

Marine Mammal Sensory Systems

Sensory systems evolved to allow animals to receive and process information from their surroundings. To understand how sensory systems operate in any given environment, we must understand how the physical characteristics of that environment affect the available information and its propagation and reception. In a very real sense we need to look at both the medium and the message (McLuhan and Fiore 1967). Signals in the marine environment can be substantially different from those in air, and the oceanic medium itself changes the message in a number of ways.

When their evolutionary paths took them into the oceans, marine mammals had to adapt sensory systems that had evolved in air into ones that were able to detect and process signals in water. The sensory systems of marine mammals are functionally similar to those of terrestrial mammals in that they act as highly selective filters. If every environmental cue available received equal attention, the brain would be barraged by sensory inputs. Instead, sensory organs are filters, selecting and attending to signals that, evolutionarily, proved to be important. Consider how predator and prey are driven to be both similar and different sensorially. Because their activities intersect in place and time, they need to have similar visual sensitivities, but different fields of view. The predator usually has binocular overlap that provides a precise judgment of distance to the prey. The

prey may forego binocular vision and accurate visual depth judgments in favor of greater lateral visual fields to detect a predator. Thus, two species may have overlapping sensory ranges, but no two have identical sensory capacities. Consequently, each animal's perceived world is only a subset of the real physical world, that is, it is a species-specific model, constructed from the blocks of data its senses can capture.

In animal behavior, this concept is called the *Umwelt* (von Uexküll 1934). As a technical term, *Umwelt* means an animal's perceptually limited construct of the world. In common usage, it simply means the environment. This dual meaning reflects the complex interaction of sensory adaptations and habitat. Senses are tuned to relevant stimuli by evolution but are limited by the physical parameters of the habitat. For example, human sensory systems are geared to diurnal, airborne cues. Humans are highly developed visually, with 38 times more optic nerve fibers than auditory nerve fibers, and a hearing range (20 to 20,000 Hz) that is narrower than that of many other animals. By observing species adapted to different habitats and analyzing their sensory biology, we can learn how they detect and use physical cues that are normally imperceptible to us. If we develop technology that translates those cues into our sensory ranges, we can glimpse at the world as other species perceive it. Marine mammals offer us a very special glimpse. In aquatic environ-

ments, our air-adapted senses are out of their element and are effectively detuned. By studying marine mammal sensory systems and abilities, we can understand how land mammal senses were evolutionarily returned to operate in water. From that knowledge, we gain a valuable window into the oceans, the most extensive and unexplored environment on earth.

In this chapter, we discuss marine mammal audition, vision, chemoreception, tactile sensation, and magnetic detection. We begin with an overview of the basic aspects of sensory receptor systems, and then, for specific sensory systems, examine how water versus air affects the parameters and propagation of related signals and discuss how air-based receptors were adapted to function effectively in an aquatic environment. Different sensory systems and different marine mammal groups (sirenians, cetaceans, pinnipeds, fissipeds, ursids) are discussed in varying detail based on the extent of data available for each.

Generally, the term sensory system refers to the peripheral, as opposed to the brain, or central, components an animal uses to detect and analyze a signal. There are four essential functions for any sensory system: (1) capture an environmental signal, (2) filter it, (3) transduce it to a neural impulse, and (4) send processed information to the central nervous system. Each function may involve more than one form of receptor or peripheral processor. The block diagram in Figure 4-1 compares a generic sensory receptor system with equivalent stages for mammalian eyes and ears. In vision, the first step, signal capture, is accomplished by the re-

fraction of light at the cornea and the pupil's ability to control the light intensity entering the eye. Second, the lens focuses light on the retina while also acting as a first-stage filter, passing only some portions of the full spectrum of light. The tapetum, a reflective layer behind the retina, reflects the photons not captured on the first passage through the retina back through for a second chance at absorption. Third, pigments within the rod and cone receptor cells absorb each wavelength with a different efficiency. Fourth, the rods or cones pass a chemical signal to horizontal or bipolar cells that modify and transmit the signal to amacrine or ganglion cells. Axons of ganglion cells make up the optic nerve, which passes signals to midbrain structures and ultimately to the cortex. In hearing, the first step is the capture of sound by the external ear. The external ear and the ear canal act as first-stage filters, attenuating some sounds based on their direction (pinna shadowing) and amplifying others according to the resonance characteristics of the outer ear and canal. Second, the middle ear components act as second stage filters. The middle ear bones mechanically transmit vibrations of the eardrum, or tympanic membrane, to the oval window, which is the acoustic entrance to the fluid-filled inner ear. This bony chain acts as a series of levers that provides a nearly 40-dB boost to the incoming signal, which compensates for the loss of acoustic power that would normally occur from a simple transmission of sound in air into fluid. The mass, stiffness, and shape of the middle ear cavity and of the middle ear ossicular chain also influence the efficiency with which different frequencies are transmitted to the inner ear. Third,

