4

Directional Hearing in Nonmammalian Tetrapods

JAKOB CHRISTENSEN-DALSGAARD

1. Introduction

The nonmammalian tetrapods—amphibians, reptiles and birds—are a diverse assembly of animals with body mass ranging from below 1 g to more than 100 kg and adapted to almost any habitat on Earth. Apart from being tetrapods, these animals do not form a natural group. However, they share an important functional characteristic—a tympanic ear with a single auditory ossicle—and, as will be outlined below, the limitations of this monossicular ear may impose common constraints on the directional hearing of these species. Another shared constraint in all vertebrates is the general, conserved organization of inner ear and central auditory pathways.

The focus of this chapter is the origin of directional hearing, the general principles of directionality of the monossicular ear, and the special characteristics of directional hearing in the different groups. The main thesis is that the primitive condition of the ear in all groups is one in which the tympana are air coupled and that a pressure-sensitive ear represents a later (derived) specialization. Also, following the current view of the independent evolution of tympanic hearing in these groups, the differences in the organization of neural processing of directional hearing are outlined. This chapter does not attempt to review the older litterature on directional hearing in detail, since it has been covered in excellent reviews (e.g., Fay and Feng 1987; Eggermont 1988; Klump 1988, 2000).

1.1 Origin of the Monossicular Ear

The earlier view of the evolution of tetrapod hearing was based on the general similarity of the tympanic ears of tetrapods and stated that tympanic hearing emerged early in the tetrapods (or even before the tetrapods, van Bergeijk 1966) and was conserved in the lineages leading to recent amphibians and amniotes (Goodrich 1930). However, this view was challenged by Lombard and Bolt (1979) and Bolt and Lombard (1985), who provided evidence from the morphology of the middle ear in recent amphibians and their tetrapod ancestors, leading to the conclusion that tympanic hearing had evolved independently in anurans (frogs and toads) and in the amniotes. Studies on fossil tetrapods have shown that a tympanic middle ear is not a primitive characteristic of tetrapods (Clack 1993) and that even the amniote ancestors probably did not have a tympanic ear (Clack 1997; Manley and Clack 2004). Therefore, the informed consensus today is that the columellar–tympanum connection has emerged independently at least five times, that is, in the lines leading to amphibians, turtles, lepidosaurs (lizards and snakes), archosaurs (crocodiles and birds), and mammals, and that the inner ear (but not the auditory organs!) and middle ear bone (columella/stapes) is homologous in the tetrapods (Lombard and Bolt 1979; Clack 1997; Manley and Köppl 1998).

In this light, the tympanic ears of all groups are independently derived traits, and, furthermore, many of the similarities of the tympanic ears in tetrapods are probably caused by convergent evolution. Also, it is not self-evident anymore that all the central auditory nuclei are homologous in the tetrapods beyond the basic homology as octaval nuclei (McCormick 1999). An obvious, but still important, point to note is that none of the extant groups can be regarded as representing the ancestral condition of any of the others.

1.2 Origin of Directional Hearing

Unfortunately, directional hearing is not linked to any specific morphological character and therefore it cannot be traced in the fossil record. It would be tempting to link the emergence of directional hearing to the emergence of the tympanic ear, but this would be incorrect, since also atympanic ears can show directionality. For example, frogs show enhanced, nontympanic directionality at low frequencies (see Section 3.3.4). Similarly, ancestral tetrapods, even if atympanic, could have had a crude (low-frequency) directional hearing, since the hair cells in their sensory maculae would encode the direction of vibrations of the skull induced by sound: stimulation along the hair cell's axis produces maximal responses with 180° phase difference for stimulation parallel and antiparallel to the hair cell's orientation (see Jørgensen and Christensen-Dalsgaard 1997b and Section 3.3.4). Thus, binaural amplitude and phase comparisons would probably already be useful to sharpen the directional response, and some of the neuronal substrate subserving directional hearing could already have been in place from the early tetrapods. However, the emergence of tympanic hearing changed directional hearing by (1) increasing sensitivity, (2) extending the frequency range, (3) enabling the auditory system to use time-of-arrival and intensity difference cues, and (4) enabling a new directional mechanism by acoustical coupling of the eardrums. Therefore, the emergence of tympanic hearing is an important landmark in the evolution of directional hearing.

The anurans (frogs and toads), the only amphibians that have a tympanic membrane, probably emerged in the Triassic. In the amniote lineages, tympanic hearing also emerged during the Triassic (Clack 1997; Manley and Köppl 1998; Manley and Clack 2004). It has been speculated that this timing coincides with the evolution of sound-producing insects (earliest orthopterans date from the Permian; Hoy 1992) and that the evolutionary push for high-frequency hearing occurred in small insectivores of the different amniote lineages. If this hypothesis is true, localization of sounds associated with prey organisms would also have been a major driving force in the initial evolution of the tympanic ear that was later exploited by secondary adaptations for sound communication in the anurans and some of the amniote lineages.

2. General Properties of the Monossicular Ear

2.1 Structure of the Ear

The structure of the auditory periphery in a representative anuran, lizard, and bird is shown schematically in Figure 4.1. Anurans and lizards show the same general configuration in that they have middle ear cavities that are connected through the mouth cavities by relatively large, permanently open Eustachian tubes, but the anuran head (and body) is generally much more transparent to sound than the head and body of the other groups (see Section 3.3). In birds

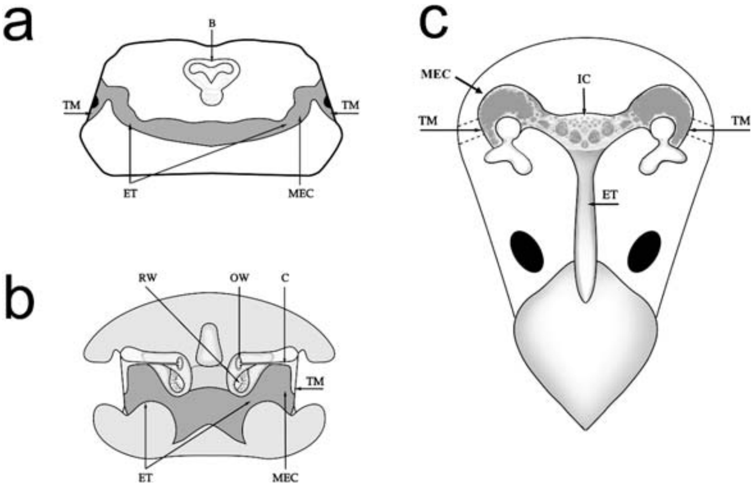


FIGURE 4.1. The middle ear of an anuran (**a**: *Rana sphenocephala*, redrawn from a section shown in Wever 1984), the middle ear of a lizard (**b**: *Sceloporus*, redrawn from Wever 1978), and bird (**c**: zebra finch, *Poephila guttata,* from a preparation, courtesy of O.N. Larsen). Note the large and continuous air spaces in frog and lizard, and the trabeculated interaural canal connecting the bird middle-ear cavities.

and crocodiles, the middle ear cavities are connected by an interaural canal that is connected to the mouth cavity through a common Eustachian tube (Kühne and Lewis 1985). Also, the avian ear has a relatively long external ear canal.

The anurans, reptiles, and birds all have a single auditory ossicle, the columella (homolog to the mammalian stapes) and an extracolumella between columella and eardrum. In reptiles and birds, the extracolumella is an incompletely ossified and complex structure with several processes, whereas in anurans it is a lump of soft cartilage. In all of these species, the columella–extracolumella link has been shown to have an essential function in the impedance matching of the ear by creating a mechanical lever (Manley 1972, 1990; Jørgensen and Kanneworff 1998).

2.2 Pressure and Pressure-Difference Receivers

Tympanic ears can be divided in two functional categories. Ears in which the tympanum lines a closed middle ear cavity are pressure receivers and nondirectional, since they respond to sound pressure, a scalar. An example of a pressure receiver ear is the mammalian ear, in which the Eustachian tubes are narrow and usually closed, resulting in functionally closed and separated middle ear cavities. In pressure receiver ears, directional information is extracted by the central nervous system (CNS) using binaural comparisons of the inputs, such as interaural time differences (ITDs) and interaural level differences (ILDs). In mammals, the duplex theory proposes that localization of low- and high-frequency sounds depends on the ITD and ILD, respectively (Wightman et al. 1987). ITD includes both interaural phase differences (IPDs) and onset time differences (OTDs). IPD is by far the most salient cue to direction at low frequencies in humans (Blauert 1997), and a localization ability based on time differences declines with frequency as would be expected by the decline in phase locking by the auditory fibers. However, at high frequencies, in which neural phase locking is decreased, OTD is probably an important cue for localization of more complex sounds, such as amplitude-modulated sounds, based on timing differences of the sound envelope.

The problem for a small animal in using a pressure receiver is that both the maximal ITDs and ILDs depend on the head size (Michelsen 1994). The simplest approximation of ITD, assuming that sound can penetrate the head, is

$$\mathrm{ITD} = \frac{2r}{c} \cdot \sin\theta$$

where r is the head radius, c is sound velocity, and θ the angle of sound incidence. If—more realistically—sound is assumed to propagate along the head perimeter, the expression becomes

$$\mathrm{ITD} = \frac{r}{c} \cdot (\sin\theta + \theta)$$

(Woodworth and Schlosberg 1962; Blauert 1997; see also Klump 2000 for more accurate approximations). For an animal with a head diameter of 2 cm, for example, the maximal ITD (contra- or ipsilateral sound incidence) is 58 μs using the simplest approximation (76 μs assuming propagation along the perimeter). For a 10° sound incidence angle, the ITD would be reduced to 10 μs. ILDs depend on the diffraction by the head and body of the animal. As a rough rule of thumb, diffraction effects are seen when the dimensions of an object is larger than 1/10 of the wavelength (Larsen 1995), for example, 3.4 cm at 1 kHz, where the wavelength is 34 cm (but note that close to this limit the effects will be very small, and robust effects are seen only for objects larger than 1/4 of a wavelength). Therefore, for most frogs, reptiles and smaller birds measurable diffraction effects are restricted to higher frequencies (above 4 kHz).

In contrast, the principle of the pressure gradient or pressure difference receiver ear is that binaural interaction takes place on the tympanum itself. Sound reaches both sides of the tympanic membrane, and the driving force for membrane motion is proportional to the instantaneous pressure difference between the two sides. Obviously, membrane motion depends on phase as well as on amplitude differences between the two sides of the membrane. The pressure gradient receiver is directional, because the phase shift between sounds reaching the two sides of the membrane is directional, and both ILD and ITD cues are larger than in a pressure receiver ear. However, the directivity (the physical directional characteristics of the receiver) is very frequency dependent. At very low frequencies, the phase difference between direct and indirect sound will be small at any direction of sound incidence, so the vibration amplitudes of the membrane will be small. At high frequencies, the phase difference between direct and indirect sound exceeds 360°; hence, the phase cues become ambiguous.

Any ear in which the two tympana are coupled through Eustachian tubes or interaural canals is potentially a pressure difference receiver. However, for the ear to exhibit any significant directionality, the sound from the contralateral ear must reach the ipsilateral ear with little excess attenuation. Evidently, if there is no diffraction or interaural attenuation, so that the amplitudes of direct and indirect sound are equal, the pressure difference will range from 0 (when direct and indirect sound is in phase) to twice the level of direct sound (when the two sides are 180° out of phase). If the indirect sound pressure is 0.5 that of direct sound pressure p, then the pressure difference ranges from $0.5p$ to $1.5\ p$ and, generally, the smaller the indirect component, the smaller the directionality (ITD as well as ILD; see Klump 2000) generated by the pressure difference receiver. However, at high frequencies where sound is diffracted around the head of the animal, the sound amplitudes reaching the shaded ear can be so small that they are comparable in amplitude to sound reaching the ear via internal pathways, even though attenuation through the internal pathways is considerable (Michelsen 1998).

Any tubelike structure such as the Eustachian tubes will exhibit frequency-dependent attenuation depending on its length and thickness, and this will limit the frequency range within which the receiver is directional. In contrast to the ideal pressure difference receiver, which is just a suspended membrane, in real-world ears the eardrums are connected by tubes and cavities, and the ears behave like a combination of a pressure and pressure-difference receiver (a pressure–pressure difference receiver; Fay and Feng 1987).

2.3 Acoustical Models

The directivity index V for a simple receiver consisting of a membrane, a cavity, and an second sound entry can be modeled by

$$V = 20 \log \frac{1 + B\cos\theta}{1 + B}$$

$$B = \frac{\Delta L}{c \cdot C_A \cdot R_A}$$

(Beranek 1986) where B is a dimensionless constant, ΔL is the distance between the eardrums, c is the speed of sound, C_A is the compliance, and R_A is the resistance of the cavity. With a large interaural resistance, B approaches zero (omnidirectional pressure receiver). Conversely, for small resistances (large B) the directivity will approach $V = 20 \log \cos\theta$, producing a figure-of-eight directionality with a null for sound coming from frontal and caudal directions.

More realistic model calculations have been based on electrical network analog of the auditory periphery of frogs and birds (Fletcher 1992; see Fig. 4.2). For an initiation into such network modeling, the reader is referred to Fletcher and Thwaites (1979) and Fletcher (1992). In brief, any acoustical system in which acoustical flow is one dimensional (such as propagation in tubes and through membranes) will have an analogous electrical circuit in which cavities correspond to capacitors, tubes to inductances (at low frequencies; for high-frequency approximations see Fletcher 1992) and sound absorbers to resistances. At high frequencies, a key assumption inherent in the electrical analogy—that the acoustical elements can be treated as lumped elements—is no longer valid. Therefore, as a rule of thumb all elements must be smaller than 0.5 * wavelength (Morse 1948), that is, 3.4 cm at 5 kHz, which means that the models are applicable only to low-frequency hearing in small animals. These kinds of models are of course strongly simplified; nonetheless, with realistic parameters they make it possible to evaluate the contributions of Eustachian tubes and mouth cavity volume to the measured response. As will be noted below, some of the network models fail to give a reasonable fit to the observed data, usually because some of the basic assumptions are violated, for example, that the sound entrances are not localized, but distributed as in the frogs. In these instances, more sophisticated models are needed.

An even more simplified model of the avian auditory periphery than the network analog was developed by Calford (1988). Here, the difference between direct sound and indirect sound, delayed and attenuated during propagation

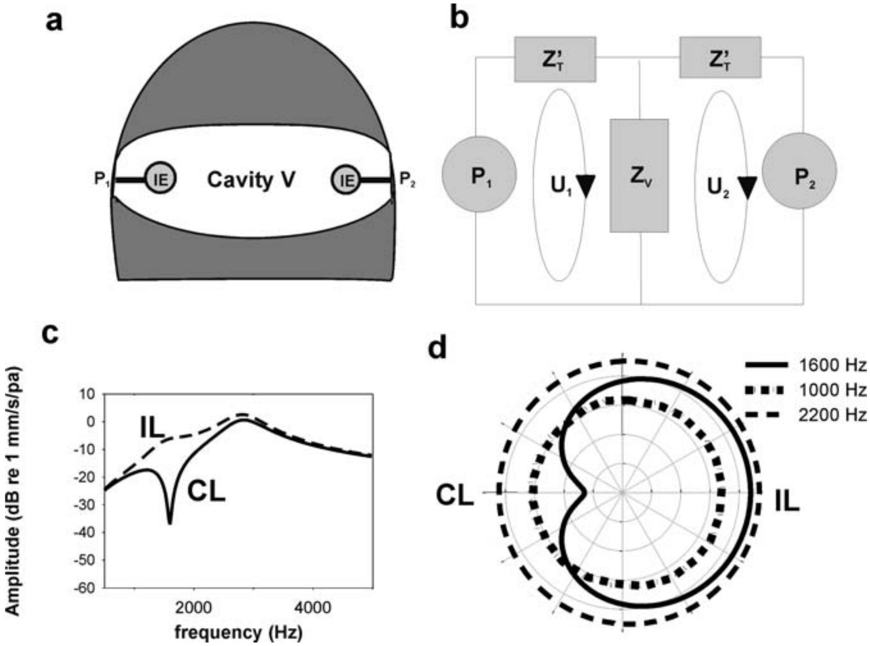


FIGURE 4.2. An example of an analog model of a very simple (lizardlike) ear with two eardrums connected by a large cavity (**a**). The equivalent electrical diagram of such an ear is shown in (**b**). Sound only enters via the tympana (p_1 and p_2) delayed by arrival-time differences, and is filtered by impedances of tympanum (Z'_T) and middle ear cavity (Z_v) before reaching the other tympanum. With 'realistic' parameters the vibration amplitude of the tympana are highly directional in a limited frequency range, as shown by the spectra (**c**) and polar plots (**d**). The parameters used are based on measurements from a lizard. (From Fletcher 1992; Christensen-Dalsgaard and Manley 2005; and unpublished data.)

through the interaural canal, was calculated. The advantages of this model are its conceptual simplicity and that no parameters need to be estimated (the only parameters entering the equations are dimensions of the interaural canal and canal attenuation; both can be measured with relative ease). The model is important, because it allows calculation of the additional delays caused by the indirect pathway. The disadvantage of the model is that the phases of direct and indirect sound are not realistic, since the complex impedances associated with inductance of the interaural canal and Eustachian tube and with the capacitance of the mouth cavity that would generate a (frequency-dependent) phase shift of the indirect signal are neglected. It may be advantageous to use the models discussed by Fletcher (1992, see e.g., pp. 208–212), since they are based on a realistic, if simplified, acoustical description of the system.

2.4 *Optimization of Directionality*

It follows from the paragraphs above that in the optimization of the auditory periphery of a small animal for directional hearing, natural selection can follow one of three courses. Either (1) the animal will be forced to use high frequencies at which diffraction by the head becomes measurable by the ears, (2) the animal will improve its time resolution to use the small ITDs available, or (3) by manipulating the dimensions of the interaural connections the ear will become inherently directional in a limited frequency range. The first solution is the mammalian, where small mammals extend their frequency range of hearing to frequencies at which diffraction produces useful directional cues (Heffner and Heffner 1992), but also used by some bird species, most notably the owls (see below). The second solution is also used by barn owls (Section 5.2) and probably by other bird species. The third solution is used by anurans, reptiles, and some bird species.

There is an obvious reason why nonmammalian tetrapods cannot extend their frequency range to that of mammals of comparable size. As shown by Manley (1972, 1990) for reptiles and birds the ear is impedance matched by insertion of the incompletely ossified extracolumella between eardrum and columella. At low frequencies vibrations of the eardrum is transferred with little loss to the columellar footplate. At higher frequencies, however, the transfer breaks down because the extracolumella–columella link flexes, and a further high-frequency limitation is that the tympanic membrane vibration tends to break up in higher vibration modes at higher frequencies (Manley 1972). In these modes, nodes can form at the extracolumellar attachment, effectively limiting the sound input to the inner ear. The high-frequency limit of the nonmammals does not exceed 12 kHz, and for most species sensitivity drops around 5 kHz. Here, the wavelength is 6.8 cm, so for the smallest animals (head size around 1 cm) diffraction might just be measurable.

2.5 *The Pressure Difference Receiver: Primitive or Derived?*

Consider the emergence of a tympanic ear in a generalized ancestral tetrapod. This animal would have a mouth cavity and a columella probably functioning as a structural element (see Clack 1997). It is likely that the first eardrums would have been especially compliant areas of skin covering fenestrations in the skull and contacted by the columella. The most compliant areas would connect directly to the mouth cavity. Thus, there would be little obstruction of sound reaching the internal surface of the eardrum, and, hence, the ear would in a certain frequency range function as a pressure difference receiver. In contrast, the pressure receiver in the terrestrial tetrapods is considerably more complicated, since it depends on a specialized structure, that is, an enclosed cavity behind the tympanic membrane. Therefore, the pressure receiver ear is probably a derived condition and the pressure difference receiver in the amphibians and reptiles reflects the primitive condition—not necessarily as a special adaptation for directional hearing, but rather as a byproduct of having an ear that is coupled to the respiratory structures. What, then, are the selection pressures that can lead to the pressure receiver?

