The Mammalian Ear: Physics and the Principles of Evolution

Physical laws govern the operation of the ear but natural selection dominates its design.

Geoffrey A. Manley

Postal:

Cochlear and Auditory
Brainstem Physiology
Department of Neuroscience
Hearing4all Research Centre
Carl von Ossietzky University Oldenburg
26129 Oldenburg
Germany

Email:

geoffrey.manley@uol.de

Andrei N. Lukashkin[1]

Email:

a.lukashkin@brighton.ac.uk

Patrício Simões[1]

Email:

p.simoes@brighton.ac.uk

George W. S. Burwood[1,2]

Email:

burwood@ohsu.edu

Ian J. Russell[1]

Email:

i.russell@brighton.ac.uk

Postal:

[1]Sensory Neuroscience Research Group
School of Pharmacy and
Biomolecular Sciences
University of Brighton, Brighton BN2 4GJ
United Kingdom

[2]*Present Address:*

Oregon Hearing Research Center
Oregon Health and Science University
3181 SW Sam Jackson Park Road
Portland, Oregon 97239
USA

Introduction

In the sensory worlds of animals and humans, there are major differences in the extent to which the laws of physics exert an influence on the function and evolution of the senses. The chemical senses of taste and olfaction depend mainly on the three-dimensional amino acid chain structure of hundreds of genetically coded receptor molecules that, in a kind of "lock-and-key" mechanism, fit with a small molecule and lead to a response in the sensory cells. In these cases, physics mainly has roles in the distribution and binding of molecules.
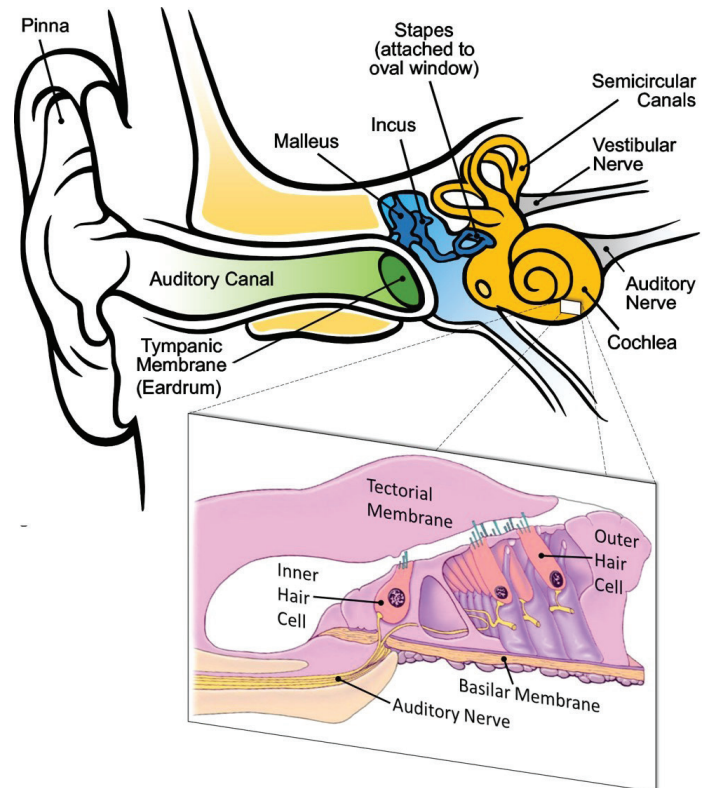

*Figure 1. Structure of the human ear. Sound energy is conveyed by the pinna and auditory canal to the tympanic membrane. Vibrations of the tympanic membrane are transmitted by the middle ear bones, the malleus, incus, and stapes, to the inner ear fluid. The cochlea is a fluid-filled duct of the inner ear responsible for hearing sensation. **Inset:** cross section of the hearing organ, the organ of Corti. The basilar membrane divides the cochlear duct along its length and separates sounds into their constitutive frequency components. It also supports the organ of Corti that contains sensory inner hair cells that transmit auditory information to the brain and outer hair cells that amplify and sharpen vibrations of the basilar membrane. During up-and-down vibrations of the basilar membrane, the tectorial membrane displaces sensory hairs of hair cells and excites them. Modified with permission from Bruce (2017). **Inset** modified from Brownell (1997).*

