The Adapted Ears of Big Cats and Golden Moles: Exotic Outcomes of the Evolutionary Radiation of Mammals

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Through the process of natural selection, diverse organs and organ systems abound throughout the animal kingdom. In light of such abundant and assorted diversity, evolutionary adaptations have spawned a host of peculiar physiologies. The anatomical oddities that underlie these physiologies and behaviors are the telltale indicators of trait specialization. Following from this, the purpose of this article is to consider a number of auditory "inventions" brought about through natural selection in two phylogenetically distinct groups of mammals, the largely fossorial golden moles (Order Afrosoricida, Family Chrysochloridae) and the carnivorous felids of the genus *Panthera* along with its taxonomic neighbor, the clouded leopard (*Neofelis nebulosa*).

In the Beginning

The first vertebrate land invasion occurred during the Early Carboniferous period some 370 million years ago. The primitive but essential scaffolding of what would become the middle and inner ears of mammals was present at this time, although the evolution of the osseous (bony) middle ear system and the optimization of cochlear features and function would play out over the following 100 million years. Through natural selection, the evolution of the middle ear system, composed of three small articulated bones, the malleus, incus, and stapes, and a highly structured and coiled inner ear, came to represent all marsupial and placental (therian) mammals on the planet thus far studied. The consequences of this evolution were extraordinary. The process of natural selection enabled an extension of the highly restricted low-frequency hearing range that tops out around 12 kHz for most nonmammalian vertebrates (although there are notable exceptions in some frogs and fishes) into the greatly expanded high-frequency space of the mammal that reaches an upper limit of about 90 kHz in some terrestrial mammals and exceeds
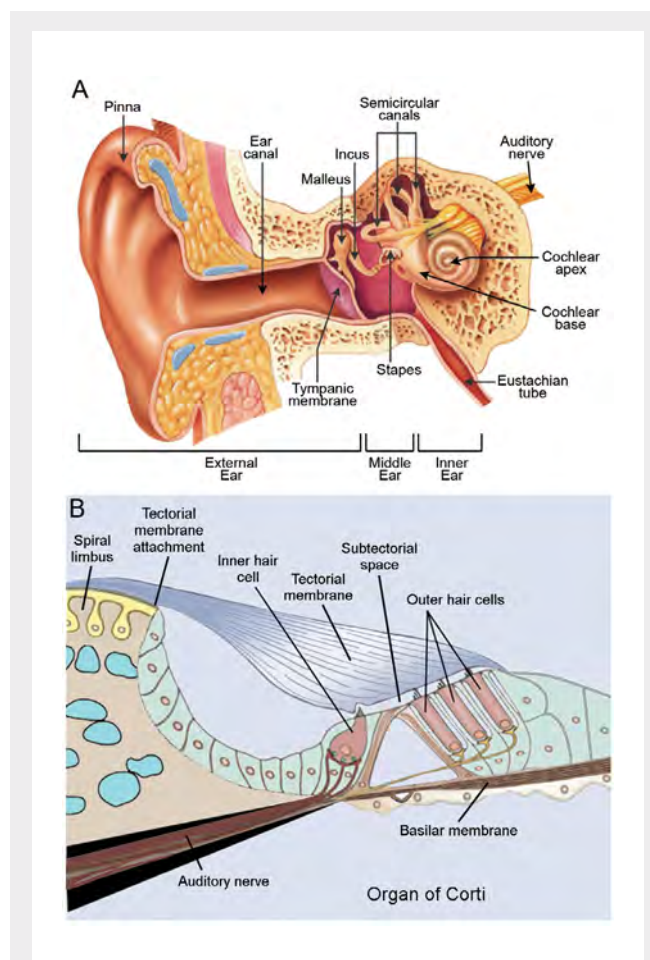

Figure 1. *Schematics of the outer, middle, and inner ears (A) and the organ of Corti in cross section (B) of a placental mammal.*

150-200 kHz in some echolocating bats and aquatic mammals. All of this was accomplished, at least partially, by the selection-driven repurposing of elementary components of the reptilian jaw into the osseous middle ear and the reconfiguration of the amphibian and basilar papillae into

a hearing organ (**Figure 1**) equipped with signal-amplifying sensory cells sensitive to displacements measured on a nanoscale ruler (Clack et al., 2016).

The story that we tell here focuses on one well-known outcome of evolution through natural selection and one outcome that is just emerging.

