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STRUCTURE AND FUNCTION IN WHALE EARS

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ABSTRACT

Ultrasonic echolocation abilities are well documented in several dolphin species, but hearing characteristics are unknown for most whales. Vocalization data suggest whale hearing spans infra- to ultrasonic ranges. This paper presents an overview of whale ear anatomy and analyzes 1) how whale ears are adapted for underwater hearing and 2) how inner ear differences relate to different hearing capacities among whales.

Whales have adaptations for rapid, deep diving and long submersion; e.g., broad-bore Eustachian tubes, no pinnae, and no air-filled external canals, that impact sound reception. In odontocetes, two soft tissue channels conduct sound to the ear. In mysticetes, bone and soft tissue conduction are likely. The middle ear is air-filled but has an extensible mucosa. Cochlear structures are hypertrophied and vestibular components are reduced. Auditory ganglion cell densities are double land mammal averages (2000–4000/mm). Basilar membrane lengths range 20–70 mm; gradients are larger than in terrestrial mammals. Odontocetes have 20–60% bony membrane support and basal ratios >0.6, consistent with hearing >150 kHz. Mysticetes have apical ratios <0.002 and no bony lateral support, implying acute infrasonic hearing. Cochlear hypertrophy may be adaptive for high background noise. Vestibular loss is consistent with cervical fusion. Exceptionally high auditory fiber counts suggest both mysticetes and odontocetes have ears "wired" for more complex signal processing mechanisms than most land mammals.

Key words: cetacean ear, inner ear, odontocete, mysticete, basilar membrane, cochlea, auditory system, auditory nerve

INTRODUCTION

Hearing provides an important sensory window on the world. The view through that window differs for each species, in part because of inner and middle ear anatomical differences shaped through evolution. Understanding how hearing capacity and auditory structures co-vary in other species, particularly in ultra- and infrasonic animals from diverse habitats, can provide important insights into fundamental mechanisms in the auditory periphery that affect hearing range and

acuity. Whales have a very special auditory view having successfully coupled an air-adapted mammalian ear to underwater sound.

The present consensus is that modern Cetacea (dolphins and whales) are descended from mesonychid condylarths, land-dwelling, carnivorous ungulates, that entered the shallows of the warm Tethys Sea in the Eocene and stayed (Gingerich et al. 1983, Barnes et al. 1985; see Ridgway 1997). In the intervening 50 to 60 million years, the air-adapted, high frequency ears of these amphibious carnivores were reshaped for good sensitivity and accurate localization of water-borne sound. Every portion of the auditory periphery was modified: pinnae and external auditory canals were lost, the middle and inner ear capsules fused, and the new ear complex migrated outward, dissociating from the skull. As cetaceans developed into obligate aquatic mammals, unable to move, reproduce, or feed on land, their ears became sufficiently specialized that modern whales and dolphins may no longer be able to detect or interpret normal air-borne signals.

There are now 76 species of whales, ranging in size from the harbour porpoise (*Phocoena phocoena*; 1 m., 55 kg.) to the blue whale (*Balaenoptera musculus*; 40 m., 93,869 kg.) (Nowak 1991). Most are odontocetes (suborder Odontoceti—toothed dolphins and whales; 65 species), which are efficient predators. All odontocetes tested to date echolocate; i.e. they "image" their environment with self-generated signals ranging to 200 kHz, and all 65 species produce ultrasonic signals (Kellogg 1959, Norris et al. 1961, Awbrey 1990, Au 1993; see also Au 1997, Dolphin 1997, Moore 1997). The second suborder, the Mysticeti (rorquals, right, and baleen whales; 11 species) are pelagic omnivores. There are no direct behavioral or physiologic measures of hearing in any mysticete; however, many species are known to produce infrasonic signals (see Edds-Walton 1997) that may be used for long-range communication or for topographic imaging and navigation. As a group, whales therefore have two important aspects for auditory investigations: 1) They have the only mammalian ears fully adapted to underwater hearing, and 2) they employ the broadest acoustic range of any known mammal group.

Considering that cetaceans function wholly in water, a dense medium in which light attenuates far faster than sound, it is not surprising that hearing is believed to be the fundamental sensory and communication channel for whales. We expect whale hearing to be highly evolved, and, given the diversity of cetaceans, it would be naive to expect to understand the scope of whale hearing from data on one species or division. Differences in sounds, habitat, behaviour, and size, particularly between odontocetes and mysticetes, imply substantial variation in their auditory anatomy and, therefore, in hearing abilities.

For practical and legal reasons, most cetaceans cannot be investigated with conventional audiometric techniques. However, anatomical data are available on some aspect of the auditory system in

26 cetacean species, including nearly half of the larger, rare, and non-captive species. Anatomical correlates of hearing characteristics in land mammals are fairly well established from comparative studies that analyzed how differences in cochlear morphometry were related to psychophysical and electrophysiological results (Manley 1972, Greenwood 1961, 1962, 1990, Fay 1988, 1992, Echteler et al. 1994). Functional correlates have also been established for ears in the few delphinids for which electrophysiologic and behavioural audiograms are available (Solntseva 1975, Solntseva and Chernova 1980, Ketten 1984, Ketten and Wartzok 1990, Ketten 1992).

Comparisons of data from these two sets of studies show that similar principles govern the response characteristics in both aquatic and terrestrial ears, which is consistent with the structural similarity of all mammalian ears. This paper provides an overview of whale peripheral auditory system anatomy from a functional perspective. The key issues addressed are: 1) how do whale ears differ from terrestrial ears, 2) how do these differences correlate with underwater sound perception, and 3) how do structural variations among whales correlate with underwater infra- and ultrasonic hearing.

Acoustic Environment—Air vs. Water

While the characteristics of each sensory system are shaped by species-specific evolutionary pressures, they are also, in a sense, limited by their environment. To understand whale hearing, it is important to consider how the physical properties of water vs. air influence intensity and pressure measures.

Sound intensity (I) is the acoustic power impinging on a surface perpendicular to the direction of sound propagation; i.e., the sound energy per second per unit area. For an instantaneous sound pressure in an outward travelling plane wave intensity is:

$$I = pv = p\ (p/c\rho) = p^2/c\rho$$

where p is the effective sound pressure, c is the sound speed, and ρ is the density of the medium. The product $c\rho$ is the characteristic impedance for that medium.

Sound speed varies significantly with any factor affecting the density of the medium. If we assume average speeds and densities for moist surface air (c = 340m/sec; ρ = 0.0013 g/cc); and for sea water (c = 1530m/sec; ρ = 1.03 g/cc):

$$I_{air} = p^2/(340\text{m/sec})(0.0013\ \text{g/cc}) = p^2/(0.442\ \text{g-m/sec-cc})$$
$$I_{water} = p^2/(1530\text{m/sec})(1.03\ \text{g/cc}) = p^2/(1575.90\text{g-m/sec-cc})$$

To hear a sound equally well in water and in air, an intensity based mammal ear would require the same acoustic power/unit time ($I_{air} = I_{water}$), or:

$$I_{air} = p_{air}^2/(0.442 \text{ g-m/sec-cc}) = p_{water}^2/(1575.90 \text{g-m/sec-cc}) = I_{water}$$
$$p_{air}^2(3565.4) = p_{water}^2$$
$$p_{air}(59.7) = p_{water}$$

which means for an equivalent intensity, the sound pressure in water must be ~60 times that in air. For technological reasons, we commonly measure the mean square pressure of the sound wave rather than intensity, and express hearing thresholds in terms of effective sound pressure level (SPL), measured in decibels (dB):

$$\text{dB SPL} = 10 \log (p_m^2/p_r^2)$$
$$= 20 \log (p_m/p_r)$$

where p_m is the pressure measured and p_r is a reference pressure. For air-borne sound , the reference is dB SPL or dB re 20 μPa rms, derived from the fact that the lowest sound level the human ear detects at 2 kHz is a diffuse field pressure of 20 μPa, which has an acoustic power density of ~1 picowatt/m^2. For underwater sound, the reference pressure is dB re 1 μPa. If reference pressures were identical, the hypothetical dual environment ear would require a sound level ~35.5 dB greater in water than in air. However, if conventional reference pressures are used, the underwater sound pressure level value would numerically be 35.5 dB + 20 (log 20) dB greater than the airborne value; i.e., 61.5 dB re 1 μPa in water ~0 dB re 20 μPa in air.

Clearly, comparisons of in-air vs. in-water hearing must consider these differences, and in terms of structural analyses, these calculations suggest that in addition to adaptations for differences in acoustic velocity and wavelength, we need to consider whether adaptations are related to the substantially greater acoustic pressures required in water for equal intensity percepts.

Functional Acoustic Divisions

Because underwater measures of auditory sensitivity are available for very few whales, peak spectra of emitted sounds were used to acoustically categorize cetaceans in this paper. Mammalian vocalizations generally have peak spectra at or near the frequency of best sensitivity for that species; therefore, spectral analyses of underwater recordings of emitted sounds provide reasonable indirect estimates of cetacean hearing (Sales and Pye 1974, Watkins and Wartzok 1985, Henson et al. 1990, Popper 1980, Tyack 1997). The most

consistent odontocete signals are used in echolocation. Based on peak spectra (the frequency of maximum energy in a typical echolocation click) (Table 1), there are two ultrasonic odontocete groups (Ketten 1984): Type I with peak spectra above 100 kHz and Type II with peak spectra below 80 kHz. These ultrasonic divisions coincide with differences in habitat and social behavior. Type I odontocetes typically are solitary, inshore phocoenids and platanistids, whereas Type II species are mostly delphinids that form large, complex social groups or pods (Ketten and Wartzok 1990).

All mysticetes are preliminarily classed as Type M, although recent analyses suggest they may have equally distinct functional acoustic divisions (Würsig and Clark 1993). Mysticete vocalizations are significantly lower in frequency than those of odontocetes (Table 1). The available data indicate baleen vocalizations are in the sonic to infrasonic range (peak spectra 12 Hz to 3 kHz) and are categorized as moans (0.4 to 40 seconds, fundamental < 200 Hz), calls (bursts or pulses; peak < 1 kHz), and songs, with complex phrasing and spectra (see Edds-Walton 1997). Infrasonic signals; i.e., below 25 Hz, are well documented in at least two species, *Balaenoptera musculus* (Edds 1982) and *Balaenoptera physalus* (Watkins 1981, Watkins et al. 1987, Edds 1988).

Cetacean Ears

There are three essential parts to the mammalian auditory periphery: 1) an outer ear which captures sound, 2) a middle ear which filters and amplifies sounds, and 3) the inner ear (cochlea) which is a mechanochemical transducer of sound that performs a spectral analysis. Although whale ears clearly follow the land mammal blueprint, they have aquatic-related adaptations at all auditory system levels.

External ear—sound channels

External auditory canals are present in all Cetacea, but it is debatable whether they are functional. Pinnae are absent, although vestigial pinnal rings occur in some individuals. A small external meatus connects with an exceptionally narrow external auditory canal. In odontocetes, the external canal is plugged with cellular debris and dense cerumen and has no observable connection with the tympanic membrane or temporal bones. In mysticetes, the proximal end of the canal flares, cloaking the "glove finger", a complex, thickened membrane derived from the pars flaccida of the tympanic membrane (Reysenbach de Haan 1956). This extensive tympanic "finger" (up to 15 cm. long in humpback whales) protrudes laterally from the middle ear cavity and in adult animals is capped by a waxy mound that increases with age.