Figure 2. Biological evolution is not like designing the innovative, first full-flying monohull sailing boat (A). It often uses unrelated components and thus more resembles a boat construction using recycled materials (B). (A) is courtesy of and with permission from ©SEAir and (B) is courtesy of and with permission from Rame Peninsula Beach Care.

For mechanoreceptors such as touch, pressure, and acoustic receptors, by contrast, the physical properties of numerous structures play major roles in capturing, transmitting, and receiving the stimulus. An examination of the complex function of the ears shows that it is their physical properties that dominate signal processing, from sound capture to sensory transduction. The specific structure of different ears is, however, by no means determined by physical laws; as we show here, it is mainly powerful biological processes that govern the evolution of the vertebrate ear. A brief description of the general anatomy and physiology of the ear is given by Bruce (2017; see **Figure 1**).

In view of the variety of the structures in ears, it might be expected that the particular constellation in various animals and the way they have evolved might be strongly, and logi-

cally, traceable to the laws of physics that govern how structures capture, transmit, and respond to sounds of different frequencies and amplitudes. Indeed, this expectation has led some authors (e.g., Lorimer et al., 2015) to propose that the physics governing the responses to sound have dominated the evolution of the structure of inner ears of mammals. In this article, we intend to show that this is a misleading concept. Although it is a given that the responses of mechanosensory organs will depend on the physical properties of their components, the mechanisms of evolution are different from the deterministic nature of physics. There is one extremely important aspect of the laws of biological evolution that can lead to evolutionary trends that a physicist might find counterintuitive; this aspect is known as *historical contingency*.

The Concept of Historical Contingency Illustrated

The idea of historical contingency can be illustrated using a hypothetical situation. Imagine that a physicist in a modern laboratory is asked to build a small, seaworthy boat. Numerous erudite works and plans might be consulted, and a boat that is both functional and appealing might be designed "from scratch," using new materials and working with the best machines (**Figure 2A**). On the other hand, there is an engineer stranded on a remote island who needs to put together an adequate flotation device using only components left scattered over the island by previous inhabitants (**Figure 2B**).

The way biological evolution works is very much akin not to the first situation but to the second (Futuyma, 2008). The evolution of any "new" structure in the biological world almost always proceeds from preexisting structures that may, indeed, originally have had a completely different function. They may only poorly correspond to what anyone may intuitively conceive of, but the changes that happen in small evolutionary steps, driven by mutations and random mixture of genomes, are adequate to provide a small advantage over previous constellations and thus provide the owner of the new structure with a reproductive advantage.

Thus, evolution is a creative and yet highly conservative phenomenon whose trajectories are greatly influenced by evolutionary coincidences rather than by any deterministic dominance of physics. As an example, chance rather than the principles of physical design determined that the mammalian middle ear has three ossicles rather than one (**Figure**

3B) and that later in its evolution, three ossicles were better than one at transmitting high-frequency sounds.

It was serendipitous that at the time of the origin of the middle ear, mammalian ancestors were changing the way they obtained and processed food in the mouth, partly by developing a new and unique jaw joint (Manley, 2010). This process resulted in the gradual loss of bones from the old jaw joint, bones that happened to lie between the skin just behind the lower jaw and the stapes that was connected to the bone surrounding the inner ear. The redundant jaw bones were co-opted into the mammalian middle ear, which arose independently of and at a different bodily location to that of nonmammalian land vertebrates and, indeed, independently in egg-laying and live-bearing mammals (Manley, 2010). Mammalian groups thus share a sensory architecture that arose from a common ancestry and, therefore, a common genetic substrate that is characteristic for mammals. The physics of the result of that evolutionary event is in almost all respects, especially regarding impedance matching between the medium of air and the medium of the inner ear fluids, not unique but fully comparable to that of nonmammals (Manley, 1995).