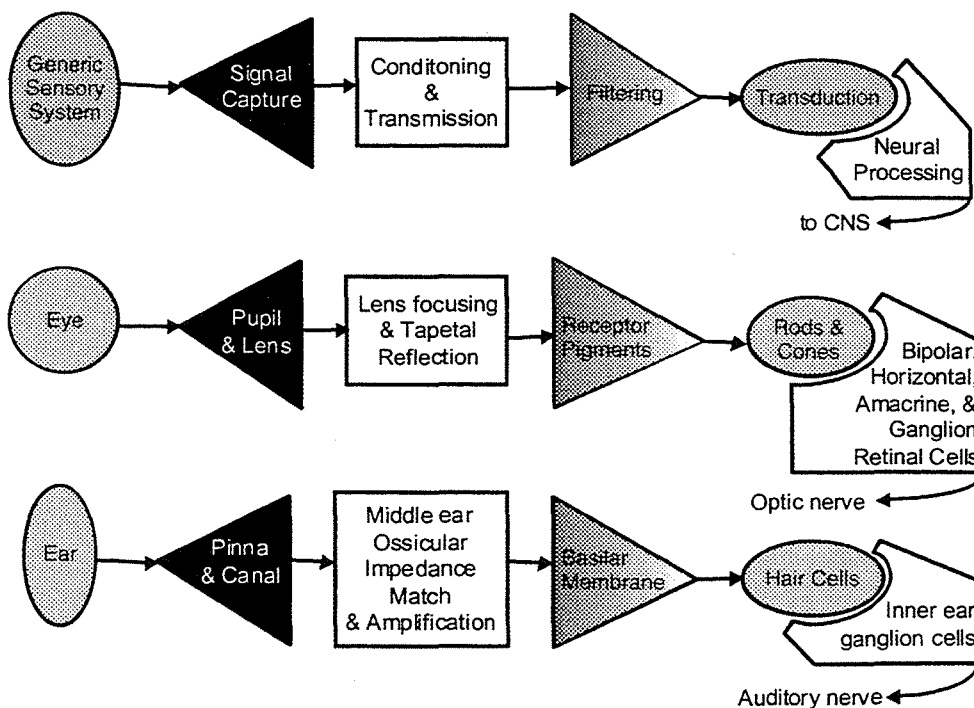


Figure 4-1. A generic sensory system is shown with parallel stages for mammalian visual and auditory systems.

at the level of the inner ear, the basilar membrane acts as a bank of filters that determine the range of frequencies the brain will ultimately process. The detectable sound or "hearing" range is dictated by the stiffness and mass characteristics of this membrane. Fourth, when sensory cells with flexible cilia, the hair cells, are bent through the motion of the basilar membrane, a chemical signal is transmitted via the auditory afferent (inward) fibers to the brainstem. Thus, in both the eye and ear, the signal goes through a minimum of three and as many as five layers of signal processing before it is transformed into a neural impulse.

For both sensory systems, there is extensive central processing as well as efferent (outward) feedback signals from the central nervous system that affect the responses at the receptor. Depending on the stimulus, the behavioral and physiologic state of the animal, and the type of receptor, a stimulus can be perceived but elicit no action, or it can prompt a set of signals to be sent to an effector that modulates the stimulus intensity, as in withdrawal from pain, pupillary contraction in bright light, or rotation of the head or pinna to enhance detection of a particular sound. Now we turn to a more detailed look at individual sensory systems.

Audition

Hearing is simply the detection of sound. "Sound" is the propagation of a mechanical disturbance through a medium. In elastic media, such as air and water, that disturbance takes the form of acoustic waves. The adaptive significance of sound cues is underscored by the ubiquity of hearing. There are lightless habitats on earth with naturally blind animals,

but no terrestrial habitat is without sound, and no known vertebrate is naturally profoundly deaf.