It is evident that some undesirable effects will result from the ears being coupled to the respiratory and food-intake pathways. One effect is that breathing will produce noise that is very efficiently coupled to the eardrum. However, it may be of equal consequence that the frequency and directional characteristics of the ear are quite variable. Inflation of the lungs and changes of the volume of the mouth cavity will change the characteristics of the ear (Rheinlaender et al. 1981, Jørgensen et al. 1991), and this instability of the ear directivity may pose a problem for the processing of directional information by the CNS. Frog calls tend to be at frequencies at which the directionality of their ear is not maximal, but stable, probably because at the frequencies where the directionality is maximal it is also quite variable (Jørgensen 1991; Jørgensen and Gerhardt 1991; see below). Thus, a step in the evolution of a pressure receiver could be to isolate the ear from the respiratory pathway (see also Clack 1997). The development of a separate interaural canal in the archosaurs (crocodiles and dinosaurs including birds) can be seen as a step in this direction.

Another disadvantage of the pressure difference receiver is that the two ears are functionally converted to one directional ear, since they are coupled. Thus, monaural directional cues generated by diffraction cannot be used. Such cues could aid the segregation of sound components from multiple sources, for example, in distinguishing between one sound source located equidistantly from the ears and two sound sources stimulating each ear equally (auditory streaming, Bregman 1990).

Obviously, an advantage of the pressure-difference receiver is that it produces a directional response at low frequencies, whereas an unspecialized ear may have few directional cues. However, the drawback is that the directionality is strongly frequency dependent. Consequently, the useful frequencies for sound localization may lie in a restricted frequency range. In the context of sound communication, the animal can place its signals within the operational range of the pressure-difference receiver. However, for animals that rely on passive hearing the sound emitted by important sources (such as high-frequency rustling noises made by prey) may lie outside of the useful frequency range. For example, it has been speculated that an evolutionary push for the development of mammalian high-frequency hearing could have been that insect prey increased the frequencies of their communication sounds into the ultrasonic range (Clack 1997). The resulting selection pressure to detect and localize such sounds would lead to improved high-frequency hearing, to a reliance on diffraction cues, and to further the functional isolation of the two ears.

3. Directional Hearing in Amphibians

Directional hearing in amphibians has only been studied in anurans (the frogs and toads). Both the urodeles (salamanders) and the caecilians lack a tympanic ear (although the columella is present), but they may still possess directional hearing comparable to the low-frequency extratympanic hearing of anurans (see Section 3.3.4). Apart from a recent study showing that the marbled newt, *Triturus marmoratus*, will perform phonotaxis toward sympatric anuran choruses (Diego-Rasilla and Luengo 2004), far less is known about these groups than about the anurans.

3.1 Behavioral Studies of Frog Directional Hearing

In almost all species of anurans, males produce advertisement calls to attract females, and the female's identification and localization of the advertisement call is a prerequisite for successful mating. Furthermore, given that the female incurs increased predation risks during her phonotactic approach, it is a reasonable assumption that natural selection should act to shorten the phonotactic approach by maximizing her efficiency in localizing conspecific calls.

It is natural, therefore, that the main focus of behavioral studies of frog directional hearing has been on localization of the mating call, especially since the only robust sound localization behavior in anurans thus far has been observed in phonotaxis. As pointed out by Gerhardt (1995), the problem with this "naturalistic" approach is that behavioral studies on anurans are difficult to compare with psychophysical experiments using conditioning in other animal groups, because there is no way to test the localizability of nonattractive signals (Klump 1995). However, it has proved to be difficult to condition anurans to acoustic stimuli. Food conditioning does not seem to work with acoustic stimuli. So far, the only quantitative results have been obtained with aversive conditioning (Elepfandt et al. 2000) and reflex modification (Megela-Simmons et al. 1985). None of these methods seem to work very robustly in frogs and they have not been applied to directional hearing studies.

In earlier phonotaxis experiments, frogs (usually gravid females) were placed in an arena and the localization path toward a loudspeaker continuously playing the advertisement call was recorded. Not all frog species work equally well in such a setup, but some of the hylid treefrogs have a very robust and consequently well-studied phonotactic behavior. It is unfortunate, though, that the ranid "laboratory" grass frogs *Rana temporaria* and *R. pipiens*, on which the bulk of physiological experiments have been performed, do not exhibit very robust phonotaxis.

A study of the sound localization behavior in two treefrog species, *Hyla cinerea* and *H. gratiosa* (Feng et al. 1976) showed that gravid females could accurately locate the sound source (a loudspeaker broadcasting the mating call continuously at a level comparable to a calling male—86 dB SPL in 2m distance). The phonotactic paths were shown, but the accuracy was not quantified.

Furthermore, the frogs were unable to locate the sound source when one eardrum was covered with vaseline (Feng et al. 1976). In this case, the frogs would turn in circles toward the unoccluded ear, indicating that interaural comparison (acoustical—by the pressure difference receiver—and neural) is necessary for a normal phonotactic response. The accuracy of phonotaxis toward the mating call was quantified in *H. cinerea* by Rheinlaender et al. (1979). The average jump error was 16.1°, but the head orientation error after head scanning movements was smaller (mean 8.4°), as was the jump error after scanning (11.8°), suggesting that scanning improves the localization accuracy. Later, azimuthal localization accuracy was quantified in the species *H. versicolor* (mean jump error angle 19.4°, Jørgensen and Gerhardt 1991), *Hyperolius marmoratus* (mean jump error angle 22.0°, Passmore et al. 1984), and, interestingly, in the small dendrobatid *Colostethus nubicola* (mean jump error angle 23.2°, Gerhardt and Rheinlaender 1980). In other words, azimuthal localization accuracy is remarkably similar in the species studied (around 20°), including in the very tiny *C. nubicola*. However, in this species the small head width (5 mm) is probably compensated for by the high-frequency advertisement call (5 to 6 kHz).

All of the studies discussed above have been so-called closed-loop experiments, in which sound is emitted continuously (Rheinlaender and Klump 1988). In closed-loop experiments the frogs can locate the sound source using lateralization by scanning movements of the head until the ears are equally stimulated, or even simply by following the pressure gradient (by moving in the direction of increasing sound level). In contrast, true angle discrimination must be investigated in open-loop experiments, in which the sound is switched off after the frog has made an orienting response (Klump 1995). Such brief sounds are not attractive in all frog species, and angle discrimination has so far been demonstrated only in the barking treefrog, *H. gratiosa*, that does respond to single sound pulses. Head orienting and jump error angles are 21.2° and 24.6°, respectively (Klump and Gerhardt 1989).

The role of head scanning for localization acuity is a matter of current debate. As mentioned above, head scanning improved localization in *Hyla cinerea* and *Hyperolius marmoratus*. However, in the open-loop study of *Hyla gratiosa*, the localization acuity without scanning was comparable to the acuity in the other species. Furthermore, lateral scanning movements were not observed in *Hyla versicolor* (Jørgensen and Gerhardt 1991).

Many arboreal frog species locate conspecifics calling from elevated sites, that is, they have to localize sound in elevation as well as in azimuth. Localization of sound in elevation was first demonstrated in *Hyla cinerea* (Gerhardt and Rheinlaender 1982). The mean jump error angle of *Hyperolius marmoratus* in a three-dimensional grid (closed-loop) was 43.0°, that is, approximately twice as large as the error angle in a two-dimensional grid (Passmore et al. 1984). In *Hyla versicolor*, the mean three-dimensional error angle was 23° (excluding vertical climbs; with vertical climbs the error angle was 36°), close to the azimuthal error angle of 19.4° (Jørgensen and Gerhardt 1991). The localization of elevated sound sources is still difficult to explain, since mechanisms such as binaural comparisons for azimuthal localization cannot be invoked. The frequency response of the eardrum (see below) seems to vary systematically with elevation (Jørgensen and Gerhardt 1991), but the frog needs a reference to utilize this cue. Vertical head scanning movements would be a possible way to compare auditory responses at different elevation angles, but such movements are not reported for *H. versicolor*. However, the frogs make quick orientation movements in response to sound onset (Jørgensen and Gerhardt 1991), and such movements might enable the frogs to compare different elevation angles. Another possibility is that the frog has some kind of acoustic memory enabling a comparison of sequential responses at different elevation angles. In both cases the elevation angle determination should work only in a closed-loop experiment. Thus, it would be interesting to investigate three-dimensional phonotaxis in an open-loop experiment.

While most of the studies reviewed so far have dealt with localization of single sources, in the real world frogs face the problem of localizing and discriminating in the presence of several sound sources, whether they be masking noise or calling males emitting sound more or less synchronously in a chorus. For example, female *H. gratiosa* were attracted and made accurate phonotactic movements toward a chorus of calling males at least 160 m away (Gerhardt and Klump 1988). The detection of the advertisement call in noise by *H. cinerea* females was shown to improve, but only 3 dB or less, with angular separation of masker and target when the separation was 45° or 90° (Schwartz and Gerhardt 1989). Other angles were not tested, but if the spatial release from masking reflects the directionality of the auditory system, an effect of angular separation should be expected at least down to the 20° found in the phonotaxis experiments.

The ability to separate simultaneously calling males has been investigated in *Hyperolius marmoratus* (Passmore and Telford 1981). Here, neither phonotactic paths nor duration of the phonotactic approach was affected by simultaneous playback of the mating call from two speakers placed 0.5 m apart (corresponding to an angular separation of approximately 35° at the release point of the frog). In a clever experiment, female *H. versicolor* was presented with advertisement calls emitted from either adjacent or spatially separated speakers (Schwartz and Gerhardt 1995). The calls were time shifted so that calls from speaker pairs overlapped, thereby obscuring the temporal pattern (in fact, changing it to the temporal pattern of *H. chrysoscelis*). The test was whether the females would choose the spatially separated pair over the adjacent pair, and it was shown that females would choose pairs separated by 120°, but not by 45°. Even at 120° the preference could be counteracted by dropping the level of one of the adjacent speakers by 3 dB. Compared to neurophysiological data (midbrain multiunit recordings) that showed a 9 dB release from masking for a 120° angular separation, the behavioral performance seems to be relatively poor. One reason may be that the behavioral experiments do not measure directionality as such, but rather female choice—not whether the sounds presented are localizable, but also whether they are attractive. For example, as mentioned by the authors, the female performance could be offset by a preference for closely spaced calling males. However, an alternative interpretation is that processing of sound from multiple sources degrades the localization accuracy, indicating that the separation of sounds emitted simultaneously from multiple sources (i.e., auditory streaming, Bregman 1990) should be difficult for the frog, maybe as a result of the acoustical coupling of the two ears.

3.2 Structure of the Frog Ear

A schematic diagram of the frog ear is shown in Figure 4.3 (see Lewis and Narins 1999 for a full review of amphibian ear structure). In brief, the two large middle-ear cavities are bounded by a tympanum and coupled through the mouth cavity by wide, permanently open Eustachian tubes (see Fig. 4.1a). Vibrations of the tympanum are coupled to the inner ear through the middle ear bone, the columella. The inner ear is encased in the otic capsule that has two major openings, the round and oval window. The columellar footplate sits in the oval window, and uniquely to the amphibians, a second movable element is inserted in the oval window. This is the operculum, which is connected to the scapula through the opercularis muscle. Vibrations generated by the columellar footplate or operculum at the oval window travel through the otic capsule to the other pressure release window, the round window.

Three inner-ear organs can be regarded as acoustic sensors: the otolithic sacculus primarily responds to low-frequency vibrations (BF 40 to 80 Hz), but can

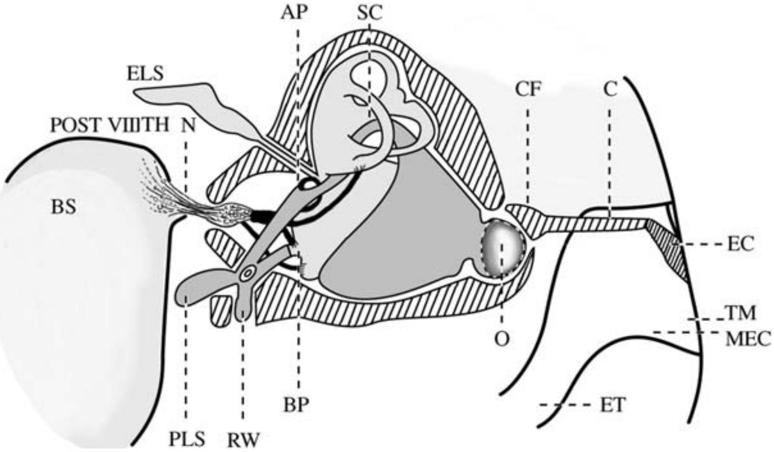


FIGURE 4.3. A diagram of the frog ear seen in transverse section at the level of the eardrum. Note that the operculum (O) is drawn in simulated 3-D (extending out of the plane of the figure). BS, brainstem; ELS, endolymphatic sac; PLS, perilymphatic sac; Post VIIIth n, posterior branch of the VIIIth nerve; SC, semicircular canals. (Redrawn and altered from a diagram by Frishkopf and Goldstein 1963. © 1963 American Institute of Physics; reprinted by permission.)

also be stimulated by intense sounds (Christensen-Dalsgaard and Narins 1993). The amphibian papilla responds to low-frequency sound (from below 100 Hz up to 1200 Hz) and vibrations, while the basilar papilla responds to high-frequency sounds (above approximately 1.5 kHz).

The amphibian papilla (AP) is by far the most complicated of the auditory organs. It contains a large sensory macula in which the best frequencies of the sensory hair cells are organized tonotopically. In contrast, the basilar papilla (BP) is probably a simple resonator that is tuned to a single best frequency, which is usually the higher frequency component of the advertisement call. The AP and BP are located close to the round window and, according to recent measurements of the acoustic flow resulting from columellar vibrations in *R. catesbeiana* (Purgue and Narins 2000), the acoustic flow is directed through the perilymphatic and endolymphatic spaces and diverges according to stimulus frequency. The frequency dependence of the acoustic flow is such that the BP contact membrane is maximally stimulated above 1100 Hz, whereas the AP contact membrane displays a peak for frequencies below 500 Hz.

3.3 Biophysics of Directional Hearing in Anurans

Understanding directional hearing in the anurans is complicated, since sound enters the frog ear by multiple pathways: through tympana, the lungs, the mouth cavity, and the nares as well as through extratympanic pathways. The following paragraphs will characterize each of these inputs.

3.3.1 The Tympanic Input

Anurans lack external ear structures and external ear canals and the tympana are located flush with the skin. In most species, the tympanic membrane is a relatively undifferentiated piece of skin, although in the aquatic clawed frog (*Xenopus laevis*) the tympanic “membrane” is a cartilaginous disk covered with normal skin and suspended in a delicate membranous frame (Wever 1985, Christensen-Dalsgaard and Elepfandt 1995). In the Southeast Asian ranid frog (*Amolops jerboa*), the tympanic membrane is very thin and transparent and clearly differentiated from normal skin (personal observation). The cartilaginous extracolumella is attached to the center of the tympanic membrane and connects it to the columella.

The columella is not driven like a piston by the membrane. Rather, the ventral edge of the columellar footplate is firmly connected to the otic capsule, and the columella rotates around this fulcrum, producing a lever ratio of approximately 6 (Jørgensen and Kanneworff 1998; Werner 2003). The rotational instead of translational movement of the columella has the consequence that inward movement of the tympanum results in outward movement of the columellar footplate, contrary to the motion in amniotes. A key element in the mechanism is that the inward movement of the eardrum is converted to a downward displacement of the distal end of the columella. This happens because the soft extracolumella slides down relative to the eardrum during inward movement of the eardrum (Jørgensen and Kanneworff 1998). However, the weakness of this mechanism probably is the same as described for reptiles and birds whose middle ear transduction also rely on a flexible extracolumella (Manley 1990). At high frequencies, the coupling between extracolumella and columella decreases, and so does the efficiency of transmission of eardrum vibrations to the inner ear.

Another factor that may limit the high-frequency transmission by the middle ear is the changes in the vibration pattern of the eardrum at high frequencies. At low frequencies, the membrane will usually vibrate in the fundamental mode in which all parts of the eardrum move in phase. However, at higher frequencies the eardrum vibration tends to break up into higher modes where parts of the eardrum move 180° out of phase (Jørgensen 1993; Purgue 1997) and the sound radiated to the internal pathways therefore may cancel. Also, in these modes, the site of attachment of the extracolumella may move very little.

3.3.2 The Lung Input

The lungs of several species of frogs vibrate as a simple resonator in the sound field with a characteristic frequency set by the lung volume (Jørgensen 1991) and hence by the size of the frog, and a corresponding low-frequency peak can be seen in the eardrum vibration spectrum (Narins et al. 1988; Jørgensen et al. 1991; Ehret et al. 1993). Furthermore, Jørgensen et al. (1991) showed that the low-frequency peak in *Eleutherodactylus coqui* could be diminished by shielding the lungs (Fig. 4.4). How sound is coupled from the lungs to the middle ear cavity is not clear. The pathway from the lungs to the middle ear cavity is obstructed by the glottal slit. During most of the respiratory cycle the glottis is closed and the lungs inflated. The glottis is open only briefly during the respiratory cycle when the lungs are emptied and refilled with air. Opening of the glottis leads to instant deflation of the lungs. Therefore, the efficient transfer of sound during the brief glottis-open periods is probably not very important in the normal function of the ear. Moreover, when the glottis is closed sound is transferred efficiently from the lungs to the middle ear cavity (Jørgensen et al.

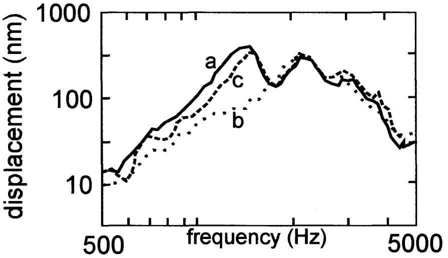


Figure 4.4. The lung input to the ear of *Eleutherodactylus coqui*. The figure shows eardrum vibration spectra measured by laser vibrometry before (*a*) and after (*b*) loading the body wall of awake frogs with Vaseline. Curve *c* shows the response after removal of the Vaseline. The low-frequency peak corresponds to the frequency of body wall vibrations. (From Jørgensen et al. 1991. © 1991 Springer-Verlag.)

1991). This idea was corroborated by the finding that blocking the glottal slit in *Xenopus* reduced the lung input to the tympanum (Christensen-Dalsgaard and Elepfandt 1995).

However, it has also been proposed that sound is transferred from the lungs to the ear through the round window (Hetherington and Lindquist 1999). The round window is isolated by a layer of muscle and connective tissue from the respiratory tract.

Another proposed pathway is through endolymphatic channels that connect directly to the inner ear (Narins et al. 1988). At present sound entry through both pathways are hypothetical and the importance of them needs to be verified by experiment. Finally, the relatively large pulsations of the lungs will generate vibrations in the adjacent tissue that may be coupled to the inner ear (for example, through the scapula and opercularis muscle), even in the absence of specialized structures.

3.3.3 Mouth Cavity and Nares

In earlier studies and models of anuran directional hearing, in addition to the tympana, the nares were regarded as the main point of entry for sound into the mouth cavity (Fletcher and Thwaites 1979; Palmer and Pinder 1984). However, blocking the nares with grease does not affect ear directionality (Aertsen et al. 1986). Furthermore, Vlaming et al. (1984) showed that the effect of stimulating inside the mouth cavity is almost identical to contralateral stimulation and suggested that sound can enter the mouth cavity through the mouth floor with little attenuation. However, it is also evident that opening the mouth obscures the coupling between the two ears and changes the directionality of the ear (Feng 1980; Feng and Shofner 1981; Vlaming et al. 1984). Thus, the mouth floor cannot be totally transparent to sound. A partial solution to this discrepancy could be that the lung input was not known at the time of the experiments of Vlaming et al. (1984). Hence, at least part of the sound entering the mouth cavity could have done so through the lung–glottis pathway described above. Rheinlaender et al. (1981) showed that altering the mouth cavity volume by inserting molds changed the directivity of the ear. They speculated that the frog could actively change the directionality by changing mouth cavity volume. However, their molds only allowed connection between the Eustachian tubes (and in one experiment the nares), so the mouth floor input or lung input was blocked. Thus, the increased directionality could also have resulted from an increased interaural transmission, because the mouth input was blocked. The idea that the frogs would be able to actively change the directionality is attractive, but probably unlikely, since the directional cues generated would be variable and thus difficult to process by the CNS (the same argument as for the variable directionality generated by the lung input; see Section 3.4).