Significantly, the middle ear of nonmammals such as birds evolved completely independently using a single element (of the same origin as, i.e., homologous to, the stapes; **Figure 3, A** and **C**) that became attached to an eardrum using new, flexible cartilage elements that also form a lever system. Both these middle ear systems thus do not represent physical systems whose structure represents some idealized "design" but are the result of the contingencies of their histories that determined the elements that were "accidentally" available. These parallel evolutionary processes in mammals and nonmammals are due to the requirements of detecting the same physical modality. Long after middle ears arose, the inner ear of mammals evolved the ability to detect high frequencies because their middle ear can transmit such frequencies. The fact that the functions of one- and three-ossicle middle ears are extremely similar in the frequency range below 10 kHz nonetheless testifies to both the creative nature and the importance of history in the evolutionary selection process.

Modern Vertebrate Groups and Their Hearing Organs Did Not Arise in a Linear Sequence

A common mistake among nonbiologists (e.g., Lorimer et al., 2015) is to represent the evolution of modern vertebrates as a staircase, which implies that in their evolution, includ-
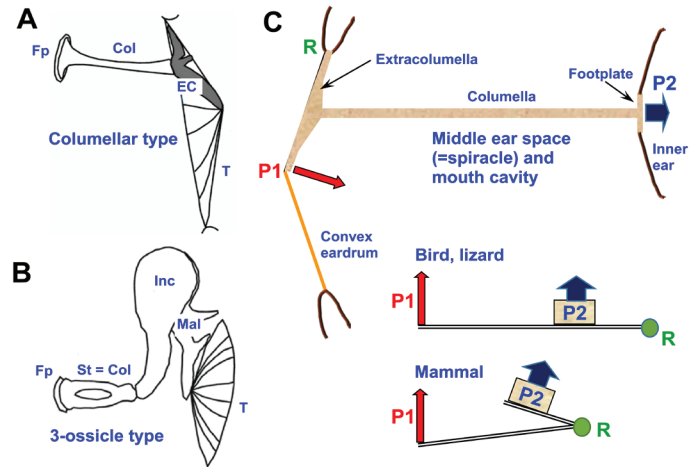

*Figure 3. Middle ear configurations and function. **A**: nonmammalian, single-ossicle type of middle ear. **B**: mammalian, three-ossicle type of middle ear. In **A** and **B**, the inner ear (not shown) is to the left and connected via the footplate (Fp) that is seated in the wall of the inner ear. T, tympanic membrane or eardrum; EC, extracolumella (gray); Col, columella = stapes (St); Mal, malleus; Inc, Incus. **C**: schematic representation of the columellar-type middle ear. Compare with lever systems shown at **bottom right** that illustrate the mode of operation. In each case, air particle velocity over the eardrum and centered at P1 (**red arrow**) provides the eardrum with an oscillatory movement. The fulcrum at R (**green**) leads to a higher oscillating pressure (P2) on the columella (**blue arrow**). **Bottom right:** equivalent lever systems for the three-ossicle mammalian middle ear. From Manley (2017), with permission.*

ing that of their hearing organs, the different modern groups represent a series of steps or a sequence of refinements leading gradually to the supposedly final improvement seen in mammals. In fact, all organs of extant land vertebrates, whether reptiles, birds, or mammals, evolved fully independently of each other, yet all originated from the same, very simple, ancestral form in the earliest reptiles (Manley and Ladher, 2008; **Figure 4**). There is, therefore, no reason whatsoever to expect that mammalian auditory organs should be the best or most sophisticated. Depending on the evolutionary pressures, which were determined by environmental strategy, predator-prey relationships, and requirements for conspecific communications, each extant group of vertebrates has found an adequate hearing solution. Acute sensitivity and sharp frequency resolution, features of hearing organs frequently associated with mammals, have evolved independently in all groups of modern land vertebrates. Indeed, the auditory nerve fibers of some lizards are among the most sharply frequency tuned of any vertebrates, including those of most mammals (Manley, 2001). Auditory sensitivity in birds of prey, especially those (such as barn owls) that rely

