

Development of Hearing. Part I: Phylogeny

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Abstract

We humans hear the way we do because of at least three major forces. The first is phylogeny, the evolutionary changes in the auditory system since its beginnings. Another is embryology, the development of the system in each individual before birth. Finally, there is the biologically determined auditory mechanism we are born with and our interaction with the environment in early postnatal life. This series of three articles reviews each aspect in turn, so we may have a fuller appreciation of how it is we come to hear the way we do. Part I reviews the evolution of human hearing through the vertebrates. Ancestral bony fish had an equilibrical organ, which was passed to subsequent classes. Both amphibians and reptiles evolved their own auditory systems based on a balance organ inherited from fish. Amphibians independently evolved an impedance-matching apparatus through a combination of eardrum and ossicle. Reptiles evolved a flexible basilar membrane for the receptor cells. Mammals added movable, external ears and expanded the frequency response range. Finally, large-brained *Homo* acquired the use of language. Part II examines embryologic development and Part III considers postnatal aspects of auditory development.

Key Words: Amphibians, evolution, fish, hearing, mammals, phylogeny, reptiles

Hearing is one of our most precious gifts. With it, we acquire the marvelous power of speech. These two abilities, hearing and speaking, afford us humans an astounding ease and range of communication with one another. This series of papers examines how we come to possess our capacity to hear.

How we hear is the result of at least three main influences. The first is evolution, that is, the development of hearing over time in uncounted species before us. A second is the formation of the organs of hearing in individuals during embryonic life according to the laws of heredity. Finally, there is the biologic, auditory system we inherit and our development after birth including the interaction with our environment. This series of articles will review each in turn—the phylogenetic, embryologic, and postnatal development of hearing—in the hope that we may appreciate more fully what a marvelous gift hearing is.

The intention is not to cover each aspect in great, technical detail. These areas are highly complex, and writings on them are not sought out or easily understood by the nonscientist. Rather, the goal is to bring together information from evolutionary biology, embryology, and infant development for the clinician or student.

The review ends at a beginning, the onset of speech at the close of the first year of life. One may imagine a curious parallel between the phylogeny and the ontogeny of hearing and speech. Just as hearing across the ages eventuated in the appearance of speech in the human species, hearing in early life permits the acquisition of speech by human individuals. Speech marks a crucial transition in the process of shedding infancy, for the term itself means “without speech” (in = “not” + fans, past participle of fari = “to speak”).

To begin, let us ask, “What is hearing?” To say it is what ears do in response to sound is hardly an explanation, for as Wever (1974) pointed out, many tissues and organs respond to sound vibrations. He said that “Hearing is the response of an animal to sound vibrations by means of a special organ for which such vibrations are the most effective stimulus” (Wever, 1974, p. 425). Individual mechanical impulses can certainly be detected better by our skin than

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by our ears. But if the impulses come fast enough frequently enough, then the ear is a far superior detector. The key here is that they must have the right frequency. The best rate of impulses for our ears is the familiar range of 20 per second to 20,000 per second. In other words, sound, as we experience it, is that range of frequencies that our ears can detect better than any other bodily tissue. In a way, then, our ears "feel" sound. There is an association, albeit a weak one, between feeling and hearing, both phylogenetically and ontogenetically. The important difference between the two is the interpretation made by special areas in the brain. In short, it is the brain that hears, not the ear.

Why concern ourselves with the phylogeny of hearing? The human auditory system is the result of how various animal ancestors developed their auditory systems. One could begin with fish, the first vertebrate to develop hearing as we know it, perhaps 350 million years ago. Perhaps, however, a better perspective is obtained by tracing the development of the ear against the backdrop of evolution itself. To help do so, the reader should make frequent reference to Figure 1. The remainder of the paper gives a simplified overview of evolution and its effect on hearing. No attempt is made to cover vertebrate hearing in detail. Animal variety is

nearly unimaginable. One should not construe this paper to imply that humans sit on the top rung of an evolutionary ladder. Evolution is not a ladder but an extremely diverse set of different directions, only one of which ends at human-kind.