TABLE 1

Acoustic Categorization of Representative Odontocete and Mysticete Vocalizations (Data compiled from Schevill et al. 1969, Møhl and Anderson 1973, Popper 1980, Norris and Leatherwood 1981, Watkins 1981, Watkins and Wartzok 1985, Watkins et al. 1987, Edds 1988, Clark 1990, Au 1993, Richardson et al. 1995)

Suborder Species	Category	Common Name	Sound Type	Frequency Range (kHz)	Frequency at Maximum Energy (kHz)
Odontoceti					
Inia geoffrensis	I	Boutu	Click	25–200	95–105
Phocoena phocoena	I	Harbour porpoise	Pulse	100–160	110–150
Delphinus delphis	II	Common dolphin	Whistle	0.2–150	4–9
			Click	0.2–150	30–60
Orcinus orca	II	Killer whale	Scream	0.25–35	12
Stenella longirostris	II	Long-beaked spinner	Click	1–160	60
			Whistle	1–20	8–12
Tursiops truncatus	II	Bottlenosed dolphin	Click	0.2–150	60–80
			Whistle	2–20	–
Physeter catodon	II	Sperm whale	Coda	16–30	–
Mysticeti					
Eschrictius robustus	M	Grey whale	Call	–	1–1.5
Balaenoptera musculus	M	Blue whale	Moan	0.2–0.20	0.012–.018
Balaenoptera physalus	M	Fin whale	Call	0.16–0.75	0.020
Balaena mysticetus	M	Bowhead whale	Call	0.1–0.580	0.14–0.34†
Eubalaena glacialis	M	Right whale	Call	–	<0.200†
Megaptera novaeanglia	M	Humpback	Song	0.05–10.0	<4.0

†Recordings below 100 Hz are not available

Reysenbach de Haan (1956) and Dudok van Heel (1962) were among the first to investigate soft tissue sound conduction in odontocetes. Reysenbach de Haan (1956) reasoned that, since the transmission characteristics of blubber and sea water are similar, using a canal occluded with variable substances would be less efficient than tissue or bone conduction. Dudok van Heel (1962) concluded the canal was irrelevant because behavioral measures of minimum audible angle in bottlenosed dolphins (*Tursiops truncatus*) were more consistent with an intercochlear than intermeatal distances.

Considerable evidence implicates the lower jaw as the primary reception path for ultrasonic signals in odontocetes (Bullock et al. 1968, Norris 1969, McCormick et al. 1970, Norris and Harvey 1974, Brill et al. 1988). A passive resonator system involving the teeth of the lower jaw has been suggested for some species (Goodson and Klinowska 1990), but it is unsuitable as a general explanation because it cannot account for good echolocation abilities in relatively toothless species; e.g., the Monodontidae (narwhals and belughas) and Ziphiidae (pelagic beaked whales). Norris (1968, 1980) observed that the odontocete mandible has two exceptional properties: a concave medial face which houses the fatty jaw liner, and a thin, ovoid, region, the "pan bone" in the posterior third of the mandible. The fats in the mandibular channel are wax esters with acoustic impedances close to sea water (Varanasi and Malins 1971). Norris (1969) speculated this mandibular fat channel acts as a preferential low impedance path to the middle ear, and the pan bone, as an acoustic window to the middle ear region that lies medial to it near the rear edge of the jaw (Figure 1). Several forms of data support this hypothesis. Evoked responses and cochlear potentials in two delphinids (Type II) were significantly greater for sound stimuli above 20 kHz placed on or near the mandible (Bullock et al. 1968, McCormick et al. 1970). Measurements of transmission characteristics from hydrophones implanted in severed bottlenosed dolphin heads had best responses from sources directed into the pan bone (Norris and Harvey 1974). Brill et al. (1988) found that encasing the lower jaw in neoprene significantly impaired echolocation performance of a captive bottlenosed dolphin. However, findings by some researchers, notably those by Popov and Supin (1990) and Bullock et al. (1968), disagreed with these conclusions. They found minimum thresholds were associated with stimuli near the external meatus. Recently, magnetic resonance imaging of several species of odontocetes revealed a second trumpet-shaped body of fats with a density equal to those in the jaw overlying the pan bone (Figure 1) (Ketten 1994). This second potential channel may explain the discrepancy in the earlier studies since the fatty lobes also lie near the meatus. The orthogonal orientations of the two channels, jaw (anterior) and lobes (lateral), suggest dolphins may have "segmented" sound conduction; i.e., the anterior channel may be specialized for

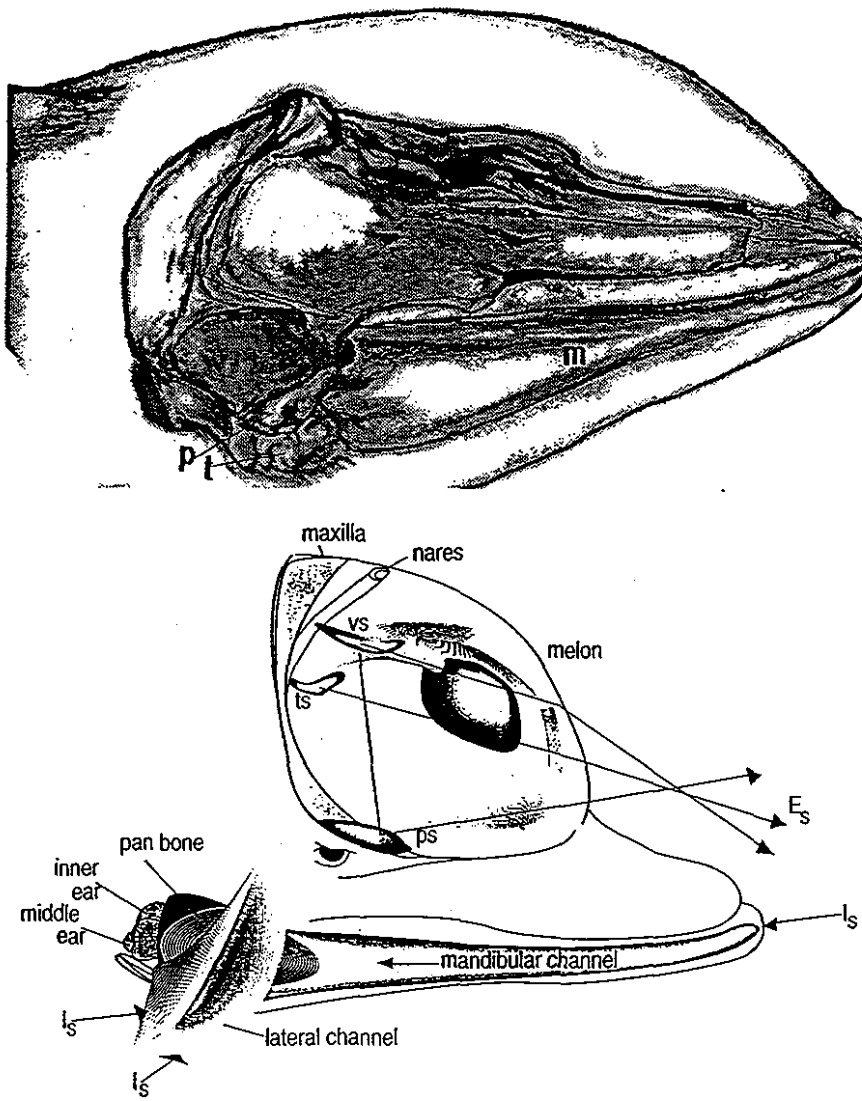


Figure 1. Proposed sound paths in the dolphin head. Out-going ultrasonic signals (Es) are generated in the vestibular (vs) and tubular (ts) nasal sac diverticulae and reflected off the cranium and premaxillary sac (ps) (Norris 1980, Au 1993). Incident sounds (I_S) from anterior targets enter the lower jaw where lipids act as preferential low impedance conduits (mandibular channel) to the ear (Varnassi and Malins 1971, Norris 1980). Lateral, trumpet-like fatty lobes (lateral channel) with densities equal to those in the jaw overlie the pan bone (Ketten 1994) and may act as preferential input channels for lower frequency incident signals from conspecifics at the rear or side of the animal. The inset shows the approximate relation of the skull and ear components to the surface of the animal. (m = mandible; p = periotic; t = tympanic) (Copyright Ketten, 1992, revised 1995)

capturing return echolocation signals, while the lateral channel may capture lower frequency communication signals from other pod members. No similar, discrete soft tissue channels to the ear have been identified in mysticetes.

Temporal bone construction and placement

The temporal bones of cetaceans are distinctive in form, construction and location. All whale ears are housed in two bulbous bones constructed of massive, porcelaneous bone. The inner ear is housed in the periotic bulla which is attached to a shell-like tympanic bulla that forms the middle ear cavity. Most important, however, this tympano-periotic bullar complex sits in an extensive peribullar cavity formed by broad, cranial wings which give the whale skull its distinctive mushroom appearance (Figure 2), and both the inner and middle ear are therefore external to the brain case.

Odontocete periotics are ovoid and dense. The tympanics are conical and thin-walled, and the major tympano-periotic suture is a partly fused hinge (Kasuya 1973, Ketten 1984, Ketten and Wartzok 1990). Differential motion between the two components is possible, but no precise relation to audition has been demonstrated. In odontocetes, the entire odontocete tympano-periotic complex is suspended in the peribullar cavity by five or more ligaments and surrounded by a spongy mucosa. This ligamentous suspension and mucosal cushion isolate the ear from bony sound conduction and hold the tympanic loosely in line with the mandibular fatty channels and pan bone (Figure 1) (Reysenbach de Haan 1956, Ketten 1984). Because the peribullar sinuses and mucosa are most developed in shallow water, ultra-high frequency species like the Amazonian boutu *Inia geoffrensis*, Oelschläger (1986) concluded their primary function is for acoustic isolation of the ear for echolocation.

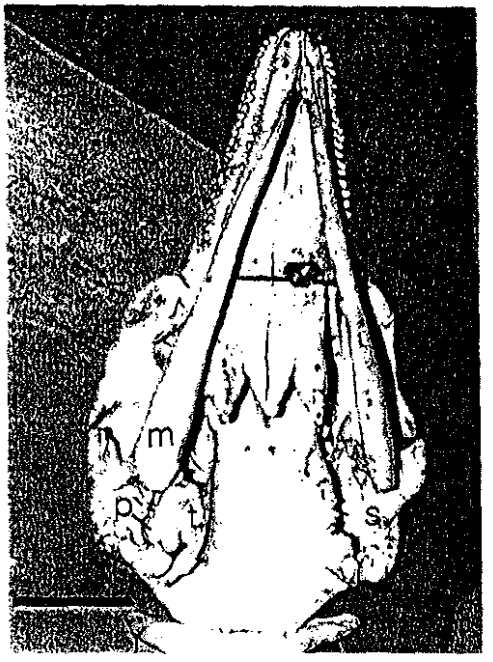
In mysticetes, the tympano-periotic sutures are fixed, and extensive anterior and posterior bony flanges wedge the periotic bulla into crevices in the skull. The tight coupling of these flanges to the skull suggest both bony and soft tissue conduction mechanisms are possible in baleen whales.