almost exclusively on hearing to detect their quarry, is superior to the sensitivity of most mammalian species (Manley, 1990). The extended frequency range of hearing in echolocating mammals is almost matched by frog species that use ultrasonic calls for communicating (Feng et al., 2006).
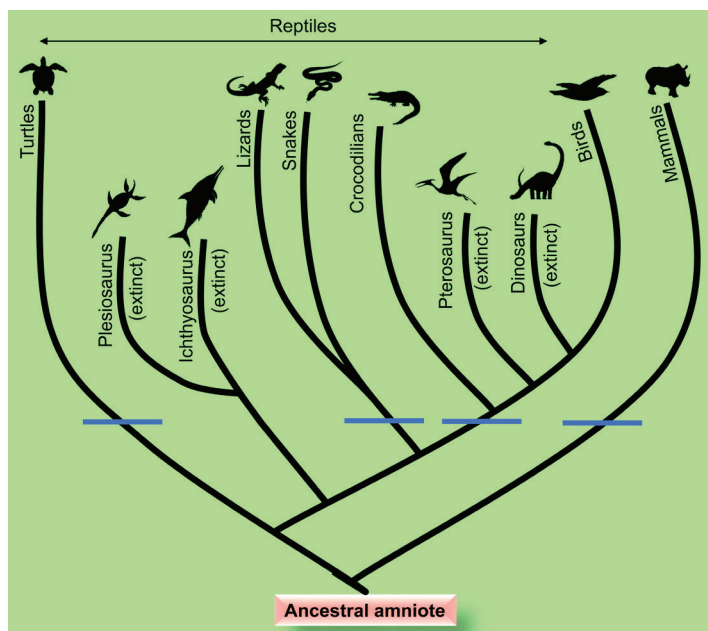

Figure 4. *Tree of life of amniotes that includes reptiles, birds, and mammals. All these classes of vertebrates evolved from the same ancestral form of the stem reptiles at the bottom of the tree.*

Did Physics Direct the Evolution of the Mammalian Cochlea?

The hearing organs of all animals perform very much the same task: that of detecting acoustic signals. However, when examined through the eye of a physicist, the adaptations that permit this may be seen as being suboptimal. For example, a physicist examining the mammalian cochlea as a fluid-filled tube in which mechanics are dominated by viscous damping might find this counterintuitive. Equally irrational is the concept of using a gel-like, energy-dissipating tectorial membrane that covers all the sensory cells (**Figure 1**) to transmit energy in the cochlea. From a physics perspective, the mammalian cochlea may be misconstrued as being poorly "designed" for its purpose.

Despite this, the mammalian cochlea fulfills its role superbly and enables species survival. Observations of seemingly unsuitable design are therefore difficult to ascribe to an organ that has evolved over millions of years by natural selection and, obviously, like the middle ear, has been continuously

modified for its purpose. The hearing part of the ear evolved from a vestibular organ whose evolutionary origin (and especially the sensory cells themselves) resembles that of the lateral line, a body surface organ used by fishes to detect fluid motion in water. The lateral line has sensory hair cells similar to those of the cochlea whose responses are strongly influenced by viscous damping and are connected by a gel-like structure; both features survived 500 million years of evolution and are common to vertebrate inner ears. The problem of damping was solved very early by the evolution of active mechanisms of the sensory cells (Hudspeth, 2008; Brownell, 2017), and linking sensory cells via a gel-like structure in fact increases both their sensitivity and their frequency selectivity (Authier and Manley, 1995).

