Environmental influences in the evolution of tetrapod hearing sensitivity and middle ear tuning

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Synopsis Vertebrates inhabit and communicate acoustically in most natural environments. We review the influence of environmental factors on the hearing sensitivity of terrestrial vertebrates, and on the anatomy and mechanics of the middle ears. Evidence suggests that both biotic and abiotic environmental factors affect the evolution of bandwidth and frequency of peak sensitivity of the hearing spectrum. Relevant abiotic factors include medium type, temperature, and noise produced by nonliving sources. Biotic factors include heterospecific, conspecific, or self-produced sounds that animals are selected to recognize, and acoustic interference by sounds that other animals generate. Within each class of tetrapods, the size of the middle ear structures correlates directly to body size and inversely to frequency of peak sensitivity. Adaptation to the underwater medium in cetaceans involved reorganization of the middle ear for novel acoustic pathways, whereas adaptation to subterranean life in several mammals resulted in hypertrophy of the middle ear ossicles to enhance their inertial mass for detection of seismic vibrations. The comparative approach has revealed a number of generalities about the effect of environmental factors on hearing performance and middle ear structure across species. The current taxonomic sampling of the major tetrapod groups is still highly unbalanced and incomplete. Future expansion of the comparative evidence should continue to reveal general patterns and novel mechanisms.

Environmental factors and hearing

In most tetrapods, the sense of hearing plays a fundamental role in predator avoidance, mate acquisition, and foraging (Dusenbery 1992). In support of such behaviors, hearing systems have adapted to a wide diversity of life histories such that the ears operate under a myriad of combinations of environmental conditions, sensitivity requirements, and size (Webster et al. 1992; Fay and Popper 1994, 1998; Dooling et al. 2000). Comparative analyses of this diversity can reveal correlations between morphological or mechanistic features of the ear and environmental factors in the habitat, indicating potential cases of adaptation.

In this review, we focus on the frequency range of hearing in tetrapods and examine the current evidence for adaptation to environmental factors. We also review the knowledge on changes to middle ear anatomy in response to environment. While inner ear allometry, mechanics, and neurophysiology also contribute to define an animal's hearing abilities (Manley 1971; Echteler et al. 1994), we will only discuss the middle ear, due to space constraints.

Measurements related to hearing sensitivity

This review will refer to studies that employed a variety of methods to measure the response of the auditory system to sound. These methods probe various points along the hearing pathway and can produce different results. It is, therefore, important to be aware of the main differences between the most frequently used measurement techniques in order to interpret their results appropriately.

Behavior

Behavioral methods often involve training an animal to produce a motor output in response to a pure-tone acoustic stimulus (Heise 1953; Masterton et al. 1969; Konishi 1970). By varying the intensity and the frequency of the stimulus and recording the individual's response, threshold curves called audiograms are produced. Behavioral audiograms reveal the minimum intensity of sound at the ear that is necessary at each frequency to evoke the trained response. This method provides a natural assessment of hearing; it is noninvasive and it quantifies high-level neural

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responses to the stimuli. Although behavioral audiograms are commonly measured in mammals and birds (Masterton et al. 1969; Konishi 1970; Fay 1988; Dooling 2002), they are rarely obtained in amphibians and reptiles (Bulog and Schlegel 2000), which are notoriously difficult to train. The extent to which behavioral audiograms represent hearing abilities can be influenced by the effectiveness of the training regime.

Electrophysiology

Neural activity may be recorded directly from various areas of the brain of animals, axons in the auditory (VIIIth) nerve, or from various locations in the inner ear, including hair cells. Electrodes can be prepared to obtain intra- or extracellular recordings from a single cell, or to record from an ensemble of cells (Kraus and McGee 1992; Eggermont and Ponton 2002). Hair cells in the main auditory sensory epithelium of all tetrapods are tonotopically organized, i.e., their frequency of peak sensitivity is a function of their position in the organ. This frequency-specific organization is conserved in the auditory nerve and in the midbrain. Assessments of the hearing range of animals through electrophysiological methods involving direct measurement from neurons, therefore, demand sampling the responses of enough cells to span the whole range of sensitivity. Such recordings tend to be in good agreement with behavioral audiograms (Konishi 1970; Dooling and Popper 2000). The neural response to sound can also be measured indirectly (without neuronal contact), through recordings of auditory-evoked responses in the brain, vestibulo-ocular reflexes and magnetic resonance imaging. Such methods are advantageous for being noninvasive, but they tend to produce results with higher thresholds than do measurements involving direct neuronal contact (Kraus and McGee 1992; Eggermont 2001; Eggermont and Ponton 2002; Todd et al. 2008). Another type of indirect technique is the recording of microphonic potentials using an electrode in the inner ear or on the round window. The combined electrical activity of the hair cells in response to mechanical excitation is then measured (Wever and Bray 1930, 1936; Tasaki et al. 1954).