The extra-cranial location of whale ears is an important adaptation for underwater sound localization. In land mammals, two important cues for localizing sound are differences in arrival time (interaural time) and in sound level (interaural intensity). Because of sound speed differences, lack of pinnae, and ear canal adaptations in whales, localization depends on somewhat different paths than those of land mammals. Heffner and Masterton (1990) found that the high frequency limit of functional hearing in most mammals is correlated with the species average interaural time distance (IATD), the distance

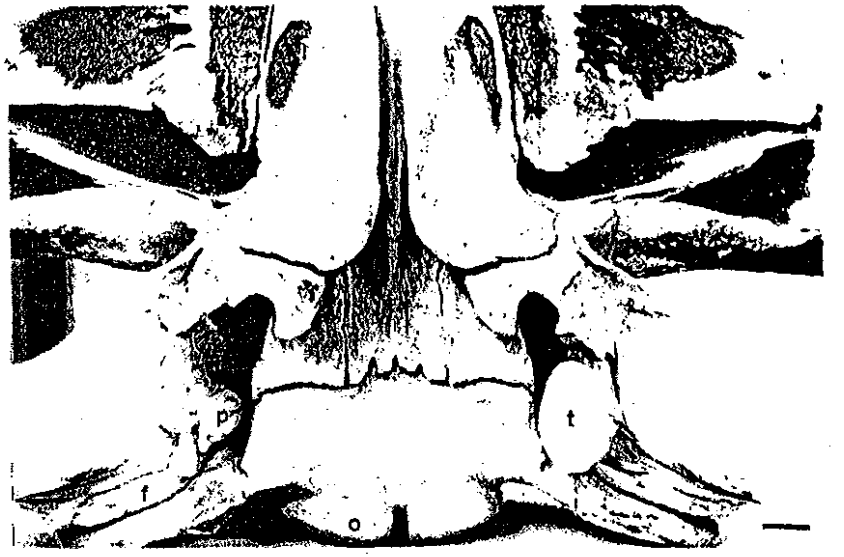
sound travels from one ear to the other divided by the speed of sound. For terrestrial species, the normal sound path is through air, around the head, pinna to pinna. The key entry point for localization cues is the external meatus, and the IATD is therefore the intermeatal (IM) distance measured around the head divided by the speed of sound in air.

In aquatic animals, sound can travel on a straight line through the head by tissue conduction, given that tissue impedances are similar to the impedance of sea water. Binaural hearing studies are relatively rare for marine mammals, but the consensus from research on both pinnipeds and odontocetes is that binaural cues are important for underwater localization and that intercochlear (IC) or inter-jaw distances are the most appropriate measure for calculating IATD values in odontocetes (Dudok van Heel 1962, Gentry 1967, Moore et al. 1995). Supin and Popov (1993) suggested that the combination of sound speeds in water with small receptor distances may preclude underwater IATD cue use for non-pinnal species; but recently, Moore et al. (1995) demonstrated that *Tursiops* has an IATD on the order of 7 μsec, which is comparable to the human value (10 μsec) and well below that of most land mammals tested. IC distances of dolphins are acoustically similar to a rat or bat IM distance in air (Ketten et al. 1992). If we use IM distances for land mammals and IC distances for cetaceans, whales appear to follow similar trends for IATD vs. high frequency limits (Figure 3).

In land mammals, level discrimination thresholds are independent of frequency, decrease with increasing sound levels, and are generally better in larger animals (Fay 1992, Heffner and Heffner 1992). Humans and macaques commonly detect intensity differences of 0.5 to 2 dB throughout their functional hearing range; gerbils and chinchillas, 2.5 to 8 dB. Behavioral and evoked potential data show intensity differences (IDT) are detectable by odontocetes at levels equal to those of land mammals and that the detection thresholds, like those of land mammals, decline with increasing level. Fay (1992) points out that the IDT data for land mammals do not quite fit Weber's Law, from which we expect a flat curve for IDT; i.e., intensity discrimination in dB should be nearly constant. The fact that whale IDT's have a similar deviation from the expected curve could be a simple reflection of a common ancestral ear, or it may mean there is common auditory advantage in both land and aquatic mammals. However, trends related to animal size appear to differ in odontocetes. Binaural behavioral studies and evoked potential recordings for *Tursiops* (mid-size, Type II dolphin) indicate an approximate IDT limit of 1–2 dB (Bullock et al. 1968; Moore et al. 1995). In *Phocoena*, which are significantly smaller Type I animals, IDT's range 0.5 to 3 dB (Popov et al. 1986). Thresholds in *Inia* (mid-size, Type I) range 3–5 dB (Supin and Popov 1993). Because of small sample sizes and



(a) The left ear has been removed to show the size of the peribullar cavity in the harbour porpoise.



(b) The right tympanic has been removed to show the periotic and flanges in the humpback. Volume and mass of the bullae are strongly correlated with animal size in each species (Ketten and Wartzok 1990). Odontocete bullae average 30 gms whereas mysticete tympano-periotics are commonly near 1 kg. (f) posterior flange; (m) mandible; (o) occipital condyle; (p) periotic; (s) squamosal; (t) tympanic. (Photography by I. Milde)

Figure 2. Ear positions in odontocetes vs. mysticetes. Each scale bar represents 50 mm. Ventral views of (a) a harbour porpoise (*Phocoena phocoena*) and (b) a humpback whale (*Megaptera novaeangliae*) skull demonstrate the extra-cranial position of the tympano-periotic complex and differences in shape, size and skull attachments between mysticetes and odontocetes.

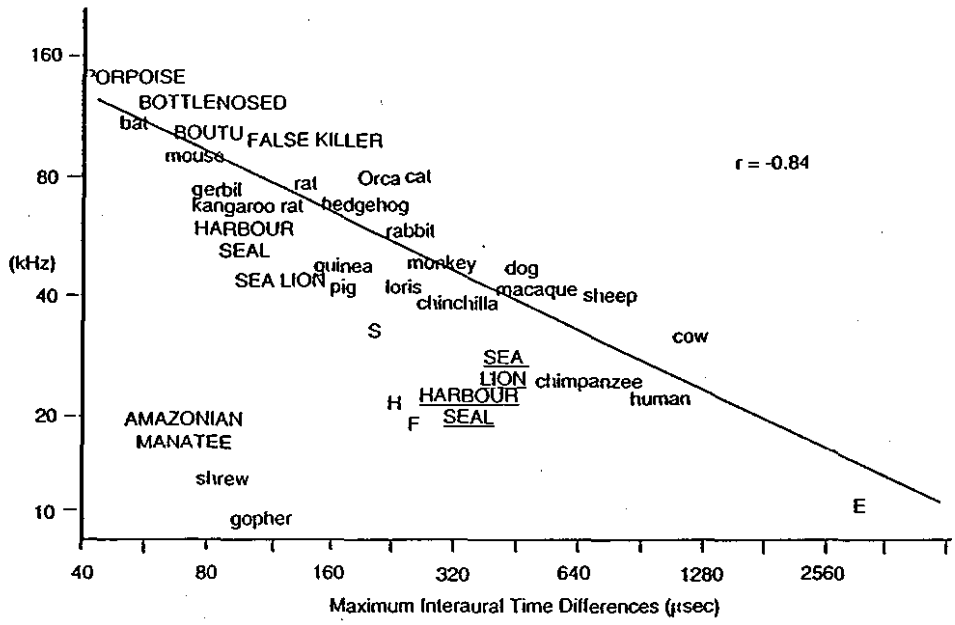


Figure 3. Interaural time differences vs. high frequency hearing limit. High frequency limits from behavioral audiograms are plotted against the calculated interaural time distances for aquatic and land mammals. For in-air limits, the frequency at 60 dB re 20 μPa was used; for animals in water, the limit was taken as the frequency corresponding to 120 dB re 1 μPa. IATD is calculated on the external intermeatal distance for all land mammals and for pinnipeds in air. Underwater IATD's are intercochlear distances. Aquatic mammals are in capital letters; in-air data points are underlined. Single letters represent theoretical points for the sperm whale (S), humpback (H), fin whale (F) and African elephant (E) based on vocalizations, cochlear models, and direct measures of ear locations. Data were compiled from Ketten (1984), Watkins and Wartzok (1985), Payne et al. (1986), Fay (1988), Heffner and Heffner (1980, 1992, pers. comm.), Heffner and Masterton (1990), Popov and Supin (1990), Richardson et al. (1991, 1995),Au (1993).

methodological differences, it is unclear whether these numbers represent true species-size differences and a reverse trend compared to land mammals.

Middle ear

Whale middle ears are heavily adapted to prevent injury from large, rapid pressure changes in diving. There are no weak-walled, pneumatized areas similar to primate mastoids. The Eustachian tubes are tough and broad-bored, reducing the probability of tube closure and large external vs. middle ear pressure differentials that lead to barotrauma. The middle ear cavity in both odontocetes and mysticetes

is lined with a thick, vascularized fibrous sheet, the corpus cavernosum. CT and MRI data suggest the intra-tympanic space is air-filled *in vivo* (Ketten 1994). If it remains air-filled in diving whales, which is likely given the Eustachian tube's configuration, it presents an interesting hearing problem. A potential acoustic difficulty for a diving mammal is that changing middle ear volumes may alter the resonance characteristics of the middle ear and, in turn, alter frequency sensitivity. Studies are underway with free-swimming beluga whales (S. Ridgway, pers. comm.) to test whether hearing thresholds change during deep dives.

Middle ear anatomy suggests there are neural specializations in whales that may prevent threshold changes by regulating middle ear volumes (Ketten 1992). Extensive nerve endings in the middle ear corpus cavernosum appear to be subdivisions of the trigeminal nerve; a mixed sensory-motor nerve, which could monitor and control corpus cavernosum distention. This added task for the trigeminal could also account for its exceptional size in whales (up to 500,000 fibers vs. 140,000 in humans) (Jansen and Jansen 1969, Morgane and Jacobs 1972).

Ossicles of odontocetes and mysticetes are massive, with wide species variations in size, stiffness, and shape (Reysenbach de Haan 1956, Belkovich and Solntseva 1970, Solntseva 1971, Fleischer 1978). In odontocetes, a bony ridge, the processus gracilis (Figure 3), fuses the malleus to the wall of the tympanic, and the ossicular joints are stiffened with ligaments. Mysticete ossicles are more massive, with none of the external stiffening agents of odontocete ossicular chains. Mysticete stapes are fully mobile with a conventional fibrous annular ligament. Further, as noted earlier, the tympanic scales with animal size, and mysticete middle ear cavities are therefore substantially larger than those of any odontocete. Thus, the mysticete middle ear consists of a voluminous cavity with massive ossicles that are loosely joined; i.e., a characteristically low frequency ear.

