

# Marine mammal ears: An Anatomical perspective on underwater hearing

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**Abstract:** Recently, concerns over anthropogenic sounds in the oceans pushed us to develop a broader knowledge of marine mammal hearing. Methods ranging from conventional audiometry to FEM modeling have been employed. The resulting data suggest marine mammal ears are more diverse and complex than previously expected, with acoustic capabilities spanning infra to ultrasonic ranges. Seals are amphibious hearers but divide into air vs aquatic adapted ears. Whales have strikingly different ears adapted exclusively to hearing underwater and have specialized tissue paths to the ear, consistent with the acoustic impedance in water. Exceptional auditory nerve densities are found in all whales, and is not exclusively found in ultrasonic echolocators.

## INTRODUCTION

Conceptually, hearing is a relatively simple chain of events: sound energy is converted by neuro-mechanical transducers (middle and inner ear) into electrical signals (neural impulses) that provide a central processor (brain) with a window on the world. The view through that window differs dramatically for every species and, in part, reflects the selection pressures that shaped its ear. Structurally, the picture is more complex. Mammalian ears are elegant structures, packing over 75,000 mechanical and electrochemical components into an average area of  $1 \text{ cm}^2$ . Structural variations in the components are essential elements in species differences in hearing abilities; therefore, comparing ears from species with different hearing ranges and habitats can provide useful insights into both specific and basic hearing mechanisms.

Marine mammals, and whales in particular, are good candidates for such analyses. "Marine mammal" is a broad categorization for over 150 species from four orders. Extant groups of marine mammals include the Pinnipedia, which includes the true seals (phocids), sea lions (otariids), and walrus (odobenids); marine Fissipedia (sea otters); Sirenia (manatees and dugongs); and Cetacea, which comprise the baleen or "moustached" (mysticete) whales and echolocating, toothed (odontocete) whales, porpoises, and dolphins. The degree of aquatic adaptation varies for each group. Many pinnipeds are amphibious, while all cetaceans and sirenians are aquatic obligates, unable to move, reproduce, or feed on land.

All marine mammals, including whales, evolved from land-based animals with air-adapted ears (1). Over the next 50 million years, as their body shapes evolved to withstand enormous pressures, preserve heat, and move efficiently in the comparatively dense, cold environment of the seas, their ears evolved in tandem to effectively processes underwater sound. Water, with a density nearly 800-fold that of air ( $\rho=1.03 \text{ g/cc}$  vs.  $0.0013 \text{ g/cc}$ ), has a sonic velocity that is on average 4.5 times faster than in air ( $c=1530 \text{ m/sec}$  vs.  $c=340 \text{ m/sec}$ ). To examine the sensory implications of these values, consider a hypothetical mammal, that hears equally well in water and in air. An animal with an intensity based ear would require the same acoustic power/unit area in water as in air to have an equal sound percept, or ( $I_{\text{air}} = I_{\text{water}}$ ):

$$I_{\text{air}} = p_{\text{air}}^2 / (0.442 \text{ g-m/sec-cc}) = p_{\text{water}}^2 / (1575 \text{ g-m/sec-cc}) = I_{\text{water}} \quad (1)$$

which implies the sound pressure in water must be 59.7 times that required in air to produce the same intensity and therefore the same sensation in this hypothetical perfectly matched amphibian ear. The units of intensity are, of course,  $\text{watts/m}^2$ , but to put this into the context of conventional hearing measures, recall that intensity is related to the mean square pressure of the sound wave over time. Most hearing studies report hearing thresholds in effective sound pressure level (SPL), expressed in decibels (dB), which in turn are complicated by arbitrary reference pressures. For air-borne sound measures, the reference is generally dB SPL or dB re  $20 \mu\text{Pa}$  rms; for underwater sound measures, the reference pressure is dB re  $1 \mu\text{Pa}$ . Thus, underwater sound pressure levels numerically are  $\sim 61.5 \text{ dB}$  greater than sound pressure levels in air for an equal intensity. In any case, whether viewed in terms of pressure or intensity, there are substantial differences for an equal percept.