Eardrum vibration measurements

The frequency response of the eardrum vibration to acoustic stimuli has been assessed with various methods, including stroboscopic illumination (von Békésy 1960), capacitive probe (von Békésy 1960), the Mössbauer technique using a radioactive source (Hillman et al. 1964), displacement measurements with laser interferometry (Khanna and Tonndorf 1972; Dragsten et al. 1974), and velocity measurements using laser Doppler vibrometry (Buunen and Vlaming 1981). Such measurements can be rapid and noninvasive, depending on the accessibility of the eardrum. While the spectral response of the eardrums to sound often coincides with the frequency ranges determined by behavioral tests or electrophysiology, it does not reflect signal losses that may occur in the ossicular chain (especially in cartilaginous middle ears), or during either signal transduction by the hair cells, or processing in the central nervous system.

Variability and body size

The diversity of hearing sensitivity spectra has been summarized for various groups of vertebrates (Fay 1988, 1992; Dooling and Popper 2000; Dooling 2002). The extent of phylogenetic coverage found in the literature varies widely among classes, limiting comparisons of hearing performance among groups.

One major difference found between the middle ears of mammals and those of other tetrapods is that the ossicular chain of mammals is composed of three ossicles (malleus, incus, and stapes), whereas in nonmammals it comprises one ossicle (stapes or columella) and one cartilaginous element (extrastapes or extracolumella; Clack and Allin 2004). Until recently, the frequency ranges of hearing sensitivity in all nonmammals were believed to be restricted to below 12 kHz, whereas in mammals they often can extend beyond 40 kHz (Fay 1992). These differences, in addition to studies on single-ossicle ears showing transmission efficiency loss at high frequencies due to flexing of the extrastapes (Manley 1972a, 1972b, 1981), lead to a common belief that the single-ossicle design prevented nonmammals from evolving hearing sensitivity above 12 kHz (Manley and Gleich 1992). This hypothesis is currently being revisited as three species of Asian frogs (*Odorrana livida*, *Odorrana tormota* and *Huia cavitympanum*, Ranidae) have been shown to detect ultrasound, with efficient transmission of frequencies up to ~40 kHz by the middle ear and acoustically evoked potentials recorded in the midbrain up to 38 kHz (Feng et al. 2006; Arch et al. 2008, 2009; Gridi-Papp et al. 2008).

Body size has been reported to have a strong inverse correlation with the frequency of peak sensitivity both among and within species (Rosowski and Graybeal 1991; Dooling 1992; Hetherington 1992; Nummela 1995; Werner et al. 1998, 2002; Nummela et al. 1999; Dooling and Popper 2000;

Werner and Igic 2002; Gleich et al. 2005; Nummela and Sanchez-Villagra 2006). The sizes of the middle ear components and the volumes of the middle ear and mouth cavities scale with body size, resulting in correlated air compliances, resonances and, ultimately, middle ear tuning (Hetherington 1992; Rosowski 1994; Hemilä et al. 1995; Nummela 1995; Nummela et al. 1999; Huang et al. 2000; Nummela and Sanchez-Villagra 2006). All major tetrapod groups show, however, extensive interspecific variation around the average relation between body size and frequency of peak sensitivity. Evidence has been reported in several groups that such variation can be partly explained by adaptation to the physical or biotic environment (Okanoya and Dooling 1987, 1988; Dooling 1992; Wilczynski et al. 1993). Body size itself can be driven by environmental factors that affect development or select individuals for body size. Tetrapods, especially ectotherms, tend to be larger in colder environments, leading to latitudinal and altitudinal patterns of gradual change both across and within species (Narins and Smith 1986; Partridge and French 1996; Angilletta et al. 2004).

The abiotic environment

Lewis and Fay (2004) provide an analytical discussion of the environmental factors that are most likely to have shaped hearing in tetrapods. We will focus on the empirical evidence of correlated variation between hearing sensitivity and environmental factors, principally medium characteristics, habitat acoustics, temperature, and noise.

Medium characteristics

Tetrapod ears operate surrounded by a medium of air, water, or soil and the performance of the same ear in different media has been quantified in a few mammals and amphibians. Behavioral audiograms show that relative to air, human auditory thresholds increase underwater and these differences increase with frequency from 18 dB at 125 Hz to 56 dB at 8 kHz (Brandt and Hollien 1967). Marine mammals vary from hearing best in water (elephant seals, *Mirounga angustirostris*, Phocidae), in air (sea lions, *Zalophus californianus*, Otariidae), or hearing equally well in both media (harbor seals, *Phoca vitulina*, Phocidae; Richardson et al. 1995; Kastak and Schusterman 1998). In amphibians, airborne and underwater hearing have been compared in bullfrogs [*Lithobates catesbeianus*, formerly *Rana catesbeiana* (Ranidae)] using multi-unit acoustically evoked responses recorded in the torus semicircularis of the midbrain (Lombard et al. 1981). They revealed underwater sensitivity to be equal or better than airborne sensitivity below 200 Hz, and up to 30 dB poorer above 200 Hz.