The problem is that "design" is often seen quite differently by a physicist and a biologist. The physicist may see the ear as a device whose construction has been based solely on physical principles (Lorimer et al., 2015). A biologist would be acutely aware of how such devices evolved naturally through historical contingencies (Manley, 2017) and avoid the notion of design. It is therefore of interest to highlight where these views of cochlear evolution oppose each other and consider some of the resulting questions to clarify the current understanding of how hearing organs evolve. Does the constraint of working within the same physical modality, such as acoustic pressure, inevitably lead to hearing organs that all have the same design? Does physics direct the evolution of hearing organ structure or are the principles of evolution different?

Genes, Evolutionary Compromise, and the Idea of Perfection

Anyone who has watched a television series on animal life will have often heard that animals are "perfectly" adapted to something. The idea is that in some way, evolutionary processes will inevitably reach an ideal situation in which no improvement is necessary or even possible. This, however, is erroneous. In any species that is adapted to something, individual animals will always vary in their genetic makeup and abilities (one basis of evolution). In addition, the object of the adaptation, say a prey organism, is also itself continuously adapting, gaining some small advantage to keep one step ahead of the predator. Thus, adaptation is always an on-going process; perfection can never be reached. Bodily processes do not evolve in isolation from each other and are subject to sometimes competing selection pressures. Hence, evolution inevitably involves compromises.

A clear example for evolutionary compromise can be seen in snakes, which have no external ear canal, and it is, falsely, supposed that snakes are deaf. Snake ancestors possessed normal middle ears and the loss of the eardrum in early snake evolution resulted in much poorer hearing. They became much less sensitive and lost the perception of frequencies above 1 kHz (Manley, 2002).

This evolutionary change was therefore unlikely to be guided by the physics of hearing, and there must be a biological explanation involving a different change that was of greater survival benefit for the snake ancestors than the disadvantages of hearing insensitivity. Snakes that were able to devour large prey survived on a single prey item for long periods during which no energy was needed to seek prey, an enormous advantage. The ingestion of such large prey was facilitated by the newly evolved ability to reversibly disarticulate the jaw and greatly stretch the tissues between the then floating jaw joints. It was obviously impossible to maintain a delicate eardrum suspended precisely where the stretch was necessary. Once the middle ear had been partially deconstructed in this way, the auditory epithelium of the inner ear was also simplified (Manley, 2002).

The design of the mammalian cochlea also provides other clear examples of compromises that ensure survival of species in their respective environment. For example, it is possible to genetically manipulate the protein structure of the tectorial membrane overlying the sensory cells and, through this, change the physics of the cochlea such as to enhance its frequency resolution (Russell et al., 2007). Why did evolution not use this opportunity? One trade-off of highly selective tuning is that the operation of the cochlea is brought close to the safety limits that ensure detection of weak signals (Lukashkin et al., 2009). Survival of an animal near the base of the food chain has a much higher dependency on detecting the sounds of a predator than using fine frequency resolution to detect which type of predator it is.

Opportunism of Evolution and Deterministic Dominance of Physics

Evolutionary compromise is not the only principle that is different from the deterministic laws of physics. Opportunism of evolution, which utilizes preexisting structures and genotypes, also makes it less providential. Any biological sensory system will be subject to evolutionary selective pressures. These pressures can be not only the direct result of the physics underlying the characteristics of the signal to be sensed and the properties of the medium transmitting that

signal but also the result of the requirements underlying the biological building blocks sensing that signal. In the case of the ear of land vertebrates, these include the outer and middle ears and the large variety of cellular and extracellular components that contribute to the structure and physiology of the sensory organ itself.

The shape of the mammalian cochlea itself is a good example of opportunism in evolution (**Figure 1**). A proposed reason for the spiraling snail-like shape of the cochlea is that it provides efficient packing of the cochlear duct within a single bone of the skull, a proposal supported by a recent study of the human cochlea (Pietsch et al., 2017).