Mechanistically, hearing is a relatively simple chain of events: sound energy is converted by biomechanical transducers (middle and inner ear) into electrical signals (neural impulses) that provide a central processor (brain) with acoustic data. Mammalian ears are elegant structures, packing more than 75,000 mechanical and electrochemical components into an average volume of 1 cm³. Variations in the structure and number of these components account for most of the hearing capacity differences among mammals (for an overview, see Webster et al. 1992).

Normal functional hearing ranges and the sensitivity at each audible frequency (threshold, or minimum intensity required to hear a given frequency) vary widely by species (Fig. 4-2). "Functional" hearing refers to the range of frequencies a species hears without entraining nonacoustic mechanisms. In land mammals, the functional range is generally considered to be those frequencies that can be heard at thresholds below 60 dB SPL. (dB SPL refers to a decibel measure of sound pressure level. The basis for this measure and how it differs in air and water are explained in detail in the next section.) For example, a healthy human ear has a potential maximum frequency range of 0.02 to 20 kHz, but the normal functional hearing range in an adult is closer to 0.04 to 16 kHz.¹ In humans, best sensitivity (lowest thresholds) occurs between 500 Hz and 4 kHz, which is also where most of the acoustic energy in speech occurs (Fig. 4-2; Schuknecht 1993; Yost 1994). To hear frequencies at the extreme ends of any animal's total range generally requires intensities that are uncomfortable, and some frequencies are simply unde-

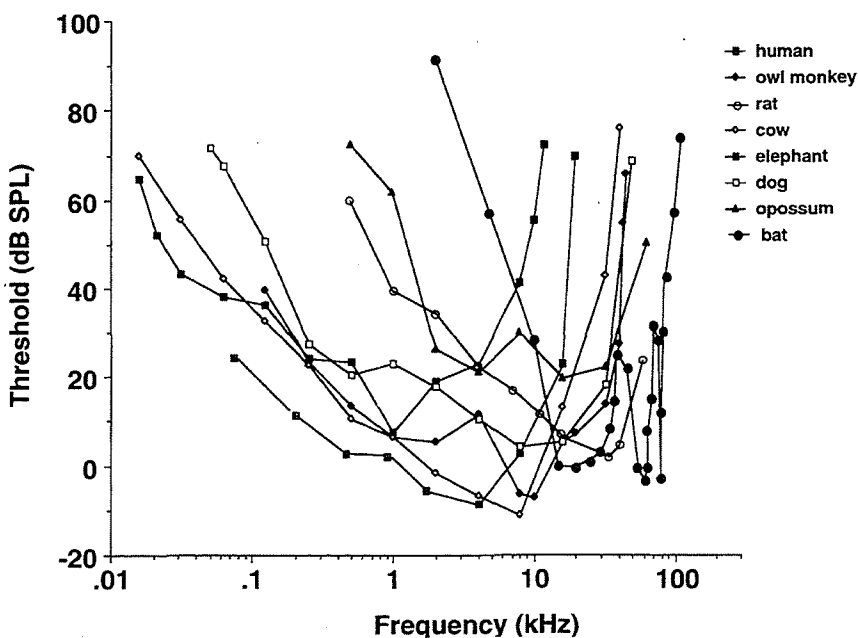


Figure 4-2. Audiograms of representative terrestrial mammals. Note that the ordinate is labeled dB SPL and therefore, thresholds are at or near 0 dB in the regions of best sensitivity for most species (data compiled from Fay 1988). The human curve ends abruptly near 100 Hz at its low-frequency end because most human hearing studies have focused on speech perception and subjects are not tested over the full human hearing range. Compare these audiograms for land mammals in air with the underwater audiograms for cetaceans and pinnipeds in Figure 4-5, taking into consideration the effect that differing reference pressures have on reported threshold values.

tectable because of limitations in the resonance characteristics of the middle and inner ear. Exceptionally loud sounds that are outside the functional range of normal hearing can sometimes be perceived through bone conduction or direct motion of the inner ear, but this is not truly an auditory sensation.