While comparing the hearing performance of a terrestrial species in air and underwater can reveal the effect of the change in medium, comparative analysis of the sensitivity and structure of specialists inhabiting each medium can point to the evolutionary changes involved in adaptation to that medium. All vertebrate inner ears are filled with fluid, which must be vibrated to stimulate the sensory hair cells (Lewis et al. 1985). The most obvious differences in structure and function exhibited by tetrapods specialized to each medium relate to the pathways taken by the acoustic input to the inner ear.

Air is a sound transmission medium with much lower impedance than the body tissues of vertebrates and therefore the direct transfer of acoustic signals from air into the tissues is minimal. Middle ears resolve the impedance mismatch between sound in air and the inner ear fluid, greatly increasing auditory sensitivity (Vlaming and Feenstra 1986; Jørgensen and Kanneworff 1998; Voss et al. 2000; Aibara et al. 2001; Koike et al. 2002; Stenfelt et al. 2002). The impedance matching is based on two features: (1) The large surface area ratio between the tympanic membrane (eardrum) which is in contact with the air, and the oval window, which contacts the inner ear fluid. (2) The vibration of the tympanic membrane is transferred to the oval window through one or two levers formed by the ossicular chain (two levers are found in amphibians, see Jørgensen and Kanneworff 1998; Mason and Narins 2002b). The problem of impedance mismatch, and therefore the importance of the middle ear, increases with body size and sound frequency. In small amphibians, external sound can cross the floor of the mouth and the tissues of the body wall to excite the air contained in the mouth and lungs (Wilczynski et al. 1987; Narins et al. 1988; Ehret et al. 1990, 1994; Hetherington and Lindquist 1999; Hetherington 2001; Mason 2006). The lungs and mouth connect to the middle ear cavity through the short and wide Eustachian tubes, that remain open at rest (but see Gridi-Papp et al. 2008), and provide an alternative acoustic pathway for auditory input (Narins et al. 1988). Middle ear structures have been secondarily lost in small species of several groups of amphibians, and this loss might be due to developmental reduction (Hetherington and Lindquist 1999). As an alternative explanation, small frogs tend to have relatively large lungs and thin body walls. Thus, their lungs might serve as an efficient conduit for sound pickup and delivery

to the middle ear, taking up the role of the eardrum in sound admission (Narins et al. 1988; Ehret et al. 1994). Such an hypothesis is supported by measurements showing that two species of frogs without eardrums have relatively low auditory thresholds (Hetherington 1992; Jaslow and Lombard 1996).

When sound propagates underwater, it passes into the body tissues of vertebrates with relatively little loss since the impedances of tissues and water are similar. The ear canal in whales and dolphins is narrow and plugged with dense cerumen (Clack 1992; Fritzsch 1992; Ketten 1997; Nummela et al. 2004) and it is believed to have lost its importance in conducting sound to the inner ears. High-frequency acoustic input in odontocetes is mainly through a channel of low-impedance fatty tissues that runs from the mid-line of the lower jaw to the temporal bones (Varanasi and Malins 1971; Norris 1980). The anatomical modifications found in the middle ears of secondarily aquatic nonmammalian vertebrates appear to be less extreme than those found in cetaceans, but a detailed mechanistic understanding of underwater hearing is still lacking in most cases (Hetherington 2008).

Fossorial animals live with their heads buried in sand or soil, which attenuates high-frequency sounds. Some fossorial insectivores, such as the African golden moles (Chrysochloridae) have evolved an extreme specialization for detection of low frequencies. The mallei in the middle ear are hypertrophied, and due to their increased mass and the fact that their center of mass is displaced from their rotatory axis, they vibrate out of phase with the skull in response to seismic vibrations, stimulating the inner ear (Mason and Narins 2001, 2002a; Willi et al. 2006b). In this mode, the relative motion between the malleus and the skull is due to the inertia of the malleus, rather than mechanical drive by the tympanic membrane.