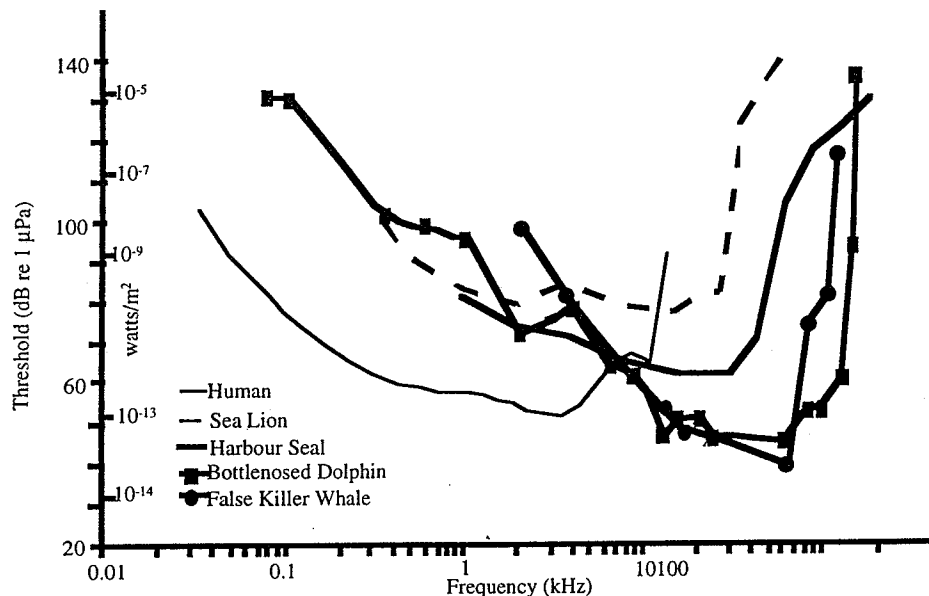
Marine mammal ears have solved this problem, as well as all the attendant differences in other acoustic cues; e.g. shortened interaural arrival times. Equally important, underwater acuity, and the level of structural adaptation that underlie these abilities, do vary among marine mammals. Some, like the sea lion, still hear better in air, while others, like the bottlenosed dolphin, are fully aquatic, that is, they are exceptionally acute processors of waterborne sound but are probably incapable of hearing in air in any normal functional sense. Therefore, teasing out differences among these ears and comparing them to those of land mammal provides an opportunity to explore how structural elements in mammal ears relate to media dependent cues important for hearing.

Until very recently, our knowledge of marine mammal hearing was driven primarily by an interest in replicating the exceptional sonar abilities of dolphins. Consequently, for nearly 50 years, the majority of studies focused detecting, measuring, and modeling dolphin sonar and therefore on the sonic to ultrasonic abilities of relatively few marine mammal species (2). In the last decade, increasing public and scientific concerns about the deployment of man-made acoustic devices in the oceans led to a realization of our lack of basic information on the hearing and sound use by most marine species. Because marine mammals have a high profile, are arguably dependent upon hearing, and, in many cases, are endangered, the concern over noise impacts for these animals became particularly acute. In the last five years, therefore, there has been a substantial increase in research effort directed at obtaining both direct and indirect measures of hearing abilities for marine mammals. The resulting data on their hearing, ear anatomy, and vocalizations suggest that marine mammal ears are more diverse and complex than previously expected, with acoustic capabilities spanning infra to ultrasonic frequencies. Therefore, they have two unique and intriguing features: 1) air-derived mammalian ears that are successfully adapted for acute underwater sound reception and localization; and 2) an auditory capacity ranging from very low infrasonic (10 Hz) to high ultrasonic (200 kHz) frequencies.

Therefore, the principal questions to be addressed here are what do we know about their hearing ability and how do they accomplish these feats. In this summary only the two best studied groups, cetaceans and pinnipeds are discussed.

### AUDIOMETRY

Underwater audiograms are available for eight odontocete and seven pinniped species (Fig. 1). Most odontocetes tested to date are delphinids, with the bottlenosed dolphin being the best investigated. There are no published audiograms for larger, deep diving odontocetes, like the sperm and beaked whales. The current data suggest odontocetes commonly have a >10 octave functional hearing ranges, compared with 8 octaves in most mammals. Best sensitivities range from 12 kHz in the killer whale (*Orcinus orca*) to over 100 kHz in bouu (*Inia geoffrensis*) and the harbour porpoise (*Phocoena phocoena*).