Analyzing how hearing abilities, habitat, and ear anatomy are linked in different species, particularly in animals from diverse habitats, provides insights into how each component in the auditory periphery functions and how different hearing capacities evolved. "Sonic" is an arbitrary term that refers to the maximal human hearing range. Frequencies outside this range are deemed infrasonic (below 20 Hz) or ultrasonic (above 20 kHz). Of course, many animals hear sounds inaudible to humans. Most mammals have some ultrasonic hearing (i.e., can hear well at ultrasonic frequencies) and a few, like the Asian elephant (*Elephas maximus*) hear infrasonic signals (Fig. 4-2).

Hearing ranges are both size and niche related. In general, mammalian ears scale with body size (Manley 1972; Ketten 1984, 1992; West 1985). In land mammals, the highest frequency an animal hears is generally inversely related to body mass; smaller animals typically have good high frequency hearing, whereas larger animals tend to have lower overall ranges (von Békésy 1960, Greenwood 1962, Manley 1972, Ketten 1984). Yet, regardless of size, crepuscular and nocturnal species typically have acute ultrasonic hearing, whereas subterranean species usually have good infrasonic hearing, and, in some cases, can detect seismic vibrations (Sales and Pye 1974, Heffner and Heffner 1980, Payne et al. 1986, Fay 1988).

How well do marine mammals mesh with this general land mammal hearing scheme? Marine mammals evolved from land-dwelling ancestors during the explosive period of mammalian radiation (see Barnes et al. 1985). Today, marine mammals occupy virtually every aquatic niche (freshwater to pelagic, surface to profundal) and have a size range of several magnitudes (e.g., harbor porpoise [*Phocoena phocoena*], 1 m and 55 kg vs. the blue whale [*Balaenoptera musculus*], 40 m and 94,000 kg; Nowak 1991). Water is a relatively dense medium in which light attenuates much faster than sound, therefore marine mammals are, in a sense, de facto crepuscular species, but we also expect to see a wide range of hearing given their diversity of animal size and habitat. Because marine mammals retained the essentials of air-adapted ears, that is, an air-filled middle ear and spiral cochlea, some similarities in hearing mechanism between land and aquatic mammals would not be surprising. In fact, hearing in marine mammals has the same basic size versus auditory structure relationship as in land mammals, but marine mammals have a significantly different auditory *bauplan*, or ear size versus

frequency relationship (Solntseva 1971, 1990; Ketten 1984, 1992). Consequently, although some marine mammals, consistent with their size, hear well at low frequencies, the majority, despite their relatively large size, hear best at ultrasonic frequencies because of unique auditory mechanisms that evolved in response to the marine environment.

Land and marine ears have significant structural differences. Because of some of these differences, a common definition of the term ear is somewhat problematic. In this chapter, ear is used in the broadest sense to encompass all structures that function primarily to collect and process sound. As marine mammal ancestors became more aquatic, air-adapted mammalian ears had to be coupled to waterborne sound for hearing to remain functional. Ear evolution took place in tandem with, and in part in response to, body reconfigurations. Just as the physical demands of operating in water exacted a structural price in the locomotory and thermoregulatory systems of marine mammals (see Pabst, Rommel, and McLellan, Chapter 2, this volume), physical differences in underwater sound required auditory system remodeling. In modern marine mammals, the extent of ear modifications parallels the level of aquatic adaptation in each group (Ketten 1984, 1992; Solntseva 1990). The greatest differences from land mammals are found in cetaceans and sirenians. As they evolved into obligate aquatic mammals, unable to move, reproduce, or feed on land, every portion of the head, including the auditory periphery, was modified. Modern cetaceans have the most derived cranial structure of any mammal (Barnes and Mitchell 1978, Barnes et al. 1985). "Telescoping," a term coined by Miller (1923), refers to the evolutionary revamping of the cranial vault as the maxillary bones of the upper jaw were transposed back to the vertex of the skull, overlapping the compressed frontal bones. As the rostrum elongated, the cranial vault foreshortened, and the nares and narial passages were pulled rearward to a dorsal position behind the eyes. Telescoping may have been related primarily to changes that allow respiration with only a small portion of the head exposed, but it also produced a multilayer skull that has a profound effect on how sound enters and leaves the cetacean head. Many land mammal auditory components, like external pinnae and air-filled external canals, were lost or reduced and the middle and inner ears migrated outward. In most odontocetes, the ears have no substantial bony association with the skull. Instead, they are suspended by ligaments in a foam-filled cavity outside the skull. Consequently, they are effectively acoustically isolated from bone conduction, which is important for echolocation. There are also few bony, thin-walled air chambers, which is important for avoiding pressure-related injuries. Specialized fatty tissues (low impedance channels for underwater sound recep-

tion) evolved that appear to function in lieu of external air-filled canals.