Golden Moles and Their Remarkable Middle Ears

The golden mole subfamily Chrysochlorinae is home to 11 species of highly specialized mammals (Bronner, 2020). Members of this taxon distinguish themselves from the only other golden mole subfamily, Amblysominae, by virtue of middle ear specializations thought to augment subterranean auditory performance. Golden moles as a group are small, insectivorous, burrowing mammals inhabiting wide-ranging climates, altitudes, and floral systems of sub-Saharan Africa. All species live a subterranean

Figure 2. Bottom: *relationship between body mass and malleus mass is shown for numerous mammals (**purple area**) and for Chrysochlorinae species (**red area**). Data obtained from Nummela, 1995; von Mayer et al., 1995; Mason, 2001, 2003; Mason et al., 2018; and Coleman and Colbert, 2010.* **Top:** *scaled reconstructions of middle ear ossicular chains (**blue**, malleus; **light blue**, incus; **yellow**, stapes) and inner ears reproduced from Crumpton et al., 2015, with permission.* **Inset:** *photograph by G. B. Rathun, reproduced with permission.*

lifestyle, save one, the Namib golden mole (*Eremitalpa granti namibensis*) that we highlight in this article (**Figure 2**, *photograph*). External ear openings of golden moles are tiny and covered with dense, iridescent hair, and they have vestigial eyes covered by tough, thick skin that render them image blind. These phenotypic features are clear indicators of their unusual, but certainly not unique, mammalian lifestyle. Their fusiform body shapes combined with specialized cranial features and appendages adapted for digging suit them ideally for a subterranean lifestyle.
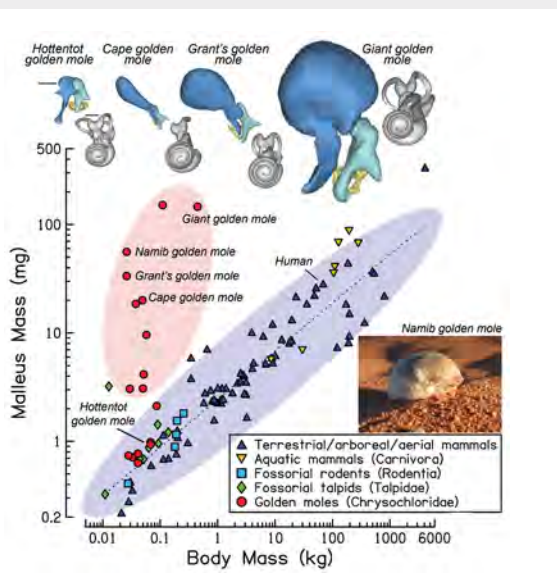
The specialization of interest here, however, has nothing to do with digging, but everything to do with the detection of subterranean "sounds" originating in the form of seismic waves in an ancient desert known as the Namib erg that extends along the Atlantic coast of Africa from Angola in the north to the northern tip of South Africa. These soilborne waves almost certainly influenced the evolution of the auditory periphery of at least some members of this taxon. The chief evolutionary outcome of this process in Chrysochlorinae species was hypertrophy of the malleus, the middle ear bone commonly referred to as the "hammer," that is set into motion by the sound-induced vibration of the tympanic membrane, commonly known as the eardrum (**Figure 1**).

In some species of Chrysochlorinae, malleus size can be remarkable (**Figure 2**). To put the incredible nature of this adaptation in perspective, consider the species *Amblysomus hottentotus*, the Hottentot golden mole. Its average body mass is over 2.5 times the mass of the Namib golden mole, the smallest of the golden mole species. Although the malleus mass of the Hottentot variety scales proportionally with body mass, as with the majority of mammals, the mass of the Namib golden mole's malleus is more than 60 times that of the Hottentot variant, which unambiguously justifies its designation as an evolutionary adaptation. Accordingly, it is reasonable to presume that a significant amount, if not the great bulk, of the malleus size difference between Hottentot and Namib varieties is the product of environmental modification, an adaptation shaped by the force of natural selection.

The Namib Golden Mole

The Namib golden mole has abandoned the inflexible underground lifestyle of its relatives; it is celebrated instead for its sand-swimming skills, so much so that they are known in colloquial terms as "sand sharks."

However, their swimming skill isn't the point of interest here. It is their peculiar style of foraging, a style enabled, presumably, by their conspicuously hypertrophied mallei. Fiercely territorial, individuals scurry about on the surface of the erg, intermittently stopping to dip their snout and small, conically shaped head beneath the surface. They are, some have suggested, listening for the low-frequency, soilborne seismic signature that might lead them to their favorite prey, the subterranean dune termite (Fielden et al., 1990).