This view, however, is counter to an elegant analysis of the physics of the spiral in a wide range of nonhuman, mammalian cochleae that revealed a correlation between the curvature gradient of the spiral (rate at which the spiral tightens) and low-frequency hearing limits (Manoussaki et al., 2008). The greater the rate of tightening of the spiral ratio, the greater the ability of the cochlear curvature to focus acoustic energy at the outer wall of the cochlear canal (whispering gallery effect) that enables sound energy to propagate toward the apex of the cochlea where low frequencies are detected. The human cochlea study (Pietsch et al., 2017) revealed that the spiral of the human cochlea varies markedly between individuals and that its shape is influenced by neighboring structures such as the large facial nerve. Does this mean the outcome of the physical-mathematical analysis on a wide variety of mammals is wrong? No. It could indicate that space preservation was paramount in determining the spiral shape of the mammalian cochlea and that selective pressure has led to further refinement of the spiral and enhanced the detection of low frequencies vital for survival of some mammalian species but not, apparently, humans. Release from this design constraint may free the human cochlea to other selective pressures, including diversity itself, in a changing communication environment.

To summarize, evolution is a creative and yet highly conservative phenomenon whose trajectories are greatly influenced by evolutionary coincidences rather than by any deterministic dominance of physics.

Convergent Evolution and "Optimal" Designs

Does the necessity of detecting the same physical modality inevitably lead to similar, convergent "optimal" designs of hearing organs? Of course, the hearing system of vertebrates provides remarkable examples of convergent evolution. For

example, the hearing and echolocation systems of bats and toothed whales are both based on the use of ultrasonics (see Simmons, 2017).

This, however, is frequently confused (e.g., Lorimer et al., 2015) with parallel evolution, which utilizes mechanisms and structures that were already present in the common ancestor. Strictly speaking, convergence, as defined by Futuyma (2008), is the evolution of similar features independently in different evolutionary lineages, usually from different antecedent features and/or by different developmental pathways. With respect to the evolution of mammalian, or even vertebrate, hearing, this is certainly not the case. In mammals, the shared sensory architecture and physiology arose from a common ancestry and not by convergent evolutionary processes. The traits involved show a high degree of conservation across the group, with specific adaptations arising from the modification of these preexisting cochlear structures and hearing processes.

For example, there is remarkable parallel evolution of the cochleae in old world (*Rhinolophidae*) bats and a single known New World bat species (*Pteronotus parnellii parnelli*) that use constant frequency echolocation calls to detect the Doppler shift in insect wing beats in acoustic clutter (Schnitzler and Denzinger, 2011). In both *Rhinolophidae* and *Pteronotus,* the basilar membrane of the cochlea, which performs frequency analysis of acoustic signals, is greatly extended and thickened in the region sensitive to the call echoes (Vater and Kössl, 2011). In *P. parnellii* at least, it forms an acoustic fovea that behaves as an acoustic laser with exceptional frequency selectivity that is over an order of magnitude sharper than that of any other mammal (Russell et al., 2004).

Two consequences arise from common ancestry. First, it establishes that the origin of the general uniformity of the structure of the mammalian organ of Corti is the result of evolutionary conservation, not of convergence. This by itself does not destroy the idea that physics guided the evolution of the mammalian hearing sensor's structure. As noted in the **Introduction**, the evolution of any sensory structure will be greatly influenced by the physics of the modality, the medium, and the structures involved. However, evolutionary conservatism stresses the importance of biological constraints that steer the evolution of these traits based on the historical contingencies that support them. In a way, the *mere existence* of a functional trait is itself a biological constraint for the evolution de novo of a trait that could eventually outperform the ancestral one. Second, the optimization of existing structures is evolutionarily more economical and,

due to the existence of well-adapted genetic "toolboxes," far more likely than the production from scratch of a new one. Although physics often constrains what evolution can do to optimize hearing, biological constraints arising from evolutionary contingencies also limit the nature and degree of the physical process involved in hearing optimization.