Evolution. The earth formed 4.65 billion years ago, when the universe was already two to four times that old. At some point in the dim past, estimated to be 3.5 billion years ago, molecules acquired the capacity to reproduce themselves. Life emerged out of previously lifeless matter. Those molecules formed the most primitive sort of single cell—only protoplasm with no nucleus (prokaryotes). Then, about 1.5 billion years ago, cells somehow acquired a nucleus (eukaryotes), perhaps by simply engulfing another cell in a symbiotic relationship. Life's diversity was expanded when cells began to reproduce sexually (i.e., through combining genetic material) rather than merely dividing. Eventually, cells began to group together in multicellular combinations to form the fungi, plant, and animal kingdoms.

As time passed, the different cells in an organism took on different functions. In other words, they became tissues. Within the animal kingdom, there was an explosion of body types

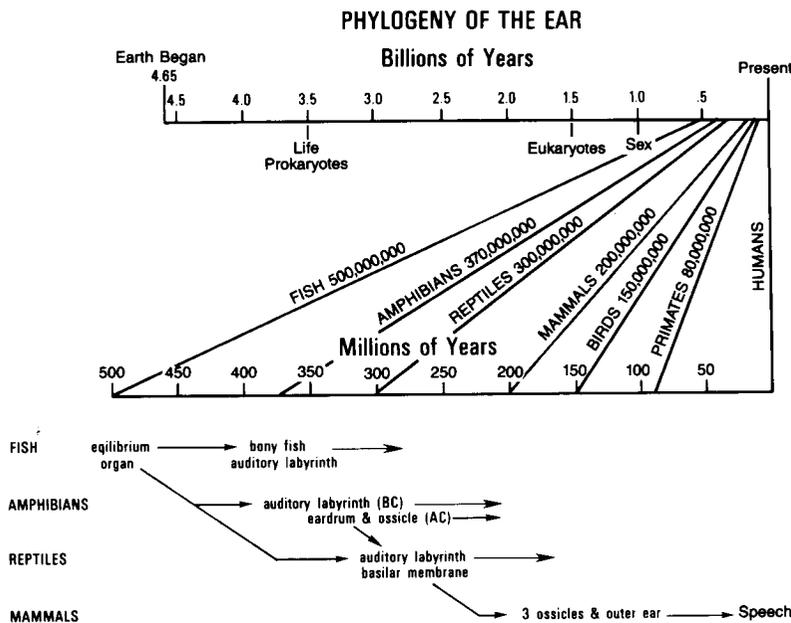


Figure 1 A time line showing the phylogeny of the ear against the age of the earth. The upper line shows time in billions of years and notes great landmarks of life's early history, from its onset with single-celled, non-nucleated prokaryotes, through nucleated eukaryotes, sexual reproduction, and, finally, the appearance of vertebrates. The lower segment shows in millions of years just the portion of the earth's history since vertebrates and the major innovations in their ear development preceding human communication. Note that fish passed along an internal equilibrational (but not auditory) organ to amphibians and to reptiles and that both of those groups evolved their own auditory labyrinths. An eardrum-ossicle complex originated with amphibians and was passed along to reptiles and mammals. Mammals received from reptiles both an auditory labyrinth and a middle ear system. Mammals modified the conductive apparatus by establishing a triple-ossicle system and by adding outer ears.

into numerous phyla. Extant phyla include, in approximate order of appearance, sponges, worms, molluscs, arthropods (such as crustaceans and insects), sea urchins, jellyfish, and, finally, our phylum, the chordates.

The major group of chordates is by far the vertebrates whose nerve cord has a segmented protective covering, the vertebral column. The vertebrates came on the scene perhaps 570 million years ago at the start of the Paleozoic ("old life") Era. There are five main classes of vertebrates; in order of appearance, they are the fishes and the tetrapods ("four-legged ones"), comprised of amphibians, reptiles, mammals, and birds.

Fish. Fish, the first vertebrates, arose between 450 and 600 million years ago, a mere one tenth of the age of our planet. Primitive fish had an internal balance organ inherited from some obscure invertebrate ancestor. Eventually, the balance labyrinth came to include an auditory receptor. Perhaps that statocyst of long ago was similar to that seen in current, simpler life forms, such as the jellyfish, and may have been the earliest sense organ of any sort to occur in an animal (Gray, 1955; Stevens and Warhofskey, 1965). Fish seem to be the first hearing animal, most notably the bony fish (osteichthyes), which appeared nearly 400 million years ago (although when they began to hear is uncertain).

As fish evolved, the labyrinth included curved canals and a utricle (both a constant finding among vertebrates), as well as a saccule and lagena (see Fig. 2).

