitive to the small, rapid changes in ambient pressure associated with a sound wave. In a sound field, the force causing the tympanum to vibrate is derived from the instantaneous difference between the air pressure acting on its external surface and the pressure behind the tympanum in the tympanic cavity. This general description holds for crickets, locusts, bush-crickets, cicadas, moths (representing several independently evolved insect auditory

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systems) and vertebrate ears. Sound localization using two such ears placed laterally depends on the production of a physiological difference between the afferent auditory responses from each ear, the sense of this difference indicating on which side of the body the sound source is located.

Many terrestrial animals have evolved systems of communication using sound signals with wavelengths many times longer than the dimensions of their bodies. In such cases, and where the two tympana are exposed to the air medium directly or via a short tube (but there are no pinnae), sound pressures reaching the external surfaces of the two tympana may be expected to be of similar amplitude regardless of the location of the source, because the attenuation of pressure due to the animal's head or body will be small. If the anatomical distance between the ears is less than about 3 cm, the maximum time delay between the onset of the pressure wave at each of the tympana will be less than 100 μs, which is an extremely short interval for reliable neural coding. To enable directional hearing in such animals, therefore, a mechanism seems necessary by means of which the amplitude of vibration of each of the auditory tympana changes according to the direction of propagation of the sound wave, despite the almost constant sound pressure reaching the external surface of each tympanum for all directions of the sound source. Such a mechanism is the pressure-gradient receiver (Michelsen, 1971; Lewis, 1974; Michelsen & Nocke, 1974), in which sound pressures of similar amplitude are applied to the front and back surfaces of the tympanum and the amplitude of its resulting vibration depends on the phase difference between the inside and outside pressures. The phase difference across the tympanum may vary according to the direction of the incident sound wave and if it becomes very small, the force driving the tympanum is sharply reduced. This mechanism enables directional hearing in crickets (Hill & Boyan, 1977), locusts (Miller, 1977) and cicadas (Fletcher & Hill, 1978). In each of these animals, sound pressures of similar amplitudes act on the front and back surfaces of each tympanum because sound is conducted between the inside surfaces of the tympana through an air space in the body, i.e. the auditory tympana are acoustically coupled internally.

In frogs, small reptiles and small birds, sound pressures on the external surfaces of the tympana will be of similar amplitudes when wavelengths are long with respect to dimensions of the head. In each of these vertebrate classes, however, the inside surfaces of the auditory tympana are connected by ducts produced by expansion of the eustachian tubes. Evidence that sound is transmitted through the head from one tympanum to the other is available in each case (e.g. Strother, 1959; Wever & Vernon, 1957; Schwartzkopff, 1952). Thus, in these vertebrates the auditory tympana ought to show characteristics of pressure-gradient receivers.

In this paper, we describe sound conduction through the auditory system in the quail *Coturnix coturnix japonica*, in order to specify the acoustic conditions existing at each auditory tympanum when sound is incident from different directions in the horizontal plane. A physical mechanism for directional hearing in this bird utilizing the principle of the pressure-gradient receiver can be demonstrated when we compute the directional response of the tympanum, to a first approximation, using measurements of the sound pressure amplitude and phase existing at the front and back surfaces of the tympanum when the bird is in a free sound field. The study is extended to the responses of auditory receptors in the following paper.

MATERIALS AND METHODS

Adult male and female quail, *Coturnix coturnix japonica*, were obtained from a commercial breeder. Birds were killed (intramuscular Nembutal) immediately prior to experiments. They were held in a natural position by cementing the cranium, exposed between the eyes, to a rigid stand made from small diameter metal tubing (see Fig. 1 A), Initially, the whole bird was mounted on the stand, the body being supported under the wings and by the feet. Most measurements, however, were made on isolated heads separated from the body about three inches below the jaw. The absence of the body did not affect sound pressures measured around the head when a loudpeaker was placed at different positions in the horizontal plane.

Sound pressure was measured at three positions in the quail's auditory system; at the external opening of the meatus, inside the meatus but external to the auditory tympanum, and inside the interaural cavity (see below) near the inside surface of one auditory tympanum. The microphone (see below) was directed vertically upwards for all measurements, and when in the required position, it was firmly clamped to the bird's stand. Feathers over and around the external opening of the meatus were removed. For measurements outside the meatus, the microphone was held against the side of the head with its end at the centre of the meatus opening. For internal measurements, neck muscles were removed on one side exposing the ventral surface of the skull or the ventral wall of the meatus. For access to the meatus, the proximal part of the lower jaw was also removed. A hole was cut in the wall of the meatus or in the ventral surface of the skull to admit the microphone, which was then clamped and sealed in position with petroleum jelly (Vaseline). Following such measurements in intact auditory systems we checked that no material was occluding cavities or in contact with the tympana as a result of locating the microphone.

Sound was presented to the bird head either unilaterally to one meatus only, or in a free field in anechoic conditions. For unilateral presentation, sound was conducted from a loudspeaker (acoustically isolated from the bird) along plastic tubing (length 3 m, bore 10 mm), the end of which was held over the meatus and sealed against the side of the head with Vaseline. In the free field, the bird was mounted on a thin metal post (approximately 1 m from the floor) in the centre of an acoustically insulated, anechoic chamber (see Results), having approximate internal dimensions of $2\cdot5 \times 2\cdot5 \times 2\cdot0$ m and lined on all internal surfaces with rockwool wedges. The loudspeaker was mounted on a pivoted arm and could be rotated through 360° in the horizontal plane at a constant $1\cdot05$ m from the position of the microphone, which was centred in the plane of rotation of the loudspeaker using a plumb-line. Calibrations were made of the sound field (see below), but in addition, bird heads were routinely mounted facing different directions in the anechoic chamber.