Biologists have, it turns out, settled on a likely explanation of just how the head-dipping behavior of the Namib golden mole might enable its hunting prowess. The hypothetical but probable answer is that some golden mole species detect seismic events by tightly coupling their heads to the substrate, taking advantage of inertial bone conduction. The low-frequency seismic waves propagating through the sand of the erg cause the bones of the skull to vibrate in unison. Movement of the loosely coupled ossicles lags behind that of the skull because of inertia, producing relative motion between the stapes footplate and the oval window of the cochlea and transferring energy to the inner ear (Bárány, 1938). We should point out, however, that compression of the bony cochlear wall and/or inner ear fluid inertia also play a role in bone conduction in at least some mammals.

Regardless, the enlarged mallei of some Chrysochlorinae species enhance sensitivity to bone conduction, presumably, but almost certainly, permitting the detection of low-amplitude, low-frequency ground vibrations (Narins et al., 1997; Mason 2003). A second ossicular adaptation contributing to and enhancing sensitivity to seismic events is the displacement of the center of mass of the ossicular chain away from its natural rotational axis. The relocation of the center of mass further amplifies ossicular motion relative to the skull and, ostensibly, augments the sensitivity of the system to low-frequency seismic signals, unlike that predicted for golden moles with smaller mallei and a center of mass that falls close to the natural rotational axis. In a remarkable tilt to the amazing power of selection-driven adaptation, it can be confidently argued that the head-dipping behavior of the Namib golden mole permits the detection of faint seismic signals produced by the wind-driven motion of dune grass mounds scattered about their territories.

Golden Mole Hearing: Can They?

Although we cannot claim to know what Namib golden moles or any other member of the Chrysochlorinae subfamily actually hear, predictions derived from Bárány's 1938 model of inertial bone conduction suggest that they do. Using morphological measurements of key middle ear structures and calculating relevant middle ear parameters required by this model, Mason (2003) predicted the frequency producing peak displacement, the strongest driving force delivered by the stapes to the fluids of the inner ear, at 300 Hz in Grant's golden mole (*Eremitalpa granti granti*), a close relative of the Namib golden mole. This frequency corresponds closely to the peak frequency of seismic signals generated by the grassy mounds of the Namib erg (Narins et al., 1997). In addition, the predicted resonant frequency of bone conduction in the Cape golden mole, *Chrysochloris asiatica*, is 220 Hz (Mason, 2003), a value nearly matching resonant frequencies of 100-200 Hz determined by direct measurements of ossicular velocity in response to vibrational stimuli (Willi et al., 2006a,b). Depending on the accuracy of these predictions, these findings point confidently to the conclusion that the middle ears of golden moles were almost certainly adapted to detect soilborne seismic events, a prediction reinforced by the directed foraging behavior of the Namib golden mole (Lewis et al., 2006).

Further support for the view that golden moles are able to hear can be found in predictions of the high-frequency limit of hearing based on a widely used model of the middle ear (Hemilä et al., 1995). Using this model, Mason (2001) computed upper limits of 5.9 kHz and 13.7 kHz for Grant's golden mole and the Cape golden mole, respectively. In addition, direct observation of frequency-dependent alterations in the mode of ossicular vibration permit, theoretically, uncompromised detection of airborne stimuli in the Cape golden mole (Willi et al., 2006b). The evolutionarily modified middle ear of some golden moles has been described by some as nothing short of ingenious.

We end this section by pointing out the obvious. Although the role of the middle ear of the golden mole family has been the topic of considerable, highly productive inquiry, a complete accounting of golden mole hearing will require a comprehensive investigation using behavioral techniques or at the systems level of physiology before a clear understanding of the auditory capacity of these fascinating mammals is available.

Is the Inner Ear of the Tiger Adapted to React Rapidly to Low Frequencies?

Although the middle ear specialization observed in golden moles is evident, even in gross anatomical terms, some adaptations are more subtle and are recognized only in behaviors or physiologies buried deep in otherwise generalist phenotypes. Discovering those traits can be challenging and are frequently revealed, as with many scientific discoveries, through serendipity. Such was the case when an unusual feature in the auditory phenotype of the tiger (*Panthera tigris*) was discovered. Its discovery suggested that the tiger may be best thought of as an auditory specialist, a question that we address in this section. When thinking about use of the term "specialist," we generally refer to any trait that differentiates the animal's performance from closely related organisms. If, for example, the shape of an animal's audiogram breaks radically from that of other related taxa and is beneficial from an ethological perspective, the animal can be thought of as specialized in that specific trait.

We start, therefore, by pointing out that many elements of the tiger auditory phenotype are typical of auditory generalists. For example, overall sensitivity to acoustic stimuli in tigers is similar to that of other cat (felid) species, and, although the high-frequency limit is lower than that of smaller felids, the shapes of their sensitivity curves are also similar (Walsh et al., 2011). It is also likely that the low-frequency limit of hearing is lower than that of smaller cats, a prediction based on structure-based scaling of the middle ear (Huang et al., 2000).