The lagena is an extension of the saccule and presumed to be the forerunner of the cochlea (Guggenheim, 1948; Wever, 1974). Eventually, some of the macular cells in both the saccule and lagena became sensitive to sound. Equally im-

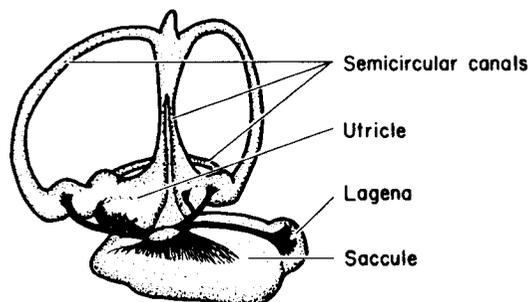


Figure 2 A diagram of the labyrinth of a modern fish (from Retzius, 1881).

portant, certain neural pathways and brain centers arose, which transmitted and interpreted signals from the sense organ in a new way, so that they were heard and not just felt (Wever, 1974).

How the change from equilibrical labyrinth to a combined auditory-equibrical labyrinth came about is unclear. Formerly, the common view was that the lateral line, the external pressure-sensing organ along the sides and head of fish, gave rise to an internal balance labyrinth in the head, which eventually included an auditory organ. Based on more recent evidence on anatomy and embryology, Schellart and Popper (1992) and Wever (1974, 1976) agree that, indeed, the balance system gave rise to the hearing system but maintain that the external lateral line did not lead to the internal labyrinth.

In any event, the early lateral line and balance mechanisms were hair cell organs. In other words, bending the tiny hairs on these unique cells triggered a sensory image in the organism. Indeed, Vinnikov (1982) feels that *all* animal exteroceptors are cytologic and molecular transformations of an original "hair" cell. That original cell, he maintains, was a flagellated protist cell (the earliest single cells to have a nucleus a few billion years ago). The cilia, used for fending off unwanted matter, balance, feeding, and locomotion, were also highly sensitive antennae. Vinnikov (1982) asserts that the ciliated cell was conscripted by the multicellular animals as exteroceptors to monitor happenings immediately around them.

The hair cell design is an exquisitely sensitive mechanoreceptor, so it is no wonder it became so widespread. In mammals, hair cells can respond when the tip of the hair bundle is moved a distance of 100 picometers (trillionths of a meter), that is, on the order of the size of hydrogen atoms (Hudspeth, 1983). Perhaps it is easier for us to relate to the experience we have all had of detecting a tiny insect as it climbed through the hairs of our arm. This is not to say that the cells and hairs of our skin are the same as sensory hair cells. The point is that slight deflections of hair-like projections can trigger a sensory response.

As far as is known, some ancient fish that had a swimbladder had their hearing coincidentally enhanced by the swimbladder. As in modern fish, the gas-filled bladder served to control buoyancy, but it also acted as a collecting chamber for vibrations entering the fish. The impulses, augmented by this "sound chamber,"

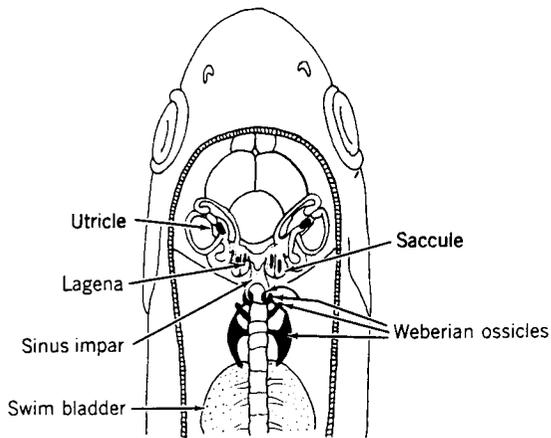


Figure 3 An illustration of the Weberian ossicles (reprinted with permission from von Frisch, 1936).

were passed to auditory receptors in the adjacent labyrinths.

Although not in the line that led to humans, one group of fish is well known for maximizing use of the sound-enhancing properties of the swimbladder. The group was the Ostariophysii, so named because of projections off a few of its vertebrae next to its swimbladder (ostareon = "little bone"; phys = "sac"). The ostarions are familiar to us through catfish, goldfish, and minnows. In ostarions of long ago, extensions of vertebrae lengthened to form a bony bridge between the swimbladder and a fluid system connecting with the labyrinths. Shown in Figure 3, these are the *Weberian ossicles*, first described by Ernst Heinrich Weber (a name known to audiologists for his discussion of the occlusion effect in bone-conduction hearing, for the Weber-Fechner Law in psychoacoustics, and for his tuning fork test). The Weberian ossicles are analogous to but not homologous to the middle ear bones in other tetrapods.