3.3.4 The Extratympanic Input(s)

Neurophysiological experiments (Lombard and Straughan 1974; Wilczynski et al. 1987) showed that the anuran ear is remarkably sensitive at low frequencies, where the eardrum shows very little sensitivity. Wilczynski et al. (1987) compared auditory nerve fiber thresholds in frogs stimulated by a coupler and by free-field stimulation with the eardrum shielded by the coupler housing. They showed that the thresholds for the two stimulation routes were similar up to 1 kHz. Also, the directionality of the low-frequency fibers is pronounced, in contrast to the small directionality measured at the eardrum (Feng 1980; Wang et al. 1996; Jørgensen and Christensen-Dalsgaard 1997a; see Section 3.5.1). Furthermore, some anurans have secondarily lost parts of the middle ear, so they do not have a functional tympanic ear (Jaslow et al. 1988; Hetherington and Lindquist 1999), yet most of these species communicate by sound. Recordings from their auditory system shows responses to acoustic stimulation with thresholds that are elevated compared to tympanate species, but not more than approximately 20 dB in the low-frequency range (Walkowiak 1980). Hence, extratympanic sensitivity obviously is important for low-frequency sensitivity and directionality. The main characteristics (inferred from neurophysiological studies) are: (1) the sensitivity is maximal in the frequency range of 100 to 400 Hz, (2) the extratympanic directionality has a figure-of-eight characteristic with a frontal null, and (3) the phase difference between ipsi- and contralateral stimulation approaches 180° (see Section 3.6.1).

The origin of the extratympanic input is still unknown, but several studies have attempted to assign it to different acoustical pathways. Most interest has centered on the operculum, a movable cartilaginous element inserted in the oval window. The operculum is connected to the scapula by the opercularis muscle. It has been proposed that the operculum could be implicated in extratympanic sensitivity, since the low-frequency sensitivity decreased after section of the opercularis muscle (Lombard and Straughan 1974). Eggermont (1988) speculated that the opercularis complex may have a resonance frequency around 2 to 300 Hz and be acted upon by sound entering through the eardrum and through the mouth cavity. Conversely, Christensen-Dalsgaard et al. (1997) reported that laser vibrometry measurements from the operculum show that it vibrates 20 dB less than the columellar footplate when stimulated with free-field sound. Moreover, the peak vibration frequencies of opercular vibrations were around 1200 to 1500 Hz. It should be noted, however, that they had to expose the operculum for the laser vibrometry measurements, which may conceivably have changed its frequency response.

Christensen-Dalsgaard and Narins (1993) proposed sound-induced substrate vibrations as the origin of the extratympanic sensitivity. However, it was later shown that the low-frequency sensitivity is essentially unchanged when the sound-induced vibrations are canceled (Christensen-Dalsgaard and Jørgensen 1996). Other putative extratympanic pathways, as yet unconfirmed by experiments, may be sound entering via the round window (Hetherington and Lindquist 1999) or via endolymphatic pathways (Narins et al. 1988). Christensen-Dalsgaard et al. (1997) reported that removal of the tympana also affects the low-frequency sensitivity, in contrast to the earlier observations of Lombard and Straughan (1974). The effect of detympanation is largest at high frequencies, but can be measured down to 150 Hz. This puzzling observation shows that the extratympanic sensitivity may be quite closely coupled to tympanic hearing. Jørgensen and Christensen-Dalsgaard (1997b) proposed an alternative model for extratympanic hearing, where the inner-ear fluids are set in motion by a combination of bone conduction and differential motion of otic capsule and columella. The directionality of such a system would result from the fact that the inner-ear fluids will show maximal vibrations when the head is displaced along the axis of the pressure release windows. A hair cell oriented along this axis would show figure-of-eight directivity and a maximal phaseshift of 180° (stimulation parallel and antiparallel to the hair cell's orientation). Frog VIIIth nerve fibers show well-defined best axes of sensitivity to vibration in three dimensions (Brandt and Christensen-Dalsgaard 2001). Manipulations of the system by severing the opercularis muscle or removing the tympanum will change the impedances as seen from the inner ear and may conceivably affect the bone-conduction pathways (e.g., by "shunting" vibrations through the operculum or columellar footplate and reducing the effective stimulus for the sensory cells).

3.4 Measurements of Eardrum Directionality

Eardrum directionality has been measured in several anuran species: *Rana esculenta* (Pinder and Palmer 1983); *R. temporaria* (Vlaming et al. 1984); *Hyla cinerea* (Michelsen et al. 1986); *Eleutherodactylus coqui* (Jørgensen et al. 1991); *R. temporaria*, *H. versicolor*, *H. chrysoscelis*, and *H. gratiosa* (Jørgensen 1991); and *Bufo calamita* (Christensen and Christensen-Dalsgaard 1997). In all species, the frequency response of eardrum vibration stimulated with free-field sound has a bandpass characteristic with one or two peaks, where the low-frequency peak usually corresponds to the frequency of lung resonance (Section 3.3.2).

The eardrum vibration spectrum varies systematically with sound direction. Generally, the resulting polar plots (Fig. 4.5) are ovoidal with a maximal difference of 6 to 10 dB between ipsi- and contralateral sound incidence, but at very low and very high frequencies, eardrum vibration amplitude as well as directionality decreases. Around the lung resonance frequency, eardrum directionality is small, as is the directionality of lung vibrations (Jørgensen 1991; Jørgensen et al. 1991). However, directionality is maximal at frequencies between the two peaks. If this directionality maximum was exploited by the frogs, the call frequencies would be expected to be placed in this frequency region, but that is not the case in any of the species investigated. Jørgensen and Gerhardt (1991) tested whether female *H. versicolor* had improved localization abilities when using these intermediate frequencies and concluded that sound localization was poorer at the intermediate frequencies, at which eardrum directionality is maximal, probably because the directionality at these frequencies is also quite variable and affected by small changes in the inflation of the lungs.

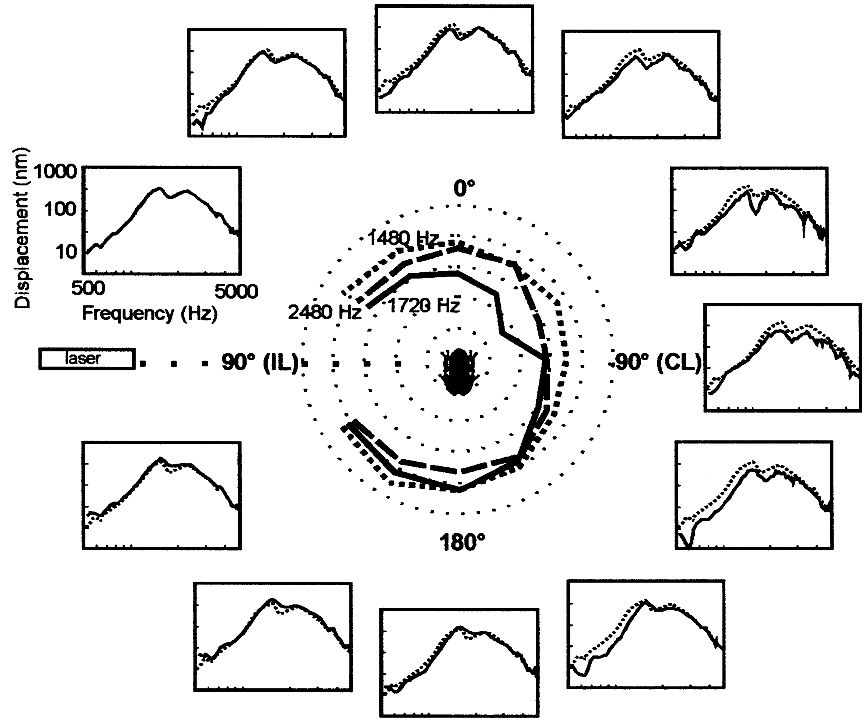


FIGURE 4.5. Directional response of the eardrum in *E. coqui* measured by laser vibrometry. The figure shows polar plots at three frequencies (5 db/circle), and the *inset* figures are vibration spectra taken at different directions. In each figure, the IL spectrum is shown as a reference (thin line). (Redrawn from Jørgensen et al. 1991. © 1991 Springer-Verlag.)

3.5 Models of Anuran Eardrum Directionality

The common characteristic of all current models of the anuran acoustic periphery (Fletcher and Thwaites 1979; Palmer and Pinder 1984; Aertsen et al. 1986) is that they rely on electrical analog models (see Section 2.3). Also, the tympanic inputs and the mouth cavity are modelled similarly in all models. The models differ, however, in the inputs. For example, a crucial element in the model by Palmer and Pinder (1984) is that the input to the mouth cavity is through the nares, that are given a tubelike radiation impedance. In contrast to this, Aertsen et al. (1986) ascribe the mouth cavity input to a delocalized, general transparency of the mouth floor to sound. Aertsen et al. incorporate the directional characteristics of the extratympanic pathway as known from neurophysiology experiments in their model and obtain, not surprisingly, a nice fit to this part of the experimental data.

All models published so far fail to give a reasonable fit to the experimental data if realistic parameters are used. The model by Palmer and Pinder (1984) predicts a figure-of-eight shaped directivity at low frequencies. This directivity is observed in neural recordings, but not in eardrum vibrations and is probably a property of the extratympanic pathway. The model of Aertsen et al predicts generally higher directionality at low frequencies. However, the eardrum vibration measurements (e.g., Jørgensen 1991; Jørgensen et al. 1991) show highest sensitivity and directionality at and between the peak frequencies and very little directionality and sensitivity at low frequencies. One explanation for the discrepancy between model predictions and the experimental data may be that the lung input needs to be incorporated in the models, but another serious problem probably is that some of the sound entrances are not very well localized and therefore cannot be approximated by a single input with a well-defined phase. For example, Vlaming et al. (1984) showed that sound enters via most of the head region. Also, the lung input would essentially cover a large area of the dorsum.

3.6 Neurophysiology of Anuran Directional Hearing

3.6.1 The Auditory Nerve

Afferent nerve fibers from the inner-ear organs are collected in the eighth or auditory nerve that enters the dorsal part of the brainstem. The number of fibers innervating the amphibian papilla ranges from 141 (*Ascaphus*) to 1548 (*R. catesbeiana*); those innervating the basilar papilla range from 31 in *Ascaphus* to 392 in *R. catesbeiana* (Will and Fritzsch 1988). In directional hearing studies, the auditory nerve must be exposed from the dorsal side to allow the animal to sit in a normal posture and to avoid decoupling the ears by opening the mouth. This type of experiments have only been undertaken in two relatively large ranid species: *R. pipiens* (Feng 1980; Feng and Shofner 1981; White et al. 1992; Schmitz et al. 1992; Wang et al. 1996; Wang and Narins 1996) and *R. temporaria* (Jørgensen and Christensen-Dalsgaard 1997a,b). Comparative studies, especially on frogs that have a well-studied phonotactic behavior (e.g., hylids), are thus badly needed.

In the following, neural coding of direction by spike rate and spike timing will be discussed. It should be realized from the outset that this separation is somewhat artificial, since spike rate and spike timing are linked through phenomena such as intensity-latency trading, in that spike latency decreases monotonically with stimulus level, whereas spike rate usually shows a monotonic increase (Feng 1982; Jørgensen and Christensen-Dalsgaard 1997b). Furthermore, in the central processing of auditory nerve information in the frogs, there is at present no evidence of separate time and intensity pathways such as reported, for example, for barn owls (see Section 5.2.4). Rather, in the CNS both response timing and response strength are integrated, for example, by inhibitory interneurons in the DMN where the output depends both on input timing and strength (see Section 3.6.2).

3.6.1.1 Spike-Rate Coding of Sound Direction

Single-cell recordings from the anuran auditory nerve using free-field stimulation have shown that the auditory fibers have two types of directional responses (Feng 1980; Jørgensen and Christensen-Dalsgaard 1997a; see Fig. 4.6). For low-frequency stimulation, a polar plot of spike rates shows a figure-of-eight directivity pattern with a frontal "null," that is, very low sensitivity to sound coming from the frontal and caudal directions, and equally high sensitivity to sound from ipsi- and contralateral directions. The axis of least sensitivity is tilted relative to the frog's symmetry axis. For high-frequency stimulation, the directivity pattern is ovoidal with the highest sensitivity for sound coming from the ipsilateral direction. The directivity pattern of a fiber depends on its char-

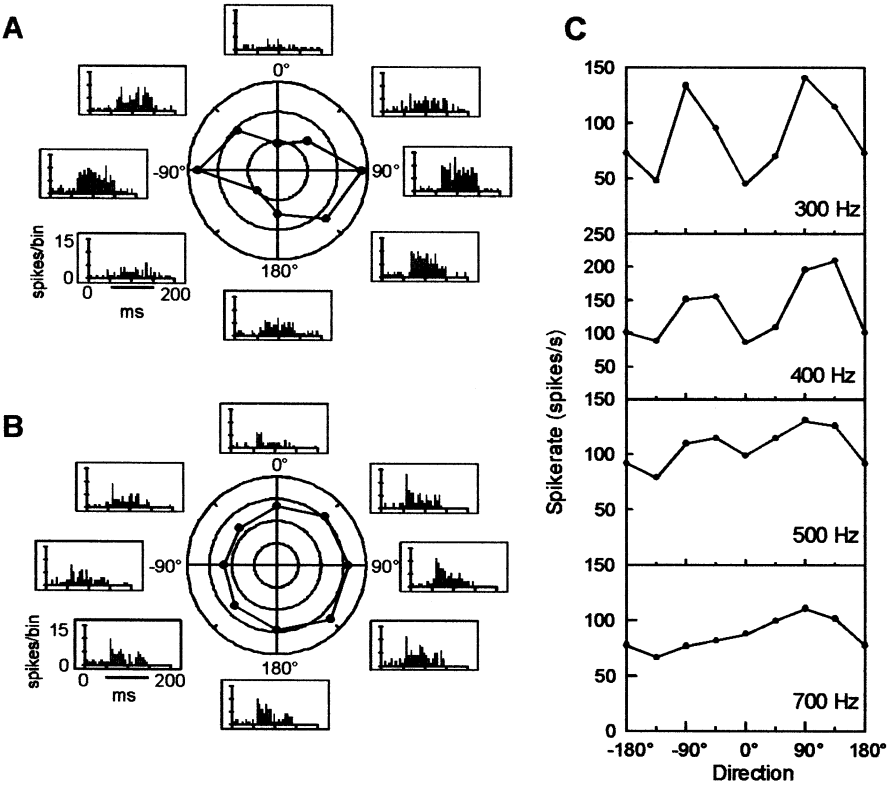


FIGURE 4.6. Response of VIIIth nerve fibers in *Rana temporaria* to directional stimulation. (**A**) Response of a low-frequency fiber stimulated at BF (300 Hz). Note the "figure-of-eight" response with low sensitivity at frontal directions. (**B**) Response of a BP fiber stimulated at its BF (1500 Hz). Here, the response is ovoidal. In (**C**) the response of a fiber stimulated at different frequencies shows that the response changes systematically with frequency. (From Jørgensen and Christensen-Dalsgaard 1997a. © Springer-Verlag.)

acteristic frequency (CF, the frequency where the cell is most sensitive) and not on stimulus frequency (Feng 1980; Jørgensen and Christensen-Dalsgaard 1997a). Accordingly, tuning curves change shape with stimulus direction (White et al. 1992).

For all fibers, the directionality depends strongly on stimulus intensity. Since almost all fibers have a relatively narrow dynamic range (median 20 dB) and saturating rate-level curves (Christensen-Dalsgaard et al. 1998), at high stimulus intensities the directionality will also show saturation and therefore decrease. Conversely, at low stimulus levels the response from some of the directions will be below threshold. Note, however, that this limited dynamic range is not necessarily a problem in the processing of directional information, since the thresholds of fibers span a range of approximately 60 dB, and, furthermore, cells with different CFs will be recruited at high stimulus intensities. When the spike rates are recalculated as equivalent decibel values by reading the levels corresponding to the measured spike rates off the fiber's rate-level curve (measured with ipsilateral stimulation) (Feng 1980), the resulting directivity is the directivity of the entire acoustic periphery and can be compared to the directivity of the tympanum such as Fig. 4.5. For the low-frequency fibers the maximal differences between ipsi- and contralateral stimulation in equivalent dB is 15 dB in *R. temporaria* (Jørgensen and Christensen-Dalsgaard 1997a) and 1 to 8 dB in *R. pipiens* (Feng 1980). For high-frequency fibers, the maximal directional difference is 10 dB in *R. temporaria* and 5 to 10 dB in *R. pipiens*. The high-frequency directivity is directly comparable in shape and magnitude to the directivity of the eardrum. However, at low frequencies, where the eardrum shows little directivity, the nerve fibers show the highest directionality and a figure-of-eight directivity pattern that is not found in the eardrum measurements. Here, the nerve fiber directivity undoubtedly reflects the directionality of the extratympanic pathway. Simultaneous single cell recordings and laser vibrometry measurements in *R. pipiens* auditory nerve fibers showed that 55% of the fibers show some degree of extratympanic directionality (Wang et al. 1996). Interestingly, however, in detympanated frogs the low frequency directionality is also changed, suggesting that detympanation also affects the extratympanic pathway (Christensen-Dalsgaard et al. 1997). When interaural transmission in *R. pipiens* is reduced by filling the mouth cavity, directionality at all frequencies decreases and the directivity patterns of the auditory fibers are ovoidal (Feng and Shofner 1981; see Fig. 4.7, second row). It may be surprising that blocking the mouth cavity also changes the directivity pattern at the low, extratympanic frequencies. However, it should be realized that filling the mouth cavity not only blocks interaural transmission. By blocking sound access to the middle ear cavity, the ear is converted to a pressure receiver, and this changes the frequency response of the eardrum and its directionality. After covering the contralateral eardrum, the directionality and directivity pattern of the low-frequency fibers was unchanged, but for mid- and high-frequency fibers directionality decreased and the directivity pattern changed to omnidirectional (Fig. 4.7, third row). When the frog's mouth was forced open, an increased directionality and a figure-of-eight

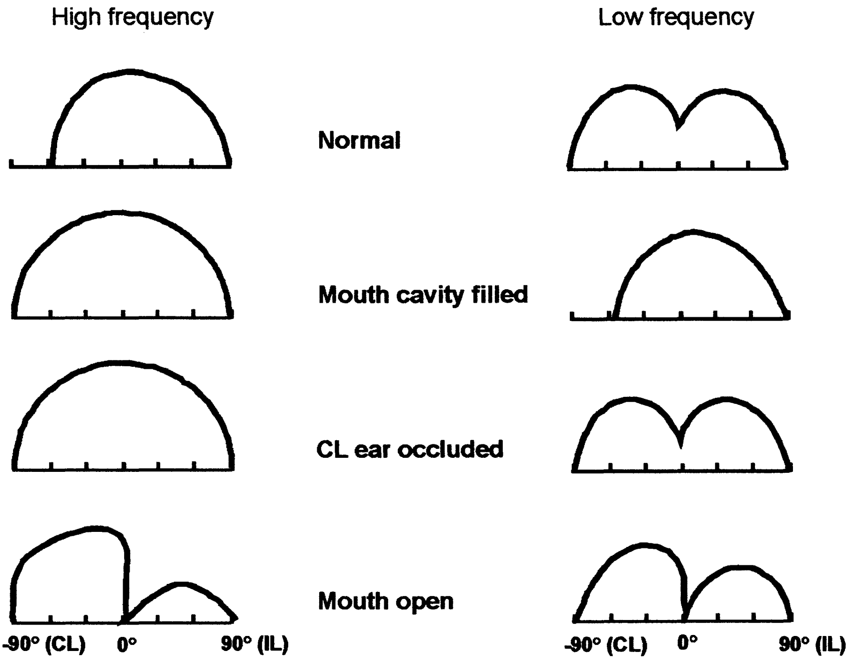


FIGURE 4.7. Directional response of *R. pipiens* auditory fibers after manipulations of the auditory periphery. (Reprinted from Feng and Shofner 1981. © 1981 with permission from Elsevier.) See text for details.

directivity pattern was found at all frequencies (Feng and Shofner 1981; Fig. 4.7, bottom row). Conceivably, opening the mouth changes the characteristics of the ear to that of a pure pressure-difference receiver, probably caused by easy access of sound to both sides of the eardrums. Interestingly, this result again suggests that the mouth floor is not transparent to sound (see above). Taken together, Feng and Shofner's experiments are consistent with the view that low-frequency directionality essentially is extratympanic, whereas directionality at higher frequencies is produced by the acoustics of the coupled middle-ear cavities and respiratory pathway resulting in combined pressure–pressure-difference receiver directivity.