Most terrestrial animals live with their ears surrounded by air, but with their feet on the ground. As the two media (air and ground) have different sound transmission properties, they can provide the animal with complementary input from the environment. For example, elephants are known to be highly sensitive to low-frequency sound (Heffner and Heffner 1980) and to produce and detect seismic signals (O'Connell et al. 1997; O'Connell-Rodwell et al. 2000, 2001). Seismic stimuli can be transmitted from the ground to the feet and up to the ears through bone conduction. The massive middle ear ossicles of elephants respond to vibration and stimulate the inner ears in a manner similar to that described above for golden moles (Reuter et al. 1998). Among the tetrapods, seismic sensitivity is currently believed to be highest in amphibians (Ross and Smith 1978, 1979; Narins and Lewis 1984; Yu et al. 1991; Narins 2001). Besides tympanic hearing, amphibians possess a second middle ear mechanism: the operecularis system. It consists, in part, of a disk-shaped bone, the operculum, which abuts a portion of the oval window of the inner ear. The distal surface of the operculum receives the insertion of the operecularis muscle, which at its other end inserts into the cartilagenous suprascapula. This forms an alternative pathway for acoustic stimuli, in which seismic vibrations are transmitted from the ground to the shoulders through bone conduction, then through the tonic operecularis muscle to the operculum and into the inner ear (Hetherington 1985, 1987; Hetherington et al. 1986). Disruption of the operecularis system produces up to 6.5–13.1 dB loss in seismic sensitivity (Hetherington 1988).

Acoustics of the habitat

The acoustics of the environment in which an animal lives and communicates can influence several aspects of sound transmission, potentially leading to adaptation of the animal's vocal and hearing systems (Richards and Wiley 1980; Penna and Solís 1996; Penna and Márquez 2007). Due to constraints of space, we will restrict this section to the well-studied case of rodents that live in tunnels, which is a clear example of repeated independent evolution of middle ear structure and function correlated with environmental acoustics.

Comparative studies in rodents have revealed a close relation between their habitat and features of their hearing, vocalizations, and anatomy (Heth et al. 1986; Heffner and Heffner 1992b, 1993; Heffner et al. 1994; Jackson et al. 1997; Lange et al. 2004, 2007; Begall and Burda 2006). Heth and colleagues investigated the acoustics in the tunnels used by blind mole rats (*Nannospalax ehrenbergi*, Spalacidae), and found that sound transmission was greatly decreased at high frequencies with best transmission at 440 Hz (Heth et al. 1986). Both the hearing range and the vocalizations of blind mole rats are shifted to low frequencies, presumably as an adaptation to the acoustics of the tunnels (Heth et al. 1986; Bruns et al. 1988). Later studies demonstrated that the patterns first observed in the blind mole rats may be generalized across rodents: subterranean species tend to have reduced sensitivity in comparison with surface dwellers, having higher sensitivity at low frequencies but much reduced

sensitivity at high frequencies. Species such as prairie dogs (genus *Cynomys*; Sciuridae), that are intermediate between subterranean and surface-dwelling rodents in the amount of time spent underground versus above the ground, also have intermediate sensitivity at low and at high frequencies. The hearing and vocal features of subterranean rodents are accompanied by modifications of the middle ear including: relatively larger eardrum lacking a pars flacida, enlarged incus, and reduced or missing middle ear muscles (Burda et al. 1992). In a recent study, Lange and colleagues (2007) evaluated the acoustics of tunnels used by subterranean rodents, and confirmed the patterns reported previously by Heth and colleagues (Heth et al. 1986), but they also found that some tunnels actually amplified sounds by up to 6.5 dB at frequencies between 200 and 800 Hz (Lange et al. 2007). They suggested that reduced peak sensitivity in subterranean rodents might be an adaptation to prevent overstimulation of the ears.

Temperature

Gerhardt (1978) studied male advertisement calls and female acoustic preferences of two sympatric sister species of gray treefrogs (*Hyla versicolor* and *Hyla chrysoscelis*, Hylidae), in which the calls differ only in note rate. He found that increasing temperature caused males of both species to produce calls with higher note rates, and females of both species to prefer calls with higher note rates. The separation between the communication systems of the two species was therefore maintained because temperature biased both signalers and receivers in the same way. Walkowiak (1980) made multi-unit recordings in two species of frogs to assess the effect of temperature on midbrain auditory responses to pure tones. He found that sensitivity increased with temperature in both species, but stabilized at different optimal temperatures. Such optimal temperatures matched the temperatures in which the frogs most frequently call in nature, indicating that the hearing systems are adapted to the temperature range to which each of several frog species is naturally exposed. Nevertheless, studies of the responses of the eighth nerve to sound as a function of temperature in various frog species demonstrated that whereas the responses of the amphibian papillar fibers were highly temperature sensitive, responses of the basilar papillar fibers were strikingly temperature-insensitive (Stiebler and Narins 1990; van Dijk et al. 1990; Benedix et al. 1994).