Pure tone, continuous sound was produced by amplifying the sinusoidal output of a waveform generator (Phillips GM 2317), passing the signal through a step-wise attenuator (Hatfield 2125), monitoring the voltage on an oscilloscope and feeding the signal to a loudspeaker (Radio Spares 243031). Frequency was set to $0\cdot1\%$ accuracy using a calibrated electronic counter (Heath, Co.). All measurements of sound pressure level and phase were made with a $\frac{1}{8}$ in. condenser microphone (Bruel and Kjaer type 4138), a $\frac{1}{3}$-octave bandpass filter set (Bruel and Kjaer type 1612) and a measuring
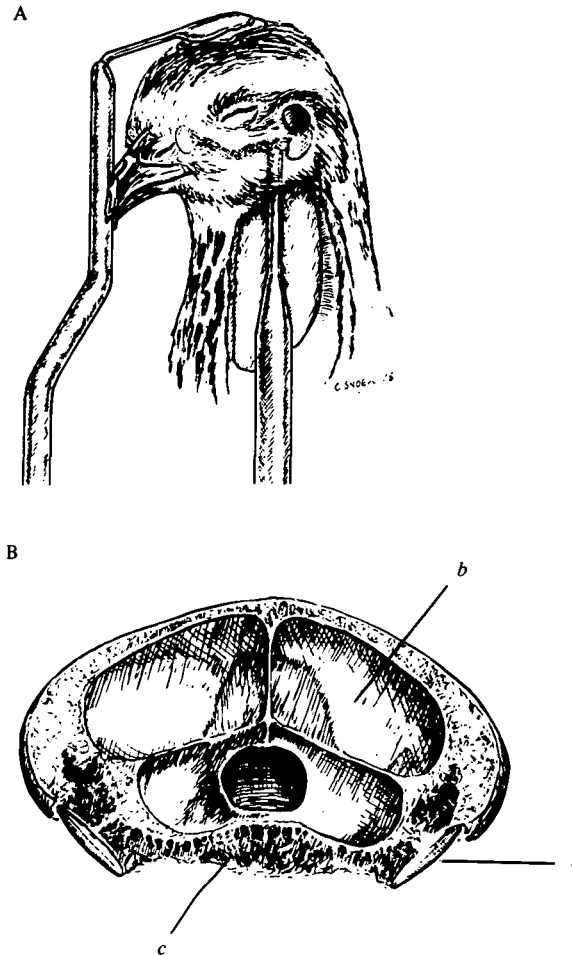
A

B

b

t

c

Fig. 1. Drawings to illustrate aspects of the auditory system in the quail. (A) Arrangement of the head mounted on a stand for measurement of sound pressure in the auditory system using a condenser microphone. (B) Appearance of a vertical, transverse section through the quail head at the level of the auditory tympana: t, tympanum; c, interaural cavity; b, braincase.

amplifier (Bruel and Kjaer type 2107). Sound pressure levels used were in the range 75–85 dB re. $2 \times 10^{-5} \mathrm{N/m^2}$. Measurements of the relative phase of the sound pressure at the microphone were made as follows. The sinusoidal signal fed to the loudspeaker was also applied to one beam of a dual beam oscilloscope (Tektronix 5441) on which the sweep speed and trigger level were adjusted at each frequency so that one complete cycle of the sine wave occupied the width of the oscilloscope screen graticule and the sweep started at a fixed point in the wave (the negative-going zero crossing). Assuming a constant phase relationship at each frequency between the voltage fed to the loud-speaker and the sound pressure produced, the voltage signal provided an arbitrary zero phase for reference at each frequency. The response of the condenser microphone was monitored from the measuring amplifier and displayed on the second beam of the oscilloscope. For each frequency, therefore, the phase of the sound pressure at the microphone, relative to an arbitrary zero phase, was indicated as a proportion of

One complete cycle by the horizontal distance between corresponding zero crossings of the two traces on the oscilloscope screen. In all measurements, the microphone was used with a short length of plastic tubing fitted over the cartridge to prevent material occluding the grid or contacting the membrane. This tube extended about 2 mm in front of (and behind) the grid. Its presence had no measurable effect on the response of the microphone at the sound frequencies used in these experiments.

For calibration of the sound field in the chamber, the microphone alone was clamped to the post and directed vertically upwards at the centre of the plane of rotation of the loudspeaker. Pressure amplitude and phase were measured for constant output of the signal generator, at each fequency used in the experiments, when the loudspeaker was shifted through 360° in steps of 30°.

The sound pressures acting on the front and back surfaces of the auditory tympanum in the quail depend on sound transmission through the meatus, past the tympanum and through the interaural cavity (see below). Transmission through each element was assessed when sound was applied unilaterally to one meatus by means of the tube. Initially, the microphone was positioned at the external opening of the meatus, the sound delivery tube was sealed in place over it and sound levels were measured at each frequency for calibrated signal voltages fed to the loudspeaker. The microphone was then positioned inside the interaural cavity near the tympanum ipsilateral to the sound source, and sound measurements were repeated using the same signal parameters. Further sets of measurements were made when the sound tube was applied to the meatus contralateral to the microphone and after each of the auditory tympana were largely removed with a pair of curved forceps.

The bird head forms an impedance at the end of the sound tube and hence, changes to the auditory system may alter this impedance and lead to changes in the sound pressure in the tube, i.e. the source pressure at the entrance to the meatus. As a control, therefore, measurements were made in the tube when positioned over one meatus, before and after the removal of both auditory tympana. Sound pressures at the entrance to the meatus before and after removal of both tympana were within 2 dB at all frequencies except 1600 Hz where a decrease of 4 dB occurred. Similarly, phase changed by less than 10% at all frequencies after removal of the tympana.