Since these early developments, there has evolved a remarkable variety of auditory systems in modern species of fish, but the basic plan of bilateral labyrinths of combined equilibrational-auditory function seems to apply (Schellart and Popper, 1992).

Why should an auditory system evolve? What was there to hear? Vinnikov (1982) states that sound detection developed along with but a step behind sound generation. Earliest marine sounds were probably caused by surface wind and surf and were likely of low value to sea dwellers. Later, sound must have been caused not only by one's locomotion, ingestion, and respiration but also by activities of other organisms close by. The animal that could better

monitor its environment had an advantage and, by natural selection, a better chance of surviving and passing along its genes to its offspring.

Amphibians. The transition from fish to amphibian seems to have involved a particular group of lobe-finned fish with a sort of fringe on the fins (crossopterygii). Speculation is that the shallow and warm fresh water those fish inhabited was oxygen poor, and they needed to supplement their oxygen intake. With rudimentary lungs, they could gulp air from time to time in the shallow ponds, or they could breathe air temporarily, as they flopped from one evaporating pond to another, more hospitable, one (Wever, 1981). Each of these two features, limbs for land locomotion and lungs for air breathing, evolved independently several other times. But it was the combination of both in Rhipidistians, a group of fringe-finned fish, that led to the first amphibians.

With the capacity to propel themselves on land and breathe air, amphibians arrived about 370 million years ago. Then as now, amphibians spent the first part of their life cycle in a water environment and took to land for the remainder of their lives. Their very name tells of their dual nature: amphi = "both sides," bios = "life," meaning they existed on both the aquatic and the terrestrial sides of life.

Even though the fish was the first vertebrate to develop an auditory labyrinth, neither the amphibians nor any of the subsequent classes of tetrapods inherited hearing inner ears from fish. It is true that all vertebrate labyrinths can be traced to the balance labyrinth of the bony fish. However, the change in the sensory-neural organization to become an auditory system occurred more than once among vertebrates, and perhaps as many as five different times, in the course of evolution (Wever, 1974, 1976). This sort of repeated adaptation to a common environmental pressure by different lineages, called convergent evolution, is quite common in nature.

The amphibia did not receive the auditory system of fish because they had branched before that line of fish possessed an auditory system. Instead, amphibia evolved an auditory labyrinth of their own, although it also involved a transformation of hair cells in the balance labyrinth and special changes in the central nervous system to become sensitive to sound (Wever, 1974, 1976; Fritzsche, 1992).

Most amphibia have not one but two groups of auditory sensory cells, a basilar papilla and

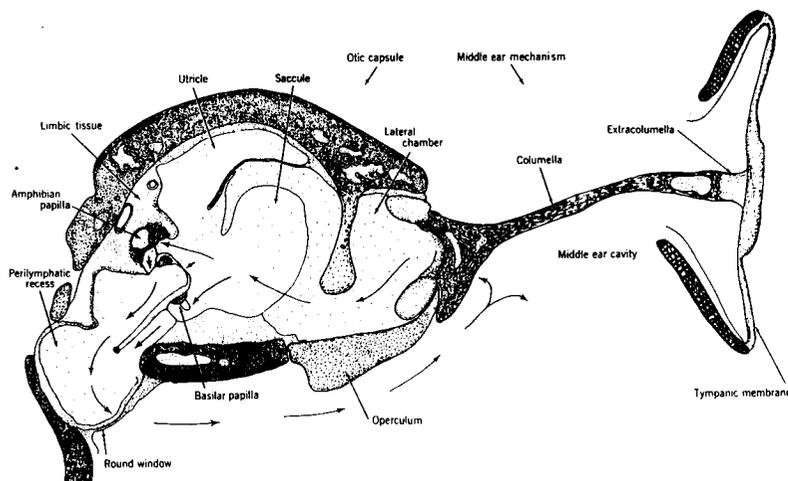


Figure 4 A diagram of the inner ear of an amphibian (frog). Note the two kinds of sensory papilla, the amphibian and the basilar papilla, in the inner ear. See also the conductive apparatus consisting of the tympanic membrane, columella, and oval window (reprinted with permission from Wever, 1974).

an amphibian papilla (see Fig. 4). The basilar papilla had its origins in ancestral fish and is present in many amphibians and all "amniotes" (animals with an amniotic membrane, including reptiles, birds, and mammals) (Fritzsche, 1992). The amphibian papilla is unique to and universal in amphibians. Indeed, the two amphibian sensory structures are so different that they may represent two separate evolutionary events (The New Encyclopaedia Britannica, 1992).