There is no clear consensus on how cetacean middle ears function. Both conventional ossicular motion and translational bone conduction have been proposed for cetaceans (Lipatov and Solntseva 1972, Fleischer 1978, McCormick et al. 1970, 1980). Based on experiments with anesthetized *T. truncatus* and *Lagenorhynchus obliquidens* (Pacific white-sided dolphin), McCormick et al. (1970, 1980) concluded that sound entering from the mandible by bone conduction produces a "relative motion" between the stapes and the cochlear capsule. In their procedure immobilizing the ossicular chain decreased cochlear potentials, but disrupting the external canal and tympanic cone had no effect. Fleischer (1978) suggested the procedure introduced an artificial conduction pathway. From anatomical studies, he concluded that sound from any path is translated through tympanic vibration to the ossicles which pulse the oval window, as in land mammals.

McCormick's theory assumes sizeable differential motion of the tympano-periotic components; Fleischer's requires a mobile stapes, distensible round window, and flexible tympano-periotic connections. Both theories incorporate some features of middle ears in some whales, but neither theory is compatible with the total structural range of whale middle ears. Consequently, no comprehensive explanation of whale middle ear function is currently available.

Inner ear

The cetacean periotic houses the membranous labyrinth of the inner ear, which is subdivided into the auditory and vestibular systems.

Vestibular system

In all cetaceans, the vestibular system is substantially reduced. While size is not a criterion for vestibular function, cetaceans are unique in having semicircular canals that are significantly smaller than the cochlear canal (Figure 4) (Boenninghaus 1903, Gray 1951, Ketten

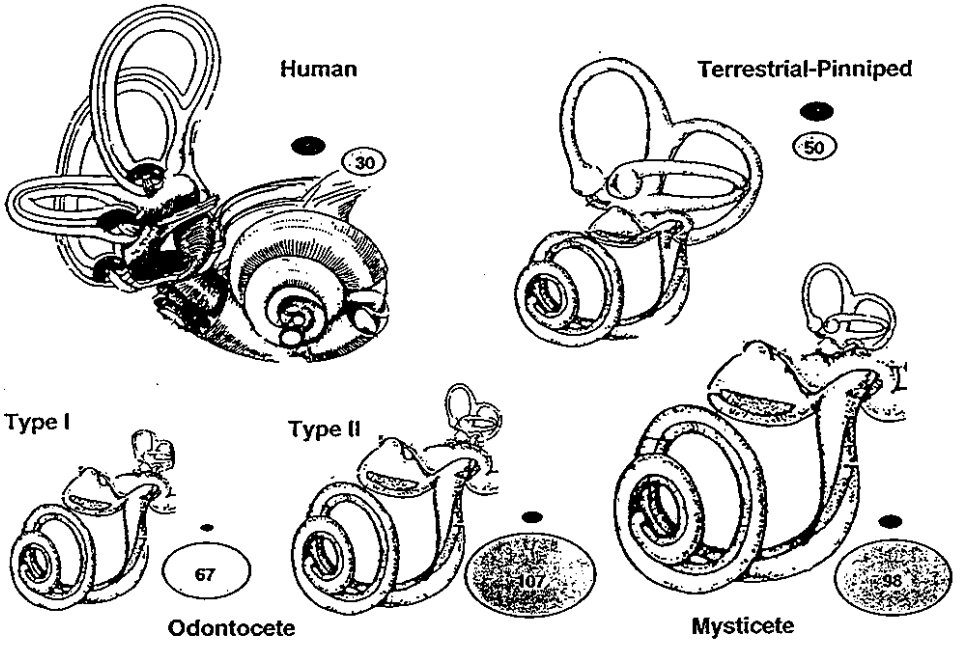


Figure 4. Scaled inner ear schematics demonstrate the relative volume of the vestibular and cochlear labyrinths in land and marine mammals. Gray ovals represent relative cross-sections of the vestibular (dark gray) and auditory (light gray) components of the VIIIth nerve. Numbers inside the ovals are the fiber counts in thousands. Human and terrestrial schematics were redrawn from Lewis et al. (1985).

1992). In odontocetes, this reduction is most extreme. The semi-circular canals in some species are incomplete, the ampullae are nearly acellular, and the vestibular fibers are commensurately reduced (Jansen and Jansen 1969, Gao and Zhou 1995, Ketten unpubl. data). Both the cell count (< 4,100) and the proportion of VIIIth nerve fibers are exceptionally low (Table 2). Less than 5% of the odontocete VIIIth nerve is devoted to vestibular fibers, compared to an average of 30% in most mammals. Semi-circular canal reduction is less extreme in the mysticetes.

No equivalent aberrations of the vestibular system have been found in any land mammal or pinniped, which argues that reduced semi-circular canals are related to a fully aquatic lifestyle. One possible explanation is that fusion of the cervical vertebrae in Cetacea resulted in limited head movements. As head rotations diminished, reduced inputs to the vestibular system may have led to a retrograde receptor loss, and whales may detect linear acceleration and gravity cues but little or no rotational acceleration cues. Studies of labyrinth-ectomized cats and of congenitally alabyrinthine humans found that the absence of functional semi-circular canals eliminates motion sickness (Graybiel 1964). An attenuated vestibular system may therefore be adaptive for whales.

These data raise two issues that need further investigation. First, because the vestibular system has been implicated in low frequency hearing (Yeowart 1976), it would be interesting to compare differences in vestibular development between mysticetes and odontocetes, but no neural data are available on the mysticetes at this time. Second, fish have widely varying canal systems, and if vestibular reduction is a function of swimming and vertebral fusion, similar reductions might be expected in some species, but vestibular characteristics in larger species that would make appropriate comparisons, like the whale shark or some rays, are also unknown (A. Popper pers. comm.).

Cochlea

Detailed descriptions of cetacean cochleae are available in Wever et al. (1971a, b, c, 1972), Ketten (1984, 1992) and Solntseva (1990). This paper summarizes the histologic findings and discusses in detail only the most salient features of whale cochleae: basilar membrane structure and neural distributions.

Cetacean cochlea have the three prototypic mammalian divisions: scala media (cochlear duct), scala tympani, and scala vestibuli. As in other mammals, these parallel tubes form an equiangular spiral, curving inside the periotic like a diminishing spiral staircase with a hollow bony axis, the modiolus, which houses the auditory branch of the VIIIth nerve. The ramp of the stair is the

TABLE 2

Auditory, Vestibular, and Optic Nerve Distributions
(Data compiled from Yamada 1953, Gacek and Rasmussen 1961, Jansen and Jansen 1961, Firbas 1972, Morgane and Jacobs 1972, Bruns and Schmieszek 1980, Dawson 1980, Ketten 1984, 1992, Vater 1988, Nadol 1988, Gao and Zhou 1991, 1992, 1995, Kössl and Vater 1995).

Species	Common Name	Cochlear Type (mm)	Membrane Length Cells	Auditory Ganglion	Density (cells/mm cochlea)	Vestibular Ganglion Cells	Vestibular-Auditory Ratio	Optic Nerve Fibers	Optic-Auditory Ratio	Optic-Vestibular Ratio
Inia geoffrensis	Boutu	I	38.2	104,832	2,744			15,500	0.15	
Lipotes vexillifer	Baiji			82,512		3,605	0.04	23,800	0.29	6.60
Neophocoena phocoenoides	Finless porpoise			68,198		3,455	0.05	88,900	1.30	25.73
Sousa chinensis	Humpbacked dolphin			70,226		3,213	0.05	149,800	2.13	46.62
Phocoena phocoena	Harbour porpoise	I	22.5	70,137	3,117	3,200		81,700	1.16	25.53
Delphinapterus leucas	Beluga		42	149,386	3,557			110,500	0.74	
Delphinus delphis	Common dolphin	II	34.9	84,175	2,412	4,091	0.05	165,600	1.97	40.48
Lagenorhynchus obliquidens	White-sided dolphin	II	34.9	70,000	2,006			77,500	1.11	
Stenella attenuata	Spotted dolphin	II	36.9	82,506	2,236					
Tursiops truncatus	Bottlenosed dolphin	II	38.9	96,716	2,486	3,489	0.04	162,700	1.68	46.63
Physeter catodon	Sperm whale		54.3	161,878	2,981			172,000	1.06	

Balaenoptera physalus	Fin whale	M	64.7	134,098	2,073			252,000	1.88	
Megaptera novaeangliae	Humpback whale	M	58	156,374	23,696			347,000	2.22	
Rhinolophus ferrumequinum	Horseshoe bat	T	16.1	15,953	991/1,750*					
Pteronotus parnellii	Mustached bat	T	14.0	12,800	900/1,900*					
Cavia porcella	Guinea pig	T	19.0	24,011	1,264	8,231	0.34			0.00
Felis domesticus	Cat	T	28.0	51,755	1,848	12,376	0.24	193,000	3.73	15.59
Homo sapiens	Human	T	32.1	30,500	950	15,590	0.51	1,159,000	38.00	74.34

*Densities at auditory fovea as described by Bruns and Schmiezek (1980)

basilar membrane, which acts as one of two membranous dividers defining the cochlear duct. The primary sensory apparatus, the organ of Corti, rests on the basilar membrane.

Odontocete cochlear duct anatomy is characterized by hypercellularity and overdevelopment. Hypertrophy of the auditory system in odontocetes may be a function of the complexity or of the importance of hearing in these animals. Wever et al. (1971a, b, c, 1972) and Reysenbach de Haan (1956) found exceptionally thick pillar cells in the lower basal turn and a greater density of support cells throughout the cochlea in several species of odontocetes. More recent studies confirmed this anatomy for a wider range of delphinids and reported similar hypertrophy for phocoenids and monodontids (Ketten 1984, 1990, Solntseva 1990). A notable feature of all odontocete ears is an exceptionally dense stria vascularis and spiral ligament with a tightly woven collagen infrastructure (Figure 5). Wever et al. (1971b) reported irregular outer hair cell distributions varying from two to four rows in *Tursiops*, but this may have been an individual phenomenon as all other reports found rows of outer hair cells throughout the cochlea in this and all other odontocete species examined (Reysenbach de Haan 1956, Bloome 1968, Solntseva 1971, Ketten 1984, 1992, 1994).

Mysticete cochlear ducts do not have the same degree of cellular development as odontocetes (Norris and Leatherwood 1981, Ketten 1992). The spiral ligament, stria vascularis, and support cells more closely resemble those of humans, with no overt support cell specializations. Although much of the current data for mysticetes comes from stranded animals with moderately long post-mortem times, it is likely that observed differences from odontocetes are correct. Inner ear material from odontocetes with similar post-mortem times retain clear evidence of hypercellularity and even with advanced decay do not resemble the ears of mysticetes.

Auditory fiber and ganglion cell counts are remarkable in all cetaceans, particularly considering, as was noted, that some counts are based on residual neural populations in stranded animals (Table 2). Auditory ganglion cell totals range from 68,000 in the harbour porpoise to over 160,0000 in fin whales. Whale auditory fiber diameters range 2–40 μ, with a mean of 12 μ in odontocetes and 5 μ in mysticetes, compared to a land mammal range of 1–15 μ with an average of 3 μ (Morgane and Jacobs 1972, Bruns and Schmieszek 1980, Ketten 1984, 1992, Vater 1988, Nadol 1988, Gao and Zhou 1992, 1995).