RESULTS

Calibration of the free sound field

Sound pressure and phase were measured in the anechoic chamber at the centre of rotation of the loudspeaker for 12 positions of the loudspeaker separated by 30°. Variations in pressure and phase for the relevant range of frequencies are shown in Table 1. Sound pressure level was generally within ± 2 dB and phase was within ± 7·5% of 2π as the loudspeaker was rotated in the chamber. For one position of the loudspeaker (270°), a greater variation in sound pressure (up to ± 3·5 dB) occurred, but only at 1630 and 2000 Hz. This is attributed to an unaviodable projection in the chamber. For any frequency, there were no abrupt changes in pressure and phase as the loudspeaker was moved through 360° and each preparation was routinely pointed in a different direction.

Table 1. *Total variation in two parameters of the sound field at the centre of the anechoic chamber when the loudspeaker was rotated through 360°*

Frequency (Hz)	Variation in sound pressure level (dB)	Variation in phase (% of 2π)
500	±0·6	±1·5
630	±1·0	±1·0
800	±0·5	±5·0
1000	±1·0	±4·0
1250	±2·0	±7·5
1630	±3·5	±6·5
2000	±3·0	±1·1
2500	±0·5	±1·5
3150	±0·6	±1·0
4000	±0·3	±1·0
5000	±0·2	±2·5
6300	±1·8	±1·5
8000	±1·5	±4·0

Anatomy of the auditory system

Anatomical aspects of the auditory system in the quail are illustrated in Fig. 1. The external opening of the meatus is a simple, ovoid hole in the side of the head, normally covered by a fan of delicate feathers. The meatus leads down and back to the tympanum, it is about 4 mm in length, it has a minimal cross-sectional area of approximately 3 mm², and it is lined with epidermis. The auditory tympanum is a light membrane, approximately ovoid and about 8 mm² in area. It is distended outward by the columella. Behind the tympanum is an air-filled cavity formed in the bone of the skull. This cavity extends dorsally and posteriorly towards the midline behind the braincase. Ventrally, the cavity extends to the midline where it is constricted; however, it connects with the cavity on the opposite side. Thus, a continuous air-filled passage runs across the head between the inside surfaces of the auditory tympana. The internal distance between the tympana is about 12 mm. The interaural cavity is bounded by the spongy matrix of the skull. The total air space between the ears extends, therefore, throughout the pneumaticized region of the skull bones.

Sound conduction through the auditory system

Sound pressure levels measured at different positions in the auditory system will depend on the extent to which the system is intact or modified and on the relative amplitudes and phases of the pressures at each ear. When sound is applied unilaterally, measurements of pressure levels at different positions along passages in the system or on each side of one of the tympana give some indication of the acoustic transmission properties of those elements. The 'gains' (differences between pairs of measurements in dB) thus obtained may not precisely characterize the elements themselves, for in each case transmission will depend on the state of the remainder of the system. The measurements to be described, however, do provide an insight into the functioning of the auditory system as a whole.

Fig. 2 shows the difference in level between the unilaterally applied sound pressure at the entrance to the meatus and the pressure just inside the position of the ablated ipsilateral tympanum. This graph indicates that sound energy entering the head
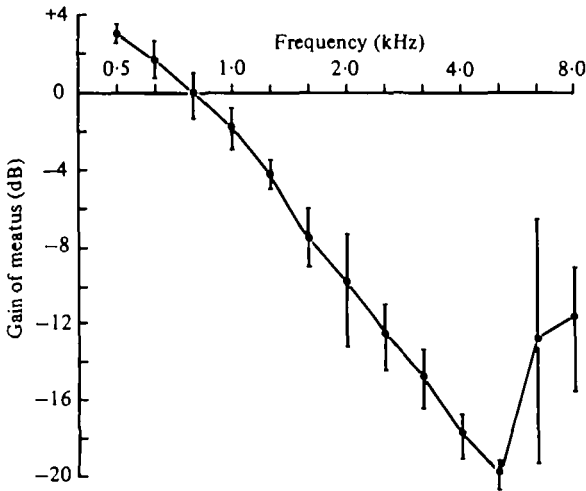
Fig. 2. Gain of the meatus, defined as the difference between the sound pressure in the inter-aural cavity near the position of the ipsilateral tympanum after ablation of the tympanum and the sound pressure at the entrance to the meatus. Sound was applied unilaterally to one meatus, the contralateral tympanum was intact. Means and standard errors are shown for six preparations.
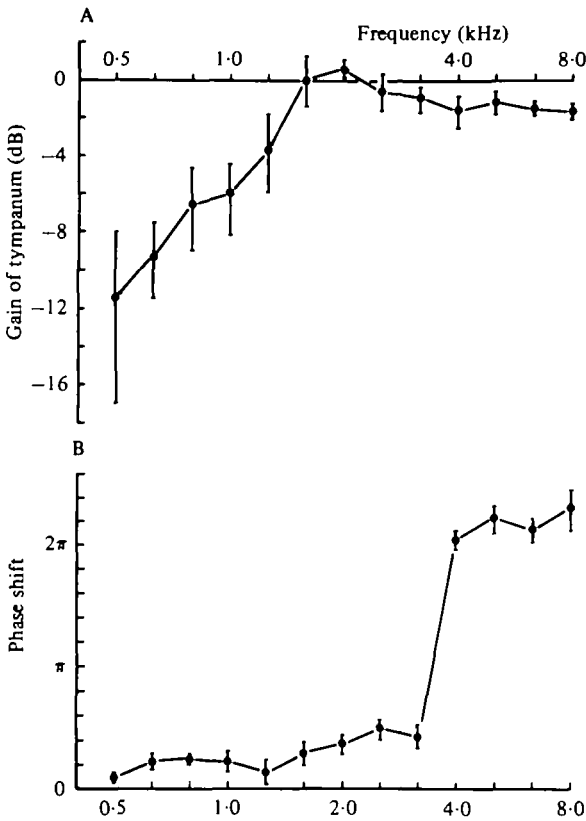