In addition to different sensory cell groups, amphibia evolved a perilymphatic system (Fritzsche, 1992). Finally, in reverse to the "usual" mode of auditory cell stimulation, sensory cells rest on a rather firm structure, and a tectorial membrane moves over them in response to sound vibrations, thereby bending the cilia of the sensory cells. Despite this commonality, auditory systems among amphibians show great variety across modern species. The reader should keep in mind that these descriptions are intentionally oversimplified. The purpose of this article is to trace, for the nonscientist, the line of evolution that led to our own auditory system.

Amphibia were the first vertebrate land dwellers. At first, their ears were poorly equipped for air-conduction hearing. The inner ear of both fish and early amphibia worked well in water, since their tissues and fluids closely matched the density of water. Vibrations traveling through water could pass virtually unimpeded through their bodies to stimulate their inner ears. But on land, any sound vibrations travelling through air met a tremendous impedance mismatch at an amphibian's body. Thus, the earliest amphibia heard much better by bone conduction than by air conduction. They spent their time either in water or creeping

along the ground. Some, when out of the water, rested their jaws on the surface, and vibrations were conducted to the labyrinth through jaw and skull bones. In others, sound vibrations may have been detected through an open mouth and subsequently caused bone conduction. In still others, sound vibrations were transmitted from the substrate to the labyrinth through limb bones. In these ways, vibrations in the ground could be sensed by bone-conduction hearing perhaps as well as by tactile sensation (Tumarkin, 1984). However, by our standards, they had a conductive hearing loss.

Evolution has shown there were a number of advantages to good hearing on land. Hearing is an excellent distance sense, working around corners, out of sight, and in darkness. It helps in obtaining food and in avoiding becoming food. Hearing is useful in territory marking, courtship, social interaction, and communication. However, the early land vertebrates had inefficient ears to take full advantage of detecting air-conducted sound.

The answer to this phylogenetic situation was the development of the conductive apparatus, one of the great landmarks of vertebrate evolution. Amphibians took advantage of pre-existing structures inherited from fish and elaborated them into a tympanic membrane and a single ossicle, the columella, to transmit vibratory energy from the air to the inner ear (Fritzsche, 1992). (Apparently, a membranous spiracular pouch for breathing became a tympanic space and tympanic membrane, and the hyoman-dibular bone for jaw bracing and the forerunner of the stapes was positioned near the labyrinth for sound transmission [Fritzsche, 1992].) The tympanic membrane, being much larger than the oval window in the inner ear, amplified the

sound energy mechanically, in effect reducing the difference in the impedances of the air outside and the contents of the labyrinth inside. Thus, the conductive mechanism served as a biologic impedance-matching transformer. Figure 4 illustrates a typical amphibian "middle ear."

Reptiles. Reptiles appeared in the late Carboniferous Period some 300 million years ago. The most common living reptiles nowadays are snakes, lizards, turtles, and crocodiles, but their most famous members, dinosaurs ("terrible lizards"), are extinct. The dinosaurs' main living heir, birds, arose perhaps 150 million years ago.

Reptilian auditory development took its own course. While it is true that reptiles inherited a balance labyrinth from amphibians, they did not inherit an auditory one. (This is analogous to amphibians inheriting an equilibrical but not an auditory system from fish.) Although not at all identical to preceding labyrinths, reptiles' auditory labyrinths were (and are) similar to earlier systems in that they included sensory hair cells in liquid-filled channels. The sensory cells were poised on a flexible, basilar membrane between two separate fluid channels in the pathway of sound energy coming through the labyrinth. The membrane and the sensory cells moved in response to sound. The relative motion between cilia and the cell body stimulated the cell (see Fig. 5).

The reptilian system is more familiar to us because it is the basic design that was passed to all descendant animals, including ourselves. However, not all reptiles have the same auditory system, any more than they have the same anatomy and function of other organ systems.