3.6.1.2 Spike Timing Coding of Sound Direction

Response timing in auditory nerve fibers of *R. pipiens* and *R. temporaria* depends on the direction of sound incidence (Schmitz et al. 1992; Jørgensen and Christensen-Dalsgaard 1997b). Schmitz et al. investigated the directionality of phase locking and showed that preferred phase, but not vector strength (i.e., the degree of phase locking), varied systematically with sound direction. Polar plots of the phase differences showed an ovoidal directivity, and the directionality of phase locking decreased with fiber CF. Contralateral stimulation always produced a phase lead relative to ipsilateral stimulation. The magnitude of the phase lead was, however, quite variable (150° to 360° in the 200 to 300-Hz range). Jørgensen and Christensen-Dalsgaard (1997b) found qualitatively similar results showing a phase lead for contralateral stimulation in 84 of 86 neurons (the remaining two showed a phase lead for ipsilateral stimulation), but a much more homogeneous distribution of phase leads. They report a mean phase shift of 140° at 200 to 300 Hz decreasing with frequency to 100° at 600 to 700 Hz. These phase shifts correspond to time shifts of 2 ms at 200 Hz and 0.5 ms at 700 Hz (see Fig. 4.8). In contrast, the maximal timeshift resulting from arrival time differences at the two eardrums is only 60 μs (assuming a 2-cm interaural distance). Measurements of the directional phase shift at the eardrum show a maximal difference of 60 to 100°. At higher frequencies, therefore, the phase shifts of the fibers are largely caused by the directionality of the frog ear. At 200 to 300 Hz, however, the phase shift is caused by the extratympanic pathway (see Section 3.4.4). Spike latencies also show systematic changes with sound direction with a difference of up to 2 ms between ipsi- and contralateral stimulation. The latency difference is probably caused by directional changes in stimulus intensity (time-intensity trading). Both the directional latency and phase changes produce large interaural time differences. Jørgensen and Christensen-Dalsgaard (1997b) calculated that a hypothetical binaural neuron in the CNS that compared inputs from two auditory fibers with equal directional characteristics would register systematic variation in interaural time differences with direction with a range of ± 1.6 ms.

These directional effects are only seen at frequencies to which the auditory fibers show robust phase locking (below 500 to 600 Hz). However, the auditory fibers also show phase locking to the envelope of amplitude modulated (AM) stimuli (Christensen-Dalsgaard and Jørgensen, in preparation). The time shift of the spikes again varies systematically with direction, but surprisingly, there is now a phase lead for stimuli from ipsilateral directions. The time shifts (up to 3 ms) are comparable to those produced by phase locking to the carrier and

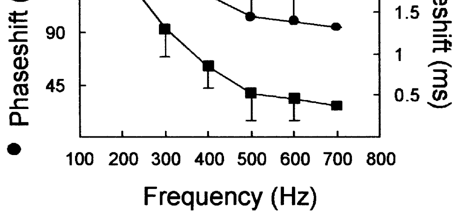


FIGURE 4.8. Ipsilateral–contralateral phase shifts in *R. temporaria* auditory fibers. The two curves show phase shifts (*circles*) and time differences calculated from the phase shifts (*squares*). Note the decline in phase difference with frequency, but also that the phase shift at the higher frequencies is much larger than expected from the head size. (From Jørgensen and Christensen-Dalsgaard 1997b. © Springer-Verlag.)

are independent of AM rate and carrier frequency. Similar directional time shifts are found for stimulation with the advertisement call, but not for stimulation with AM noise. If the AM time shifts were caused by time-intensity trading, so the effects were due to directional changes in stimulus intensity, the time shifts should be smaller, with high AM rates producing shorter rise–fall times and should be independent of the carrier (tone/noise). Since this is not the case, the time shifts are generated by an unknown mechanism, perhaps related to short-term adaptation during the AM stimulus.

3.6.2 Processing of Directional Information in the Dorsal Medullary Nucleus (DMN)

The first auditory nucleus, the DMN (see Fig. 4.9) (also called the dorsolateral or dorsomedial nucleus), is also the first stage in the processing of directional information (for a review of central auditory processing, see Feng and Schellart 1999). DMN has traditionally been homologized with the mammalian cochlear nucleus, but it is now realized that the "homology" is as octaval nucleus (Will 1988; McCormick 1999) and does not imply similarity in processing of auditory stimuli, given the independent origin of tympanic hearing in the two groups. Also, in contrast to its mammalian counterpart (the cochlear nucleus) the DMN is innervated by commissural fibers from the contralateral DMN (Feng 1986; Will 1988). Anatomical studies of the DMN have shown that the nucleus is heterogeneous in that it has six different cell types (Feng and Lin 1996), although it does not exhibit the clear subdivisions found in its amniote counterparts (Will 1988). So far, nothing is known about the location and morphology of the binaural cells in the DMN. Dichotic stimulation (where the ears were uncoupled by opening the mouth) of neurons in the DMN in *Rana catesbeiana*

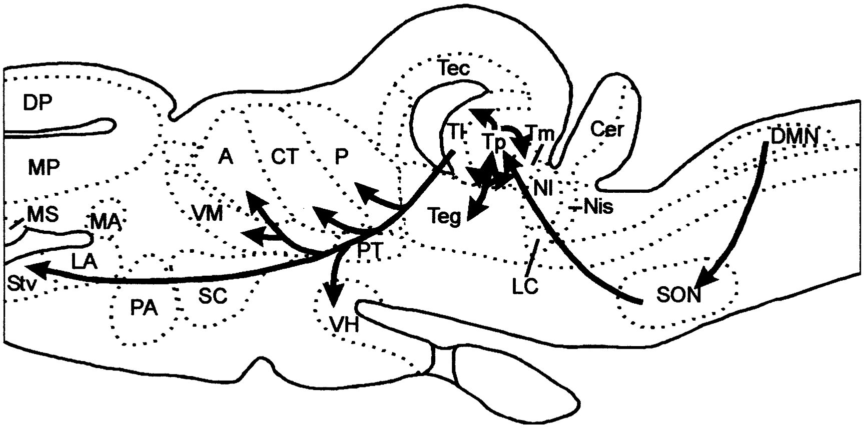
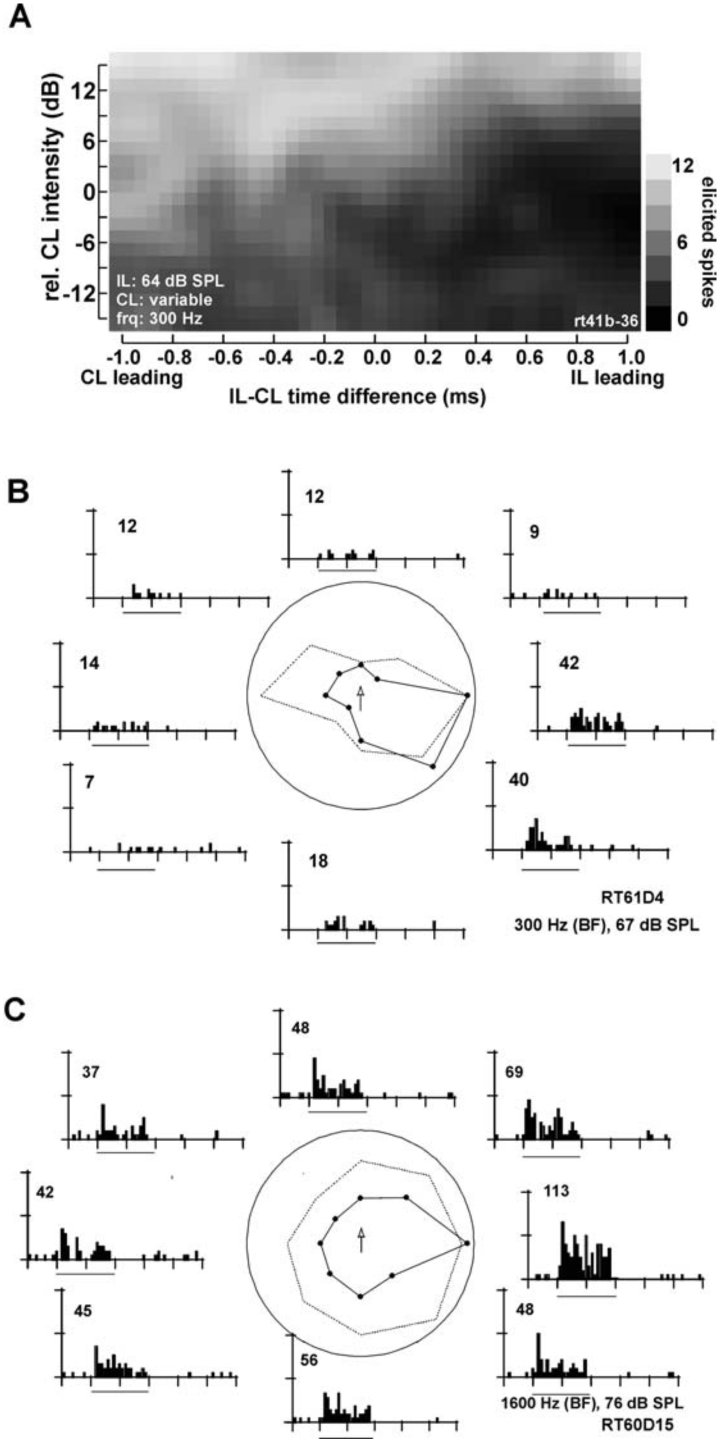


FIGURE 4.9. Diagram of the ascending auditory connections in the anuran brain. (Redrawn from Endepols et al. 2000. © 2000, with permission from Elsevier.)

(Feng and Capranica 1976) showed that approximately half of the cells studied were monaural and that most of these cells were excited by the ipsilateral ear. Of the binaural cells, most were EI cells (excitatory = inhibitory, meaning that they were excited by one ear and inhibited by the other). In most of these cells, the contralateral ear was excitatory. The EI cells were sensitive to interaural time differences of 150 μs and interaural level differences of 3 dB. Recently, binaural cells in *R. temporaria* have been studied using both closed-field and free-field stimulation (Christensen-Dalsgaard and Kanneworff 2005; Kanneworff and Christensen-Dalsgaard, in preparation). A subset of cells is inhibited by a combination of ITD and ILD (Fig. 4.10a). ITD responses are always seen as inhibition, and the cells probably respond to IPD (the ITD response is repetitive with the stimulus cycle). Interestingly, the responses are similar to recent data from mammals (Brand et al. 2002) where ITD sensitivity is generated by precise, fast inhibition. Using closed-field stimulation, it is possible to separate neural interaction from acoustical interaction resulting from coupling of the ears. However, it may be difficult to relate the results to natural, free-field stimulation. In a pilot study of free-field responses of DMN neurons, Christensen-Dalsgaard and Kanneworff (2005) report that the directionality in many cases was not much different from the directionality of VIIIth nerve fibers (Fig. 4.10b, c). However, most low-frequency neurons (Fig. 4.10b) showed ovoidal directivity in contrast to the figure-of-eight directivity of the auditory nerve fibers. Also, some of their high-frequency neurons (Fig. 4.10c) show increased directionality that probably is caused by inhibition. Such a sharpening probably is caused by the EI neurons. Note that the minimal ITD where inhibition in EI neurons was observed in Feng and Capranica's study (1976) was only 150 μs. As stated above, in a free sound field the directional interaural time difference found in the auditory nerve fibers can be much larger (up to 2 ms latency differences; Jørgensen and Christensen-Dalsgaard 1997b). If the latency difference of the DMN neurons to contra- and ipsilateral stimulation is 1 to 2 ms (reported by Feng and Capranica 1976, for the EE [excitatory-excitatory] neurons) the response of an EI neuron could range from total inhibition (inhibitory side leads) to a shortened excitatory response (excitatory side leads), depending on inhibitory and excitatory strength. Conversely, the EE cells that receive excitatory input from both ears probably do not increase the directionality compared to the auditory nerve fibers, unless they are coincidence detectors that have so far not been reported from the anuran

▶

FIGURE 4.10. Responses of neurons in the DMN of *R. temporaria* to dichotic stimuli (**A**) and free-field stimulation (**B**, **C**). (**A**) is an ITD–ILD response area; the number of spikes elicited at each combination is indicated by a grayscale code. This low-frequency neuron is inhibited at ITDs from 0.4 to 1 ms, IL leading. (**B**, **C**) shows the response of two DMN neurons to free-field sound. The thin line is the average response of VIIIth nerve fibers at the same best frequencies (**B**: 300 Hz, **C**: 1500 Hz), indicating a sharpening of directional sensitivity already at this stage. (From Christensen-Dalsgaard and Kanneworff 2005. © 2005, with permission from Elsevier.)


A
rel. CL intensity (dB)
12
6
0
-6
-12
IL: 64 dB SPL
CL: variable
frq: 300 Hz
rt41b-36
12
6
0
elicited spikes
-1.0 -0.8 -0.6 -0.4 -0.2 0.0 0.2 0.4 0.6 0.8 1.0
CL leading
IL leading
IL-CL time difference (ms)
B
12
12
9
14
42
7
40
18
RT61D4
300 Hz (BF), 67 dB SPL
C
48
37
69
42
113
45
48
56
1600 Hz (BF), 76 dB SPL
RT60D15

DMN. Note also that, in contrast to avian and mammalian auditory systems, there is no evidence of a segregation of time and intensity pathways at this stage. Rather, the response of the EI cells depend both on level and time difference.

3.6.3 Processing of Directional Information in the Superior Olivary Nucleus (SON)

The SON of anurans (Fig. 4.9) receives projections bilaterally from the dorsolateral nuclei with most prominent projections from the contralateral DMN (Will 1988). It has no subdivisions comparable to the lateral and medial olivary nucleus of amniotes, but is tonotopically organized (Wilczynski 1988). The SON has traditionally been homologized with the amniote SON, but as for the DMN, the homology is disputed (Will 1988; McCormick 1999), as is the homology of the SON within the amniotes (Carr and Code 2000). Only one study of directional processing in the SON has been published (Feng and Capranica 1978). Here, responses of SON neurons in *H. cinerea* to dichotic stimulation were investigated. A little less than half of the cells were binaural, and most of these were EI cells. Generally, the directional response characteristics of these cells are very similar to those of the DMN cells. From the limited data available there is no indication of a sharpening of the directionality or a separation in time and intensity pathways as reported for the SON of birds and mammals, but further investigations of the directional processing in the SON are obviously needed.

3.6.4 Processing of Directional Information in the Torus Semicircularis (TS)

The anuran midbrain auditory center TS in anurans is homologous to the inferior colliculus (IC) of mammals and birds and to the torus semicircularis in reptiles (Carr and Code 2000). It is subdivided into five nuclei of which three—the principal (T_p), magnocellular (T_m) and laminar nuclei (T_l)—are auditory (see Fig. 4.9). The principal nucleus receives most of the inputs from the caudal brainstem nuclei, for example, direct projections bilaterally, but predominantly from the contralateral DMN and from the ipsilateral SON. The arborizations of cells in the principal nucleus are small and projections are found mainly within the torus (Luksch and Walkowiak 1998). This nucleus is tonotopically organized. The magnocellular and laminar nuclei receive most of their ascending projections from the thalamus and have descending projections to the DMN and SON (Feng and Lin 1991). The cells in these nuclei differ in their projection patterns, one cell type in each having mainly intrinsic projections within the TS (Luksch and Walkowiak 1998). To summarize, the principal nucleus is the input layer of the TS, whereas the other nuclei serve audiomotor functions, the laminar nucleus probably being the main output station of toral auditory processing (Luksch and Walkowiak 1998). (Note, however, that the organization of the TS in the aquatic frog *Xenopus laevis* is apparently totally different. Here, the laminar nucleus receives all ascending projections from the DMN, and the principal and magnocellular nuclei receive projections from the lateral line nucleus [Edwards and Kelley 2001]). In contrast to the paucity of data from the lower auditory stations in the CNS, the accessibility of the TS has generated a wealth of neurophysiological data on processing of directional information. Kaulen et al. (1972) made single-cell recordings from TS with dichotic (coupler) stimulation in "the frog"and found that most of the cells were monaural. Approximately 40% were binaural, and half of these were EE cells. Of the rest, almost all were EI cells (ipsilateral inhibitory). Unfortunately, in these experiments as in some of the later studies, the mouth was closed during the recordings, so the ears were coupled acoustically. This probably leads to an overrepresentation of EE cells (Epping and Eggermont 1985), but could also influence the responses of EI cells. With free-field stimulation, most cells in the TS show direction-dependent changes in firing rates and/or latencies (Feng 1981). The units were distributed over the principal, magnocellular and laminaris nuclei and showed two major classes of directional responses. Most (with CFs ranging from 135 to 2100 Hz) had ovoidal directional responses, usually with highest sensitivity from the contralateral side. The rest (CFs ranging from 295 to 1950 Hz) had "V-shaped" (i.e., figure-of-eight) directional responses. Note that these types of directional responses are also found in auditory nerve fibers (see Section 3.5.1). In auditory nerve fibers, however, the directivity pattern is frequency specific (V-shaped at low and ovoidal at high frequencies), and V-shaped directional TS responses at high frequencies reflects additional processing by the CNS. Mellsen and Epping (1990), using closed-field dichotic stimulation in *R. temporaria* found that almost all units were binaural. Of the binaural units, most were EI units with BFs uniformly distributed between 100 and 3000 Hz and most sensitive to IIDs from −4 to 4 dB. Forty percent of the units showed intensity-invariant responses. Gooler et al. (1993) showed that tuning curves of single neurons in the TS (free-field stimulation) varied systematically with sound direction; the tuning curves were broader with contralateral than with ipsilateral stimulation. Similarly, the isointensity frequency response showed a narrower bandwith for ipsilateral than for contralateral stimulation (Xu et al. 1994). That these effects are due to neural interactions, especially ipsilateral inhibition mediated by γ-aminobutyric acid (GABA), has recently been shown in a series of elegant experiments (Zhang et al. 1999). However, it is also suggested that binaural interactions probably takes place in lower stations in the brainstem, maybe also by GABA-mediated inhibition, or more likely by faster inhibitory transmitters such as glycine. While most of these studies deal with ILDs, it should be noted that there is apparently not a clear division of time and level processing in the anuran auditory pathway. Rather, as discussed for the auditory nerve and DMN, directional phase and level changes are coupled. Furthermore, the effects of inhibition probably are intensified by the large timeshifts that accompany directional changes in level in the auditory nerve. Approximately half of the units in the TS showed intensity-invariant responses to click stimulation, and most ITD-selective units showed a well-defined latency of the response to the excitatory, contralateral stimulus (Melssen and Epping 1992). The inhibitory, ipsilateral stimulus depressed activity within a time window of a few milliseconds following excitation. Whether there is a spatiotopic organization of the TS neurons (i.e., an auditory space map) is controversial. Pettigrew et al. (1981) found spatiotopy in multiunit recordings from the TS of *R. temporaria* and *Rana esculenta*. They also proposed the simple explanation that if the best direction of a neuron varied systematically with frequency, this would produce a spatial map because of the tonotopicity in TS. This idea was corroborated by field potential recordings in *B. marinus* by Pettigrew and Carlile (1984) suggesting that the optimal stimulus angle changed with frequency. However, other studies (Wilczynski 1988) have shown that the tonotopicity in TS is not very pronounced, and furthermore, Pettigrew and Carlile probably included areas outside the TS in their data. To conclude, it is probably safe to say that no robust spatiotopy is found in the anuran TS and that the data are compatible with a model in which sound direction (encoded in the spike rate of individual TS neurons; Feng 1981) is processed in separate frequency channels (since the TS neurons are tuned) and encoded by neuronal ensemble activity. At the population level the directional information is sharpened by inhibition in the TS that will produce strong lateralization cues.