Mysticete ears are also specialized but they appear to have been shaped more by size adaptations than by special hearing functions. Sirenian ears are not as well understood, but they too appear to have many highly derived adaptations for underwater sound reception. Today, cetacean and sirenian ears are so specialized for waterborne sound perception that they may no longer be able to detect or interpret airborne sound at normal ambient levels. On the other hand, ears of sea otters (*Enhydra lutris*) and some otariids have very few anatomical differences from those of terrestrial mammals, and it is possible these ears represent a kind of amphibious compromise or even that they continue to be primarily air adapted.

That brings us to three major auditory questions: (1) How do marine and terrestrial ears and hearing differ?; (2) How do these differences relate to underwater sound perception?; and (3) How do amphibious species manage hearing in both domains? To address these questions requires collating a wide variety of data. Behavioral and electrophysiological measures are available for some odontocetes and pinnipeds, but there are no published hearing curves for any mysticete, sirenian, or marine fissiped. Anatomical correlates of hearing are fairly well established (Greenwood 1961, 1962, 1990; Manley 1972; for reviews, see Fay 1988, 1992; Echteler et al. 1994). Anatomical data are available on some aspects of the auditory system for approximately one-third of all marine mammal species, including nearly half of the larger, non-captive species. Therefore, to give the broadest view of current marine mammal hearing data, both audiometric and anatomical data are discussed. An outline of physical measures of sound in air versus water and of the basic mechanisms of mammalian hearing are given first as background for these discussions.

Sound in Air Versus Water

In analyzing marine mammal hearing, it is important to consider how the physical aspects of sound in air versus water affect acoustic cues. Basic measures of sound are frequency, speed, wavelength, and intensity. Frequency (f), measured in cycles/sec or hertz (Hz), is defined as:

$$f = c/\lambda, \quad (\text{equation 1})$$

where c = the speed of sound (m/sec) and λ = the wavelength (m/cycle). The speed of sound is directly related to the density of the medium. Because water is denser than air, sound in water travels faster and with less attenuation than sound in air. Sound speed in moist ambient surface air is approximately 340 m/sec.² Sound speed in seawater aver-

ages 1530 m/sec, but varies with any factor affecting density. The principal physical factors affecting density in seawater are salinity, temperature, and pressure. For each 1% increase in salinity, speed increases 1.5 m/sec; for each 1°C decrease in temperature, speed decreases 4 m/sec; and for each 100 m depth, speed increases 1.8 m/sec (Ingmanson and Wallace 1973). Because these factors act synergistically, the ocean has a highly variable sound profile that may change both seasonally and regionally (Fig. 4-3). For practical purposes, in-water sound speed is 4.5 times faster than in air and, at every frequency, the wavelength is 4.5 times greater than in air.

How do these physical differences affect hearing? Mammalian ears are primarily sound-intensity detectors. Intensity, like frequency, depends on sound speed and, in turn, on density. Sound intensity (I) is the acoustic power (P) impinging on surface area (a) perpendicular to the direction of sound propagation, or power/unit area ($I = P/a$). In general terms, power is force (F) times velocity ($P = Fv$). Pressure is force/unit area ($p = F/a$). Therefore, intensity can be rewritten as the product of sound pressure (p) and vibration velocity (v):

$$I = P/a = Fv/a = pv \quad (\text{equation 2})$$

For a traveling spherical wave, the velocity component becomes particle velocity (u), which in terms of effective sound pressure can be defined as $p/\rho c$ where ρ is the density of the medium. The product ρc is called the characteristic impedance of the medium.