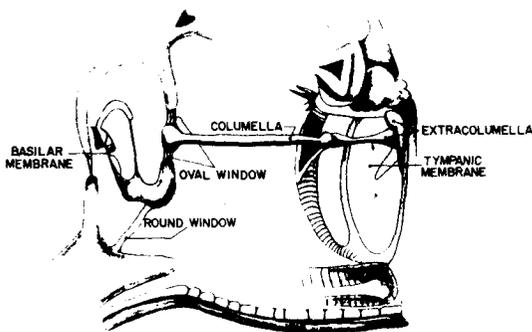


Figure 5 A diagrammatic illustration of a reptilian auditory mechanism. Note the sensory end organ on the basilar membrane (from Weber, 1965).

Still, their auditory systems have common elements, while showing great variation in detail.

Mammals. Members of one early group of reptiles—pelycosaurs—evolved some mammal-like characteristics. Their descendants were the Therapsida (ther = "beast" or "mammal" + aphis = "arch," because of the mammal-like form of the arch of the skull). The Therapsida, "mammal-like reptiles," began the line that eventuated in animals who are warm-blooded, develop some sort of coat for insulation, and suckle their young—mammals. Mammals seem to have appeared around 200 million years ago. Perhaps 80 million years ago, some placental mammals branched off and became the order of Primates (McLoughlin, 1985). The family of man (Hominidae) includes creatures that use two legs as their usual means of locomotion (bipedalism). Hominids certainly existed 3.5 million years ago (Pilbeam, 1984) and perhaps as long as 6 million years ago (McLoughlin, 1985). The starting point of the genus, *Homo*, cannot be fixed with certainty, but our species, *Homo sapiens*, was here perhaps 300,000 years ago (Pilbeam, 1984; Weaver and Brill, 1985). Individuals indistinguishable from us appeared in the last 45,000 years (Pilbeam, 1984). Figure 6 summarizes in a highly simplified and schematized fashion what is widely believed to be our evolutionary pathway, showing those key transitions from one type of animal to another. One ought not to view this as *the* direction in evolution but merely as *a* direction, one that happens to lead to humans.

When mammals appeared, they brought with them the auditory labyrinth design of the reptile (as did birds later). The basic plan remained unchanged, hair cells on a basilar mem-

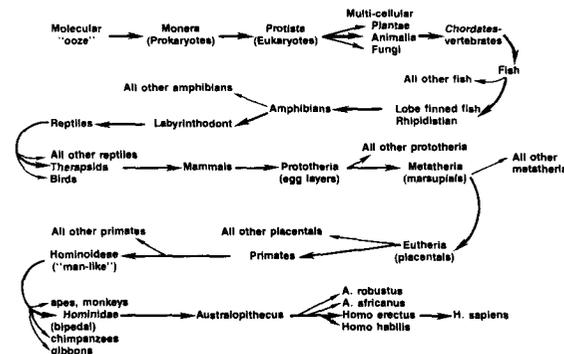


Figure 6 A highly simplified diagram showing a probable evolutionary pathway to our species *Homo sapiens*.

brane. Yet the organ of Corti is a mammalian specialization (Brownell, 1990), with its rows of different hair cells. There were no distinct inner hair cells (IHCs) before mammals (Tumarkin, 1984). Differences in inner and outer hair cells (OHCs) make one wonder if they represent different evolutionary products. They differ in number, shape, innervation, function, and response. For example, the IHCs supply output from the organ of Corti, whereas the OHCs are mechanical tuner-amplifiers that influence IHC response (Romand et al, 1987; Brownell, 1990). That the two types of hair cells may represent different evolutionary events may be a curious parallel to the two different types of sensory papillae in amphibians (also speculated to be distinct phylogenetically, as mentioned above). Another sensorineural characteristic of at least some mammals seems to be a separate cochlear division of the VIIIth cranial nerve (Tumarkin, 1984).