**Figure 1.** Two representative odontocete and pinniped behavioural audiograms are plotted with a typical human minimum audible field in-air audiogram, using a common ordinate of intensity as well as the conventional dB re 1  $\mu$ Pa. Note the apparent species and group differences in range as well as absolute sensitivity. The data suggest that sensitivities evolved in parallel to average ambient levels in each major frequency division. (Data compiled from 2,3,4)

Echolocation performances in bottlenosed dolphins (*Tursiops truncatus*) are similar to that microchiropteran bats and 6 to 8 dB lower than that expected from an ideal receiver (2). Angular resolution is generally 1° to 4°. Intensity discrimination is equal to human (1 dB); temporal discrimination (~8% of signal duration) is superior to human. Frequency discrimination varies from 0.28 to 1.4% rdl for frequencies between 1-140 kHz; best values are found between 5 and 60 kHz (4). Odontocetes have more critical bands and the critical ratios are generally smaller

than in humans, although they are relatively constant at ~0.25 to 0.35 octaves/mm of basilar membrane (11). Odontocete critical bandwidths approach 0 and are not a constant factor of the ratio at different frequencies. The best critical ratios to date (8 to 40 dB) are for the false killer whale, *Pseudorca crassidens*, which is also the species that has performed best in echolocation discrimination tasks (5, 6).

Auditory evoked potentials (AEP) are useful in marine mammals for the same reasons as in infants, namely, they are rapid, minimally invasive, and require no training by the subject. The most recent work, using continuous amplitude modulated stimuli (AMS) at low frequencies, found odontocetes can extract envelope features at higher modulation frequencies than other mammals (7). Anatomical correlates of EFRs have not been identified, but the data suggest auditory central nervous system adaptations in dolphins may include low as well as high frequency specialized regions.

Pinnipeds are interesting because they are faced with two acoustic environments. One theory is that pinnipeds have dual systems, operating independently for aquatic vs. air-borne stimuli. If so hearing might be expected to be equally acute but possibly have different frequency ranges related to behaviors in each medium; e.g., feeding in water vs. the location of a pup on land. An alternative to the dual-equal hearing option is that each species is adapted primarily for one environment and has a compromised or lesser facility in the other. Renouf (8) argued that there is an "a priori justification for expecting otariids and phocids" to operate with different sensory emphases given that phocids are more aquatic in general. Audiometric data for these groups are consistent with this speculation.

Peak sensitivities in phocids tested underwater (harbour seal, *Phoca vitulina*; harp seal, *P. groenlandica*; ringed seal, *P. hispida*; monk seal, *Monachus schauinslandi*) occurred between 10 and 30 kHz (3). Low frequency limits are not yet well established for phocids; however, the fact that all current plots show remarkably little decrease in sensitivity below peak frequency suggests further lower frequency testing is needed. Recent data from harbour and elephant seals (*Mirounga angustirostris*) suggest the elephant seal has significantly better underwater low frequency hearing thresholds than other pinnipeds tested to date but is less acute in air (9), which is consistent also with anatomical differences in the external canal and middle ears in these species (Ketten, unpub.). When air and underwater audiograms are compared on the basis of intensity measures, the thresholds for phocids in water are, on average, significantly better than in air, suggesting they are adapted primarily for underwater hearing.

Air vs. underwater audiograms for otariids suggest the opposite. California sea lions (*Zalophus californianus*) and northern fur seals, *Callorhinus ursinus*, have functional high frequency underwater hearing limits between 35-40 kHz with peak sensitivities from 15-30 kHz (3). In air, otariid peak sensitivities shift, as do phocid, to lower frequencies in air, but levels are similar or slightly more sensitive, suggesting that otariids developed parallel, equipotent hearing strategies for air and water or, as is clearly suggested by the *Zalophus* data, "opted" evolutionarily for better aerial hearing.

Pinnipeds perform less well than odontocetes in discrimination tasks (3). Angular resolution is generally 4° to 6°. There is wide individual variability and no consistent trend for aerial vs aquatic stimuli. Intensity discrimination (3 dB) by *Zalophus* is poorer than that of dolphins or humans. Frequency discrimination limits (1-2% rdl) are similar to some of the bottlenosed dolphin data but are less sensitive than those for harbor porpoise. In northern fur seals, underwater critical ratios over a fairly narrow range (2-30 kHz) were on a par with odontocetes (18-35 dB) at the same frequencies.