The kaleidoscope of structural configurations seen in modern groups of reptiles, birds, and mammals and their respective subgroups is the result of the unique histories of each group (Manley and Köppl, 1998). At every stage, evolutionary selection pressures worked on the physiological result of the input from the ear to the brain. If the input is adequate, in that it provides the sensory basis for survival and reproduction, the particular construction principles of each type of ear are not only unimportant but they are not even "seen" by evolution. Thus, it is of no surprise that in many very important respects, such as auditory sensitivity and frequency selectivity, the *functional* differences between the ears of mammals, birds, and reptiles are, despite large differences in structure, quite small (Manley, 2017). Hence, there is no single "optimal" solution for the realization of "ideal" hearing organs simply because the solutions are so massively, and usually irreversibly, influenced by history.

How Uniform Is the Construction of the Mammalian Cochlea?

The idea of convergence toward a physics-guided "optimal" design of the hearing periphery is not supported by the diversity of hearing organ structure that serves the enormous diversity of lifestyles across the animal kingdom. Even mammalian cochleae (**Figure 1**) are far from uniform (West, 1985). For example, the number of turns in the cochlear coils (1.7-4.5) and sensory cell rows (3-4) vary even within single taxonomic families such as rodents (West, 1985).

The mammalian cochlea shows, as do the inner ears of reptiles and birds, a diversity concomitant with the variety of lifestyles and thus the variety of selection pressures of different families, indeed of different individual species. Prey animals such as golden moles (*Chrysochloridae*) and mole rats (*Heterocephalus glaber*) use infrasound to detect predators (Narins et al., 1997). At the other extreme, predators such as the fishing bat *Noctilio* and some toothed whales use sounds in excess of 200 kHz to locate their prey (Thomas et al., 2003).

Bats provide another fine example of selective pressure driven by predator-prey relationships that shaped their hearing organs but also shaped the ultrasonic detection of bats by some noc-

turnal moths. These moths, prey to bats, have an ear with just two auditory sensory neurons tuned selectively to bat calls. This selective pressure has resulted in a spiraling competitive "war" between bats and moths and involve physics-based acoustic tricks (ter Hofstede and Ratcliffe, 2016; Pollack, 2017). Accordingly, "Evolutionarily speaking, insects have responded to selective pressure from bats with new evasive mechanisms, and these very responses in turn put pressure on bats to 'improve' their tactics" (Miller and Surlykke, 2001, p. 570).

How to Deal with the Evoked Signal Complexity

Survival in a complex acoustic environment requires plasticity of the central nervous system, including learning and memory. This flexibility permits designs of the hearing periphery that may be suboptimal from a physics point of view but sufficient from an evolutionary perspective. The hearing organs of vertebrates are dedicated to the sensory transduction and transmission to the brain of all components that are detected in a complex acoustic signal. These include those produced as a by-product of the hearing organ's own nonlinear properties, e.g., the generation of intermodulation distortion products by the nonlinear transfer function at the level of single sensory cells (Jaramillo et al., 1993).

Why are there no filtering mechanisms in the hearing organs of vertebrates to remove processing artifacts? The biological answer to this question is that any auditory signal processed by the cochlea (external or intrinsic) will act as a selection pressure to a lesser or greater extent. Complexities in signals, such as the distortion products, are not filtered at the cochlear level. To apply filtering, one has to know a priori the origin of a signal. Natural signals (e.g., birdsong, speech), however, are generally very broadband and their interpretation by the brain involves both learning and memory to make decisions about which frequencies are important and which are not. Under these circumstances, determining the difference between an internal signal generated due to distortion compared with the same frequency originating in the outside world is clearly unrealistic. Moreover, distortion components tend to be more than 40 dB smaller than primary signals and vertebrate ears cope with them because other advantages they offered were favored by natural selection. In addition, remarkably, mosquitoes exclusively use distortion products to hear (Simões et al., 2016).