In addition to any variances in inner ear morphology, perhaps even more substantial differences between mammals and their forerunners were in middle and outer ear anatomy. The Therapsids independently evolved a mammalian tympanic ear. However, as in all evolutionary steps, those transitional mammals took advantage of pre-existing structures to form their own "versions" of a middle ear system (Allin and Hopson, 1992). As a result, whereas reptiles have several jaw bones and one auditory ossicle, mammals have one jaw bone and three auditory ossicles. The multiple jaw bones of the reptile, save one which became the mandible, were modified into mammalian ossicles. A trace of this origin can be seen in the unity of the mandible and malleus during the fetal stage of mammals. The mammalian ossicles became less massive and more delicately supported to form a middle ear system slightly more efficient than that of the reptiles. For protection, tympanic membranes became recessed within canals (generally true also of birds, many of whom added a feather covering). Another distinguishing mammalian feature was a movable outer ear, one that could be positioned for most favorable sound reception. That ability has been lost in the hominids, including humans, save for the infrequent individual with the unusual ability to "wiggle" his ears.

Vertebrates Compared. Our purpose here is not to compare vertebrate auditory abilities but rather to trace the pathway of auditory development to humans; however, a brief glance

at comparative hearing abilities helps put our human hearing in perspective. As a very rough generality, the later the appearance of the vertebrate class, the more complex and capable the auditory system (Masterton et al, 1969; Wever, 1974; Stebbins, 1976). For example, Wever (1974) notes a trend toward more sensory cells across vertebrate classes from fish to mammals. However, a common misconception is that evolution inevitably leads to a better product—in this case, hearing. "Better" may be true, if functionally defined as improved adaptations to one's environment with resulting increased chances of reproduction. Nature incorporates chance changes (mutations) that prove beneficial through what Darwin termed "natural selection." In some instances, "better" may even mean a reduction in structure or function (e.g., loss of limbs or eyes in certain species, which better suits the animal to its environment).

Hearing has been honed in most hearing animals over the eons to be extremely acute. For example, Fay (1988), in comparing current species of all vertebrate classes, finds a wide diversity of auditory capabilities but no clear phylogenetic trends in sensitivity (Figs. 7, 8 and 9),

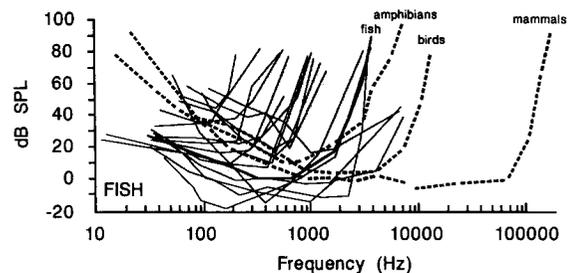


Figure 7 Audiograms of fish as compared to the other vertebrate classes. (Adapted with permission from Fay, 1988.)

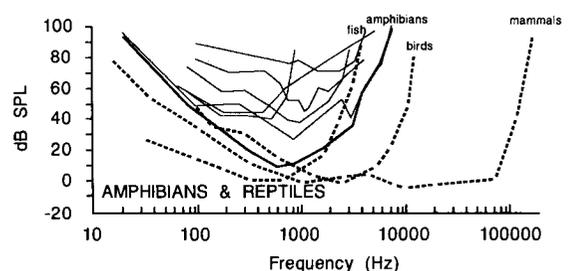


Figure 8 Audiograms of amphibians and a reptile as compared to the other vertebrate classes. (Adapted with permission from Fay, 1988.)

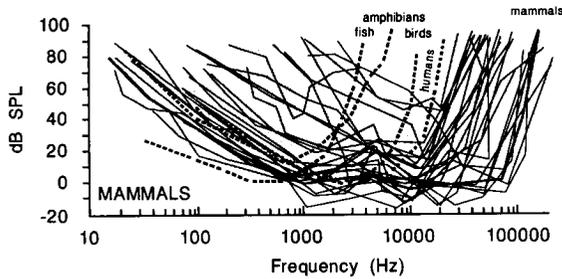


Figure 9 Audiograms of mammals, including humans, as compared to the other vertebrate classes. Note human sensitivity is markedly poorer in high frequencies as compared to many other species. (Adapted with permission from Fay, 1988).

intensity discrimination (Figs. 10 and 11), frequency discrimination (Fig. 12), frequency selectivity, or certain aspects of temporal resolution.