Fig. 3. (A) Gain of the auditory tympanum averaged for six preparations. With sound applied unilaterally, pressure behind the intact ipsilateral tympanum, relative to that at the same position after ablation of the tympanum, is appreciably diminished at low frequencies (0·5–1·0 kHz). At higher frequencies, loss of sound pressure across the tympanum is very small. (B) Difference between the phase of the pressure behind the intact ipsilateral tympanum for unilateral sound input and the phase of the pressure at the entrance to the meatus. From 2000 to 3150 Hz, the phase shift across the tympanum (and the meatus) is close to $\pi/2$. At higher frequencies, reversion to smaller observed phase differences are interpreted as phase shifts greater than 2π. In both cases data are obtained from six preparations.
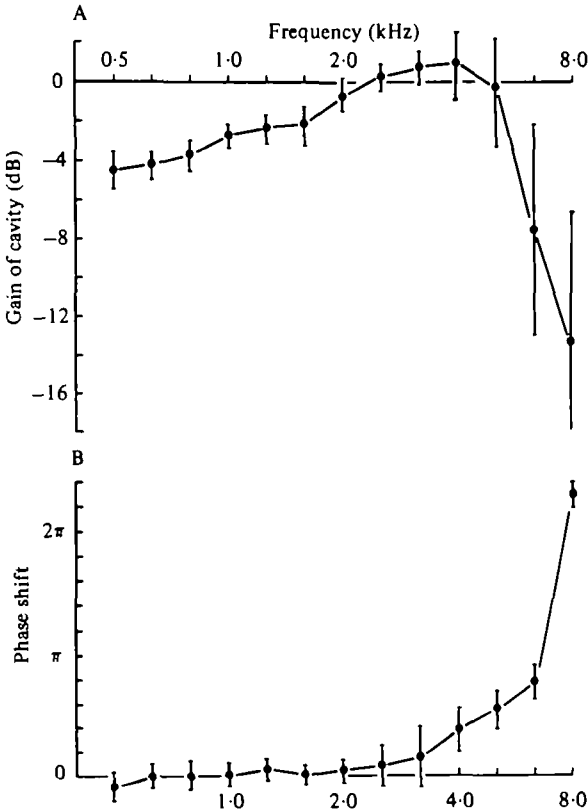
Fig. 4. (A) Gain of the interaural cavity measured for unilateral sound input in six preparations. Transmission of sound through the head cavity improves up to 5000 Hz and at higher frequencies sharply declines. (B) Phase shift across the interaural cavity. Little difference occurs between the phase of the sound pressure at each side of the head cavity for frequencies up to 2000 Hz. At higher frequencies an increasing phase shift is observed.

cavity through the meatus is attenuated at frequencies above 800 Hz, the attenuation increasing with frequency at near 6 dB per octave. From 5000 to 8000 Hz there is a reversal of this trend, possibly due to some resonance in the system.

Fig. 3 indicates the transmission of sound pressure past the auditory tympanum (the gain of the tympanum). Fig. 3 A shows the difference between the sound pressure levels measured just inside the position of the tympanum before and after its ablation, for a constant unilateral sound input at the ipsilateral meatus. This difference indicates that at low frequencies there is normally a large drop in sound pressure across the tympanum. As the frequency is increased to 1630 Hz, however, attenuation of the pressure behind the tympanum reduces to zero and remains within 2 dB up to 8000 Hz. Fig. 3 B shows the phase of the pressure behind the intact tympanum relative to that at the entrance to the meatus. Note that in the range 2000–3150 Hz the phase shift down the meatus and across the tympanum is close to $\pi/2$. We have plotted the phase shift at 4000 Hz as a sudden jump to just beyond 2π: possibly, the shift actually declined to just above zero. The point is immaterial to our major conclusions, however, and an increased phase shift at higher frequencies seemed more probable.