We can then redefine intensity (equation 2) for an instantaneous sound pressure for an outward traveling plane wave in terms of pressure, sound speed, and density:

$$I = pv = p(p/\rho c) = p^2/\rho c \quad (\text{equation 3})$$

Recall that for air $c = 340$ m/sec and for seawater $c = 1530$ m/sec; for air, $\rho = 0.0013$ g/cm³; for seawater, $\rho = 1.03$ g/cm³. The following calculations using the intensity-pressure-impedance relation expressed in equation 3 show how the differences in the physical properties of water versus air influence intensity and acoustic pressure values:

$$\begin{aligned} I_{\text{air}} &= p^2 / (0.0013 \text{ g/cm}^3)(340 \text{ m/sec}) \\ &= p^2 / (0.442 \text{ g-m/sec-cm}^3) \\ I_{\text{water}} &= p^2 / (1.03 \text{ g/cm}^3)(1530 \text{ m/sec}) \\ &= p^2 / (1575 \text{ g-m/sec-cm}^3) \end{aligned}$$

To examine the sensory implications of these differences, we will construct a hypothetical mammal, the neffin ("never found in nature"), that hears equally well in water as in air. For this to be true, the neffin, 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 ($I_{\text{air}} = I_{\text{water}}$):

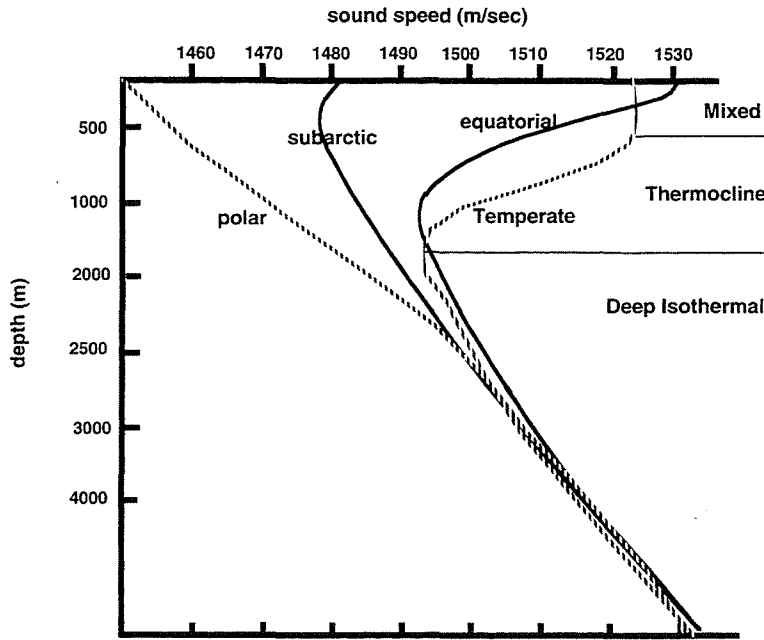


Figure 4-3. Sound speed profiles for temperate, tropical, and polar conditions. In polar waters, there is an inverse trend close to the surface where the water is near freezing; density and therefore, velocity decrease. (Adapted from Ingmanson and Wallace 1973 and Jensen et al. 1994.)

$$\begin{aligned}
 I_{\text{air}} &= p_{\text{air}}^2 / (0.442 \text{ g-m/sec-cm}^3) = I_{\text{water}} \\
 &= p_{\text{water}}^2 / (1575 \text{ g-m/sec-cm}^3) \\
 p_{\text{air}}^2 (3565.4) &= p_{\text{water}}^2 \\
 p_{\text{air}} (59.7) &= p_{\text{water}}
 \end{aligned}
 \quad (\text{equation 4})$$

This implies that the sound pressure in water must be approximately 60 times that required in air to produce the same intensity and therefore, the same sensation in the neffin ear.

For technological reasons, received intensity, which is measured in watts/m², is difficult to determine. Consequently, to describe hearing thresholds, we capitalize on the fact that intensity is related to the mean square pressure of the sound wave over time (equation 3) and use an indirect measure, effective sound pressure level (SPL) (for discussion, see Au 1993). Sound pressure levels are conventionally expressed in decibels (dB), defined as:

$$\begin{aligned}
 \text{dB SPL} &= 10 \log (p_m^2 / p_r^2) \\
 &= 20 \log (p_m / p_r),
 \end{aligned}
 \quad (\text{equation 5})$$

where p_m is the pressure measured and p_r is an arbitrary reference pressure. Currently, two standardized reference pressures are used. For airborne sound measures, the reference is dB SPL or dB re 20 μ Pa rms, derived from human hearing.³ For underwater sound measures, the reference pressure is dB re 1 μ Pa. Notice that decibels are expressed on a logarithmic scale based on a ratio that depends on reference pressure.