Echoes, also, can be a bane or a boon. In reverberant environments, the brains of most animals suppress echoes so that auditory perception is dominated by the primary or leading sounds. The leading sound is enhanced and all that follows within a brief window of time is suppressed—but not in bats. Echolocation by bats relies on the timing of echoes to enable them to detect and locate prey and other sound-reflecting features of their environment (Neuweiler, 2003). The leading sound, or a signal generated by motor neurons that control the echolocation call, gates a brief window of time during which the echo responses of neurons in the auditory pathway are facilitated. Rather like the spatial representation of the visual system, where the retina is mapped onto neurons in visual brain areas, bats have echo-delay neurons mapped according to the time delays due to the distance between the bat and the target (Neuweiler, 2003; Simmons, 2017). This is true also of the incredibly sharply tuned cochlear mechanical resonance at the dominant frequency of the echolocation calls, around 61 kHz, of *P. parnellii*. Because of cochlear ringing, such high-frequency resolution is accomplished at the expense of losing temporal resolution. However, neural inhibition enables a specialized subpopulation of duration-tuned neurons tuned to the bat's 61-kHz cochlear resonance to escape the spectrotemporal trade-off (Macías et al., 2016). These remarkable neurons are the result of the inherent plasticity of the central nervous system and its programming. Clearly, the brains of vertebrates have evolved processing complexities that are able to provide an auditory performance that is not predictable from knowing the inherently limited capabilities of the cochlea itself.

Conclusions

Hearing organs, being sound detectors, must obey the general laws of physics. In this sense, physics imposes limits for evolution but does not direct it as such or necessarily leads to the selection of one "optimum design." Vertebrate hearing organs arose from preexisting vestibular sensory epithelia that, over hundreds of millions of years, were slowly modified in adaptation to higher frequency stimuli, first in water, then in air. The principles of evolution are not in the toolbox of physics and obey completely different laws that are derived from genetics and thus historical contingency. The resultant variety of hearing organs is concomitant with the variety of ways of life in the animal kingdom.

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Biosketches

Geoffrey A. Manley was educated in Cambridge, UK, and Princeton, NJ, before holding a postdoctoral position in Australia and a professorship at McGill University, Montreal. He is the founding professor of the Institute for Zoology at the Technische Universitaet Muenchen, Germany, from which he retired in 2011. His research emphasis is on a comparative approach to the middle and inner ears of amphibians, reptiles, birds, and mammals, for which he received the Award of Merit from the Association for Research in Otolaryngology in 2016.

Andrei Lukashkin is a reader in neuroscience at the University of Brighton, UK. He received a Wellcome Studentship in mathematical biology and completed his PhD at the University of Sussex, UK, where he also gained his postdoctoral experience. He is interested in the physiology and biophysics of the cochlea, with the main research focus on cochlear micromechanics and otoacoustic emissions.

Patrício Simões is a research fellow in the Sensory Neuroscience Research Group at the University of Brighton, UK. He holds a PhD in zoology from the University of Cambridge, UK (2013), with a focus on insect neuroecology. His current interests are the physiology of vertebrate cochlear supporting cells and hearing function in mosquitoes.
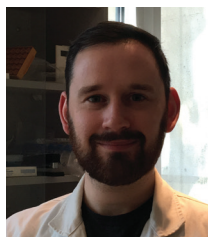
George Burwood received his BSc (Hons) in medical neuroscience from the University of Sussex, UK, and his PhD in auditory physiology from the University of Brighton, UK. He is currently working as a postdoctoral researcher in the Nuttall lab at the Oregon Health and Science University, Portland. His present research uses optical coherence tomography to study the mechanics of the low-frequency region of the inner ear and cochlear blood flow in deafness mutants.

Ian Russell is a professor of neurobiology at the University of Brighton, UK. At the University of Sussex, UK, he instigated majors in neurobiology and cognitive and medical neuroscience. He founded a research laboratory where three members initiated cochlear research that led to their appointments to the Fellowship of the Royal Society. Russell received the Award of Merit from the Association for Research in Otolaryngology in 2010. He investigates the workings of the cochlea related to normal and impaired hearing. He also studies the acoustic behavior and underlying physiology in mosquitoes and the cochlear mechanisms involved in bat echolocation.