Auditory, vestibular and optic nerve fiber counts (Table 2) suggest that a disproportionately large neural investment in the auditory system in cetaceans is accompanied by diminished vision and vestibular function. As indicated earlier, vestibular counts in all cetaceans are exceptionally low. Whale vestibular to auditory ratios are approximately 1/10 those of land mammals. Optic to auditory ratios in Type II odontocetes and mysticetes are one-half to one-third

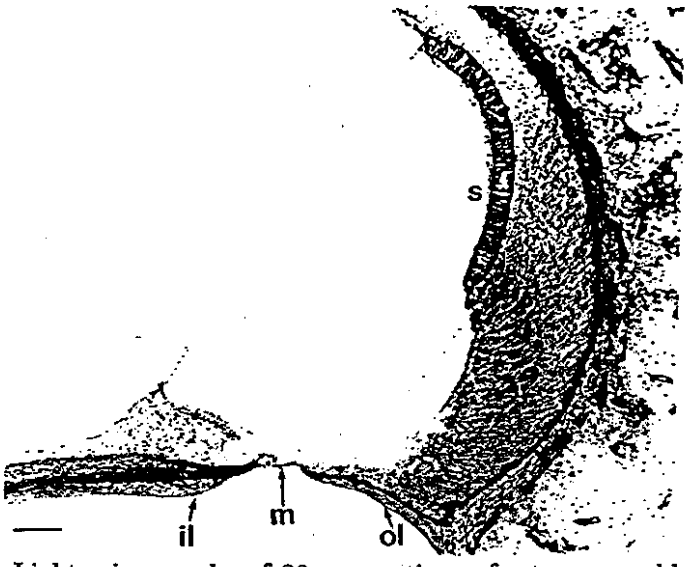


Figure 5(a). Light micrographs of 20 μm sections of cetacean cochlear ducts. Scale bars represent 100 μm. A section from the upper basal turn of an Atlantic white-sided dolphin (*Lagenorhynchus acutus*, Type II odontocete) illustrates the classic odontocete features of a narrow basilar membrane (m) stretched between substantial inner (il) and outer osseous lamina (ol), well-developed stria vascularis (s), and heavily collagenous spiral ligament (l). The membrane is 15 μ × 70 μ at this point.

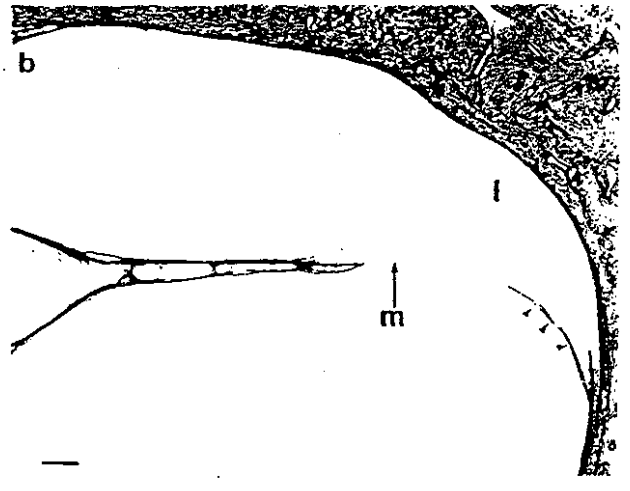


Figure 5(b). Light micrographs of 20 μm sections of cetacean cochlear ducts. Scale bars represent 100 μm. In the right whale (*Eubalaena glacialis*, a mysticete) at an equivalent position, the basal basilar membrane (m) is 5 μ × 125 μ. A narrow outer ossified spiral lamina (arrows) is attached to the tympanal edge of the spiral ligament (l) but does not contact the basilar membrane.

those of land mammals, while ratios in Type I odontocetes (0.2–0.3) are nearly a magnitude lower. The most extreme contrast in optic-auditory ratios is the 200-fold difference between the vision top-heavy human value of 38.0 vs. the 0.15 ratio for *Inia*, a riverine Type I odontocete that forages in the muddy varzea lakes of the Amazon and has the lowest visual acuity of any aquatic mammal (Mass and Supin 1989). Optic to vestibular ratios for all cetaceans (25–45), except *Inia* (6.6), are mid-way between those of cats (15.6) and humans (74.3), suggesting that, on average, similar reductions occurred in both optic and vestibular fibers in whales.

Most important, both odontocete and mysticete auditory innervation densities are significantly greater than those of other mammals. Auditory ganglion cell densities in Type I odontocetes average 2900 cells/mm; for Type II odontocetes, the average is 2600 cells/mm; and for mysticetes, 2300 cells/mm. Given 100 inner hair cells/mm and 3 rows of outer hair cells/inner hair cell in whales, these data imply a ganglion to hair cell ratio of early 7.3:1 for Type I species, 6.5:1 for Type II and 5.7:1 for Type M. The human ratio is 2.4:1; for cats, it is 3.7:1; and for bats, 4:1 (Firbas 1972, Bruns and Schmiezek 1980). Since 90–95% of all afferent spiral ganglion cells innervate inner hair cells, the average ganglion cell:inner hair cell ratio is 27:1 for cetaceans, or more than twice the average ratio in bats and three times that of humans.

Wever et al. (1971c) speculated that additional innervation is required in the odontocete ear to relay greater detail about ultrasonic signals to the CNS in echolocation analyses. Electrophysiological results are consistent with this speculation. Bullock et al. (1968) found three distinct categories of response units in the inferior colliculus of dolphin; i.e., those that were signal duration specific, those that responded to changes in signal rise time, and those that were specialized to short latencies with no frequency specificity. This division of signal properties among populations of neurons is consistent with, although not identical to, observations in bats of multiple categories of facilitation and analysis neurons (Suga 1983). Clearly, it is reasonable to assume that high ganglion cell ratios in odontocetes are related to the complexity of information extracted from echolocation signals; but this does not explain similar innervation patterns in mysticetes. Similarities in odontocete and mysticete ganglion cell densities suggest that baleen whales have equally complex auditory processing, which, in turn, suggests cetacean innervations are related largely to the physics of underwater sound or that baleen whales extract equally complex data from low to infrasonic signals; i.e., they may be infrasonic echolocators.

Cetacean basilar membranes are highly differentiated structures with substantial variations in length, thickness, and width (Table 3). Basilar membrane lengths in Cetacea range from 20 to 70 mm. As in

terrestrial mammals, lengths are strongly correlated with animal size ($0.8 < r < 0.95$), but length is not a functional correlate of hearing ranges (Ketten 1984). Functional correlates of hearing include basilar membrane thickness and width and lengths of bony auxiliary support for the membrane (Ketten 1984, Ketten and Wartzok 1990). In all mammalian cochleae, the basilar membrane is a tonotopic resonator, in which frequency distributions are related to membrane stiffness and mass characteristics. Since the basilar membrane has a fairly uniform cellular substructure, stiffness and mass are dictated largely by thickness and width, which vary inversely from base to apex. The membrane is narrow and thick at the base and gradually thins and broadens towards the apex. Highest frequencies are encoded in the stiffer basal end with progressively lower frequencies encoded as the membrane becomes more pliant apically. For some land mammals (termed generalists), frequency distributions have been estimated from one parameter; e.g., length or width, primarily because length, width and thickness co-vary regularly in these ears (Greenwood 1961, 1962, 1990, Manley 1972, West 1985, Fay 1992). Land mammal derived, single parameter estimators are insufficient for cetacean ears. For example, Greenwood's method predicts an upper frequency hearing limit of approximately 15.6 kHz for bottlenosed dolphins, which, in reality, hear well up to 160 kHz. Functional analyses of odontocete cochleae showed not only that cetaceans have a different membrane morphometry but also that when all three membrane aspects, thickness, width, and length, are incorporated into membrane-frequency distribution analyses, hearing estimates for any mammal ear, including aquatic and specialist ears, are significantly improved (Ketten 1994).

Based on current data, cetaceans have a 10 to 11 octave functional hearing range and a 10 to 14-fold increase in basilar membrane width with a 5 to 6-fold decrease in thickness, base to apex. Humans, by comparison, have an 8 to 9 octave range with 5-X width, 2-X thickness membrane gradients. In the typical odontocete, basilar membrane widths vary from 30 μm at the base to 400 μm apically. This basal width is similar to that in bats and is one-third that of humans (Firbas 1972, Schuknecht and Gulya 1986). The apical width is approximately 80% that of humans and is consistent with relatively poor sensitivity below 150 Hz reported for some odontocetes (Au 1997). Odontocete membrane thicknesses range from 25 μm at the base to 5 μm at the apex (Table 3). Therefore, a prototypical odontocete basilar membrane has a nearly square cross-section at the base and is rectangular at the apex.

Mysticete membranes are thin oblongs throughout their length. Widths vary from 100 μm at the base broadening to over 1500 μm at the apex with a thickness gradient of 7 μm at the base to 2 μm at the apex (Figure 6). Mysticete basal dimensions are similar to those of

TABLE 3

Cochlear Morphometry in Whales vs. Land Mammals
(Data compiled from Wever et al. 1971a, b, Firbas 1972, Bruns and Schmieszek 1980, Norris and Leatherwood 1981, Ketten 1984, 1992, 1994, West 1985, Vater 1988, Nadol 1988, Echteler et al. 1994, Kössl and Vater 1995)

Species	Common Name	Ear Type	Turns	Membrane Length (mm)	Outer Lamina (mm)	Base Thickness/ Width (μm)	Apex Thickness/ Width (μm)	Basal Ratio	Apical Ratio
Inia geoffrensis	Boutu	I	1.5	38.2	†				
Phocoena phocoena	Harbour porpoise	I	1.5	22.5	17.6	25/30	5/290	0.83	0.017
Grampus griseus	Risso's dolphin	II	2.5	41.0	†	20/40	5/420	0.50	0.012
Lagenorhynchus albirostris	White-beaked dolphin	II	2.5	34.8	8.5	20/40	5/360	0.50	0.014
Stenella attenuata	Spotted dolphin	II	2.5	36.9	8.4	20/40	5/400	0.50	0.013
Tursiops truncatus	Bottlenosed dolphin	II	2.25	38.9	10.3	25/35	5/380	0.71	0.013
Physeter catodon	Sperm whale		1.75	54.3	†				
Balaenoptera acutorostrata	Minke whale	M	2.25	50.6	–/100	–/1500			
Balaena mysticetus	Bowhead whale	M	2.25	56.5	<10††	7.5/120	2.5/1670	0.06	0.001
Balaenoptera physalus	Fin whale	M	2.5	64.7		–/100	–/2200		
Eubalaena glacialis	Right whale	M	2.5	54.1	<8††	7/125	2.5/1400	0.06	0.002

Rhinolophus ferrumequinum	Horseshoe bat	Æ	2.25	16.1	†	35/80	2/150	0.44	0.013
Pteronotus parnellii	Mustached bat	Æ	2.75	14.0	†	22/50	2/110	0.44	0.018
Spalax ehrenbergi	Mole rat	Sb	3.5	13.7		–/120	–/200		
Cavia porcella	Guinea pig	T	4.25	18.5		7.4/70	2/250	0.11	0.008
Felis domesticus	Cat	T	3	28.0	†	12/80	5/370	0.15	0.014
Homo sapiens	Human	T	2.5	33.0		–/120	–/550		

Width—pars arcuata and pectinata
Thickness—pars pectinata maximum
†Outer osseous lamina present, length unknown
††Laminar remnant present but not in contact with basilar membrane
I—aquatic >100 kHz II—aquatic <90 kHz M—aquatic < 2 kHz
Æ—æolian >20 kHz Sb—subterranean T—terrestrial

humans, implying a maximal functional high frequency capacity of 20 to 30 kHz, but apical widths in mysticetes are five-fold broader than in odontocetes, three-fold greater than in humans, and 1.5 times the estimated apical widths of basilar membranes in African elephants, which are known to perceive infrasonics (Ketten 1992, Payne et al. 1986).