3.6.5 The Processing of Directional Information in the Forebrain

Next to nothing is known about directional processing in the forebrain. Lesion experiments have shown that female toads (*B. americanus*) will perform phonotaxis after complete removal of the telencephalon and dorsal diencephalon (Schmidt 1988). However, Walkowiak et al. (1998) showed that phonotaxis in *H. versicolor* was affected by lesions in the septum (MS, see Fig. 4.9) and the striatum (Stv) and abolished completely by lesions in the preoptic area (PA), but apparently unaffected by lesions in the dorsomedial pallium (DP, MP). Lesions of the thalamus (A, C, P) did not affect phonotaxis, whereas even small lesions in the torus produced a degraded phonotactic response (Endepols et al. 2003). In summary, the forebrain lesions seem to affect only the initiation or control of the phonotactic response. The experiments do not permit any evaluation of whether directional hearing as such is degraded (as would, e.g., lesion experiments showing that the frogs showed phonotaxis, but that localization accuracy was reduced), but show that all the processing necessary for sound direction determination likely occurs in the TS. The question then is how pattern recognition (i.e., mating call identification) and localization are integrated in the TS (apparently, there are no specialized centers for spatial hearing and pattern recognition), and, even more fundamentally: How is the directional information "read out"? Obviously, the contralateral inhibition found in the TS (Zhang et al. 1999) can generate a robust lateralized response in a "winner takes all" fashion. However, such a simple lateralization does not explain the behavioral results showing true angle discrimination (Klump and Gerhardt 1989). The absence of any robust spatiotopy as well as the generally distributed nature of frequency representation in the TS might suggest that directional information is processed in separate frequency bands (since the directional input is strongly frequency dependent, see above; note also that all the directionally sensitive TS cells are tuned) and integrated with pattern recognition subsystems to generate a direction-specific (but probably distributed) excitation pattern. Each excitation pattern could then elicit a pattern of muscle activity turning the frog in the relevant direction. Whether the frog would move or not would then be controlled by inhibition (i.e., forebrain structures). Interestingly, a simulation experiment on visual orientation in salamanders showed that a relatively small network consisting of 300 neurons (100 optic tectum [OT] neurons with "coarse coding," i.e., large receptive fields, 100 interneurons, 100 motoneurons, and 4 muscles) and incorporating neuroanatomical and physiological features of the salamander visual brain can be trained to localize moving prey (Eurich et al. 1995). The model does not incorporate a motorneuron map. Rather, all neurons participate in coding of prey location, and the distributed coding of the tectal neurons is transformed directly into a distributed activation of the muscles. It remains to be shown whether phonotaxis in anurans can be explained by similar models. What is needed is probably simultaneously recordings from many neurons under directional stimulation.

4. Directional Hearing in "Reptiles"

The reptiles do not form a "natural" taxonomic group, since they are amniotes united by primitive characteristics (i.e., a paraphyletic group; see Manley 2004). Thus, crocodiles are more closely related to birds than to the other reptile groups, and turtles and tortoises are as distantly related to other reptiles as to mammals. This section concentrates on lacertids (the lizards), since the (few) data available on reptile directional hearing have been obtained in this group.

4.1 Behavioral Investigations of Lacertid Directional Hearing

Only in one case has a behavioral use of directional hearing been demonstrated in any lizard (or reptile). It was shown that Mediterranean geckos (*Hemidactylus tursicus*) will intercept calling crickets and also perform phonotaxis toward a speaker playing cricket songs (carrier frequency 6.6 kHz; Sakaluk and Belwood 1984). Interestingly, the data suggest that the behavior is acquired, since only adults show a significant phonotactic response. The members of one lacertid family, the true geckos (Gekkonidae) are highly vocal, but no phonotaxis (or indeed any clear responses) to call playbacks have been shown so far. Investigations of hearing using conditioned responses to sound in the reptiles have met with as little success as in the anurans (Manley 2000). However, one experimental approach seems to work, namely that lizards open their eyes in response to sounds (Berger 1924). An audiogram from *Tiliqua rugosa* based on this paradigm matches the neural audiogram reasonably well (Manley 2000). This approach has so far not been applied to directional hearing studies, but it would be interesting in the future to investigate, for example, directional release from masking or habituation.

4.2 The Lacertid Ear

Lizards do not have an external ear, although some species have an external ear canal, while in other species the eardrum is flush with the surrounding skin. The tympanic membrane is usually delicate and clearly distinct from normal skin and is usually convex. The single auditory ossicle, the columella, is connected to the eardrum by an extracolumella, that is generally not strongly ossified and with up to four fingerlike processes (Wever 1978; Manley 1990; Saunders et al. 2000). The extracolumella is probably essential for the impedance matching of the ear by being one arm in a second-order lever system with a lever ratio of approximately 3 in *Gekko gecko* (Manley 1990) and 2 in an eublepharid and a pygopodid gekko species (Werner et al. 1998). An essential feature of the lever system is that there is a flexible connection between extracolumella and columella. At low frequencies (below 4 kHz) the extracolumella pivots as a stiff rod around a fulcrum and pushes the columella. As pointed out by Manley (1990), the system is less efficient at high frequencies, because the energy is lost in flexion at the extracolumella–columella joint and thus poorly transmitted. A limited high-frequency response thus appears to be an inherent drawback of the design.

4.3 Biophysics of Lacertid Directional Hearing

Very little information exists on lizard directional hearing. Wever (1978), noting the very wide Eustachian tubes, suggested that the ear of some lizards could operate as a pressure-difference receiver. However, most of the earlier studies of the eardrum response were made using closed field stimulation. Preliminary data from a free-field investigation of midbrain auditory neurons in *G. gecko* is reviewed by Manley (1981), who together with co-workers found highly directional units in the torus semicircularis. These units exhibited ovoidal directivity with activity almost completely suppressed at (mostly) ipsilateral angles. However, as Manley (1981) pointed out, the responses are probably both due to neural inhibition and acoustical interaction. Recently, Christensen-Dalsgaard and Manley (2005) have studied the directional characteristics of the tympanum in four lizard species stimulated with free-field sound. The tympana of all species showed bandpass characteristics and a remarkable directivity (Fig. 4.11a). In some of the animals, the difference between ipsi- and contralateral stimulation exceeded 25 dB in the frequency range from 1 to 3 kHz, and the directivity is dependent on acoustical coupling of the eardrum. In this frequency range, sound shadowing hardly contributes to the difference. The directivity pattern of the eardrum is ovoidal and highly asymmetrical around the midline (i.e., with a

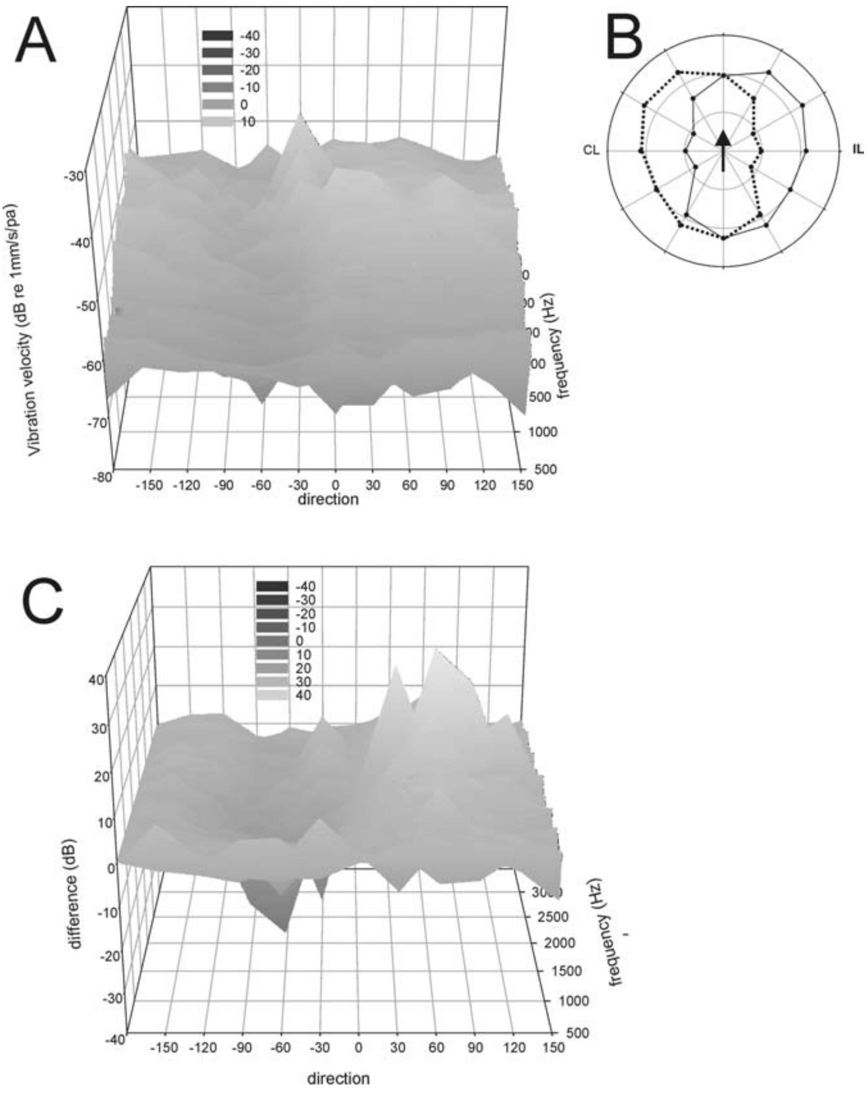


FIGURE 4.11. Directivity of eardrum vibrations in the iguanid *Ctenosaura* measured with laser vibrometry and free-field stimulation. The three-dimensional plots in (**A**) and (**C**) show the response as a function of frequency and direction (vibration amplitude is indicated by a grayscale), and each *horizontal line* corresponds to a polar plot. The eardrum has its maximal sensitivity and directionality around 2 kHz, but as shown in (**A**), contralateral sensitivity is generally depressed. A special feature of the directivity is that it is highly asymmetrical with the highest sensitivity in the IL frontal quadrant, as shown in the polar plot (**B**). If the inputs from the two ears are subtracted, the asymmetry produces a considerable sharpening of the directivity (**C**). Here, the reflection along the midline is subtracted from the response. (Redrawn from Christensen-Dalsgaard and Manley 2005 and unpublished data.)

large difference between, e.g., 30° ipsilateral and 30° contralateral, Fig. 4.11b). Any mechanism that performs binaural subtraction (as, e.g., an EI neuron) will exaggerate this directivity. A simplified model of the output of such a neuron is shown in the interaural vibration amplitude difference (IVAD) plot (Fig. 4.11c), where a mirror image of the directivity plot is subtracted from itself (Jørgensen et al. 1991). Note that the shape of the IVAD plot is generally similar to the eardrum directivity, but that (because of the asymmetrical directivity) the directionality is much sharper, with up to 40 dB difference between 30° ipsilateral and 30° contralateral. In conclusion, the fact that all investigated lizard species essentially show a similar, pressure-difference characteristic and furthermore, that the characteristic reflects a primitive organization of the periphery (i.e., that the middle ear cavities are almost continuous with the pharynx) suggests that a pressure difference characteristic and the associated low-frequency directionality is a feature of most lizard ears. The larger species, for example, some of the iguanids and varanids, should be able to exploit ILDs generated by diffraction and also have large ITDs resulting from arrival time differences at the ears. Consequently, it could be expected that some of these species would have developed uncoupled, pressure sensitive ears during the course of evolution, but that does not seem to be the case; also in the larger species (such as *Iguana iguana*) the middle ear cavities are connected through wide Eustachian tubes (G.A. Manley, personal communication).

4.4. Neuroanatomy and Neurophysiology of Lizard Directional Hearing

Apart from the study on TS neurons mentioned above (Manley 1981) the processing of directional information in the lizard (or reptile) CNS has not been studied. The same divisions of the cochlear nucleus (CN) (i.e., in a nucleus angularis and magnocellularis) as in the birds have been described (see review in Carr and Code 2000). In birds, the division in nucleus angularis and magnocellularis reflect a functional division of time and intensity processing, at least in the barn owl, and it is hypothetized that the nuclei in reptiles should serve a similar functional division (Carr and Code 2000). At least in the alligator lizard (*Gerrhonotus multicarinatus*) there is anatomical evidence that two types of auditory afferents (low-frequency tectorial and high-frequency free standing fibers) project differently in the cochlear nucleus (Szpir et al. 1990). Endbulb terminations were found only in the tectorial fibers and only in the magnocellular nucleus. This finding should be noted, since endbulb swellings with the associated, very efficient synaptic transmission is a characteristic of cochlear nucleus cells in the time coding pathway in birds and mammals. It should also be noted, however, that most lizard nucleus magnocellularis cells are small to medium-sized and therefore may not be functionally equivalent to the avian magnocellularis cells, even if the nuclei are homologous (which by no means can be assumed). Furthermore, it could be argued that the special characteristics of the pressure difference receiver and the high directionality of the periphery in the lizards would necessitate a different central processing, with emphasis, for example, on EI cells that could sharpen the directionality considerably (as shown by the IVAD plots above). Therefore, it would be of considerable interest to investigate the directional processing in the CNS of lizards. Physiological data from the CN (reviewed in Manley 1981) show that the CN in *G. gecko* (and probably also in other lizards) is tonotopically organized. All neurons are tuned, many have primary-like (i.e., phasic-tonic) responses to sound, but very phasic responses also are common. The anatomical data from *Iguana iguana* (Foster and Hall 1978) and *Varanus exanthematicus* (ten Donkelaar et al. 1987) show that the earliest stage of binaural interaction probably is at the level of the trapezoid body or SON (the trapezoid body was included in the SON by ten Donkelaar et al 1987) that receives projections from both ipsi- and contralateral nucleus angularis. Note, however that the *I. iguana* SON apparently lacks structures similar to the MSO in mammals and the nucleus laminaris (NL) in crocodiles and birds (Foster and Hall 1978). From the SON, bilateral projections to the TS have been found in both lizard species, where highly directional cells have been found in *G. gecko*, as outlined above (Manley 1981).

5. Directional Hearing in Birds

For a general review of directional hearing in birds, the reader is referred to Knudsen (1980) and to a recent review in this series (Klump 2000). The aim of the present section is to provide a counterpoint to that review by focusing on the biophysics of directional hearing and especially the evidence for pressure difference/ pressure sensitivity of the avian ear.

5.1 Biophysics of Directional Hearing in Birds

The structure of the avian ear is similar to the lizard ear. Birds usually have no external auditory structures (with the exception of some of the owls, see below). However, an ear canal is always present, but short (2 to 7 mm, Saunders et al. 2000). The single ossicle (columella) is connected to the eardrum via an especially complex extracolumella with three processes, which probably improves the lever ratio of the ear, but probably also limits the high-frequency sensitivity of the ear, depending on the flexibility of the columella–extracolumella connection (Manley 1990).

In birds, arising from an archosaur–dinosaur lineage, the ancestral condition probably is that the middle ears are partially isolated from the respiratory pathway, but connected via an interaural canal that is also found in crocodilians (Wever 1978) and probably in nonavian dinosaurs including *Tyrannosaurus rex* (Larsen and Pettigrew 1988; J.D. Pettigrew, personal observation). Reflecting this ancestral condition, all birds have an interaural canal and the eardrums of all birds are therefore to some extent coupled acoustically. To what extent the acoustic coupling produces usable pressure-difference receiver directivity has been debated extensively. The evidence is reviewed in the following paragraphs.

5.1.1 Directivity of the Auditory Periphery

Studies of directivity roughly fall into two groups. One group of researchers has shown that the directionality is greater than expected from diffraction effects and have compared the directivity to that of a pressure-difference receiver. Another group of researchers found generally small directionality that could result from diffraction and assumed that the ears are functionally uncoupled pressure receivers.

5.1.1.1 Evidence for Pressure-Difference Receiver Operation of the Auditory Periphery

The pioneering studies on bird directional hearing were performed by Schwartzkopff (1950, 1952), who found that the bullfinch (*Pyrrhula pyrrhula*) auditory periphery showed higher directionality than expected from diffraction, but, surprisingly, that this directionality did not change on ear occlusion. Consequently, he concluded that the ears operated as independent pressure receivers. Coles and co-workers (Coles et al. 1980; Hill et al. 1980) showed pronounced directionality of the quail (*Coturnix coturnix*) auditory periphery. Hill et al. (1980) measured sound transmission through the quail head using inserted microphones and found less than 5 dB interaural canal transmission attenuation at frequencies below 5 kHz. At higher frequencies, attenuation increased above 20 dB. From the attenuation data, they predicted strongly asymmetrical directivity with 10- to 20-dB directional difference in the 1- to 4-kHz range. Cochlear microphonics in anesthetized quail showed a variety of directivity patterns, cardioid at lower frequencies and figure-of-eight shaped at high frequencies. The directivities were altered when one eardrum was blocked. Larsen and Popov (1995) found very similar results using laser vibrometry and sound diffraction measurements from quail. They reported an enhancement of interaural delay of 40 µs and an interaural canal attenuation of 6 dB at 1 kHz. Interaural coupling was also inferred by Calford (1988) from a study of frequency selectivity in the IC of nine different bird species. All species except owls exhibited a poorly represented frequency range, which was correlated with the dimensions of their interaural canal. Model calculations based on the interaural canal dimensions showed that the “missing” frequency ranges corresponded to frequency regions in which tympanic directionality generated by interaural coupling was poor. The proposed model, which was based on the addition of direct and indirect sound components (delayed by propagation time and attenuated by the interaural canal), was subsequently used to calculate interaural delays, which were shown to be frequency dependent and, especially at low frequencies, much larger than travel-time delays. Pettigrew and Larsen (1990) reported that neurons in the IC of the plains-wanderer (*Pedionomus torquatus*) showed very directional responses to low-frequency sound (300 Hz) and ascribed the directionality to the large interaural canal in this species. Similarly, Hyson et al. (1994) measured bilateral cochlear microphonics in the chicken and found larger ITDs (up to 200 µs at low frequencies) than expected from travel time differences. They also report up to ±30% (±3dB) directional change of IID (relative to frontal stimulation), and effects of contralateral tympanum occlusion at low, but not on high frequencies, and conclude that interaural coupling enhances the sound localization cues. Finally, Larsen et al. (1997) showed that the interaural coupling and normal operation of the tympanum of budgerigars was very dependent on the intracranial air pressure (ICA) (Fig. 4.12). This is a very important finding, because the ICA tends to decrease in anesthetized birds, unless they are vented. The result is that tympanic vibrations are impeded (the tympanum is sucked inwards), and interaural coupling decreases by around 20 dB and tympanal directivity by 6 dB or more in nonvented compared to vented birds.