Although the middle ear transforms sound energy collected from the outer ear and transfers it to the inner ear, the cochlea functions as a frequency-analyzing system that is commonly modeled as an array of bandpass filters reflecting the resonant properties of the basilar membrane (BM; **Figure 1B**), the vibratory membrane supporting the organ of Corti, on which sit the sensory cells for hearing. The resonant properties of the BM reflect the continuously changing mass and stiffness of the membrane along the length of the cochlea (**Figure 1A**), which increases and decreases, respectively, along a basoapical gradient. This system, coupled with the voltage-dependent motility of a subset of cochlear sensory cells (outer hair cells) that amplifies BM motion and produces sharp inner ear filters (Brownell, 2017), can be
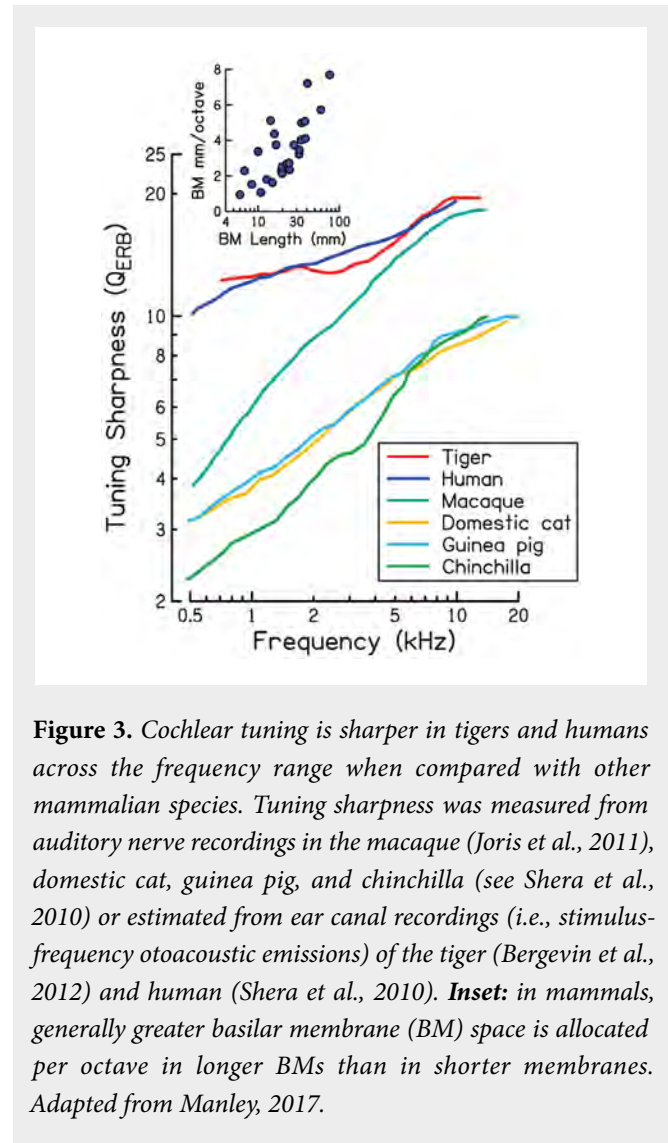

Figure 3. *Cochlear tuning is sharper in tigers and humans across the frequency range when compared with other mammalian species. Tuning sharpness was measured from auditory nerve recordings in the macaque (Joris et al., 2011), domestic cat, guinea pig, and chinchilla (see Shera et al., 2010) or estimated from ear canal recordings (i.e., stimulus-frequency otoacoustic emissions) of the tiger (Bergevin et al., 2012) and human (Shera et al., 2010).* **Inset:** *in mammals, generally greater basilar membrane (BM) space is allocated per octave in longer BMs than in shorter membranes. Adapted from Manley, 2017.*

thought of as the gateway to audition. The output of these filters determines precisely what a species can detect in the soundscape, a property that, to a large extent, determines if a selective advantage can be gained by enhanced sensitivity to a particular frequency band or by a mechanism that enhances frequency selectivity, for example.

In this regard, as shown in **Figure 3**, cochlear filter sharpness in the tiger far exceeds that observed in the much smaller domestic cat, *Felis catus*, as well as most other common and small laboratory animals (Bergeven et al., 2012). On the face of this finding, it may be tempting to conclude that the tiger inner ear filters have undergone specialization and are more frequency selective than in many other mammals.