Thickness to width ratios are a more significant correlate of frequency than any single basilar membrane dimension (Ketten 1984, Ketten and Wartzok 1990). Echolocators have significantly higher basal ratios than mysticetes, and differences in basal ratios among bats and odontocetes are consistent with species-specific differences in maximal functional hearing and peak spectra of echolocation signals (Tables 1, 3). Type I odontocetes have basal ratios > 0.8, peak spectra > 100 kHz, and a functional hearing range maximum near 200 kHz. Type II odontocetes have ratios of 0.5–0.7, peak spectra between 40–80 kHz, and functional hearing limits < 160 kHz. Little data is available except for specialist eared bats, but *Rhinolophus ferrumequinum* (horseshoe bat), a CF/FM bat, has a 0.3 basal ratio and an ear devoted largely to frequencies from 80–90 kHz. All three echolocators have apical ratios near 0.01. Mysticete ratios range 0.06 to 0.001, base to apex; i.e., mysticete basal ratios begin at a point nearly halfway along the thickness/width membrane gradients of ultrasonic echolocators and decrease exponentially to a value one-tenth that of the odontocete apex. The extraordinarily low apical ratio in Type M ears is consistent with a broad, flaccid membrane that responds to infrasonics.

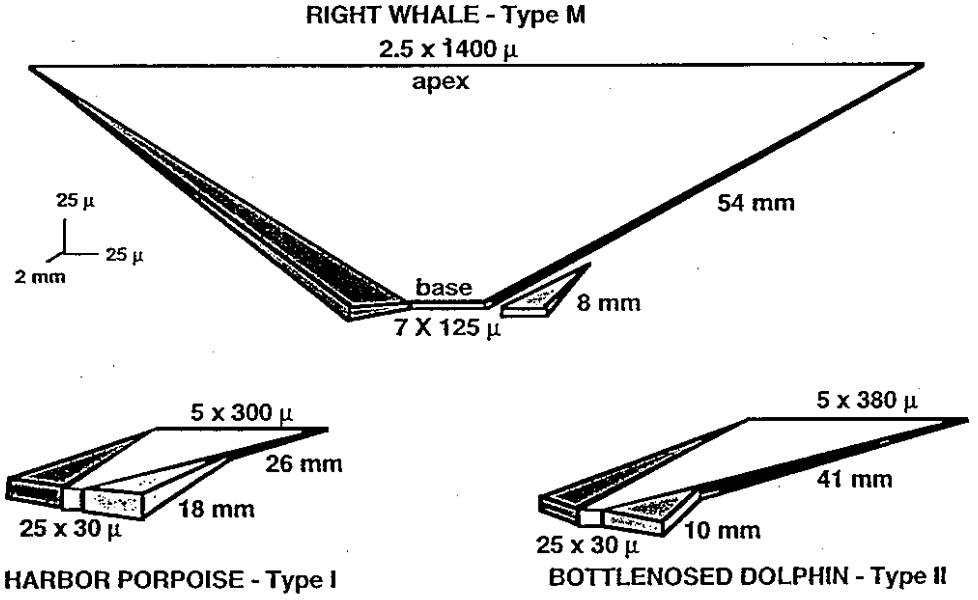


Figure 6. Basilar membrane and bony spiral laminae distributions in whales. Two-dimensional schematics summarize basilar membrane construction and support element differences in Type I, Type II, and Type M inner ears.

A second important feature of odontocete basilar membranes is the variation in outer bony laminar support. In terrestrial mammals, ossified outer spiral laminae are a common characteristic of high frequency ears (Reysenbach de Haan 1956, Sales and Pye 1974). In odontocetes, the proportion of basilar membrane in contact with the outer lamina is directly correlated with species ultrasonic hearing ranges (Table 3) (Ketten and Wartzok 1990). In the basal region of the cochlea, odontocete basilar membranes resemble thick girders, stiffened by rigid bony buttresses at both margins (Figure 5). In Type I echolocators, the bony outer lamina is doubled in the basal most regions and extends for 60% of the membrane length (Table 3). In Type II echolocators, a thinner outer lamina anchors the membrane for < 30% of the duct. The Type I basilar membrane therefore is coupled tightly to a stiff ledge for twice as much of its length as a Type II membrane. Like membrane ratios, differences in the extent or proportion of outer bony laminae are important, direct mechanistic keys to ultrasonic hearing capacities that override membrane length.

Both inner and outer laminae are present in mysticete ears but they are morphologically and functionally very different from those of odontocetes. Mysticete inner laminae are riddled with large channels, producing a spongy appearance in cross-section (Figure 5). Mysticete outer laminae are narrow spicules located on the tympanal edge of the spiral ligament. They do not attach to the basilar membrane and disappear within the first half turn. The broad, thin mysticete basilar membrane attaches only to a flexible spiral ligament. It is likely that the spike-like outer lamina in mysticetes is a remnant of an ancestral condition rather than a functional acoustic structure and that differences in apical basilar membrane ratios are the principal determinants of mysticete hearing ranges. Although relatively few mysticete ears have been analyzed, the consensus of data argues strongly that virtually all mysticete ears are adapted for good low to infrasonic hearing.

CONCLUSIONS

Aquatic influences are most evident in the gross anatomy of cetacean auditory systems. There are no pinnae. All cetacean periotics, tympanics, and ossicles are constructed of dense, compact bone with no minor, thin-walled pneumatized areas. The odontocete tympanoperiotic complex is isolated acoustically from the skull, which is adaptive for aquatic echolocation. Odontocetes may be segmented, dual-channel receivers. The position and isolation of odontocete bullae support the "pan bone" theory of ultrasonic signal reception via a fatty acoustic wave guide in the mandible. Lateral fat channels may be specialized for lower frequencies. Sound reception mechanisms in

mysticetes are unknown, but they have bony skull connections and a highly derived tympanic membrane that connects to the external auditory canal. The extra-cranial location of the ear in all whales is consistent with increased sound speed in water.

Cetacean middle ears can be grossly divided into low vs. high frequency composites that follow the suborders. Inner ear anatomy varies more by species. Cochlear length correlates with animal size, ranging 20 to 70 mm. Turns range from 1.5 to 2.5 and are independent of animal size. Odontocete cochlear duct structures are well-developed. The stria vascularis and spiral ligament are hypercellular, both of which suggest relatively rapid metabolic or repair processes consistent with the importance of hearing to these animals and with moderately high background noise in many ocean regions. Auxiliary outer osseous laminae support 20 to 60% of the basilar membrane length in odontocetes. In mysticetes, the spiral ligament is less well-developed and outer osseous laminae are absent or reduced. Spiral ganglion cell densities are significantly greater in whales than in land mammals, ranging from 2000–4000 cells/mm. Greatest densities are found in the highest frequency odontocetes, but all whales have densities and fiber diameters that are significantly greater than those of land mammals. It is unclear whether these adaptations are driven primarily by the physics of water as a denser medium or by more complex auditory processing. Vestibular structures and neural components are disproportionately small in all whales, possibly reflecting reduced azimuthal cues commensurate with cervical fusion and limited head rotations. Cetacean optic to auditory fiber ratios are also small, reflecting the predominant role of hearing in these animals.

Modern Cetacea have three inner ear structural formats which coincide with major acoustic groups: low to infrasonic Type M mysticetes; upper range ultrasonic Type I odontocetes; and lower range ultrasonic Type II odontocetes. Type I and Type II cochleae are clearly adapted for ultrasonic ranges with exceptionally stiff basilar membranes and extensive outer osseous laminae. Basilar membrane thickness to width ratios are higher for the basal turn of odontocetes than for any other mammal. Mysticete (Type M) cochleae have exceptionally wide, thin basilar membranes with no stiffening agents, implying they are adapted to low to infrasonic frequencies.

These cochlear formats and frequency ranges also coincide with habitats and feeding behaviors. Type I formats are found in the inshore phocoenid and riverine platanistid dolphins (Purves and Pilleri 1983, Ketten 1984, Feng et al. 1989). These species live in turbid waters and use ultrahigh frequency, short wavelength signals consistent with analyzing fine details of nearby objects. Type II formats are common in offshore and pelagic delphinids. Their slightly broader, less rigid membranes suggest better mid to low sonic range hearing than Type I ears as well as lower frequency ultrasonic ranges.

These hearing characteristics are consistent with highly social species that use 1–10 kHz communication signals and lower frequency, longer wavelength ultrasonic signals that can resolve predators and prey at greater distances than the Type I signals.

Are these format differences uniquely aquatic? Structurally, yes; functionally, perhaps not. Superficially, bat and dolphin echolocation signals and processing appear to have little in common. Dolphin echolocation signals are generally shorter, broader band waveforms with higher peak spectra (~50 μsec, 40–150 kHz) than bat signals (several msec, 16–80 kHz). Bats and dolphins are comparable at discriminating shape and size, but dolphins are superior at detecting target range and composition and may be better at detection in noise (Au 1993). However, if we put performance data together with anatomy, habitat and hunting characteristics, there are several intriguing parallels.

Basic echolocation frequency differences between the groups are consistent with wavelength differences in the two media and with prey sizes; i.e., the frequencies used by dolphins are only two to three-fold higher than those of most bats, not 4.5 fold, but moth wings are, acoustically, proportionately smaller than most fish profiles. Concerning habitat and prey parallels, source energy flux density of a Type II *Tursiops* signal (–21 dB re 1 j/m^2) is greater than in other dolphins and substantially different from that of the Type I Phocoena signal (–74 dB re 1 j/m^2) (Au 1993). In bats, *Eptesicus*, the big brown bat, is the *Tursiops* parallel with a larger efd than that of other bats (–66.4 dB re 1 j/m^2). *Tursiops* is primarily an open water forager; *Eptesicus* (FM bat) is a field gleaner. Both use comparatively high energy, lower range ultrasonic signals tolerant to Doppler shift in an open environment. By comparison, both *Phocoena* and its parallel, *Rhinolophus* (the horseshoe bat, CF/FM), have low energy, high frequency, narrow band signals. Both also have good discrimination and deal with imaging small objects in "clutter", the time-smeared echoes from twigs, leaves, etc.. Most important structurally, *Phocoena* and *Rhinolophus* both have highly specialized basilar membrane structures with foveal regions and high ganglion cell densities. These comparisons are tenuous, but the similarities in trends in signals and cochlear anatomy in these bats and dolphins raise interesting questions about how overtly different habitats may have had common selection pressures that led to parallel echolocation strategies. They also suggest cross-species hunts for task-related auditory adaptations in different habitats could be a useful tool for understanding fundamental auditory mechanisms.