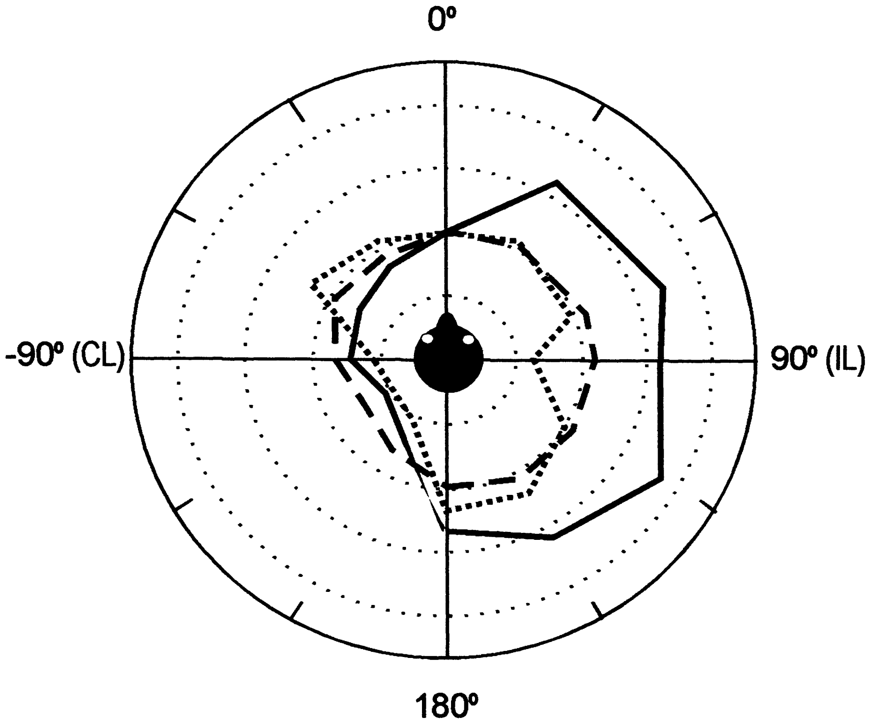


Figure 4.12. Effect of interaural air pressure on sensitivity in budgerigar. The polar plots show laser measurements of eardrum vibrations at 1 kHz before (*dashed line*) and after (*solid line*) venting of the middle-ear cavity. The *dotted line* shows the sound pressure. Note the large difference in directivity and sensitivity before and after venting. Scale: 3 dB/unit circle. (Redrawn from Larsen et al. 1997 © World Scientific Publishers, reprinted by permission.)

5.1.1.2 Experiments Showing Small Effects of Interaural Coupling

Owls have large interaural canals, and earlier studies (Payne 1971) assumed that acoustical coupling of the ears would contribute to the directionality. However, Moiseff and Konishi (1981) recorded from monaural cells in the "cochlear nucleus" of barn owls and showed that interaural attenuation (measured as the difference between the unit's threshold to ipsi- and contralateral stimulation via couplers) increased with frequency from 13 dB at 3.5 kHz to 63 dB at 7 kHz. Measurements with probe microphones also showed large interaural attenuation at higher frequencies. Thus, at behaviorally relevant frequencies, the ears would be functionally isolated pressure receivers. In contrast, Coles and Guppy (1988) report that directionality in the barn owl, measured by cochlear microphonics, exceeds the directionality produced by the external ear and suggest that interaural coupling is important for the directionality also at high frequencies. The reason for the discrepancy between the measurements of Moiseff and Konishi (1981) and Coles and Guppy (1988) is not clear. However, microphonic recordings are inherently unstable and the level can fluctuate during the time needed to measure directional sensitivity in the entire frontal hemifield. Therefore, it would be important to know about the reproducibility of the directional patterns, but this information is not given in the paper by Coles and Guppy. In contrast, threshold comparisons are probably much more reliable. Also, since head-related transfer functions generate virtual space stimulation in the owl with identical responses to free-field sound and virtual stimulation (Keller et al. 1998; Poganiatz et al. 2001) interaural coupling cannot be very important. Rosowski and Saunders (1980) used cochlear microphonics to measure interaural transmission in the chicken and found virtually no attenuation by the interaural canal, but 15- to 20-dB attenuation by the tympanum. With such an impedance mismatch by the tympanum, the directionality should be negligible, which contrasts with Hyson et al.'s (1994) data from the chicken. However, the level of the microphonics measured by Rosowski and Saunders are much lower than the levels measured by Hyson et al. (1994), suggesting that the ears had not been working optimally. Thus, the 15- to 20-dB attenuation is probably too high. Lewald (1990) investigated the directionality of cochlear microphonics in anesthetized pigeons and found less than 5 dB effects of interaural sound transmission and small effects of blocking the contralateral ear. Perhaps the most convincing case for a bird with uncoupled ears was presented by Klump and Larsen (1991) in their work on the starling. They used laser vibrometry to measure free-field directional characteristics of the eardrum in anesthetized starlings and showed that the largest directionality when corrected for sound diffraction by the animal was 3.4 dB (average 1.13 dB). These results in anesthetized birds were paralleled by cochlear microphonics from awake birds. To summarize, there is solid evidence that some species (quail, chicken, and budgerigar) have enhanced peripheral directionality caused by interaural coupling. However, it is also evident that there is considerable species variation, and that some species (barn owl, starling) probably have functionally separate ears. Most importantly, perhaps, the results of Larsen et al. (1997) have reopened the field, since many of the earlier measurements on anesthetized animals need to be redone with appropriate venting of the middle ear cavities.

5.2 Directional Hearing in Barn Owls and Other Birds

The barn owl is a model organism within the field of neuroethology and directional hearing studies. The reason for this is that the barn owl is extremely specialized for directional hearing (Payne 1971; Wagner 2002) and exhibits a very robust sound localization behavior associated with prey capture. This behavior and the associated neurophysiology has lent itself to rigorous, careful laboratory studies for three decades, with the consequence that probably more is known about sound localization in the barn owl than in any other organism. Any discussion of bird directional hearing, therefore, would be clarified by investigating similarities and dissimilarities between directional hearing in the barn owl and that of other birds, summarized in Table 4.1. The field has been extensively reviewed, however, and is only outlined briefly here. The reader is referred to Klump (2000), Wagner (2002) and, especially, to reviews by Konishi (1973, 2000) and Knudsen (2002).

5.2.1 Sound Localization Behavior

Early experiments (reviewed in Payne 1971) demonstrated that barn owls can locate prey accurately using acoustical cues (i.e., the rustling noises made by

TABLE 4.1. Specializations of the owl localization pathway.

Feature	Reference
Extended high-frequency hearing	Konishi (1973); Köppl et al. (1993)
Very low thresholds (−20 dB SPL)	Konishi (1973)
Asymmetrical auditory periphery	Konishi (1973)
Sound-reflecting facial ruff	Konishi (1973)
Increased phase-locking properties of auditory-nerve fibers (up to 9 to 10 kHz)	Köppl (1997)
Longest basilar papilla	Smith et al. (1985)
Overrepresentation of high-frequency range in basilar papilla ("auditory fovea")	Köppl et al. (1993)
Large size and convoluted shape of NA	Köppl (2001)
Multiple layering of NL	Carr and Konishi (1990)
Kv 3.1 channels in NM that reduces the duration of action potentials	Parameshwaran et al. (2001)
Segregation of time and intensity pathways	Sullivan and Konishi (1984)
Small receptive fields and ordered spatiotopic representation in the ICC	Knudsen and Konishi (1978a,b)
Sharp spatial tuning in ICx	Wagner (1993)
Spatial map in ICx and SCC	Knudsen (1982)

the prey). The accuracy of striking the target depends on the stimulus bandwidth; a 4-kHz noise band centered on 7 kHz was most efficient (Konishi 1973). Later, Konishi, Knudsen and co-workers used a setup in which the turning angle of perched owls was measured (Knudsen et al. 1979). These behavioral studies have shown that the orientation error of the barn owl for noise is approximately 5°, but around three times as large for tones (Knudsen and Konishi 1979). Furthermore, occluding the right ear produced an orientation bias downwards and to the left; occluding the left ear produced an orientation bias upwards and to the right. Finally, removing the ruff feathers of the facial mask only disturbed localization in elevation. Recent studies using a pupillary dilation response have found minimum audible angles of approximately 3° (Bala et al. 2003).

The performance of other birds in sound localization tasks vary among the investigated species, but are not as acute as in the barn owl. Early experiments on bullfinches (Schwartzkopff 1950) showed minimal angular resolution of 25°, and minimal resolution angles of 20° in Great tits (*Parus major*) were reported by Klump et al. (1986). The authors suggested that the ITD cues generated by comparing the inputs from two uncoupled ears (18 μs at 25°, approximately twice the minimal ITD in barn owls) are sufficient to explain the localization accuracy. Park and Dooling (1991) reported minimal resolution angles (noise stimulation) of 17° and 25°, respectively, in budgerigar (*Melopsitaccus undulatus*) and canary (*Serinus canarius*), at 1 and 2 kHz, the minimal resolution angles were larger. Outside the owls, the smallest minimal resolution angles were found in other aerial predators like the marsh hawk (*Circus cyaneus*) (2°) and red-tailed hawk (*Buteo jamaicensis*) (8 to 10°) (Rice 1982; see also Klump 2000, Table 6.1). Note, however, that a study of the passerine bird *Pipilo erythrophtalmus* (Towhee) showed much higher acuity than that of other songbirds: 5 to 9° azimuth as well as accurate estimation of distance (Nelson and Stoddard 1998); the authors suggest that birds would use vision at short distances and therefore might not attend to auditory stimuli.

5.2.2 External Ear in the Owls

The auditory periphery of barn owls and some other owl species (Volman and Konishi 1990) has a very special feature that is unique among the tetrapods. The ears are asymmetric, that is, the left and right ear opening differ in size and/or placement. The function of the ear asymmetry is to enable the owl to locate sound accurately in elevation. For an animal that has two symmetrical ears, the region of equal intensity for all frequencies is a plane aligned with the medial plane of the animal, that is, no binaural comparisons can resolve sound elevation. For the asymmetrical ears of the owl, however, the iso-intensity plane is a complex contour that changes with sound frequency: the plane is almost horizontal at high frequencies and almost vertical at lower frequencies (below 6 kHz). For the lower frequencies, the ongoing time difference varies systematically with azimuth because of the differences in travel distance to the two ears. Thus, (low-frequency) ITD and (high-frequency) IID define the two axes of a coordinate system (Moiseff 1989), and a particular location is uniquely defined in elevation and azimuth by its low-frequency ITD and high-frequency IID (which explains why the localization of tones is inherently more difficult for the barn owl than the localization of noise). Furthermore, some of the owls have a well-developed feathered facial mask or ruff that is a parabolic sound reflector. The ruff of the barn owl amplifies some frequencies by more than 10 dB (Volman and Konishi 1990). It should be noted that the effect of the asymmetrical ear and of the facial ruff is only seen at frequencies above 3 to 4 kHz.

5.2.3 The Auditory Papilla and Auditory Nerve

The bird basilar papilla or cochlea is an elongated structure containing the sensory epithelium of hair cells covered by a tectorial membrane. The papilla of the barn owl is longer than the papilla of all other birds—11 mm (Köppl et al. 1993) compared to 3.1 mm in pigeon and 3.7 mm in chicken (Gleich and Manley 2000)—which reflects the extended high-frequency hearing (Smith et al. 1985; Fischer et al. 1988). The auditory papilla is tonotopically organized, and in the barn owl papilla the high frequency range (5 to 10 kHz) is highly overrepresented in an “acoustic fovea” (Köppl et al. 1993), whereas the low-frequency part of the papilla is comparable to that of other birds (Gleich and Manley 2000). The auditory nerve contains an ordered array of fibers tuned to different CFs, but the directional characteristics of avian auditory nerve fibers have not been studied. Avian fibers phase-lock to relatively high frequencies; 4 kHz in the starling (Gleich and Narins 1988) and up to 10 kHz in the barn owl (Köppl 1997). The physiological basis of the specialization for high-frequency phase locking is at present unknown.

5.2.4 Nucleus Angularis (NA) and Magnocellularis (NM)

In the barn owl, information on spike timing and spike rate becomes first segregated in the auditory nuclei in the sense that NA cells show weak phase locking, large dynamic range and high rate-level slopes, whereas NM cells phase lock up to 9 kHz, and their response is almost independent of the intensity of the stimulus (Sullivan and Konishi 1984). The strong phase locking in the NM cells is inferior compared to the auditory nerve input (Köppl 1997). Anatomically, four major classes of cell types have been described from the barn owl NA, classified by the branching pattern of their dendrites *in* (two morphological types), *across*, and *vertical* to the isofrequency plane (Soares and Carr 2001). The same cell types are found in the chicken NA and the morphological types also have distinct physiological properties (Soares et al. 2002). A recent study has identified five distinct physiological response types in the NA of the barn owl, and the nucleus is probably not dedicated to sound level processing (Köppl and Carr 2003). However, some of the NA cells innervate the posterior nucleus of the ventral lateral lemniscus (VLVp), the first site of binaural computation of ILD in the owl (Manley et al. 1988; Mogdans and Knudsen 1994). The NM cells have very characteristic, regular branching patterns sending off collaterals that enter the NL at equidistant points along the tonotopic band (Carr and Konishi 1990). The NM cells have morphological specializations for relaying time information efficiently, notably large and calyx-shaped synapses (endbulbs of Held) and specialized potassium channels that reduce the duration of action potentials (Carr et al. 2001; Parameshwaran et al. 2001). Functionally, NM neurons in the owl are delay lines that, together with the contralateral NM neurons, interface on NL neurons. The NM cells are tonotopically organized and project to specific isofrequency bands in the NL (Carr and Konishi 1990). In other birds and crocodilians, only the contralateral NM neurons are delay lines, whereas the ipsilateral NM neurons have a fixed delay (Overholt et al. 1992; Kubke et al. 2002; see also Fig. 4.13).

5.2.5 Nucleus Laminaris

As a second-order auditory nucleus, the NL is equivalent to the MSO of mammals. NL cells have large, oval cell bodies and short dendrites (Carr and Konishi 1990) and discharge when action potentials arriving from the ipsi- and contralateral NM neurons coincide in time (Carr and Konishi 1990). The cells are often described as ITD-sensitive, but they really encode IPDs, since stimulus cycle time ITD shifts will produce identical coincidences, and the output of NL cells do show multiple peaks at ITD intervals corresponding to the cycle time of the stimulus. As the NL neurons are stimulated by appropriately delayed coincident action potentials from the IL and CL NM, they project an ordered array of IPDs to the IC. NL is hypertrophied in owls compared to other birds (chicken; see Fig. 4.13), where the cells form a single layer of bipolar neurons (Carr and Konishi 1990; Joseph and Hyson 1993), probably the primitive avian pattern (Kubke et al. 2002). However, also in other birds the mechanism of coincidence detection has been reported (Joseph and Hyson 1993). The hypertrophy of the owl NL occurs during a “second phase” in development; the first phase produces the plesiomorphic NL and is similar in chicken and owl (Kubke et al. 2002). Probably the owl NL reflects specialization for high-frequency IPD processing (Köppl 1997; Kubke et al. 2002) or just improves the sensitivity by parallel calculation of IPD in many cells (Carr and Code 2000).

With the current focus on ITD processing by fast (glycinergic) inhibition in the mammalian MSO (Brand et al. 2002), it may be worthwhile to note that avian NL neurons do receive inhibitory inputs, but the inhibition is relatively slow (GABAergic), controlled from the SON and most likely used to control the sensitivity of the NL cells (Brückner and Hyson 1998; Carr et al. 2001).

5.2.6 The Posterior Nucleus of the Ventral Lateral Lemniscus (VLVp or LLDp)

The VLVp receives projections from the NA and process ILD. The physiological properties of cells in the VLVp have only been studied in the barn owl (Manley et al. 1988; Mogdans and Knudsen 1994). The cells receive excitatory inputs from the CL NA and inhibitory inputs from the IL NA. The strength of

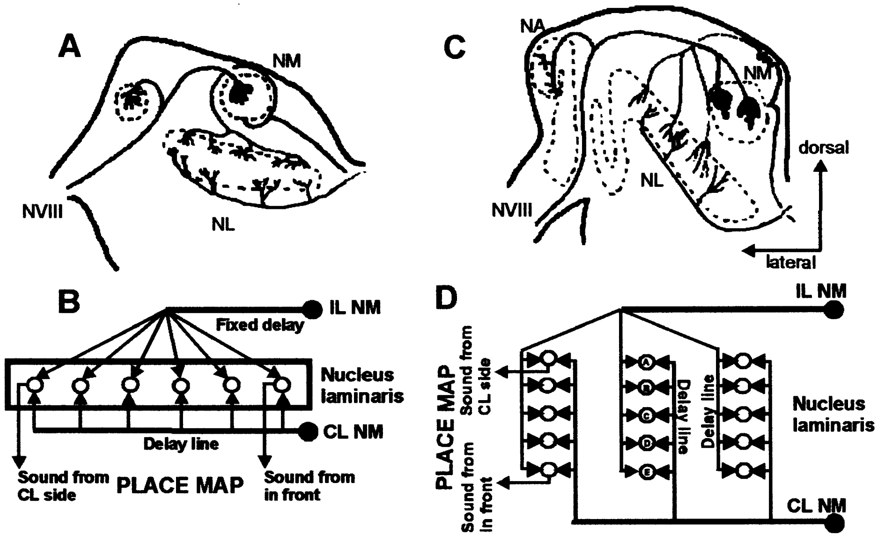


FIGURE 4.13. Comparison of NL ITD coding in chicken (**A**, **B**) and barn owl (**C**, **D**). In both chicken and owl, the NL detects coincidence between inputs from the IL and CL nucleus magnocellularis and conforms to a Jeffress model (**B**, **D**). In the chicken (schematic cross section in **A**), the NL is only a monolayer, and the IL magnocellularis input has a fixed delay. In the barn owl (schematic cross section in **C**), the NL is hypertrophied with several rows of coincidence detectors and a delay line input from both IL and CL NM. (Redrawn from Kubke and Carr 2000. © 2000, with permission from Elsevier.)

inhibition received from the IL side decrease with depth in the nucleus, and consequently, a map of ILD is generated in the nucleus (Manley et al. 1988). The cells have chopperlike discharges and show level-dependent discharge patterns (so the response to a weak monaural tone can be distinguished from the response to a loud binaural tone) (Mogdans and Knudsen 1994).

5.2.7 The Inferior Colliculus (IC)

The avian IC is homologous to the IC in mammals and to the torus semicircularis in fish, amphibians, and reptiles. In the literature, it is also called nucleus mesencephalicus dorsalis (MLD) or torus. The IC is divided into an external nucleus (ICX) and a central nucleus consisting of a lateral shell (ICCls), central core (ICCc) and medial shell (ICCms) (Carr and Code 2000). The ICCc receives projections both directly and indirectly from the NL, and the ICCms and ICCls from the NA and is still tonotopically organized. The ILD and ITD pathway converges in the ICX, where the information is combined across frequency to produce spatial receptive fields, ITD giving the azimuthal and ILD the elevational component (Takahashi et al. 1984). Also, the IPD information is converted to true ITD by comparing IPD responses across frequencies, since they will align at the shortest ITD (Wagner et al. 1987; Konishi 2000). The space-sensitive neurons in ICX have an excitatory center and an inhibitory surround (Knudsen and Konishi 1978b). The receptive fields of the space-sensitive neurons vary from 7 to 40° azimuth and 23° to “unrestricted” elevation (Knudsen and Konishi 1978a) and are organized into a spatiotopic map. The ICX is probably also an important site for plasticity and instruction by visual input, since owls that are reared with prisms show changes in the ITD coding in ICX, but not in ICC (Gold and Knudsen 2000; Knudsen 2002). The other owl species that have been studied have comparable ICX maps, but owls with a symmetrical periphery, such as the great horned owl (*Bubo virginianus*) have broad or no elevation sensitivity in ICX (Volman and Konishi 1989, 1990). In other birds, a comparable map has not been found in the IC, though directionally sensitive cells have been found (Coles and Aitkin 1979).

5.2.8 Optic Tectum (Superior Colliculus)

The OT or the superior colliculus is bimodal, and most cells in the barn owl OT respond to both visual and auditory stimuli. The cells show space-specific responses independent of the type of sound or its intensity. The width of the receptive field is narrow, and lesions in the map produce behavioral deficits (but the owls can recover) (Wagner 1993). Also, the auditory and visual maps are generally aligned. It has been shown both in behavioral experiments (Gold and Knudsen 2000) and neurophysiological experiments (Hyde and Knudsen 2000) that the visual tectal neurons control the auditory map by projecting an instructional signal back into the IC in juvenile owls (Knudsen 2002). Pigeons (*Columba livia*) also have a map of auditory space in the OT that is aligned with the visual map (Lewald and Dörrscheidt 1998). The units are very broadly tuned, however (width 43 to 166° azimuth, 16 to 186° elevation).