In the earlier hypothetical example, with identical reference pressures, the neffin needed a sound level approximately 35.5 dB greater in water than in air (from equation 4,

10 log 3565.4) to hear equally well in both. However, if conventional references for measuring levels in air versus water are used, the differences in reference pressure must be considered as well. This means that to produce an equivalent sensation in a submerged neffin, the underwater sound pressure level in water would need to be 35.5 dB + 20 (log 20) dB greater than the airborne value. That is, a sound level of 61.5 dB re 1 μ Pa in water is equivalent to 0 dB re 20 μ Pa in air. To the neffin, they should sound the same because the intensities are equivalent. Thus, underwater sound intensities with conventional 1 μ Pa reference pressures must be reduced by 61.5 dB for gross comparisons with in-air sound measures using a 20 μ Pa reference pressure.

It is important to remember that these equations describe idealized comparisons of air versus waterborne sound. In comparing data from different species, bear in mind that experimental conditions can significantly impact hearing data. Both subtle and gross environmental effects (salinity, temperature, depth, ambient noise, surface reflection, etc.) as well as individual state (motivation, age, pathology) influence results. Comparisons of terrestrial and marine mammal hearing data are particularly difficult because we have no underwater equivalent of anechoic chambers; results are often obtained from few individuals, and test conditions are highly variable.

Basic Hearing Mechanisms

Hearing capacities are the output of the integrated components of the whole ear. All mammalian ears, including those

of marine mammals, have three basic divisions: (1) an outer ear, (2) an air-filled middle ear with bony levers and membranes, and (3) a fluid-filled inner ear with mechanical resonators and sensory cells. The outer ear acts as a sound collector. The middle ear transforms acoustic components into mechanical ones detectable by the inner ear. The inner ear acts as a band-pass filter and mechanochemical transducer of sound into neural impulses.

The outer ear is subdivided conventionally into a pinna or ear flap that assists in localization and the ear canal. The size and shape of each component in each species is extraordinarily diverse, which makes any generalized statement about the function of the outer ear debatable. In most mammals, the pinnal flaps are distinct flanges that may be mobile. These flanges act as sound diffractors that aid in localization, primarily by acting as a funnel that selectively admits sounds along the pinnal axis (Heffner and Heffner 1992).

The middle ear is commonly described as an impedance-matching device or transformer that counteracts the approximately 36-dB loss from the impedance differences between air and the fluid-filled inner ear, an auditory remnant of the original vertebrate move from water onto land. This gain is achieved by the mechanical advantage provided by differences in the middle ear membrane areas (large tympanic vs. small oval window) and by the lever effect of the ossicular chain that creates a pressure gain and a reduction in particle velocity at the inner ear.

Improving the efficiency of power transfer to the inner ear may not, however, be the only function for the middle ear. Recent studies on land mammals have led to a competing (but not mutually exclusive) theory called the peripheral filter-isopower function, in which the middle ear has a "tuning" role (for comprehensive discussions, see Zwillocki 1981, Rosowski 1994, Yost 1994). The middle ear varies widely among species in volume, stiffness (K), and mass (M). Each species has a characteristic middle ear resonance based on the combined chain of impedances, which, in turn, depends on the mechanical properties of its middle ear components. For any animal, the sum of impedances is lowest (i.e., middle ear admittance is greatest and energy transmission most efficient), at the middle ear's resonant frequency (f). As expected, this frequency also tends to be at or near the frequency with the lowest threshold (best sensitivity) for that species (Fay 1992).

Stiffness and mass have inverse effects on frequency in a resonant system:

$$f = \left(\frac{1}{2} \pi \right) \sqrt{K/M}. \quad (\text{equation 6})$$

Put another way, mass-dominated systems have a lower resonant frequency than stiffness-dominated systems. Increasing stiffness in any ear component (membranes, ossicles,

cavity) improves the efficiency of transmission of high frequencies. Adding mass to the system (e.g., by increasing cavity volume or increasing ossicular chain mass) favors low frequencies. Consequently, in addition to impedance matching, middle ears may be evolutionarily tuned by different combinations of mass or stiffening agents in each species. Ultrasonic species, like microchiropteran bats and dolphins, have ossicular chains stiffened with bony struts and fused articulations (Reysenbach de Haan 1956, Pye 1972, Sales and Pye 1974, Ketten and Wartzok 1990). Low frequency species, like heteromyid desert rodents, mole rats, elephants, and mysticetes, have large middle ears with flaccid tympanic membranes (Webster 1962; Hinchcliffe and Pye 1969; Webster and Webster 1975; Fleischer 1978; Ketten 1992, 1994).