Type M inner ear formats are known only in large, pelagic whales. A specific use for infrasonic frequencies by whales has not yet been demonstrated, although several possibilities exist. Low frequencies could be used to communicate over long distances and even

to echolocate seabed and coastal topographic details as aids for offshore navigation and long-range migrations (Watkins and Wartzok 1985, Clark 1990, Ketten 1992). Whatever the present function, ultra-low frequency hearing in mysticetes may simply have evolved as an outgrowth of mechanical constraints imposed by larger ear size. Mysticetes appear geologically near the time new oceans opened in southern latitudes (Fordyce 1977, 1980). Even today, these high latitude waters are terrifically productive, but they are also colder than the temperate seas in which whales first evolved. Since surface area increases more slowly than volume, bigger mammals have a substantial metabolic advantage in cold water; i.e., a larger whale is a warmer whale. It is likely that increased body size coincided with successful adaptation to cold seas. Inner ear membranes scale with animal size, and, with less pressure to detect prey in more productive waters, decreased sensitivity to higher frequencies in a large cochlea would not be a major disadvantage. If basilar membranes broadened and lengthened without thickening as a consequence of increasing animal size and decreased pressure for high frequency hearing, a lower frequency cochlea would result. At the same time the tympanic grew. Therefore, as larger whales evolved, ear scaling may have forced inner ear and middle resonance characteristics to progressively lower frequencies, ultimately reaching the practical and profound limits of the blue whale.

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REFERENCES

Au, W. W. L. (1993). *The Sonar of Dolphins*. Springer-Verlag; New York.

Au, W. W. L.. (1997). Echolocation in dolphins, with a dolphin-bat comparison. *Bioacoustics*, 8, 137–162.

Awbrey, F. T. (1990). Comparison of hearing abilities with characteristics of echolocation signals. In *Sensory Abilities of Cetaceans: Laboratory and Field Evidence* (J. A. Thomas and R. A. Kastelein, eds.). Plenum Press; New York, pp. 427–435.

Barnes, L. G., Domning, D. P., & Ray, C. E. (1985). Status of studies on fossil marine mammals. *Mar. Mamm. Sci.*, **1**, 15–53.

Belkovich, V. M. & Solntseva, G. N. (1970). Anatomy and function of the ear in dolphins, U.S. Gov. Res. Develop. Rep. **70**(11), 275–282 (read as Eng. summ.).

Bloome, K. A. (1968). *The Gross Anatomy and Fine Structure of the Auditory Apparatus of the Delphinid Ear*. Ph.D. thesis, UCLA.

Boenninghaus, G. (1903). Das Ohr des Zahnwales, zugleich ein Beitrag zur Theorie der Schalleitung. *Zool. Gahrb.(Anatomie)*, **17**, 189–360. (not read in original).

Brill, R. L., Sevenich, M. L., Sullivan, T. J., Sustman, J.D. & Witt, R. E. (1988). Behavioral evidence for hearing through the lower jaw by an echolocating dolphin, *Tursiops truncatus*. *Mar. Mamm. Sci.*, **4**, 223–230.

Bruns, V. & Schmieszek, E. (1980). Cochlear innervation in the greater horseshoe bat: Demonstration of an acoustic fovea. *Hearing Res*, **3**, 27–43.

Bullock, T. H., Grinnell, A. D., Ikezono, E., Kameda, K., Katsuki, Y., Nomoto, M., Sato, O., Suga, N. & Yanagisawa., K., (1968). Electrophysiological studies of central auditory mechanisms in cetaceans. *Z. Vergl. Physiol.*, **59**, 117–156.

Clark, C. W. (1990). Acoustic behavior of mysticete whales. In *Sensory Abilities of Cetaceans: Laboratory and Field Evidence* (J. A. Thomas and R. A. Kastelein eds). Plenum Press; New York, pp. 571–584.

Dawson, W. W. (1980). The Cetacean Eye. In *Cetacean Behavior*. (L. M. Herman, ed). John Wiley and Sons; New York, pp. 54–99.

Dolphin, W. F. (1997). Electrophysiological measures of auditory processing in odontocetes. *Bioacoustics*, **8**, 79–101.

Dudok van Heel, W. H. (1962). Sound and Cetacea. *Neth. J. Sea Res.*, **1**, 407–507.

Echteler, S. W., Fay, R. R. & Popper, A. N. (1994). Structure of the Mammalian Cochlea. In *Comparative Hearing, Mammals* (R. R. Fay and A. N. Popper eds). Springer-Verlag; New York, pp. 134–171.

Edds, P. L. (1982). Vocalizations of the blue whale, *Balaenoptera musculus*, in the St. Lawrence River. *J. Mamm.*, **63**, 345–347.

Edds, P. L. (1988). Characteristics of finback *Balaenoptera physalus* vocalizations in the St. Lawrence Estuary. *Bioacoustics*, **1**, 131–149.

Edds-Walton, P. L. (1997). Acoustic communication signals of mysticete whales. *Bioacoustics*, **8**, 47–60.

Fay, R. R. (1988). *Hearing in Vertebrates, A Psychophysics Databook*. Hill-Fay Associates; Winnetka, Illinois.

Fay, R. R. (1992). Structure and function in sound discrimination among vertebrates. In *The Evolutionary Biology of Hearing* (D. Webster, R. R. Fay and A. N. Popper, eds). Springer-Verlag; New York, pp. 229–263.

Feng, W., Liang, C, Wang, X. & Chen, P. (1989). Morphometric and stereoscopic studies on the spiral and vestibular ganglia of the Baiji, *Lipotes vexillifer*. In *Biology and Conservation of the River Dolphins* (W. F. Perrin, R. L. Brownell, K. Zhou and J. Liu, eds). IUCN; Gland, Switzerland, pp. 119–123.

Firbas, W. (1972). Über anatomische Anpassungen des Hörorgans an die Aufnahme hoher Frequenzen. *Monatsschr. Ohr. Laryn.-Rhinol.*, **106**, 105–156.

Fleischer, G. (1978). Evolutionary principles of the mammalian middle ear. *Adv. Anat. Embryol. Cell Biol.*, **55**, 1–70.

Fordyce, R. E. (1977). The development of the Circum Antarctic Current and the evolution of the Mysticeti (Mammalia, Cetacea). *Palaeogeog., Palaeoclim., Palaeoecol.*, **21**, 265–271.

Fordyce, R. E. (1980). Whale evolution and Oligocene southern ocean environments, *Palaeogeog., Palaeoclim., Palaeoecol.*, **31**, 319–336.

Gacek, R. R. & Rasmussen, G. L. (1961) Fiber analysis of the statoacoustic nerve of guinea pig, cat, and monkey. *Anat. Rec.*, **13**, 455.

Gao, G. & Zhou, K. (1991). The number of fibers and range of fiber diameters in the cochlear nerve of three odontocete species. *Can. J. of Zool.*, **69**, 2360–2364.

Gao, G. & Zhou, K. (1992). Fiber analysis of the optic and cochlear nerves of small cetaceans. In *Marine Mammal Sensory Systems* (J. Thomas, R. Kastelein and A. Supin, eds). Plenum Press; New York, pp. 39–52.

Gao, G. & Zhou, K. (1995). Fiber analysis of the vestibular nerve of small cetaceans. In *Sensory Systems of Aquatic Mammals* (R. Kastelein, J. Thomas and P. Nachtigall, eds). DeSpil; Woerden, The Netherlands, pp. 447–453.

Gentry, R. L. (1967) Underwater auditory localization in the California sea lion (*Zalophus californianus*). *J. Aud. Res.*, **7**, 187–193.

Gingerich, P. D., Wells, N. A., Russell, D. E. & Shah, S. M. (1983). Origin of whales in epicontinental remnant seas, New evidence from the early Eocene of Pakistan. *Science*, **220**, 403–406.

Goodson, A. D. & Klinowska, M. (1990). A proposed echolocation receptor for the bottlenose dolphin (*Tursiops truncatus*), Modelling the receive directivity from tooth and lower jaw geometry. In *Sensory Abilities of Cetaceans: Laboratory and Field Evidence* (J. A. Thomas and R. A. Kastelein eds). Plenum Press; New York, pp. 255–269.

Gray, O. (1951). An introduction to the study of the comparative anatomy of the labyrinth. *J. Laryng. Otol.*, **65**, 681–703.

Graybiel, A. (1964). Vestibular sickness and some of its implications for space flight. In *Neurological Aspects of Auditory and Vestibular Disorders* (W. S. Fields and R. R. Alford, eds). Charles C. Thomas; Springfield, Mass., pp. 248–270.

Greenwood, D. G. (1961). Critical bandwidth and the frequency coordinates of the basilar membrane. *J. Acoust. Soc. Am.*, **33**, 1344–1356.

Greenwood, D. G. (1962). Approximate calculation of the dimensions of traveling-wave envelopes in four species. *J. Acoust. Soc. Am.*, **34**, 1364–1384.

Greenwood, D. G. (1990). A Cochlear frequency-position function for several species—29 years later. *J. Acoust. Soc. Am.*, **87**, 2592–2605.

Heffner, R. & Heffner, H. (1980). Hearing in the elephant (*Elephas maximus*). *Science*, **208**, 518–520.

Heffner, R. S. & Heffner, H. E. (1992). Evolution of sound localization in mammals. In *The Evolutionary Biology of Hearing* (D. Webster, R. R. Fay and A. N. Popper, eds). Springer-Verlag; New York, pp. 691–715.

Heffner, R. S. & Masterton, R. B. (1990). Sound localization in mammals, Brain-stem mechanisms. In *Comparative Perception* (M. A. Berkley and W. C. Stebbins, eds). John Wiley and Sons; New York, pp. 285–314.

Henson, O. W., Koplas, P. A., Keating, A. W., Huffman, R. F. & Henson, M. M. (1990). Cochlear resonance in the mustached bat: Behavioral adaptations. *Hear. Rsch.*, **50**, 259–274.

Jansen, J. & Jansen, J. K. S. (1969). The nervous system of Cetacea. In *The Biology of Marine Mammals* (H. T. Anderson, ed). Academic Press; New York, pp. 175–252.

Kasuya, T. (1973). Systematic consideration of recent toothed whales based on the morphology of tympano-periotic bone. *Sci. Rep. Whales Res. Inst.*, **25**, 1–103.

Kellogg, W. N. (1959). Auditory perception of submerged objects by porpoises. *J. Acoust. Soc. Am.*, **31**, 1–6.

Ketten, D. R. (1984). *Correlations of morphology with frequency for odontocete cochlea: Systematics and Topology*. Ph.D. thesis, The Johns Hopkins University, Baltimore.

Ketten, D. R. (1992). The marine mammal ear: Specializations for aquatic audition and echolocation. In *The Evolutionary Biology of Hearing* (D. Webster, R. R. Fay, and A. N. Popper, eds). Springer-Verlag; New York, pp. 717–754.