6. Summary and Perspectives

The main point of the present review is that directional hearing in the recent tetrapods reflects the independent origin of tympanic hearing in the different groups (but note that even the primitive, nontympanic tetrapods can have had a crude directional hearing based on sound-induced vibrations of the skull, similar to the directional hearing of their fish ancestors). Furthermore, in the three groups reviewed here, the primitive organization of the auditory periphery is probably one where the middle ears are coupled, potentially producing pressure-difference receiver directionality. That the directionality of anurans and lacertids is produced by acoustical interaction of the two ears is beyond dispute. However, in some bird species, at least, evolution has led to functional isolation of the two ears, most notably in auditory specialists like the barn owl and relatives. Whether this functional isolation is caused by selection against the coupled ear (which has disadvantages; see Section 2.5) or is just caused by adaptation that shifts sensitivity to higher frequencies where transmission through the interaural canal happens to be attenuated, is unknown at present. In most of the other birds studied, however, the degree of interaural coupling is disputed at present. Large values of interaural attenuation (20 dB or more) have been reported and this would mean that the ears were functionally isolated. However, from simple considerations of the acoustics of a system with two receivers coupled by a pipe (Fletcher 1992) it is difficult to accept that these large attenuations should apply throughout the entire frequency range. Also, recent findings showing that the acoustics of the periphery is highly sensitive to anesthesia, causing the Eustachian tubes to close (Larsen et al. 1997), necessitate a reevaluation of the older data, preferably in combination with realistic models based on electrical analogs. On the other hand, it is likely that bird groups other than the owls have evolved functional isolation of the ears, and hence the mechanisms of directionality should be expected to vary among different bird groups.

Very recently, it has been shown that the neural processing underlying acute ITD sensitivity in mammals is very different from the processing in barn owls. In mammals binaural interaction is probably mediated by fast and precise inhibition of neurons in the MSO, and ITD is encoded by the spike rate rather than by the activity of characteristic cells in an ordered array of best ITDs (Brand et al. 2002). Similarly, binaural interaction based on inhibition is also found in the frog DMN (Christensen-Dalsgaard and Kanneworff 2005). Thus, apparently, the Jeffress-type coincidence detectors found in the avian NL are unique in the tetrapods (Grothe 2003). The processing of directional hearing probably reflects independent, convergent evolution in the different groups of tetrapods based on ancestral features. Also in the tetrapod ancestors, bilateral neural comparison and computation of the relative level of excitation on the two sides of the animal could have been important, so that neural mechanisms subserving bilateral interaction may be a fundamental and plesiomorphic feature that can be coopted by evolving auditory systems.

The central processing of directional information apparently varies among the three groups. In the well-characterized sound localization pathway of birds, intensity and time cues are segregated at the level of the first auditory nuclei with a specialized structure, NL, for ITD processing using delay lines. In barn owls, spatiotopy in the IC and in the OT has been demonstrated. Anurans have binaural interaction already at the level of the first auditory nucleus, apparently no clear segregation of time and intensity pathways, and no robust spatial map. In the lacertid reptiles, binaural interaction starts like in the archosaurs at the level of the SON. However, some lacertids, at least, lack specialized structures comparable to the MSO in mammals and NL in archosaurs that function in temporal (ITD) processing. While essentially nothing is known of the central processing of directional information in lizards, it could be argued that a useful directionality could result from binaural difference (EI) cells, since the eardrum directivity is markedly asymmetrical and the directionality therefore will be enhanced by such cells (Fig. 4.10b, c).

The point is that the neural computation of directionality with a pressure-difference input could be radically different from the computation using a pressure-sensitive ear such as the barn owl's. For example in the first case, the directionality (IID as well as ITD) will be strongly frequency dependent, so it would be sensible to compare binaural inputs in separate frequency channels and compute a direction for each of them. Since the ITD would be strongly frequency dependent, it might not be advantageous to have a specialized time pathway. To address these questions, much more comparative work will be needed in the future.

The organization of the sound localization pathways and the amount of neural tissue devoted to the processing of sound direction in the species reviewed here probably accurately reflects the magnitude of selection pressures for directional hearing. While it is obviously always of some advantage to be able to determine the direction to a sound source, the extreme selection pressure for directional hearing in a barn owl that has to locate moving prey has led to specialization for directional hearing at every stage of the auditory pathway. In contrast, the magnitude of selection pressures for frog directional hearing is less easy to assess. Even if a female frog has to locate a calling male to reproduce—so there is a selection pressure for directional hearing—much of the burden of communication is on the sender, which has to call nonstop for hours, and whose communication calls are probably tailored to be maximally audible and localizable (Wilczynski et al. 2001). Furthermore, in some frog species, mate localisation will probably be largely carried out using nonacoustic cues, and the selection pressure for a sharpened directional hearing in those species is unknown, as in the nonvocal lizards. A related major question in anuran hearing is the extent to which the auditory system is dedicated to the processing of conspecific calls. Specialization of the auditory system for communication might be suggested by the ubiquity of call communication within the anurans and the virtual absence of response to noncommunication sound, but the fact that nongekkonid lizards, that do not communicate by sound or show any robust behavioral response to sound, have very sensitive and directional ears, should caution us: A major and primitive function of audition in the vertebrates might not be related to communication, but rather simply to the necessity of collecting information about changing features of the environment.

Acknowledgments. I thank Geoffrey A. Manley for comments on the manuscript and Nina Krogh for the drawings in Figures 4.1 and 4.3.

Abbreviations

A	anterior thalamic nucleus
AM	amplitude Modulated
AP	amphibian papilla

BP	basilar papilla
C	columella
Cb	cerebellar nucleus
Cer	cerebellum
CF	characteristic frequency
CL	contralateral
CN	cochlear nucleus
CoF	columellar footplate
CT	central thalamic nucleus
DMN	dorsal medullary nucleus
DP	dorsal pallium
EC	extracolumella
EE	excitatory-excitatory
EI	excitatory-inhibitory
ET	Eustachian tube
GABA	γ-aminobutyric acid
HRTF	head-related transfer function
IC	inferior colliculus
ICA	intracranial air pressure
ICc	inferior colliculus, core
ICx	inferior colliculus, external nucleus
IL	ipsilateral
ILD	interaural level difference
IPD	interaural phase difference
ITD	interaural time difference
IVAD	interaural vibration amplitude difference
LA	lateral amygdala
LC	locus coeruleus
LPv	lateral pallium, ventral portion
MA	medial amygdala
MEC	middle ear cavity
MP	medial pallium
MS	medial septum
NA	nucleus angularis
NI	isthmal nucleus
Nis	secondary isthmal nucleus
NL	nucleus laminaris
NM	nucleus magnocellularis
NVIII	VIIIth nerve
O	operculum
OT	optic tectum
P	posterior thalamic nucleus
PA	preoptic area
PT	posterior tuberculum
RW	round window

SON	superior olivary nucleus
Stv	ventral striatum
Tec	optic tectum
Teg	tegmentum
TM	tympanic membrane
TS	torus semicircularis
VH	ventral hypothalamic nucleus
VM	ventromedial thalamic nucleus

References

Aertsen AMHJ, Vlaming MSMG, Eggermont JJ, Johannesma PIM (1986) Directional hearing in the grassfrog (*Rana temporaria* L.). II. Acoustics and modelling of the auditory periphery. Hear Res 21:17–40.

Bala ADS, Spitzer MW, Takahashi TT (2003) Prediction of auditory spatial acuity from neural images on the owl's auditory space map. Nature 424:771–774.

Beranek LL (1986) Acoustics. New York: American Institute of Physics.

Berger K (1924) Experimentelle Studien über Schallperzeption bei Reptilien. Z Vergl Physiol 1:517–540.

Blauert J (1997) Spatial Hearing. Cambridge, MA: MIT Press, pp. 372–392.

Bolt JR, Lombard RE (1985) Evolution of the amphibian tympanic ear and the origin of frogs. Biol J Linn Soc 24:83–99.

Brand A, Behrend O, Marquardt T, McAlpine D, Grothe B (2002) Precise inhibition is essential for microsecond interaural time coding. Nature 417:543–547.

Brandt C, Christensen-Dalsgaard J (2001) Responses to three-dimensional vibrations and sound stimuli in single fibers from the 8th cranial nerve of the grass frog, *Rana temporaria.* In: Elsner N, Kreuzberg GW (eds), Göttingen Neurobiology Report 2001. Stuttgart: Georg Thieme Verlag, p. 386.

Bregman A (1990) Auditory Scene Analysis. The Perceptual Organization of Sound. Cambridge, MA: The MIT Press.

Brückner S, Hyson RL (1998) Effect of GABA on the processing of interaural time differences in nucleus laminaris neurons in the chick. Eur J Neurosci 10:3438–3450.

Calford MB (1988) Constraints on the coding of sound frequency imposed by the avian interaural canal. J Comp Physiol A 162:491–502.

Carr C, Code RA (2000) The central auditory system of reptiles and birds. In: Dooling RJ, Fay RR, Popper AN (eds), Comparative Hearing: Birds and Reptiles. New York: Springer-Verlag, pp. 197–248.

Carr CE, Konishi M (1990) A circuit for detection of interaural time differences in the brain stem of the barn owl. J Neurosci 10:3227–3246.

Carr CE, Soares D, Parameshwaran S, Perney T (2001) Evolution and development of time coding systems. Curr Opin Neurobiol 11:727–733.

Christensen KR, Christensen-Dalsgaard J (1997) Directional hearing in the natterjack toad, *Bufo calamita*. In Elsner N, Wässle H (eds), Göttingen Neurobiology Report 1997. Stuttgart: Georg Thieme Verlag, p. 334.

Christensen-Dalsgaard J, Elepfandt A (1995) Biophysics of underwater hearing in the clawed frog, *Xenopus laevis*. J Comp Physiol A 176:317–324.

Christensen-Dalsgaard J, Jørgensen MB (1996) Sound and vibration sensitivity of VIIIth nerve fibers in the grass frog, *Rana temporaria*. J Comp Physiol A 179:437–445.

Christensen-Dalsgaard J, Kanneworff M (2005) Binaural interaction in the frog dorsomedullary nucleus. Brain Res Bull (in press).

Christensen-Dalsgaard J, Manley GA (2005) Directionality of the lizard ear. J. Exp Biol 208:1209–1217.

Christensen-Dalsgaard J, Narins PM (1993) Sound and vibration sensitivity in the frogs *Leptodactylus albilabris* and *Rana pipiens pipiens*. J Comp Physiol A 172:653–662.

Christensen-Dalsgaard J, Kanneworff M, Jørgensen MB (1997) Extratympanic sound sensitivity of frog auditory fibers. In: Lewis ER, Long GR, Lyon RF, Narins PM, Steele CR, Hecht-Poinar E (eds), Diversity in Auditory Mechanics, Singapore: World Scientific, pp. 64–68.

Christensen-Dalsgaard J, Jørgensen MB, Kanneworff M (1998) Base response characteristics of auditory nerve fibers in the grass frog (*Rana temporana*). Hear Res 119:155–163.

Clack JA (1993) Homologies in the fossil record: the middle ear as a test case. Acta Biotheor 41:391–409.

Clack JA (1997) The evolution of tetrapod ears and the fossil record. Brain Behav Evol 50:198–212.

Coles RB, Aitkin LM (1979) The response properties of auditory neurones in the midbrain of the domestic fowl (*Gallus gallus*) to monaural and binaural stimuli. J Comp Physiol 134:241–251.

Coles RB, Guppy A (1988) Directional hearing in the barn owl (*Tyto alba*). J Comp Physiol A 163:117–133.

Coles RB, Lewis DB, Hill KG, Hutchings ME, Gower DM (1980) Directional hearing in the Japanese quail (*Coturnix coturnix japonica*). II. Cochlear physiology. J Exp Biol 86:153–170.

Diego-Rasilla FJ, Luengo RM (2004) Heterospecific call recognition and phonotaxis in the orientation behavior of the marbled newt, *Triturus marmoratus*. Behav Ecol Sociobiol 55:556–560.

Edwards CJ, Kelley DB (2001) Auditory and lateral line inputs to the midbrain of an aquatic anuran; neuroanatomic studies in *Xenopus laevis*. J Comp Neurol 438:148–162.

Eggermont JJ (1988) Mechanisms of sound localization in anurans. In: Fritzsch B, Ryan MJ, Wilczynski W, Hetherington TE, Walkowiak W (eds), The Evolution of the Amphibian Auditory System. New York: John Wiley & Sons, pp. 307–336.

Ehret G, Keilwerth E, Kamada T (1993) The lung-eardrum pathway in three treefrog and four dendrobatid frog species: some properties of sound transmission. J Exp Biol 195: 329–343.

Elepfandt A, Eistetter I, Fleig A, Günther E, Hainich M, Hepperle S, Traub B (2000) Hearing threshold and frequency discrimination in the purely aquatic frog *Xenopus laevis* (Pipidae): measurement by means of conditioning. J Exp Biol 203:3621–3629.

Endepols H, Walkowiak W, Luksch H (2000) Chemoarchitecture of the anuran auditory midbrain. Brain Res Rev 33:179–198.

Endepols H, Feng AS, Gerhardt HC, Schul J, Walkowiak W (2003) Roles of the auditory midbrain and thalamus in selective phonotaxis in female gray treefrogs (*Hyla versicolor*). Behav Brain Res 145:63–77.

Epping WJM, Eggermont JJ (1985) Relation of binaural interaction and spectro-temporal characteristics in the auditory midbrain of the grassfrog. Hear Res 19:15–28.

Eurich C, Roth G, Schwegler H, Wiggers W (1995) Simulander: a neural network model for the orientation movement of salamanders. J Comp Physiol A 176:379–389.

Fay RR, Feng AS (1987) Mechanisms for directional hearing among nonmammalian vertebrates. In Yost WA, Gourevitch G (eds), Directional Hearing. New York: Springer-Verlag, pp. 179–213.

Feng AS (1980) Directional characteristics of the acoustic receiver of the leopard frog (*Rana pipiens*): a study of the eighth nerve auditory responses. J Acoust Soc Am 68: 1107–1114.

Feng AS (1981) Directional response characteristics of single neurons in the torus semicircularis of the leopard frog (*Rana pipiens*). J Comp Physiol 144:419–428.

Feng AS (1982) Quantitative analysis of intensity-rate and intensity-latency functions in peripheral auditory nerve fibers of northern leopard frogs (*Rana p. pipiens*). Hear Res 6:241–246.

Feng AS (1986) Afferent and efferent innervation patterns of the cochlear nucleus (dorsal medullary nucleus) of the leopard frog. Brain Res 367:183–191.

Feng AS, Capranica RR (1976) Sound localization in anurans. I. Evidence of binaural interaction in the dorsal medullary nucleus of the bullfrog (*Rana catesbeiana*). J Neurophysiol 39:871–881.

Feng AS, Capranica RR (1978) Sound localization in anurans. II. Binaural interaction in superior olivary nucleus of the green tree frog (*Hyla cinerea*). J Neurophysiol 41: 43–54.

Feng AS, Lin WY (1991) Differential innervation patterns of three divisions of frog auditory midbrain (torus semicircularis). J Comp Neurol 306:613–630.

Feng AS, Lin WY (1996) Neuronal architecture of the dorsal nucleus (cochlear nucleus) of the frog (*Rana pipiens pipiens*). J Comp Neurol 366:320–334.

Feng AS, Schellart NAM (1999) Central auditory processing in fish and amphibians. In: Fay RR, Popper AN (eds), Comparative Hearing: Fish and Amphibians. New York: Springer-Verlag, pp. 218–268.

Feng AS, Shofner (1981) Peripheral basis of sound localization in anurans. Acoustic properties of the frog's ear. Hear Res 5:201–216.

Feng AS, Gerhardt HC, Capranica RR (1976) Sound localization behavior of the green treefrog (*Hyla cinerea*) and the barking treefrog (*H. gratiosa*). J Comp Physiol 107: 241–252.

Fischer FP, Köppl C, Manley GA (1988) The basilar papilla of the barn owl *Tyto alba*: a quantitative morphological SEM analysis. Hear Res 34:87–101.

Fletcher NH (1992) Acoustic systems in biology. Oxford: Oxford University Press.

Fletcher N, Thwaites S (1979) Physical models for the analysis of acoustical systems in biology. Q Rev Biophys 12:25–65.

Foster RE, Hall WC (1978) The organization of central auditory pathways in a reptile, *Iguana iguana*. J Comp Neurol 178:783–832.

Frishkopf LS, Goldstein MH (1963) Responses to acoustic stimuli from single units in the eighth nerve of the bullfrog. Acoust Soc Am 35:1219–1228.

Gerhardt HC (1995) Phonotaxis in female frogs and toads: execution and design of experiments. In: Klump GM, Dooling RJ, Fay RR, Stebbins WC (eds), Methods in Comparative Psycho-Acoustics, Basel: Birkhäuser Verlag, pp. 209–220.

Gerhardt HC, Klump (1988) Phonotactic responses and selectivity of barking treefrogs (*Hyla gratiosa*) to chorus sounds. J Comp Physiol A 163:795–802.

Gerhardt HC, Rheinlaender J (1980) Accuracy of sound localization in a miniature dendrobatid frog. Naturwissenschaften 67:362–363.

Gleich O, Manley GA (2000) The hearing organs of birds and crocodilia. In: Dooling

RJ, Fay RR, Popper AN (eds), Comparative Hearing: Birds and Reptiles. New York: Springer-Verlag, pp. 70–138.

Gleich O, Narins PM (1988) The phase response of primary auditory afferents in a songbird (*Sturnus vulgaris* L.) Hear Res 32:81–91.

Gold JI, Knudsen EI (2000) A site of auditory experience-dependent plasticity in the neural representation of auditory space in the barn owl's inferior colliculus. J Neurosci 20:3469–3486.

Goodrich (1930) Studies on the Structure and Development of the Vertebrates, Vol. 1. New York: Dover (reprint 1958).

Gooler DM, Condon CJ, Xu J, Feng AS (1993) Sound direction influences the frequency-tuning characteristics of neurons in the frog inferior colliculus. J Neurophysiol 69: 1018–1030.

Grothe B (2003) New roles for synaptic inhibition in sound localization. Nat Rev Neurosci 4:1–11.

Heffner RS, Heffner HE (1992) Evolution of sound localization in mammals. In: Webster DB, Fay RR, Popper AN (eds), The Evolutionary Biology of Hearing. New York: Springer-Verlag, pp. 691–715.

Hetherington TE, Lindquist E (1999) Lung-based hearing in an 'earless' anuran amphibian. J Comp Physiol 184:395–401.

Hill KG, Lewis DB, Hutchings ME, Coles RB (1980) Directional hearing in the Japanese quail (*Coturnix coturnix japonica*). I. Acoustical properties of the auditory system. J Exp Biol 68:135–151.

Hoy (1992) The evolution of hearing in insects as an adaptation to predation from bats. In: Webster DB, Fay RR, Popper AN (eds), The Evolutionary Biology of Hearing. New York: Springer-Verlag, pp. 115–129.

Hyde PS, Knudsen EI (2000) Topographic projection from the optic tectum to the auditory space mapin the inferior colliculus of the barn owl. J Comp Neurol 21:8586–8593.

Hyson RL, Overholt EM, Lippe WR (1994) Cochlear microphonic measurements of interaural time differences in the chick. Hear Res 81:109–118.

Jaslow AP, Hetherington TE, Lombard RE (1988) Structure and function of the amphibian middle ear. In: Fritzsch B, Ryan MJ, Wilczynski W, Hetherington TE, Walkowiak W (eds), The Evolution of the Amphibian Auditory System. New York: John Wiley & Sons, pp. 69–91.

Jørgensen MB (1991) Comparative studies of the biophysics of directional hearing in anurans. J Comp Physiol A 169:591–598.

Jørgensen MB (1993) Vibrational patterns of the anuran eardrum. In: Elsner N, Heisenberg M (eds), Gene-Brain-Behaviour. Proceedings of the 21st Göttingen Neurobiology Conference. Stuttgart: Georg Thieme Verlag, p. 231.