However, it can, and should, be argued that the trait differences shown in **Figure 3** can be misleading when body size differences are not taken into consideration. When scaling factors are considered, the frequency-selectivity differences between the domestic cat and the tiger are not particularly surprising. In accordance with the principle of allometric growth in which the growth of one feature relative to another is proportional, it is notable that small animals generally exhibit proportionally shorter cochlear lengths and, in some cases, higher upper frequency hearing limits than larger animals. The best way to think about these differences is probably within the framework of inner ear frequency-mapping constants (i.e., the length of the BM devoted to a given frequency bandwidth; **Figure 3**, *inset*). Because the BM of tigers is longer than that in domestic cats and other typical laboratory animals (Ulehlová et al., 1984; Walsh et al., 2004) and because the high-frequency hearing limit is lower than that observed in common laboratory animals, the mapping constant of tigers is, theoretically, significantly larger than that in domestic cats, assuming other cochlear variables are comparable. The upshot of this consideration is that there is no evidence suggesting that inner ear filter outputs break the uniform mold of other less famous felids if, that is, we frame the question in terms of biological scaling.

Tiger findings considered here are also of interest when thinking about earlier claims that inner ear mechanical filters are unusually sharp in humans. As also seen in **Figure 3**, the sharpness of inner ear filters in the tiger closely approximates the cochlear sharpness measured in humans. This finding suggests that the predicted cochlear mapping constant of tigers is much like that observed in humans (von Békésy, 1960; Shera et al., 2010), a finding with considerable scientific importance when biological scaling questions arise. These results also suggest that other cochlear features contributing to tuning, such as longitudinal coupling via tectorial membrane traveling waves, are also most likely comparable when humans and tigers are considered (Sellon et al., 2019); again, body size matters.

On the surface, therefore, for all of their otherwise magnificence, tigers are not, it would seem, particularly noteworthy from an auditory performance/processing perspective. However, all of that changes when the analytical lens shifts to focus on the timing or latency of neural responses following stimulation in the frequency realm. In the real world, response timing can make the difference between life and death or between a successful hunt and an empty stomach, for example. When concentrating on response timing, the generalist impression is at least partially upended. Outcomes of studies examining response timing in the stimulus frequency space of tigers reveal nonmonotonic profiles (**Figure 4A**). Increasing from highly unanticipated short-response latencies to low-frequency stimulation, latencies reach a maximum in the midfrequency range and steadily decrease with increasing frequency such that the latency to the highest frequency studied is higher than the latency to the lowest frequency studied. This stands in stark contrast with findings from other mammals (Ruggero and Temchin, 2007) studied thus far; latencies generally decrease exponentially with frequency, as shown for the modern day workhorse laboratory animal, the mouse (*Mus musculus*; **Figure 4B**), as well as in a squirrel monkey (*Saimiri sciureus*; **Figure 4C**). The differences are striking, and they are confusing in light of contemporaneous models of inner ear mechanics.

Although space limits won't permit an in-depth consideration of a similar discovery made recently in the clouded leopard (*Neofelis nebulosa*), the implications of the finding (**Figure 4D**) may have real relevance in efforts to understand the evolution of the timing trait observed in tigers (Walsh et al., 2017). Not only is the resemblance of response-timing profiles, in our view, stunning, it takes on evolutionary relevance when the taxonomic proximity of the genus *Neofelis* to *Panthera* is considered. Based on the close taxonomic relationship between tigers and

Figure 4. *The relationship between auditory response latencies and stimulus frequency taken from scalp recordings for tigers (**A**), a laboratory mouse (**B**), a squirrel monkey (**C**), and clouded leopards (**D**). SPL, sound pressure level. Recordings in **A**-**C** were made at the same location using the same setup.*
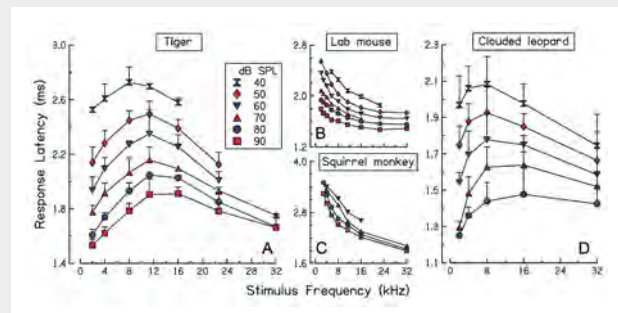
clouded leopards and unpublished findings from our laboratory suggesting that other members of *Panthera* may exhibit the same trait, the unusual timing relationship considered here may have been passed to tigers and other large cats but may have washed out of the taxonomic flow in the other felid lineages in which the trait has not been observed.