Ketten, D. R. (1994). Functional analyses of whale ears: Adaptations for underwater hearing. *I.E.E.E Proceedings in Underwater Acoustics*, **1**, 264–270.

Ketten, D. R. & Wartzok, D. (1990). Three-dimensional reconstruction of the dolphin cochlea. In *Sensory Abilities of Cetaceans: Laboratory and Field Evidence* (J. A. Thomas and R. A. Kastelein, eds). Plenum Press; New York, pp. 81–105.

Kössl, M. & Vater, M. (1995). Cochlear structure and function in bats. In *Hearing by Bats* (R. R. Fay and A. N. Popper, eds.), Springer-Verlag; New York, pp. 191–234.

Lipatov, N. V. & Solntseva, G. N. (1972). Some features of the biomechanics of the middle ear of dolphins. *Makhachkala.*, **2**, 137–140 (read as Eng. summary).

Manley, G. A. (1972). A review of some current concepts of the functional evolution of the ear. *Evolution*, **26**, 608–621.

Mass, A. M. & Supin, A. Ya. (1989). Distribution of ganglion cells in the retina of an

Amazon river dolphin, *Inia geoffrensis*. *Aquatic mammals*, **15**, 49–56.
McCormick, J. G., Wever, E. G., Palin, G. & Ridgway, S. H. (1970). Sound conduction in the dolphin ear. *J. Acoust. Soc. Amer.*, **48**, 1418–1428.
McCormick, J. G., Wever, E. G., Ridgway, S. H. & Palin G. (1980). Sound reception in the porpoise as it relates to echolocation. In *Animal Sonar Systems* (R-G. Busnel and J.F. Fish, eds). Plenum Press; New York, pp. 449–467.
Møhl, B. & Andersen, S. (1973). Echolocation: High-frequency component in the click of the harbor porpoise (*Phocoena ph.* L.). *J. Acous. Soc. Amer.*, **57**, 1368–1372.
Moore, P. W. B. (1997). Review of cetacean auditory psychophysics. *Bioacoustics*, **8**, 61–78.
Moore, P. W. B., Pawloski, D. A. & Dankiewicz, L. (1995). Interaural time and intensity difference thresholds in the bottlenose dolphin (*Tursiops truncatus*). In *Sensory Systems of Aquatic Mammals* (R. Kastelein, J. Thomas and P. Nachtigall, eds), DeSpil Publishers; Woerden, The Netherlands, pp. 11–25.
Morgane, P. J. & Jacobs, M. S. (1972). The comparative anatomy of the cetacean nervous system. In *Functional Anatomy of Marine Mammals* (R. J. Harrison, ed). Academic Press; New York, pp. 109–239.
Nadol, J. B. (1988). Quantification of human spiral ganglion cells by serial section reconstruction and segmental density estimates. *Amer. J. of Otolaryngol.*, **9**, 47–51.
Norris, J. & Leatherwood, K. (1981). Hearing in the bowhead whale, *Balaena mysticetus*, as estimated by cochlear morphology. *Hubbs Sea World Rsch. Inst. Tech. Rpt.*, no. 81–132: 15.1–15.49.
Norris, K. S. (1968). The evolution of acoustic mechanisms in odontocete cetaceans. In *Evolution and Environment* (E. T. Drake, ed), Yale University Press; New Haven, pp. 297–324.
Norris, K. S. (1969). The echolocation of marine mammals. In *The Biology of Marine Mammals* (H. J. Andersen, ed). Academic Press; New York, pp. 391–424.
Norris, K. S. (1980). Peripheral sound processing in odontocetes. In *Animal Sonar System* (R-G. Busnel and J. F. Fish, eds). Plenum Publishing Co ; New York, pp. 495–509.
Norris, K. S. and Harvey, G. W. (1974). Sound transmission in the porpoise head. *J. Acoust. Soc. Am.*, **56**, 659–664.
Norris, K. S., Prescott, J. H., Asa-Dorian, P. V. & Perkins, P. (1961). An experimental demonstration of echolocation behavior in the porpoise, *Tursiops truncatus*, Montagu. *Biol. Bull.*, **120**, 163–176.
Nowak, R. M. (1991). *Mammals of the World, Volume II*. 5th edition. The Johns Hopkins University Press; Baltimore.
Oelschläger, H. A. (1986). Comparative morphology and evolution of the otic region in toothed whales, Cetacea, Mammalia. *Am. J. Anat.* **177**, 353–368.
Payne, K. B., Langbauer, W. J., Jr. & Thomas, E. M. (1986). Infrasonic calls of the Asian elephant (*Elephas maximus*). *Behav. Ecol. Sociobiol.*, **18**, 297–301.
Popov, V. V., Ladygina, T. F. & Supin, A. Y. (1986). Evoked potentials of the auditory cortex of the porpoise, *Phoeoena phoeoena*. *J. Comp. Physiol.*, **158**, 705–711.
Popov, V. V. & Supin A. Y. (1990). Localization of the acoustic window at the dolphin's head. In *Sensory Abilities of Cetaceans: Laboratory and Field Evidence* (J. A. Thomas and R. A. Kastelein, eds). Plenum Press; New York, pp. 417–427.
Popper, A. N. (1980). Sound emission and detection by delphinids. In *Cetacean Behavior, Mechanisms and Function* (L. M. Herman, ed), John Wiley and Sons; New York.
Popper, A. N., Hawkins, H. L. & Gisiner, R. C. (1997). Questions in cetacean bioacoustics: Some suggestions for future research. *Bioacoustics*, **8**, 163–182.
Purves, P. E. & Pilleri, G. E. (1983). *Echolocation in Whales and Dolphins*. Academic Press; London.
Reysenbach de Haan, F. W. (1956). Hearing in whales. *Acta Otolaryngol Suppl.*, **134**, 1–114.
Richardson, W. J., Greene, C. R., Jr., Malme, C.I. & Thomson, D. H. (1991). Effects of

noise on marine mammals. USDI/MMA/OCS Study 90-009, LGL Ecological Research Assoc., Bryan, Texas.

Richardson, W. J., Greene, C. R., Jr., Malme, C.I. & Thomson, D. H. (1995). *Marine Mammals and Noise*. Academic Press; New York.

Ridgway, S. (1997). Who are the whales. *Bioacoustics*, 8, 3–20.

Ridgway, S. H., Bullock, T. H., Carder, D. A., Seeley, R. L., Woods, D. & Galambos, R. (1981). Auditory brainstem response in dolphins. *Proc. Natl. Acad. Sci.*, 78, 1943–1947.

Sales, G. & Pye, D. (1974). *Ultrasonic Communication by Animals*. John Wiley and Sons; New York.

Schevill, W. E., Watkins, W.A. & Ray, C. (1969). Click structure in the porpoise, *Phocoena phocoena*. *J. Mammal.*, **50**, 721–728.

Schuknecht, H. F. & Gulya, A. J. (1986). *Anatomy of the Temporal Bone with Surgical Implications*. Lea and Feibiger; Philadelphia.

Solntseva, G. N. (1971). Comparative anatomical and histological characteristics of the structure of the external and inner ear of some dolphins. Tr. Atl. Nauchno Issled Inst. Rybn. Khoz. Okeanogr.

Solntseva, G. N. (1975). Morphofunctional aspects of the hearing organ in terrestrial semi-aquatic, and aquatic mammals. *Zool. Zh.* 54, 1529–1539

Solntseva, G. N. (1990). Formation of an adaptive structure of the peripheral part of the auditory analyzer in aquatic, echo-locating mammals during ontogenesis. In *Sensory Abilities of Cetaceans: Laboratory and Field Evidence* (J. A. Thomas and R. A. Kastelein, eds). Plenum Press; New York, pp. 363–384.

Solntseva, G. N. & Chernova, O. F. (1980). Morphofunctional analysis of auricular glands in some mammals. *Zool. Zh.*, **59**, 1230–1240.

Suga N. (1983). Neural representation of bisonar (sic) information in the auditory cortex of the mustached bat. *J. Acoust. Soc. Am.*, 74(S1), 31.

Supin, A. Y. & Popov, V. V. (1993). Direction-dependent spectral sensitivity and interaural spectral difference in a dolphin: Evoked potential study. *J. Acoust. Soc. Am.*, **93**, 3490–3495.

Tyack, P. L. (1997). Development and social functions of signature whistles in bottlenose dolphins *Tursiops truncatus*. *Bioacoustics*, 8, 21–46.

Varanasi, U. & Malins, D. G. (1971). Unique lipids of the porpoise (*Tursiops gilli*): Differences in triacyl glycerols and wax esters of acoustic (mandibular canal and melon) and blubber tissues. *Biochem Biophys Acta*, **231**, 415.

Vater, M. (1988). Cochlear physiology and anatomy in bats. In *Animal Sonar, Processes and Performance* (P. E. Nachtigall and P. W. B. Moore, eds). Plenum Press; New York, pp. 225–241.

Watkins, W. A. (1981). The activities and underwater sounds of fin whales. *Sci. Rep. Whales Res. Inst.*, **33**, 83–117.

Watkins, W.A. & Wartzok, D. (1985). Sensory biophysics of marine mammals. *Mar. Mamm. Sci.*, **3**, 219–230.

Watkins, W. A., Tyack, P., Moore, K. E. & Bird, J. E. (1987). The 20 Hz signals of finback whales (*Balaenoptera physalus*). *J. Acoust. Soc. Am.*, 82, 1901–1912.

West, C. D. (1985). The relationship of the spiral turns of the cochlea and the length of the basilar membrane to the range of audible frequencies in ground dwelling mammals. *J. Acoust. Soc. Am.*, 77, 1091–1101.

Wever, E. G., McCormick, J. G., Palin H. & Ridgway, S. (1971a). The cochlea of the dolphin *Tursiops truncatus*: The basilar membrane. *Proc. Natl. Acad. Sci., USA*, 68, 2708–2711.

Wever, E. G., McCormick, J. G., Palin, H. & Ridgway, S. (1971b). The cochlea of the dolphin *Tursiops truncatus*: general morphology. *Proc. Natl. Acad. Sci., USA*, 68, 2381–2385.

Wever, E. G., McCormick, J. G., Palin, H. & Ridgway, S. (1971c). The cochlea of the dolphin *Tursiops truncatus*, hair cells and ganglion cells. *Proc. Natl. Acad. Sci., USA*, 68, 2908–2912.

Wever, E. G., McCormick, J. G., Palin, H. & Ridgway, S. (1972). Cochlear structure in the dolphin *Lagenorhynchus obliquidens*. *Proc. Natl. Acad. Sci., U.S.A.*, **69**, 657–661.

Würsig, B. & Clark, C. (1993). Behavior. In *The Bowhead Whale* (J. Burns, J. Montague and C. Cowles, eds). Society for Marine Mammalogy, spec. publ. no. 2, Allen Press; Lawrence, pp. 157–200.

Yamada, M. (1953). Contribution to the anatomy of the organ of hearing of whales, *Sci. Rep. Whales Res. Inst., Tokyo*, 8, 1–79.

Yeowart, N. S. (1976). Thresholds of hearing and loudness for very low frequencies. In *Infrasound and Low Frequency Vibration* (W. Tempest, ed). Academic Press; London, pp. 37–64.