Noise

Abiotic noise produced by wind, flowing water, or rains typically has a broad spectrum with a low frequency peak. In response to abiotic background noise, hearing systems have been suggested to adapt by shifting their sensitivity ranges toward high frequencies (Langemann et al. 1998; Feng et al. 2006; Arch et al. 2009). One could also expect animals to evolve enhanced critical masking ratios at frequencies that are most biologically relevant to them, and in fact, parakeets, horseshoe bats, and green treefrogs have lowest critical masking ratios at the frequencies in which their absolute sensitivity is greatest, which correspond to the dominant frequencies of their calls (Dooling and Saunders 1975; Long 1977; Moss and Simmons 1986). This simple match is not a general pattern; however, as in most other mammals and birds that have been studied to date the critical masking ratio tends to simply increase with frequency (Dooling 1980; Okanoya and Dooling 1987; Klump 1996).

Besides their adverse effect in masking communication, natural abiotic acoustic sounds can also benefit animals by carrying relevant information about the environment. In the Namib Desert, substrate vibrations that are produced when the wind passes over vegetation-topped sand mounds result in seismic signals in the substrate that are detected at a distance by golden moles (Narins et al. 1997; Lewis et al. 2006). These animals cue in on spectral differences between the vibrations produced by the wind blowing over naked sand mounds versus over sand mounds topped with vegetation. By detecting wind-produced vibrations, the golden moles are able to localize and approach vegetation-covered mounds, within which their arthropod prey are most abundant. Many species of golden moles have extraordinarily hypertrophied mallei, which make them highly sensitive to seismic vibrations of the substrate (Mason and Narins 2002a; Mason 2003a, 2003b; Willi et al. 2006b).

The biotic environment

Biotic factors include heterospecific, conspecific, or self-generated sounds to which the animal must be sensitive, and acoustic interference by sounds that other animals generate.

Heterospecific sounds

Cases of hearing sensitivity shaped by predator sounds have been reported in noctuid moths that rely on ultrasonic sensitivity to detect the echolocation calls of bats and initiate escape maneuvers

(Roeder 1962, 1966; Spangler 1988; Hoy 1992). The frequency ranges of sounds produced by predators and prey are also commonly found to match the hearing abilities of tetrapods. While many bats rely on echolocation to locate prey, some species cue in to the sounds produced by the insects or frogs that they consume. Echolocation calls are mostly ultrasonic and bats' ears are correspondingly tuned to high frequencies (Dalland 1965; Neuweiler 1984). Some bats present a second sensitivity peak at low frequencies (8–20 kHz). This secondary sensitivity peak has been suggested to be an adaptation to wide-range social communication, as audible frequencies transmit farther in the atmosphere than does ultrasound, or to locate prey items based on their sounds (Brown et al. 1978; Guppy and Coles 1988; Fuzessery et al. 1993; ter Hofstede et al. 2008). The frog-eating bat *Trachops cirrhosus* can be attracted to loudspeakers broadcasting low-frequency frog calls or pure tones. These bats' hearing sensitivity decreases from 15 to 5 kHz and increases again from 5 to 0.2 kHz, which is the range of most frog calls (Ryan et al. 1983).

Some of the highest acoustic sensitivities have been documented in nocturnal predators, which are greatly dependent on hearing to detect and seize prey (Neff and Hind 1955; Dalland 1965; Konishi 1973; van Dijk 1973; Neuweiler 1984; Dyson et al. 1998). High-frequency sensitivity in mammals has been suggested to be, in general, an adaptation for precise predator and prey localization based on vocalizations and wide-band sounds produced by animals moving on the substrate (Heffner and Heffner 1992a, 2008). The highly mobile external ears of most mammals are also believed to reflect the importance of detecting and locating heterospecifics (Flynn and Elliott 1965; Coles and Guppy 1986; Guppy and Coles 1988; Musicant et al. 1990).

Conspecific sounds

When analyzed across species, the frequency of highest sensitivity of the auditory system often exhibits a close match with the dominant frequency of conspecific calls (Konishi 1970; Dooling et al. 1971; Dooling and Saunders 1975; Okanoya and Dooling 1988; Wilczynski et al. 1993). This pattern could be partly due to stabilizing selection by conspecifics, and partly by allometry, as both vocal fold length and middle ear size scale with body size and correlate inversely with the tuning of calls and ears.

When examined between the sexes, within a species, however, the frequency of best sensitivity does not always match the frequency of the calls. In several species of frogs, the peak sensitivities obtained through recordings of evoked potentials in the midbrains of females were tuned to lower frequencies than the average male calls (Gerhardt and Doherty 1988; Ryan and Wilczynski 1988; Ryan 1990; Ryan and Rand 1990; Wilczynski et al. 2001). Such female midbrain recordings closely approximated the female's acoustic preferences. And several studies have found female acoustic preferences to be biased toward low frequency calls (Ryan 1980; Robertson 1986; Dyson and Passmore 1988; Gerhardt and Doherty 1988; Morris and Yoon 1989; Ryan et al. 1992). Female frogs, in these species, are larger than males, and this has been suggested to be the basis for sexual selection for large males: females, being larger than males, have their auditory systems tuned to lower frequencies than the average male call, and become maximally excited by the lowest pitched calls, which are produced by the largest males (Ryan et al. 1992).