## ANATOMICAL CORRELATES

As models become more sophisticated, anatomical data becomes more useful, particularly for species that are essentially inaccessible, like the blue whale. Major issues that are unresolved but for which anatomy is providing some useful indicators are what are the paths to the ear, how is localization accomplished, and what is the function of the middle ear.

Whales have no external ear and the canal is blocked by debris and wax. It is fairly clear that fatty jaw channels play a role in ultrasonic perception for dolphins (10), but CT and MRI data suggest there may be at least one additional channel (11). No discrete soft channels have yet been identified in seals, although Møhl and Ronald (12) found that underwater, the most sensitive region was not the canal but a region parallel to it.

Logically, it would seem that whales, with the possibility of fluid to fluid coupling have little need for the classic amplification role of the middle ear, but CT shows the middle ear of dolphins is air-filled *in vivo*. Mass and stiffness of the ossicles and the size and shape of the eardrum vary widely among marine mammals. None are overtly degenerate or vestigial. The most extreme development of middle ear structures is found in baleen whales which have a large, fibrous, everted eardrum ("glove finger") capped by a distinctive wax plug.

Marine mammal inner ears (cochlea and vestibular system) have the same general format as land mammal ears, but again, there are unusual extremes, particularly in basilar membrane construction. Anatomically, cetacean ears are divided into three structural formats that are consistent with audiometric data or with peak spectra of vocalizations. Type I ears, found in the highest frequency animals, have narrow, thick basal membranes with ratios >0.8 and

substantial inner laminae, consistent with ultrasonic hearing. Type II ears have less acute basal membranes (ratio ~0.6) and slightly wider apices, consistent with the broader hearing range and bi-modal signaling noted in many social odontocetes. Type M ears, common to the baleen whales, have broad (up to 2200  $\mu$ ), thin membranes with apical ratios near 0.002, consistent with infrasonic resonances. Many mysticete species produce infrasonic signals, but their hearing abilities have not been directly tested.

Seal inner ears have not been extensively studied, but preliminary data indicate that like other mammals, pinnipeds include both high and low frequency adapted species as well as aerial vs. aquatic specialists.

In land mammals, two cues that are vimportant for localizing sound are interaural arrival time and intensity differences. Because of sound speed differences, small or absent pinna, and ear canal adaptations in marine mammals, localization mechanisms could be substantially different from those of land mammals.

Interaural time distances (IATD) clearly depend upon the sound conduction path in the animal and on the media through which sound travels. For land mammals, the key entry point is the external auditory meatus and the normal sound path is through air, around the head, pinna to pinna. The IATD is therefore the intermeatal (IM) distance around the head divided by the speed of sound in air. In aquatic animals, sound could travel through the head by tissue conduction, given tissue impedances similar to that of sea water. Recently, Moore *et al.* (13) demonstrated that bottlenosed dolphins have an IATD of ~7  $\mu$ sec, well below that of most land mammals, including humans (10  $\mu$ sec). Straight line intercochlear (IC) and interjaw distances of dolphins, taking into account sound speeds, are effectively equal to rat or bat IM distance, which is consistent with their interaural data. If IM distances are used for land mammals and otariids in air and IC distances are used for cetaceans and underwater phocid data, marine mammal and land mammal data for IATD vs. high frequency limits follow the same regression as land mammal data (11).

In summary, marine mammals are acoustically diverse with wide variations in ear anatomy that are consistent with diverse hearing characteristics. All ear components are heavily modified from those of land mammals, but the essential plan is the same. It is possible that inner ear hypertrophy in some species provides some protective mechanisms from high intensity noise, but no data are yet available that directly address this issue. In general, the range of each animal's hearing is fundamentally linked passive monitoring of the ambient as well as to active tasks such as finding prey, detecting predators, or communicating with conspecifics. This relationship is especially apparent for the echolocating odontocetes in which the peak frequency of the echolocation signal is tightly coupled to the habitat characteristics; i.e., species that live in muddy rivers or harbours are generally Type I species capable of using ultra-high frequencies. By contrast, Type II odontocetes use lower ultrasonic frequencies that are consistent with detecting larger objects at greater distances. Finally, mysticete ears (Type M) appear geared to infrasonics and, interestingly enough are just as neurologically complex as those of echolocators. This may mean that mysticetes are able to use low frequencies for very long-range communications or perhaps assess large scale topography with sound.

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