Fig. 4 shows the gain of the interaural cavity measured with both the tympana
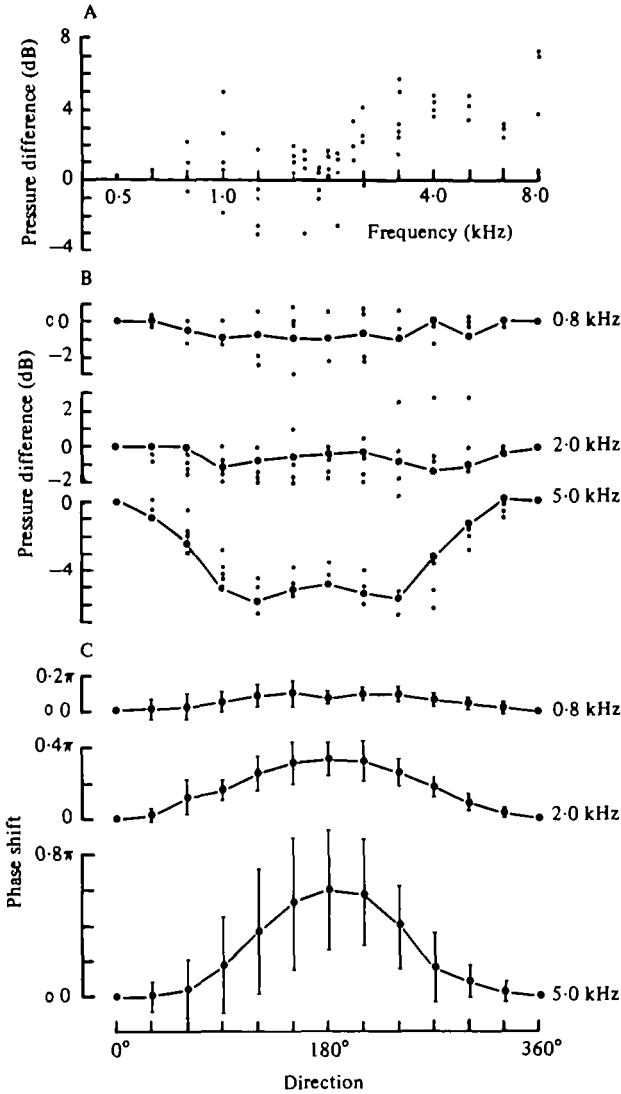
Fig. 5. (A) Differences between the sound pressure level in the meatus ipsilateral to the source and that in the meatus when contralateral to the source in a free field. Data are shown for five preparations. The interaural difference tends to increase with increasing frequency up to about 5 dB at 800 Hz. (B) Relative sound pressure level in the meatus for twelve directions of sound (0° = ipsilateral) measured at three frequencies (indicated in kHz). Data are shown for five preparations and for one preparation larger dots are connected by a solid line. The interaural difference (assuming binaural symmetry) is indicated by points 180° apart. No appreciable interaural difference occurs up to 2000 Hz. (C) Phase of the sound pressure in the meatus for different directions of sound relative to that when the source is ipsilateral to the meatus (0° = ipsilateral) measured at three frequencies (indicated in kHz). The pressure reaching the meatus contralateral to the source shows a phase lag which is greater at higher frequency. Means are obtained from five preparations.
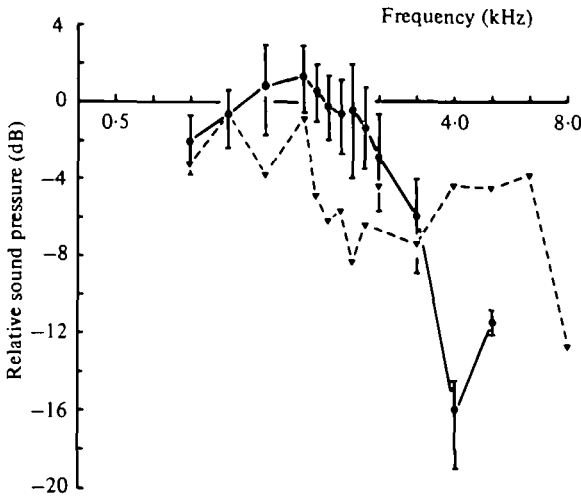
Fig. 6. Sound pressure measured inside the interaural cavity in the free field: dots, pressure behind the tympanum ipsilateral to the source relative to the ambient field; triangles, pressure behind the tympanum contralateral to the source relative to the pressure in the adjacent meatus. At most frequencies in the range 500–6300 Hz, sound pressures on each side of the tympany are within about 6 dB.

ablated. Fig. 4A shows the difference between the sound pressure levels at one side of the interaural cavity for sound presented at the ipsilateral and contralateral meatus. From 500 to 5000 Hz, attenuation of sound across the interaural cavity is within 5 dB, and it is within 3 dB from 1000 to 5000 Hz. Slight positive gain between 2500 and 5000 Hz suggests standing waves in the cavity. At the frequencies above 5000 Hz, attenuation in the cavity sharply increases. The phase shift across the inter-aural cavity is shown in Fig. 4B. Over most of the frequency range, the phase shift oscillates around zero. Above 3150 Hz a sharply increased phase shift is evident.