Mismatches between auditory sensitivity and dominant song frequency have also been reported in house sparrows (e.g., Henry and Lucas 2008). The authors suggested that the mismatch in this species may reflect selection for high-frequency song and relaxed selection for a close match between sender and receiver due to small territory size.

Self-produced sounds

Echolocating animals are unique in making intensive use of the vocal and auditory mechanisms in a self-matched manner (Konishi and Knudsen 1979; Au 1993; Grinnell 1995). Some species exhibit an extraordinary peak of auditory sensitivity at the echolocation call frequencies (Pollak et al. 1972). Such high sensitivity is not aimed at the echolocation calls themselves, but at the dim echos which reflect from the target objects. Synchronously with the emission of each echolocation call, the middle ear muscles contract to avoid overloading the ears before receiving the echos (Henson 1965; Suga et al. 1974).

Self-hearing is also important for vocal learning in birds and humans (Nottebohm 1972; Marler and Slabbekoorn 2004), and for stimulating ovulation in ring doves (Cheng 1992). The frequency content of these sounds overlaps, however, with that of sounds produced by conspecifics during communication. It seems, therefore, unlikely that the need to hear self would generate any unique selective pressure on hearing frequency sensitivity that could lead to specialization.

Biotic noise

Biotic noise is often produced by a large number of individuals emitting advertisement calls or making sound as they move. It tends to have a narrower spectrum than abiotic noise sources such as wind or rain.

In multi-species breeding assemblages, acoustic communication may be hindered by the noise produced by heterospecific advertisement calls. Several studies have described interspecific acoustic variation in such assemblages as acoustic resource partitioning, but few of them have actually attempted to test the hypothesis underlying this ecological term, i.e., verifying if the distribution of acoustic traits is more regular than expected by chance (Duellman and Pyles 1983; Heller and Helversen 1989; Kingston et al. 2000; Chek et al. 2003). In addition, the existing evidence is based on advertisement calls and does not address hearing. It is tempting to consider, however, that partitioning of the acoustic space for calls should also lead to adaptation of hearing, as the frequency ranges of advertisement calls and hearing tend to be highly correlated when compared across species (Konishi 1970; Dooling et al. 1971; Dooling and Saunders 1975; Okanoya and Dooling 1988; Wilczynski et al. 1993).

Additional evidence is available from studies of reproductive character displacement in advertisement calls. In frogs, these calls are frequently the main or the only species-isolation mechanism between two species, and in some cases the acoustic structure of the advertisement calls is more divergent in the zone of contact than in allopatry (Littlejohn 1965; Blair 1974; Fouquette 1975). Several studies have also assessed the acoustic preferences of the females, and found them to favor the divergence of the calls in sympatry (Gerhardt 1994; Márquez and Bosch 1997; Pfennig 2000; Höbel and Gerhardt 2003; Pfennig and Ryan 2007). When the fitness of the hybrids is reduced, female preferences should be selected to avoid hybrid matings. Hearing sensitivity spectrum could be involved in changes in female preferences for the frequencies of male calls (Capranica and Moffat 1983) although the available examples of acoustic character displacement (cited above) only involve divergence of temporal characters of the call.

Multiple sensitivity peaks

While most tetrapods exhibit a single peak with hearing sensitivity gradually rolling off at higher and lower frequencies, some animals exhibit multiple sensitivity peaks, which can reflect different ecological pressures. Several species of bats have been found to exhibit two hearing sensitivity peaks the higher one matching the frequency range of the echolocation calls and the lower one matching the frequency range of social signals or sounds produced by prey (see Biotic environment: Heterospecific sounds).

Ears that are selected to respond with high sensitivity to more than one frequency range can be especially informative about limitations and versatility of the auditory system. As mentioned before (Abiotic factors: Noise), golden moles have hypertrophied mallei and are highly sensitive to low-frequency seismic vibrations. These animals produce vocalizations with fundamental frequencies ~1–2.2 kHz and considerable energy up to 20 kHz in some calls (Willi et al. 2006a). While enlargement of the malleus is a key aspect of their seismic sensitivity, such an adaptation could have compromised acoustic hearing, since the massive mallei should resist vibration at high frequencies. As an ingenious solution to this problem, the mallei of golden moles rotate around different axes in response to acoustic or seismic stimuli (Willi et al. 2006a). The large mass of the malleus is centered in relation to the acoustic rotation axis but it remains displaced relative to the seismic rotation axis. This arrangement allows for high seismic sensitivity with minimal loss of acoustic sensitivity.