Jørgensen MB, Christensen-Dalsgaard J (1997a) Directionality of auditory nerve fiber responses to pure tone stimuli in the grassfrog, *Rana temporaria*. I. Spike rate responses. J Comp Physiol A 180:493–502.

Jørgensen MB, Christensen-Dalsgaard (1997b) Directionality of auditory nerve fiber responses to pure tone stimuli in the grassfrog, *Rana temporaria*. II. Spike timing. J Comp Physiol A 180:503–511.

Jørgensen MB, Gerhardt HC (1991) Directional hearing in the gray tree frog *Hyla versicolor*: eardrum vibrations and phonotaxis. J Comp Physiol A 169:177–183.

Jørgensen MB, Kanneworff M (1998) Middle ear transmission in the grass frog, *Rana temporaria*. J Comp Physiol A 182:59–64.

Jørgensen MB, Schmitz B, Christensen-Dalsgaard J (1991) Biophysics of directional hearing in the frog *Eleutherodactylus coqui*. J Comp Physiol A 168:223–232.

Joseph AW, Hyson RL (1993) Coincidence detection by binaural neurons in the chick brain stem. J Neurophysiol 69:1197–1211.

Kaulen R, Lifschitz W, Palazzi C, Adrian H (1972) Binaural interaction in the inferior colliculus of the frog. Exp Neurol 37:469–480.

Keller CH, Hartung K, Takahashi TT (1998) Head-related transfer functions of the barn owl: measurement and neural responses. Hear Res 118:13–34.

Klump GM (1995) Studying sound localization in frogs with behavioral methods. In: Klump GM, Dooling RJ, Fay RR, Stebbins WC (eds), Methods in Comparative Psycho-Acoustics. Basel: Birkhäuser Verlag, pp. 221–233.

Klump GM (2000) Sound localization in birds. In: Dooling RJ, Fay RR, Popper AN (eds), Comparative Hearing: Birds and Reptiles. New York: Springer-Verlag, pp. 249–307.

Klump GM, Gerhardt HC (1989) Sound localization in the barking treefrog. Naturwissenschaften 76:35–37.

Klump GM, Larsen ON (1991) Azimuthal sound localization in the European starling (*Sturnus vulgaris*): I. Physical binaural cues. J Comp Physiol A 170:243–251.

Klump GM, Windt W. Cuno E (1986) The great tit's (*Parus major*) auditory resolution in azimuth. J Comp Physiol A 158:383–390.

Knudsen EI (1980) Sound localization in birds. In: Popper AN, Fay RR (eds), Comparative Studies of Hearing in Vertebrates. Berlin: Springer-Verlag, pp. 289–322.

Knudsen EI (1982) Auditory and visual maps of space in the optic tectum of the owl. J Neurosci 2:1177–1194.

Knudsen EI (2002) Instructed learning in the auditory localization pathway of the barn owl. Nature 417:322–328.

Knudsen EI, Konishi M (1978a) A neural map of auditory space in the owl. Science 200:795–797.

Knudsen EI, Konishi M (1978b) Center-surround organization of auditory receptive fields in the owl. Science 202:778–780.

Knudsen EI, Konishi M (1979) Mechanisms of sound localization in the barn owl (*Tyto alba*). J Comp Physiol 133:13–21.

Knudsen EI, Blasdel GG, Konishi M (1979) Sound localization by the barn owl (*Tyto alba*) measured with the search coil technique. J Comp Physiol 133:1–11.

Konishi M (1973) How the owl tracks its prey. Am Scientist 61:414–424.

Konishi M (2000) Study of sound localizaton by owls and its relevance to humans. Comp Biochem Physiol A 126:459–469.

Köppl C (1997) Phase locking to high frequencies in the auditory nerve and cochlear nucleus magnocellularis of the barn owl, *Tyto alba*. J Neurosci 17:3312–3321.

Köppl C, Carr CE (2003) Computational diversity in the cochlear nucleus angularis of the barn owl. J Neurophysiol 89:2313–2329.

Köppl C, Gleich O, Manley GA (1993) An auditory fovea in the barn owl cochlea. J Comp Physiol A 171:695–704.

Kubke MF, Massoglia DP, Carr CE (2002) Developmental changes underlying the formation of the specialized time coding circuits in barn owls (*Tyto alba*). J Neurosci 22:7671–7679.

Kühne R, Lewis B (1985) External and middle ears. In: King AS, McLelland J (eds), Form and Function in Birds, Vol. 3. London: Academic Press, pp. 227–271.

Larsen ON (1995) Acoustic equipment and sound field calibration. In: Klump GM, Dooling RJ, Fay RR, Stebbins WC (eds), Methods in Comparative Psycho-Acoustics. Basel: Birkhäuser Verlag, pp. 31–45.

Larsen ON, Popov AV (1995) The interaural canal does enhance directional hearing in quail (*Coturnix coturnix japonica*). In: Burrows M, Matheson T, Newland PL, Schüppe H (eds), Neural systems and behavior. Proceedings of the 4th International Conference in Neuroethology. Stuttgart:Georg Thieme Verlag, p. 313.

Larsen ON, Dooling RJ, Ryals BM (1997) Roles of intracranial air pressure in bird audition. In: Lewis ER, Long GR, Lyon RF, Narins PM, Steele CR, Hecht-Poinar E (eds), Diversity in Auditory Mechanics. Singapore: World Scientific, pp. 11–17.

Lewald J (1990) The directionality of the ear of the pigeon (*Columba livia*). J Comp Physiol A 167:533–543.

Lewald J, Dörrscheidt GJ (1998) Spatial-tuning properties of auditory neurons in the optic tectum of the pigeon. Brain Res 790:339–342.

Lewis ER, Narins PM (1999) The acoustic periphery of amphibians: anatomy and physiology. In: Fay RR, Popper AN (eds), Comparative Hearing: Fish and Amphibians. New York: Springer-Verlag, pp. 101–154.

Lombard RE, Bolt J (1979) Evolution of the tetrapod ear: an analysis and reinterpretation. Biol J Linn Soc 11:19–76.

Lombard RE, Straughan IR (1974) Functional aspects of anuran middle ear structures. J Exp Biol 61:71–93.

Luksch H, Walkowiak W (1998) Morphology and axonal projection patterns of auditory neurons in the midbrain of the painted frog, *Discoglossus pictus*. Hear Res 122:1–17.

Manley GA (1972) The middle ear of the tokay gecko. J Comp Physiol 81:239–250.

Manley GA (1981) A review of the auditory physiology of the reptiles. Prog Sens Physiol 2:49–134.

Manley GA (1990) Peripheral Hearing Mechanisms in Reptiles and Birds. New York: Springer-Verlag.

Manley GA (2000) The hearing organs of lizards. In: Dooling RJ, Fay RR, Popper AN (eds), Comparative Hearing: Birds and Reptiles. New York: Springer-Verlag, pp. 139–196.

Manley GA (2004) The lizard basilar papilla and its evolution. In: Manley GA, Popper AN, Fay RR (eds), Evolution of the Vertebrate Auditory System. New York: Springer-Verlag, pp. 200–224.

Manley GA, Clack J (2004) An outline of the evolution of vertebrate hearing organs. In: Manley GA, Popper AN, Fay RR (eds), Evolution of the Vertebrate Auditory System. New York: Springer-Verlag, pp. 1–26.

Manley GA, Köppl C (1998) Phylogenetic development of the cochlea and its innervation. Curr Opin Neurobiol 8:468–474.

Manley GA, Köppl C, Konishi M (1988) A neural map of interaural intensity difference in the brainstem of the barn owl. J Neurosci 8:2665–2677.

McCormick CA (1999) Anatomy of the central auditory pathways of fish and amphibians. In: Fay RR, Popper AN (eds), Comparative Hearing: Fish and Amphibians. New York: Springer-Verlag, pp. 155–217.

Megela-Simmons A, Moss CF, Daniel KM (1985) Behavioral audiograms of the bullfrog (*Rana catesbeiana*) and the green treefrog (*Hyla cinerea*). J Acoust Soc Am 78:1236–1244.

Melssen WJ, Epping WJM (1990) A combined sensitivity for frequency and interaural intensity difference in neurons in the auditory midbrain of the grassfrog. Hear Res 44:35–50.

Melssen WJ, Epping WJM (1992) Selectivity for temporal characteristics of sound and interaural time difference of auditory midbrain neurons in the grassfrog: a system theoretical approach. Hear Res 60:178–198.

Melssen WJ, Epping WJM, van Stokkum IHM (1990) Sensitivity for interaural time and intensity difference of auditory midbrain neurons in the grassfrog. Hear Res 47:235–256.

Michelsen A (1994) Directional hearing in crickets and other small animals. Fortschr Zool 39:195–207.

Michelsen A (1998) Biophysics of sound localization in insects. In Hoy RR, Popper AN, Fay RR (eds), Comparative Hearing: Insects. New York: Springer-Verlag, pp. 18–62.

Michelsen A, Jørgensen M, Christensen-Dalsgaard J, Capranica RR (1986) Directional hearing of awake, unrestrained treefrogs. Naturwissenschaften 73:682–683.

Mogdans J, Knudsen EI (1994) Representation of interaural level difference in the VLVp, the first site of binaural comparison in the barn owl's auditory system. Hear Res 74: 148–164.

Moiseff A (1989) Bi-coordinate sound localization by the barn owl. JComp Physiol A 164:637–644.

Moiseff A, Konishi M (1981) Neuronal and behavioral sensitivity to binaural time differences in the owl. J Neurosci 1:40–48.

Morse PM (1948) Vibration and sound, 2nd ed (reprint 1986). New York: American Institute of Physics.

Narins PM, Ehret G, Tautz J (1988) Accessory pathway for sound transfer in a neotropical frog. Proc Natl Acad Sci USA 85:1255–1265.

Nelson BS, Stoddard PK (1998) Accuracy of auditory distance and azimuth perception by a passerine bird in natural habitat. Anim Behav 56:467–477.

Overholt EM, Rubel EW, Hyson RL (1992) A circuit for coding interaural time differences in the chick brainstem. J Neurosci 12:1698–1708.

Palmer AR, Pinder AC (1984) The directionality of the frog ear described by a mechanical model. J Theor Biol 110:205–215.

Parameshwaran S, Carr CE, Perney TM (2001) Expression of the Kv3.1 potassium channel in the avian auditory brainstem. J Neurosci 21:485–494.

Park TJ, Dooling RJ (1991) Sound localization in small birds: absolute localization in azimuth. J Comp Psychol 105:121–133.

Passmore NI, Telford SR (1981) The effect of chorus organization on mate localization in the painted reed frog (*Hyperolius marmoratus*). Behav Ecol Sociobiol 9:291–293.

Passmore NI, Capranica RR, Telford SR, Bishop PJ (1984) Phonotaxis in the painted reed frog (*Hyperolius marmoratus*). J Comp Physiol A 154:189–197.

Payne RS (1971) Acoustic location of prey by barn owls. J Exp Biol 54:535–573.

Pettigrew AG, Anson M, Chung SH (1981) Hearing in the frog: a neurophysiological study of the auditory response in the midbrain. Proc R Soc Lond B 212:433–457.

Pettigrew AG, Carlile S (1984) Auditory responses in the torus semicircularis of the cane toad, *Bufo marinus*. I. Field potential studies. Proc R Soc Lond B 222:231–242.

Pettigrew JD, Larsen ON (1990) Directional hearing in the plains-wanderer *Pedionomus torquatus*. In: Rowe M, Aitkin L (eds), Information Processing in Mammalian Auditory and Tactile Systems. New York: Alan R. Liss, pp. 179–190.

Pinder AC, Palmer AR (1983) Mechanical properties of the frog ear: vibration measurements under free- and closed-field acoustic conditions. Proc R Soc Lond B 219:371–396.

Poganiatz I, Nelken I, Wagner H (2001) Sound-localization experiments with barn owls in virtual space: influence on interaural time difference on head-turning behavior. J Assoc Res Otolaryngol 2:1–21.

Purgue A (1997) Tympanic sound radiation in the bullfrog, *Rana catesbeiana*. J Comp Physiol A 181:438–445.

Purgue A, Narins PM (2000) Mechanics of the inner ear of the bullfrog (*Rana catesbeiana*): the contact membranes and the periotic canal. J Comp Physiol A 186:481–488.

Rheinlaender J, Klump G (1988) Behavioral aspects of sound localization. In: Fritzsch B, Ryan MJ, Wilczynski W, Hetherington TE, Walkowiak W (eds), The Evolution of the Amphibian Auditory System. New York: John Wiley & Sons, pp. 297–305.

Rheinlaender J, Gerhardt HC, Yager DD, Capranica RR (1979) Accuracy of phonotaxis by the green treefrog (*Hyla cinerea*). J Comp Physiol 133:247–255.

Rheinlaender J, Walkowiak W, Gerhardt HC (1981) Directional hearing in the green treefrog: a variable mechanism? Naturwissenschaften 68:430–431.

Rice WR (1982) Acoustical location of prey by the marsh hawk: adaptation to concealed prey. Auk 99:409–413.

Rosowski JJ, Saunders JC (1980) Sound transmission through the avian interaural pathway. J Comp Physiol A 130:183–190.

Sakaluk SK, Bellwood JJ (1984) Gecko phonotaxis to cricket calling song: a case of satellite predation. Anim Behav 32:659–662.

Saunders JC, Duncan RK, Doan DE, Werner YL (2000) The middle ear of reptiles and birds. In: Dooling RJ, Fay RR, Popper AN (eds), Comparative Hearing: Birds and Reptiles. New York: Springer-Verlag, pp. 13–69.

Schmidt R (1988) Mating call phonotaxis in female American toads: lesions of central auditory system. Brain Behav Evol 32:119–128.

Schmitz B, White TD, Narins PM (1992) Directionality of phase locking in auditory nerve fibers of the leopard frog *Rana pipiens pipiens*. J Comp Physiol A 170:589–604.

Schwartz J, Gerhardt HC (1989) Spatially mediated release from auditory masking in an anuran amphibian. J Comp Physiol A 166:37–41.

Schwartz J, Gerhardt HC (1995) Directionality of the auditory system and call pattern recognition during acoustic interference in the gray tree frog, *Hyla versicolor*. Audit Neurosci 1:195–206.

Schwartzkopff J (1950) Beitrag zur Problem des Richtungshörens bei Vögeln. Z Vergl Physiol 32:319–327.

Schwartzkopff J (1952) Untersuchungen über die Arbeitsweise des Mittelohres und das Richtungshören der Singvögel unter verwendung von Cochlea-Potentialen. Z Vergl Physiol 34:46–68.

Smith CA, Konishi M, Schuff N (1985) Structure of the barn owl's (*Tyto alba*) inner ear. Hear Res 17:237–247.

Soares C, Carr CE (2001) The cytoarchitecture of the nucleus angularis in the barn owl (*Tyto alba*). J Comp Neurol 429:192–203.

Soares D, Chitwood RA, Hyson RL, Carr CE (2002) Intrinsic neuronal properties of the chick nucleus angularis. J Neurophysiol 88:152–162.

Sullivan WE, Konishi M (1984) Segregation of stimulus phase and intensity coding in the cochlear nucleus of the barn owl. J Neurosci 4:1787–1799.

Szpir MR, Sento S, Ryugo DK (1990) Central projections of cochlear nerve fibers in the alligator lizard. J Comp Neurol 295:530–547.

Takahashi T, Moiseff A, Konishi M (1984) Time and intensity cues are processed independently in the auditory system of the owl. J Neurosci 4:1781–1786.

ten Donkelaar H, Bangma GC, Barbas-Henry HA, de Boer-van Huizen R, Wolters JG (1987) The brain stem in a lizard, *Varanus exanthematicus*. Adv Anat Embryol Cell Biol 107:56–60.

van Bergeijk WA (1966) Evolution of the sense of hearing in vertebrates. Am Zool 6: 371–377.

Vlaming MSMG, Aertsen AMBJ, Epping WJM (1984) Directional hearing in the grassfrog (*Rana temporaria* L.). I. Mechanical vibrations of tympanic membrane. Hear Res 14:191–201.

Volman SF, Konishi M (1989) Spatial selectivity and binaural responses in the inferior colliculus of the great horned owl. J Neurosci 9:3083–3096.

Volman S, Konishi M (1990) Comparative physiology of sound localization in four species of owls. Brain Behav Evol 36:196–215.

Wagner H (1993) Sound-localization deficits induced by lesions in the barn owl's space map. J Neurosci 13:371–386.

Wagner H (2002) Directional hearing in the barn owl: psychophysics and neurophysiology. In: Tranebjærg L, Christensen-Dalsgaard J, Andersen T, Poulsen T (eds), Genetics and the Function of the Auditory System. Proceedings of the 19th Danavox Symposium. Copenhagen: Holmens Trykkeri, pp. 331–351.

Wagner H, Takahashi TT, Konishi M (1987) Representation of interaural time difference in the central nucleus of the barn owl's inferior colliculus. J Neurosci 7:3105–3116.

Walkowiak W (1980) The coding of auditory signals in the torus semicircularis of the fire-bellied toad and the grass frog: responses to simple stimuli and to conspecific calls. J Comp Physiol 138:131–148.

Walkowiak W, Berlinger M, Schul J, Gerhardt HC (1998) Significance of forebrain structures in acoustically guided behaviour in anurans. Eur J Morphol 37:177–181.

Wang J, Narins PM (1996) Directional masking of phase locking in the amphibian auditory nerve. J Acoust Soc Am 99:1611–1620.

Wang J, Ludwig TA, Narins PM (1996) Spatial and spectral dependence of the auditory periphery in the northern leopard frog. J Comp Physiol A 178:159–172.

Werner YL (2003) Mechanical leverage in the middle ear of the American bullfrog, *Rana catesbeiana*. Hear Res 175:54–65.

Werner YL, Montgomery LG, Safford SD, Igic PG, Saunders JC (1998) How body size affects middle-ear structure and function and auditory sensitivity in gekkonoid lizards. J Exp Biol 201:487–502.

Wever EG (1978) The Reptile Ear. Princeton: Princeton University Press.

Wever EG (1985) The Amphibian Ear. Princeton: Princeton University Press.

White TD, Schmitz B, Narins PM (1992) Directional dependence of auditory sensitivity and frequency selectivity in the leopard frog. J Acoust Soc Am 92:1953–1961.

Wightman FL, Kistler DJ, Perkins ME (1987) A new approach to the study of human sound localization. In: Yost WA, Gourevitch G (eds), Directional Hearing. New York: Springer-Verlag, pp. 26–48.

Wilczynski W (1988) Brainstem auditory pathways in anuran amphibians. In: Fritzsch

B, Ryan MJ, Wilczynski W, Hetherington TE, Walkowiak W (eds), The Evolution of the Amphibian Auditory System. New York: John Wiley & Sons, pp. 209–231.

Wilczynski W, Resler C, Capranica RR (1987) Tympanic and extratympanic sound transmission in the leopard frog. J Comp Physiol A 161:659–669.

Wilczynski W, Rand AS, Ryan MJ (2001) Evolution of calls and auditory tuning in the *Physalaemus pustulosus* species group. Brain Behav Evol 58:137–151.

Will U (1988) Organization and projections of the area octavolateralis in amphibians. In: Fritzsch B, Ryan MJ, Wilczynski W, Hetherington TE, Walkowiak W (eds), The Evolution of the Amphibian Auditory System. New York: John Wiley & Sons, pp. 185–208.

Will U, Fritzsch B (1988) The eighth nerve of amphibians. In: Fritzsch B, Ryan MJ, Wilczynski W, Hetherington TE, Walkowiak W (eds), The Evolution of the Amphibian Auditory System. New York: John Wiley & Sons, pp. 159–183.

Woodworth RS, Schlosberg H (1962) Experimental Psychology. New York: Holt, Rinehart and Winston, pp. 349–361.

Xu J, Gooler DM, Feng AS (1994) Single neurons in the frog inferior colliculus exhibit direction-dependent frequency selectivity to isointensity tone bursts. J Acoust Soc Am 95:2160–2170.

Zhang H, Xu J, Feng AS (1999) Effects of GABA-mediated inhibition on direction-dependent frequency tuning in the frog inferior colliculus. J Comp Physiol A 184: 85–98.