Regardless, efforts to begin considering potential mechanisms that might underlie this unusual physiology require us to briefly review a few key elements in inner ear biomechanics for those who may be less familiar with the process. The prevailing textbook explanation of the standard mammalian latency-frequency relationship borrows from classical filter theory and derives from a notably large and consistent inner ear biomechanics literature. Sensory scientists have known from the time of von Békésy (1960) that vibrations on the BM propagate as traveling waves in a base to apex direction, consuming time as they travel toward inner ear mechanical filters that match stimulation frequencies and toward their so-called characteristic place along the BM. Therefore, travel time is a clear and relevant term in the latency/frequency equation, but it is not the only relevant timing factor. In addition to passive cochlear delays, timing is influenced by active cochlear filter-response times that are dependent on outer hair cell electromotility (Brownell, 2017), the mechanism that amplifies responses near the characteristic place and sharpens filter responses. The ultimate outcome of all of this from a response-timing perspective is that high-frequency propagation times are normally shorter than times associated with lower frequency responses (cf. **Figure 4**, **B** and **C**). Clearly, some members of the *Panthera* lineage, including the tiger and clouded leopard, settled on a different auditory timing strategy than other mammals.

The natural questions emerging from this finding are, first, where in the inner ear does this presumed adaptation originate, and second, what specific inner ear structure, if any, underwent adaptation? To attempt to answer this question, we turn our attention to morphological features in the organ of Corti in search for evidence of adaptation, and particular attention will be paid to the base of the cochlea, the region responsive to high- and mid-range frequencies. The decision to concentrate on basal regions was driven primarily by preliminary findings from a masking study conducted in our laboratory on a Bengal tiger (*Panthera tigris tigris*).
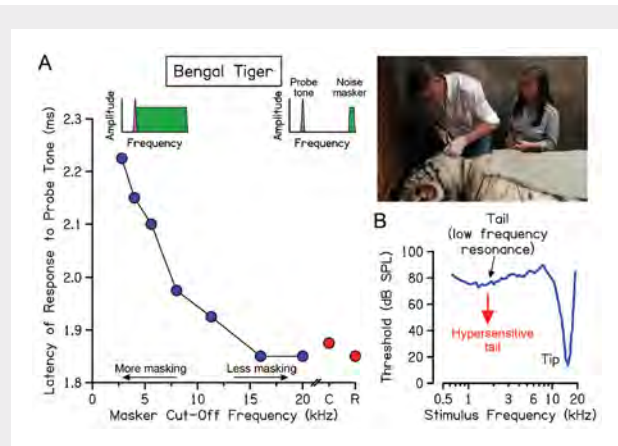

Figure 5. A: *results of a study showing that the basal half of the tiger's cochlea contributes substantially to the latency of a response to a relatively low-frequency tone (2 kHz).* **Insets:** *extremes of the stimulus spectra shown schematically (*pink, *signal or "probe tone";* green, *high-pass noise masker). Starting with a relatively broadband noise that masks responses from all cochlear regions basal to the probe tone (***A, bottom left***), the noise cutoff frequency was increased, decreasing the area of the cochlea being masked (***A, bottom right***), and resulting in faster response times.* **Red circles,** *latencies of the control (C) and recovery (R) responses to the probe tone recorded before and after the masker was presented, respectively.* **B:** *example of a tuning curve recorded from an auditory nerve fiber of a domestic cat, indicating the "tip" and "tail" resonances.* **Red arrow,** *direction of threshold shift of a hypersensitive tail.* **Inset:** *photograph of the authors preparing to record brain potentials from a tiger.*

Although preliminary in large measure because of the limited access to these very large and endangered animals, findings from that effort suggest that a substantial signal from the basal half of the tiger cochlea contributes considerably to the fast response times to low frequencies in this big cat (**Figure 5A**). A hypothetical scenario based on a few key relevant findings is offered in **A Hypothetical Answer to the Response-Timing Conundrum**.