Sound pressures in the auditory system in a free field

The sound pressure in the meatus in the free field, when the sound source is at different directions in the horizontal plane, is described in Fig. 5. The difference between the pressure levels measured in the meatus for ipsilateral and contralateral presentation is shown in Fig. 5A. Results for five preparations are plotted together and indicate some scatter. The attenuation of the sound pressure reaching the contra-lateral meatus is greater at higher frequencies, however, it reaches only about 5 dB by 8000 Hz. In Fig. 5B, results for the same five preparations are plotted together and show the relative sound pressure in the meatus for each direction of the source for three frequencies. Up to 2·0 kHz, there is no consistent reduction of pressure on the contralateral side. At 5·0 kHz the pressure in the contralateral meatus is reduced by about 5 dB. The phase of the pressure in the meatus also changes with the direction of the source. The phase in the meatus for each direction relative to the phase when the source is ipsilateral is shown for three frequencies in Fig. 5C. When the source is shifted from the ipsilateral direction (0°), there is a phase delay which reaches a maximum when the source is at or near the contralateral direction, i.e. when the path length from the loudspeaker to the microphone has been increased by
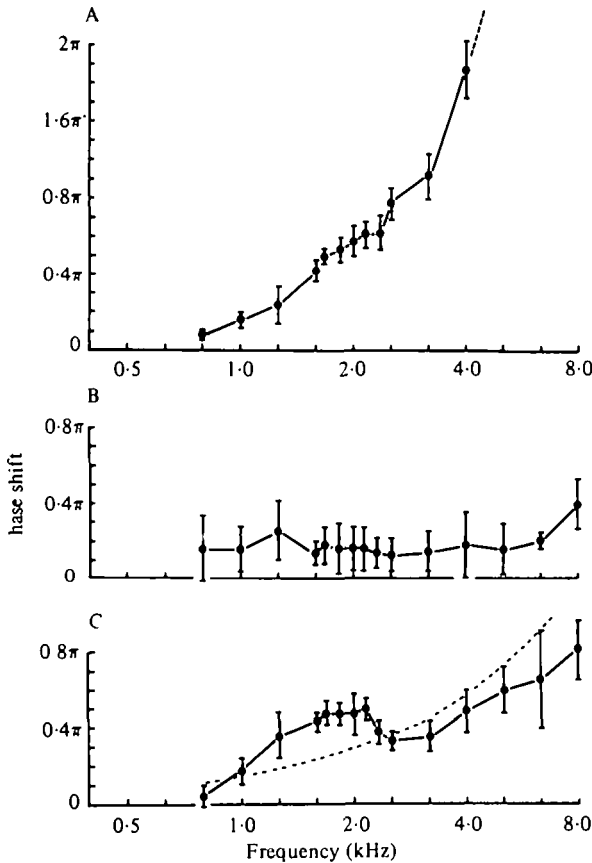
Fig. 7. (A) Phase of the sound pressure behind the tympanum ipsilateral to the source relative to that in the ipsilateral meatus in the free field. The phase shift across the ipsilateral tympanum steadily increases with increasing frequency and crosses $\pi/2$ in the region of 1760 Hz. At high frequencies, reversion to smaller observed phase differences are interpreted as phase shifts greater than 2π. (B) Phase shift across the tympanum contralateral to the source in the free field. The comparatively small difference between the phase of the internal and external sound pressures at the contralateral tympanum leads to the conclusion that the effective driving pressure would be relatively diminished (see text) and is consistent with a diminished vibration response at the contralateral tympanum. (C) Difference between the phase of the pressure behind the tympanum contralateral to the source and that of the pressure in the meatus ipsilateral to the source, i.e. the phase shift through the auditory system to the inside of the contralateral tympanum. The dashed line shows the calculated phase lag to a sound pressure wave travelling 2·5 cm (approximate distance between the ears) around the head. When the source is lateral, the effective phase shift imparted to the pressure reaching the inner surface of the contralateral tympanum appears to be matched over a wide frequency range to the phase shift observed in a wave reaching the outer surface of the contralateral tympanum.

the distance around the head. At higher sound frequencies, the extent of the phase delay is progressively greater when the source is contralateral to the microphone, i.e. the extra path length around the head is a greater proportion of a wavelength at higher sound frequencies. Phase delays measured in the contralateral meatus at different frequencies, of which only three are illustrated in Fig. 5C, agree well with phase delays expected in a wave travelling the extra distance around the head (see Fig. 7C).
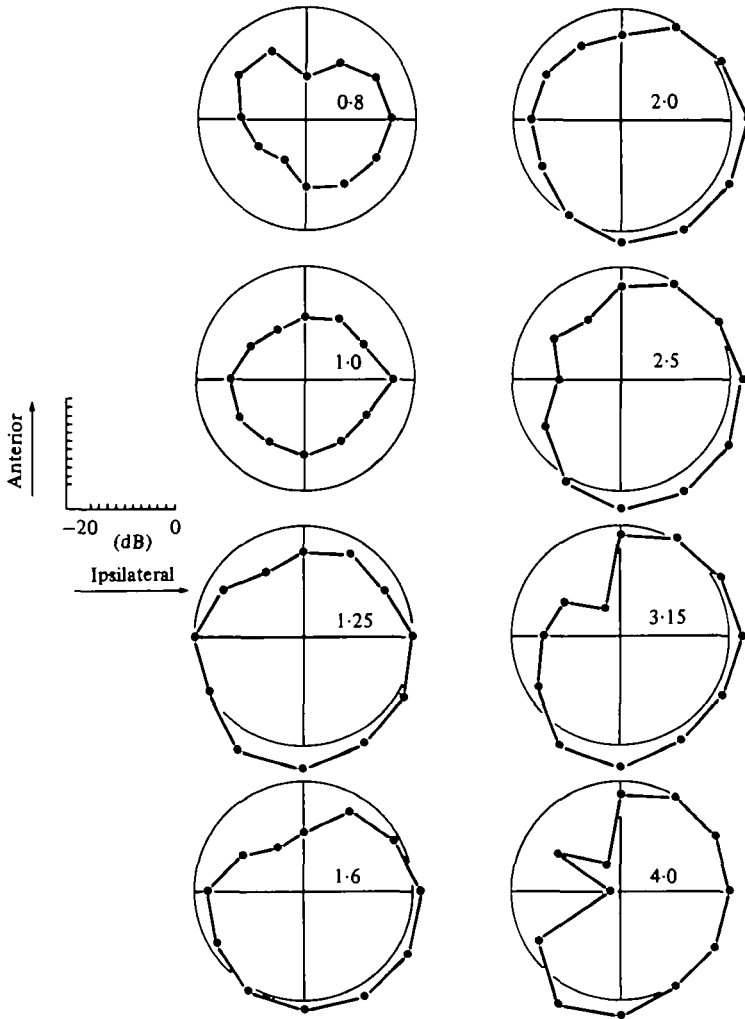
Fig. 8. The calculated effective driving pressure at the tympanum (see text) as a function of the direction of the sound source, plotted for several frequencies (indicated in kHz) on polar coordinates. Effective pressures were calculated using the measured amplitude and phase of the inner and outer sound pressures at the tympanum. At frequencies above 1600 Hz, the effective pressure on the tympanum is reduced when the source is on the contralateral side relative to that when the source is ipsilateral. Note that in some cases the maximum interaural difference in sensitivity to be deduced from these plots occurs when the source is slightly anterior to the lateral direction; also, that interaural differences in sensitivity of about 10–20 dB are predicted.