Studies of auditory sensitivity in frogs, based on midbrain auditory-evoked potentials, often reveal two sensitivity peaks (Mudry and Capranica 1987; Wilczynski et al. 1993, 2001). The double sensitivity in this case, however, is believed not to reflect multiple ecological selective pressures, but multiple hearing organs. The low-frequency peak corresponds to the sensitivity range of the amphibian papilla whereas the high-frequency peak corresponds to the sensitivity of the basilar papilla (Capranica and Moffat 1983). It has been suggested that low frequencies excite the ear predominantly via the extratympanic route and that high-frequencies preferentially enter the ear through the tympanic route thereby exciting the basilar papilla (Wilczynski et al. 1987).

Dynamic middle ear tuning

Besides evolving changes to the structure of the middle ear, vertebrates can behaviorally adjust their peripheral auditory mechanics according to environmental constraints. The best known behavioral mechanism of this type is the acoustic reflex, in which the middle ear muscles contract to restrain the movement of the middle ear elements

(Borg 1972; Nuttall 1974; Oeckinghaus and Schwartzkopff 1983). The acoustic reflex produces extensive attenuation at low frequencies and little or no gain at high frequencies. It is triggered by intense external sound, but similar contractions of the middle ear muscles can be produced in the absence of external sound, by command from the central nervous system, in synchrony with vocalizations (Suga et al. 1974; Borg and Zakrisson 1975).

In addition to direct muscular action on the middle ear elements, a novel mechanism has been recently described (Gridi-Papp et al. 2008). Compared with mammals, most frogs possess large tympanic membranes and compressed middle ear cavities which connect to the mouth through short and wide Eustachian tubes. Such a connection was believed to remain permanently open, but the Chinese concave-eared torrent frog (*O. tormota*) has been shown to actively close its Eustachian tubes (Gridi-Papp et al. 2008). The isolation of the middle ear cavity significantly diminishes its compliance, producing extensive attenuation (~26 dB) of low frequencies (Fig. 1). With the tiny middle ear cavity isolated from the mouth, the resonant