A Hypothetical Answer to the Response-Timing Conundrum

That a relatively narrow band of low-frequency, moderate-level sounds drive up discharge rates of individual auditory nerve fibers tuned to high frequencies is a well-known phenomenon in auditory neuroscience circles. This so-called

second neural resonance, often referred to as the "tail" of tuning curves, is easily differentiated from the sharply tuned primary resonance, as seen in an auditory nerve fiber tuning curve (**Figure 5B**). The mechanism responsible for the appearance of the tail has been linked to a second inner ear traveling wave, this one on the tectorial membrane (TM; Allen and Fahey, 1993), a gelatinous, acellular matrix of striated connective tissue that couples the mechanosensitive hair bundles associated with outer hair cells to motions of the BM and playing an important role in the enhancement of cochlear sensitivity (**Figure 1B**). The importance of this linkage in the context of this discussion is heightened by noting that many studies have shown significant effects on cochlear sensitivity and tuning as well as the expression of the second resonance in transgenic mice exhibiting altered TM composition or detachment of the structure from its mooring on the spiral limbus (Richardson et al., 2008). Moreover, tail hypersensitivity has been reported in animals under conditions of reduced mechanical coupling between the TM and hair bundles resulting from outer hair cell loss or stereocilia damage. This tight connection between the TM and the expression of the second resonance leads, it can be reasonably argued, to the proposition that specialization of the TM might alter its influence on the expression of the second low-frequency resonance.

We do know that the mammalian TM is a viscoelastic structure with electrokinetic, piezoelectric-like properties (Sellon et al., 2019). That is, deformation of the TM creates an electric response within the solid matrix of the structure. We also know that the biomechanical properties are influenced by the concentration of fixed charges associated with the structure; the greater the fixed charge, the greater the electrokinetic effect. This brings us to ask the provocative question: if evolutionary processes led to the exaggeration of fixed charge in the tiger's TM, could a powerful electrokinetic force enhance the sensitivity of the low-frequency resonance and trigger basal turn responses to low-level, low-frequency stimuli? Could such a system explain, at least partially, the strange case of response timing in tigers and their close relatives? Efforts to address this question are underway, but those efforts are complicated by the relative unavailability of subjects.

Conclusion

Over the course of the past 200 million years or so, mammalian hearing was shaped and refined by the forces of natural selection. The process culminated in the evolution of hearing organs with remarkable sensitivity, extraordinary dynamic range, and an operational range spanning a 10-octave frequency range in some mammalian species. Layer on top of this accounting of evolution the diverse expression of adaptation rarities witnessed in response to virtually every territory invaded by mammals as their populations radiated from one ecosystem to another and the inventiveness of natural selection clarifies. This article has concentrated on one well-understood and much-studied evolutionary wonder, the Namib golden mole, whose middle ear is a true marvel of nature, of evolution, and of natural selection. We also focused on a mysterious, poorly understood twist on our contemporaneous model of inner ear biomechanics, one trait that, potentially, differentiates the tiger and the clouded leopard, and possibly other big cats, from the rest of the mammalian class. One is the material of textbooks, the other remains shrouded in mystery, awaiting the careful scrutiny of science.

Acknowledgments

References

Allen, J. B., and Fahey, P. F. (1993). A second cochlear-frequency map that correlates distortion product and neural tuning measurements. *The Journal of the Acoustical Society of America* 94(2), 809-816.

Bárány, E. H. (1938). A contribution to the physiology of bone conduction. *Acta Oto-Laryngologica Supplement* 26, 1-233.

Bergevin, C., Walsh, E. J., McGee, J., and Shera, C. A. (2012). Probing cochlear tuning and tonotopy in the tiger using otoacoustic emissions. *Journal of Comparative Physiology A* 198(8), 617-624.

Bronner, G. N. (2020). *Golden Moles*. IUCN Afrotheria Specialist Group. Available at http://www.afrotheria.net/golden-moles/. Accessed January 15, 2020.

Brownell, W. E. (2017). What is electromotility? – The history of its discovery and its relevance to acoustics. *Acoustics Today* 13(1), 20-27. Available at https://bit.ly/39AZp0h.

Clack, J. A., Fay, R. R., and Popper, A. N. (Eds.) (2016). *Evolution of the Vertebrate Ear: Evidence from the Fossil Record*. Springer International Publishing, Cham, Switzerland.

Coleman, M. N., and Colbert, M. W. (2010). Correlations between auditory structures and hearing sensitivity in non-human primates. *Journal of Morphology* 271(5), 511-532.

Crumpton, N., Kardjilov, N., and Asher, R. J. (2015). Convergence vs. specialization in the ear region of moles (Mammalia). *Journal of Morphology* 276(8), 900-914.

Fielden, L. J., Perrin, M. R., and Hickman, G. C. (1990). Feeding ecology and foraging behaviour of the Namib Desert golden mole, *Eremitalpa granti namibensis* (Chrysochloridae). *Journal of Zoology* 220(3), 367-389.

Hemilä, S., Nummela, S., and Reuter, T. (1995). What middle ear parameters tell about impedance matching and high frequency hearing. *Hearing Research* 85(1-2), 31-44.

Huang, G. T., Rosowski, J. J., and Peake, W. T. (2000). Relating middle-ear acoustic performance to body size in the cat family: Measurements and models. *Journal of Comparative Physiology A* 186(5), 447-465.