Sound pressure developed inside the head cavity just behind the tympanum, relative to the strength of the free field, is shown in Fig. 6. For frequencies from 800 to 3150 Hz and the source located ipsilateral to the position of the microphone in the interaural cavity, the measured pressure is within 6 dB of the ambient sound field. When the source is contralateral to the microphone, the pressure inside the tympanum is within 8 dB of the pressure in the meatus from 800 to 6300 Hz.

The difference between the phases of the pressure on the external surface and on the internal surface of the tympanum ipsilateral to the source is shown in Fig. 7A. In the

free field, the phase difference across the ipsilateral tympanum increases from a low value at 800 Hz, it crosses $\pi/2$ at 1725 Hz and increases towards π at 3150 Hz. At higher frequencies, the phase difference across the ipsilateral tympanum rapidly increases further and (presumably) crosses 2π. The phase difference across the tympanum contralateral to the source in the free field is shown in Fig. 7B. It is distinctly different to that at the ipsilateral tympanum. Over the frequency range 800–6300 Hz, the phase difference across the contralateral tympanum remains comparatively small and it is within $\pi/4$. In Fig. 7C, the phase of the internal pressure near the tympanum contralateral to the source is plotted relative to the phase of the pressure at the entrance to the meatus ipsilateral to the source, indicating the phase shift in the sound transmission through the auditory system to the inside of the contralateral tympanum. For comparison, the dashed curve in Fig. 7C shows the expected phase shift, as a function of frequency, in a sound wave propagated 2·5 cm through air, i.e. the extra distance around the head from the ipsilateral side to the contralateral meatus. Over the range 500–8000 Hz the net phase shift via the path through the head approximates to that expected in a wave travelling around the head.

DISCUSSION

Free measurements of sound pressure in the auditory meatus of the quail, for frequencies up to 8000 Hz, show that the pressure reaching the outside surface of the tympanum contralateral to a sound source is attenuated by up to about 5 dB relative to that at the ipsilateral tympanum. In the range 800–3150 Hz, which covers most of the spectrum of male vocalizations in *C. c. japonica* (unpublished results), attenuation at the contralateral tympanum is only 0–3 dB. In addition, however, sound pressure develops at the inside surface of each tympanum and the amplitude of the internal pressure is within about 8 dB of the pressure in the meatus over the frequency range 800–6300 Hz. It is clear, therefore, that the auditory tympana in the quail, and in other birds where similar acoustic conditions may apply, respond to the influence of sound pressure on both sides and must be considered as pressure-gradient receivers. The amplitude of the tympanal vibration and the response of auditory receptors will depend, therefore, on the vector sum of the forces on the tympanum arising from the internal and external sound pressures. The effective driving pressure on an auditory tympanum, expressed in dB, sharply declines when the phase difference between interacting pressures of similar amplitude is small (see Nocke, 1975; Hill & Boyan, 1977; Miller, 1977). Since a balanced, asymmetrical pressure-gradient receiver (sensu Michelsen & Nocke, 1974) has substantial inherent directionality, a pair of such receivers operating reciprocally can provide a significant interaural difference in effective intensity. For the quail, this would be a far more reliable cue for sound localization than the traditional cues of interaural time difference of tens of microseconds or intensity difference external to the tympanum due to head shadowing, which is only about 1–3 dB up to 3150 Hz. In the quail, the development of a reciprocal pair of asymmetrical, pressure-gradient receivers results from internal acoustic coupling of the auditory tympana via the cavity through the floor of the skull. This basis for directional hearing appears to be an evolutionary strategy employed by most if not all small animals communicating with sounds of wavelength much greater than body

size (from anatomical and physiological studies of insects and anatomical considerations of frogs, reptiles and birds).

Measurements of sound transmission through the auditory system of the quail permit some qualitative characterization and a calculation to a first approximation of the expected directionality of the vibration response of the auditory tympana. The meatus is essentially a short tube extending almost vertically upwards from the tympanum. It has the effect of placing the entry port of sound into the auditory system much nearer the centre of the side of the head than would be the case if the ventrally placed tympana were exposed more directly. Hence, the meatus may serve to maximize the phase delay to the sound wave travelling around the head to the contralateral ear (the significance of which is apparent below). Acoustically, the meatus may constitute a small mass of confined air that is oscillated back and forth with the tympanum and which has some damping effect due to friction at the walls of the tube. Its effect on the passage of sound to the tympanum (Fig. 2) is to increase attenuation at slightly more than 6 dB per octave up to 5000 Hz. The factors responsible for this filtering effect are unknown.

The auditory tympanum is coupled to the columella and to the cochlea. The sound pressure developed behind the tympanum in the interaural cavity, when sound is applied to only one meatus, suggests the manner in which the tympanum behaves as a part of the auditory mechanism. At low frequency (500 Hz) its response is relatively weak and the phase of the pressure behind the tympanum suggests that it moves nearly in phase with the incident pressure (Fig. 3). As the frequency is increased, the response of the tympanum increases to a broad maximum at around 2000 Hz and its displacement appears to lag the phase of the incident pressure by about $\pi/2$. To this stage, the inferred response of the tympanum is similar to that of a simple driven oscillator having a highly damped resonance at 2000 Hz. At higher frequencies, the response declines only slightly and the phase lag appears to suddenly increase beyond 2π. This behaviour, however, is not consistent with that of a simple driven oscillator and may indicate effects on the tympanum due to its mechanical link with the receptors and the complex interaural cavity.

The interaural cavity has some similarity with a low pass filter with a sharp cut off above 5000 Hz. It introduces only small phase shifts to the pressure traversing the head for frequencies up to 5000 Hz. At higher frequencies, where attenuation in the interaural cavity increases, rapidly increasing phase shifts are observed.