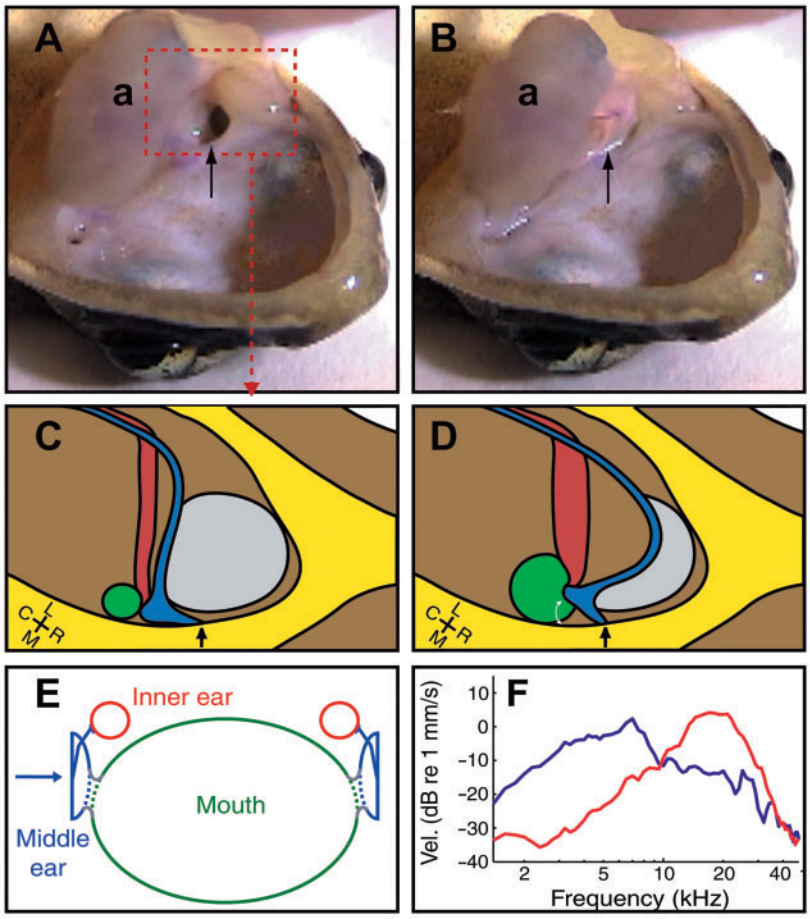

Fig. 1 Active Eustachian tube (ET) closure shifts middle ear tuning in the frog *O. tormota*. (**A**) Awake male with the mouth open, showing the wide ET opening (arrow) in the roof of the mouth; "a" labels the tongue. (**B**) The same male seconds after A, with the ET fully closed. (**C**) Schematic representation of the anatomy within the hashed red rectangle in A, depicting the anatomy involved in ET closure; the perimeter of the ET (gray) is delimited by the skull (yellow) rostrally, laterally and medially, but the caudal perimeter is delimited by the flexible anterior hyoid horn (blue), which has a narrow attachment to the skull (arrow); the submaxillary muscle (red) inserts in the caudal thickening of the hyoid near its attachment to the skull, next to the petrohyoid muscles (green), which form an angle with the plane of the hyoid cartilage. Coordinates: R = rostral, C = caudal, M = medial, L = lateral. (**D**) Contraction of the submaxillary muscle causes the hyoid cartilage to bend and pivot on its attachment to the skull, closing the ET. The movement is enhanced with pressure exerted by the petrohyoid muscles during contraction. (**E**) ET closure isolates the middle ear cavity from the mouth cavity, drastically reducing the volume of air and the compliance of the cavity behind the eardrums (blue arrow). (**F**) Vibration velocity of the TM in response to acoustic stimulation by a pure tone at various frequencies. In relation to the resting condition with the ET open (blue curve), closure of the ET (red curve) produces up to 26 dB attenuation below 10 kHz and up to 20 dB gain above 10 kHz. (Figure modified from Gridi-Papp et al. 2008, with permission. Copyright 2008 National Academy of Sciences, USA).

properties of the ear are altered and a gain of up to 20 dB is produced at high frequencies.

Diversity and evolution

Phylogenetic history explains significant portions of the diversity observed in the structure and the hearing sensitivity spectra of the middle ear of tetrapods. Middle and external ears evolved late after the initial vertebrate colonization of land and it occurred multiple times, thereby conferring structural differences among tetrapods (Clack and Allin 2004). Vertebrate classes also exhibit important differences in the mechanics and organization of the sensory epithelia of the inner ear (Manley and Clack 2004). These differences are maintained across most modern taxa and they can potentially bias the evolutionary response of species to environmental selection pressures (i.e., represent evolutionary constraint *sensu* Maynard-Smith et al. 1985).

This review found evidence of various environmental transitions that relate to changes in hearing ranges or in middle ear structure in tetrapods. Both phylogeny and environment should, therefore, be considered in a comprehensive explanation of the diversity in tetrapod hearing. The contributions of phylogeny and environment to hearing diversity can be estimated quantitatively, through the analysis of pools of taxa that represent independent transitions between environmental conditions (Felsenstein 1985).

Conclusions

The number of species for which data on hearing performance and middle ear mechanics is available is still small. The extent of taxonomic sampling is variable among vertebrate groups and widely diverging designs have been found. The generality of some patterns of environmental effects on hearing can already be established, but several others should emerge with the continued publication of measurements on additional species.

Body size is inversely correlated with frequency range of hearing and directly with the size of the middle ear structures in all major tetrapod groups. Such relationships should not be seen as confounding factors to be removed from the analysis of environmental effects, because body size itself is frequently driven by abiotic or biotic environmental factors. Such environmental factors can, therefore, alter the hearing of animals via changes in body size.

Tetrapods inhabit media (air, water, or underground) that differ drastically in impedance and sound transmission properties, factors that affect hearing sensitivity and the frequency range of detectable stimuli. Various vertebrate groups exhibit anatomical specializations of the middle ear that relate to coupling of the stimulus to the inner ear or to frequency range. Such specializations appear to represent adaptations for enhanced stimulus detection.

The current literature also provides various levels of support for the influence of biotic environmental factors on hearing frequency range. Such factors include interactions among species, within species and even the perception of self-produced signals reflected by the environment. Hearing systems appear to adapt both when individuals are selected to better detect a given signal, or when they are selected to cope with acoustic interference.

Two mechanisms of behavioral middle ear tuning have been described, both with suggested protective roles, one involving muscular restraint of the ossicular chain, and the other involving an increase of the impedance of the air cavity behind the eardrum.

As measurements accumulate on hearing spectrum, middle ear morphology and acoustic ecology of tetrapods, it becomes feasible to estimate the proportion of variation in middle ear structure and hearing range that can be associated with a given environmental factor.

Accelerating the development of knowledge on the relations between vertebrate hearing and the environment is a pressing necessity, as fast technological developments are resulting in rapid alteration of the acoustics in most environments and potentially risking the health of humans and animals. The study of hearing structure and function in additional taxa will expand the comparative basis of evidence and add power to the analysis of environmental effects on hearing. Such taxonomic sampling should continue to reveal unexpected novel mechanisms and extreme adaptations to environmental factors. In depth studies of such extreme adaptations may reveal general principles not readily observed in less extreme species, or in the words of the Danish Nobel laureate August Krogh: ''For many problems, there will be an animal for which it can be most conveniently studied''. The study of additional species should, therefore, be intensified until most vertebrate groups, geographic areas and environmental factors are sampled.

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