As mentioned above, there seems to have been a weak trend toward more sensory cells across vertebrate classes. An increasing number of hair cells was accommodated by an ever-enlarging auditory labyrinth. A space-saving curvature came along (the cochlea = "snail"), ranging from a mild bend in birds to up to four coils in some mammals. With more sensory cells, sensitivity improved and range of frequency response widened, especially in high frequencies, except in primates, in which frequency range has actually retrogressed (Masterton et al, 1969; Stebbins, 1976). Most nonprimate mammals can hear frequencies far above the human range of hearing. As a rule, high-frequency hearing above 16 kHz is unique to mammals. The total area of the "audible field" (formed by a combination of sensitivity and frequency range) increased until 60 million

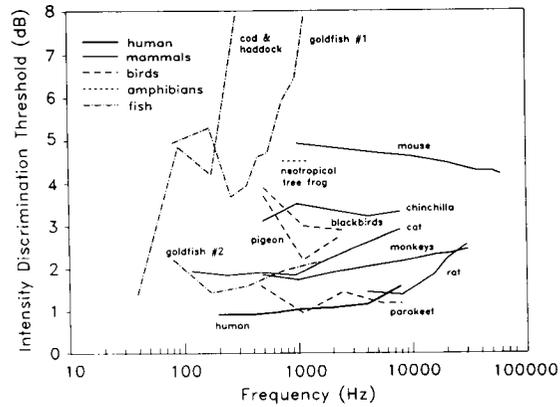


Figure 11 Intensity discrimination thresholds as a function of frequency of various animals from the vertebrate classes, except reptiles. (Adapted with permission from Fay, 1988.)

years ago, after which it declined in primates (Masterton et al, 1969). The disadvantage (if there was one) of the trend toward a narrower frequency range in primates may have been offset by improved ability to identify small differences in frequency, intensity, and complexity of an acoustic signal (Stebbins, 1976). Such expanded abilities were not due just to the peripheral system but also to changes in the central nervous system. With regard to our recent lineage, the last 5 million years have seen an enormous increase in both the size and complexity of the hominid brain. Our human brain is a wonder of collective abilities to appreciate sound in its myriad aspects and to attach meaning to it. As was mentioned at the outset, we do, indeed, hear with our brains, not with our ears.

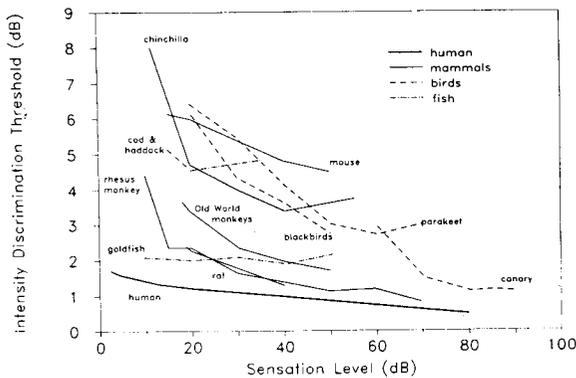


Figure 10 Intensity discrimination thresholds as a function of sensation level of various fish, birds, and mammals. (Adapted with permission from Fay, 1988.)

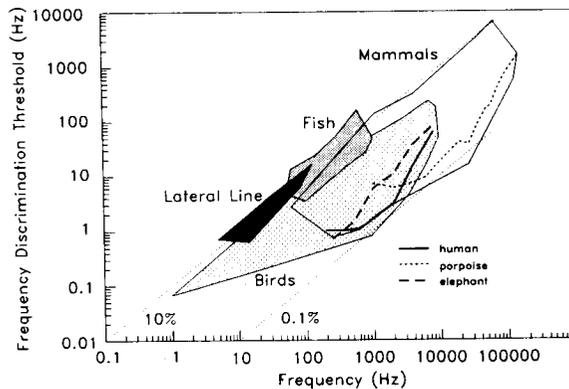


Figure 12 Frequency discrimination thresholds as a function of frequency for different fish, birds, and mammals. (Adapted with permission from Fay, 1988.)

How long humans have been producing and perceiving "speech" sounds to communicate is difficult to say. Communication is a behavior, and behaviors do not leave fossils. However, the development of an acoustic symbol system for communication—language—is probably the prime evolutionary change in the past 2 million years that led to our full humanity (Isaac, 1978). Language may have appeared around the time of fire, use of fine tools, and coordinated group hunting, perhaps 500,000 years ago (Washburn, 1960). Noted anthropologist Richard Leakey (1983) speculates that language may be even older in view of the relative success of hominids, which came before us.

In this first article, we have examined the evolution of the hearing mechanism. In Part II of this series, we trace the embryology of the auditory system.

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