When the bird is subjected to sound in a free field, the significance for directional hearing of the characteristics of the auditory system becomes apparent. The pressure developed inside the interaural cavity is substantially higher in the free field situation than for unilateral input (compare Figs. 2 and 6). This is due to sound input via two ports (both tympana) when the source is on the medial axis, or to stiffening of the contralateral tympanum (see below) when the source is located laterally. These conditions do not apply when sound is applied to only one meatus. In steady state conditions, each tympanum is acted upon by an internal and an external sound pressure which are of similar amplitude at some frequencies over a wide frequency range (Fig. 6). Furthermore, the external and internal pressures at the tympanum ipsilateral to the source differ in phase by more than $\pi/6$ for frequencies above 1200 Hz. In contrast, external and internal sound pressures at the contralateral tympanum differ in phase

by *less* than $\pi/6$ for each frequency in the range 800–5000 Hz (Fig. 7). The effective pressure causing the tympanum to vibrate is indicated by the instantaneous difference between the interacting pressures. Using the measured amplitude and phase of the internal and external sound pressures for different locations of the sound source, we have calculated the amplitude of the net pressure on the auditory tympanum in individual preparations using the equation

$$P_{net} \cdot \sin (\omega t + \phi') = P_1 \cdot \sin \omega t - P_2 \cdot \sin (\omega t + \phi),$$

where t and ω refer to time and angular frequency respectively, P_1 and P_2 represent the relative absolute amplitudes of the measured internal and external pressures at the tympanum and ϕ represents the phase difference between them. An example of the relative amplitude of P_{net} calculated for different directions and at different frequencies of sound and then expressed in dB, is shown on polar coordinates in Fig. 8. The calculated effective pressure on the tympanum varies with the direction of the source over a wide frequency range and at some frequencies it shows significant reduction when sound is from the contralateral direction. There is a clear trend of greater effective pressure on the ipsilateral side, and reduced effective pressure on the contralateral side. From two ears acting reciprocally in this manner, unambiguous directional information would be available to the central nervous system due to an effective interaural intensity difference for lateral sound of from 10 to 20 dB.

The essential features of the auditory system in the quail responsible for this directionality of the tympana are: (1) the interaural head cavity which conducts sound between the ears so that pressures of similar amplitude exist at the outer and inner surfaces of each tympanum and (2) the net phase shift imparted to the pressure reaching the inside of the tympanum when it is contralateral to a sound source so that the internal pressure is at a similar phase to the external pressure, which has travelled the extra distance around the head. The similarity of the net phase shift through the head and phase shift around the head (Fig. 7C) depends on a maximum external path of about 2·5 cm when the source is lateral. Maximizing this distance may be one function of the meatus.

A similar degree of directional sensitivity in the response of the auditory tympanum can be expected in other small vertebrates in which acoustic conditions at the tympanum are similar to those in the quail, e.g. frogs (Strother, 1959; Chung, Pettigrew & Anson, 1978), caimans (Wever & Vernon, 1957) and lizards, which also have the appropriate anatomy. Chung *et al.* (1978) claimed that the buccal cavity of the frog, to which the eardrums are coupled, shows strong resonance at the frequency of the species' call. They also tentatively suggested, however, that the directional response of the frog tympanum depended upon the pressure gradient principle. The frog auditory system is analogous to that of the bladder cicada *Cystosoma saundersii* (two auditory tympana coupled to a common air cavity) and in both cases, males propagate narrowly tuned acoustic signals utilizing their resonant air cavities (the frog vocal sac – Martin, 1972; the cicada abdomen – Young & Hill, 1977; Fletcher & Hill, 1978). Because of resonance in the air cavity when exposed to sound at the frequency of the species' call, the pressure gradient at the tympanum of the cicada does not produce a directional response (Fletcher & Hill, 1978), and the male cicada has non-directional hearing to the species' song frequency (Young & Hill, 1977). The incompatibility

between the strong resonance in the interaural cavity and directionality in the response
of the tympana suggests that the resonance in the frog's buccal cavity be re-evaluated.

This physical mechanism for the directional sensitivity of the quail auditory system
has also been adopted by insects that communicate with comparatively low frequency
sounds. Not surprisingly, it is also a mechanism for directionally sensitive micro-
phones. Payne (1971) noted that the ears of barn owls are connected by a cavity in
the head which should permit sound transference from one ear to the other. However,
he restricted his considerations with regard to directional hearing to sound pressure
entering the meatus as a function of direction and did not consider the pressure-
gradient principle. Since the feathers surrounding the external opening of the meatus in
the owl may have an acoustic function and furthermore, since barn owls appear to rely
on comparatively high frequencies (5000–7000 Hz) for acoustic location (Konishi, 1973),
the exact mechanism of directional hearing in owls may differ from the simple model
presented here (see also Coles *et al.* 1980). At 3 kHz sound frequency, Schwartzkopff
(1962) found that simultaneous cochlear microphonic recording in the two ears of
the owl *Asio otus* indicated a difference of about 10 dB between the effective sound
pressures at each tympanum. These experiments did not examine the role of the head
cavity in the directionality of the ears. Some owls, however, appear to have other
specializations for high directional acuity which are not general to the auditory
systems of birds, so modification in owls to the basic pressure-gradient system might
be expected. Schwartzkopff (1952) noted the possibility that the auditory tympana in
finches would function as pressure-gradient receivers as a result of sound transmission
through the interaural cavity. He specifically tested for the amount of sound trans-
mission between the ears and concluded that the internal sound pressure at each
tympanum would be too low to effect the response of the tympanum. Since his
measurements were of the cochlear microphonic and not directly of the sound
pressure we cannot account for the difference between his and our conclusions. In
the following paper (Coles *et al.* 1980), the directional sensitivity of the cochlear
microphonic in the quail is shown to depend on sound transmission across the inter-
aural cavity.

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