Joris, P. X., Bergevin, C., Kalluri, R., Mc Laughlin, M., Michelet, P., van der Heijden, M., and Shera, C. A. (2011). Frequency selectivity in Old-World monkeys corroborates sharp cochlear tuning in humans. *Proceedings of the National Academy of Sciences of the United States of America* 108(42), 17516-17520.

Lewis, E. R., Narins, P. M., Jarvis, J. U. M., Bronner, G., and Mason, M. J. (2006). Preliminary evidence for the use of microseismic cues for navigation by the Namib golden mole. *The Journal of the Acoustical Society of America* 119(2), 1260-1268.

Manley, G. A. (2017). Comparative auditory neuroscience: Understanding the evolution and function of ears. *Journal of the Association for Research in Otolaryngology* 18(1), 1-24.

Mason, M. J. (2001). Middle ear structures in fossorial mammals: A comparison with non-fossorial species. *Journal of Zoology* 255(4), 467-486.

Mason, M. J. (2003). Bone conduction and seismic sensitivity in golden moles (Chrysochloridae). *Journal of Zoology* 260(4), 405-413.

Mason, M. J., and Narins, P. M. (2001). Seismic signal use by fossorial mammals. *American Zoologist* 41(5), 1171-1184.

Mason, M. J., Bennett, N. C., and Pickford, M. (2018). The middle and inner ears of the Palaeogene golden mole *Namachloris*: A comparison with extant species. *Journal of Morphology* 279(3), 375-395.

Narins, P. M., Lewis, E. R., Jarvis, J. J., and O'Riain, J. (1997). The use of seismic signals by fossorial southern African mammals: A neuroethological gold mine. *Brain Research Bulletin* 44(5), 641-646.

Nummela, S. (1995). Scaling of the mammalian middle ear. *Hearing Research* 85(1-2), 18-30.

Richardson, G. P., Lukashkin, A. N., and Russell, I. J. (2008). The tectorial membrane: One slice of a complex cochlear sandwich. *Current Opinion in Otolaryngology and Head and Neck Surgery* 16(5), 458-464.

Ruggero, M. A., and Temchin, A. N. (2007). Similarity of traveling-wave delays in the hearing organs of humans and other tetrapods. *Journal of the Association for Research in Otolaryngology* 8(2), 153-166.

Sellon, J. B., Ghaffari, R., and Freeman, D. M. (2019). The tectorial membrane: Mechanical properties and functions. *Cold Spring Harbor Perspectives in Medicine* 9(10), a033514.

Shera, C. A., Guinan, J. J., and Oxenham, A. J. (2010). Otoacoustic estimation of cochlear tuning: validation in the chinchilla. *Journal of the Association for Research in Otolaryngology* 11(3), 343-365.

Ulehlová, L., Burda, H., and Voldrich, L. (1984). Involution of the auditory neuro-epithelium in a tiger (*Panthera tigris*) and a jaguar (*Panthera onca*). *Journal of Comparative Pathology* 94(1), 153-157.

von Békésy, G. (1960). *Experiments in Hearing*. McGraw-Hill, New York.

von Mayer, A., O'Brien, G., and Sarmiento, E. E. (1995). Functional and systematic implications of the ear in golden moles (Chrysochloridae). *Journal of Zoology* 236(3), 417-430.

Walsh, E. J., Armstrong, D. L., and McGee, J. (2011). Comparative cat studies: Are tigers auditory specialists? *The Journal of the Acoustical Society of America* 129(4), 2447.

Walsh, E. J., Armstrong, D. L., Robertson, H. E., and McGee, J. (2017). The low frequency auditory life of big cats. *4th International Symposium on Acoustic Communication by Animals*, Omaha, NE, July 18, 2017, p. 125.

Walsh, E. J., Ketten, D. R., Arruda, J., Armstrong, D. L., Curro, T. G., Simmons, L. G., Wang, L. M., and McGee, J. (2004). Temporal bone anatomy in *Panthera tigris*. *The Journal of the Acoustical Society of America* 115, 2485-2486.

Willi, U. B., Bronner, G. N., and Narins, P. M. (2006a). Middle ear dynamics in response to seismic stimuli in the Cape golden mole (*Chrysochloris asiatica*). *The Journal of Experimental Biology* 209(2), 302-313.

Willi, U. B., Bronner, G. N., and Narins, P. M. (2006b). Ossicular differentiation of airborne and seismic stimuli in the Cape golden mole (*Chrysochloris asiatica*). *Journal of Comparative Physiology* 192(3), 267-277.

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