Inner ears are similarly tuned, in that inner ear stiffness and mass characteristics are major determinants of species-specific hearing ranges. The inner ear consists of the cochlea (primary hearing receptor; Fig. 4-4) and the vestibular system (organs of orientation and balance). Mammalian inner ears are precocial, that is, they are structurally mature and functional at birth and may be active in utero. The cochlea is a fluid-filled spiral containing a primary resonator, the basilar membrane, and an array of neuroreceptors, the organ of Corti (see Fig. 4-7). When the basilar membrane moves, cilia on the hair cells of the organ of Corti are deflected eliciting chemical changes that release neurotransmitters. Afferent fibers of the auditory nerve (cranial nerve VIII) synapsing on the hair cells carry acoustic details to the brain, including frequency, amplitude, and temporal patterning of incoming sounds. Efferent fibers also synapse with the hair cells, but their function is not yet fully understood.

A key component in this system is the basilar membrane. Interspecific differences in hearing ranges are dictated largely by differences in stiffness and mass that are the result of basilar membrane thickness and width variations along the cochlear spiral. Because the cochlea is a spiral with a decreasing radius, the spiral portion with the largest radius (closest to the oval and round windows) is referred to as the base or basal turn; the section with the smallest radius (farthest from the middle ear) is the apex or apical turn. From base to apex, changes in the construction of the basilar membrane in each mammal mechanically tune the ear to a specific set of frequencies. Each membrane region has a particular resonance characteristic and consequently greater deflection than other regions of the membrane for a particular input frequency. For an animal to be sensitive to a sound, its basilar membrane must have resonance capabilities matching that sound at some point along the cochlear spiral.

For any input signal within the hearing range of the animal, the entire basilar membrane responds to some degree. At any one moment, each region of the membrane has a dif-

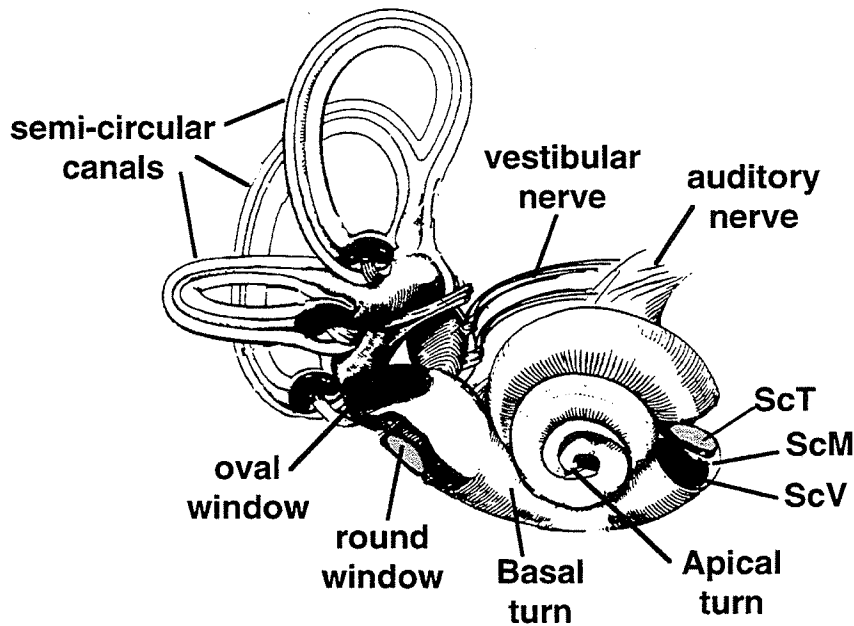


Figure 4-4. The drawing illustrates the fundamental structure of a mammalian inner ear with a 2.5 turn cochlea and 3 semicircular canals. A wedge has been removed from the basal turn to show the three chambers or scalae in the cochlea. (See Fig. 4-7 for additional intracochlear detail.) ScM, scala media; ScT, scala tympani; ScV, scala vestibuli. (Figure was redrawn to scale based on illustrations of human and guinea pig ears in Lewis et al. 1985.)

ferent amount of deflection and a different phase related to the input signal. Over time, changes in amplitude and phase at each point give the impression of a traveling response wave along the cochlea, but because the membrane segments that have resonance characteristics closest to frequencies in the signal have greater displacements than other segments of the membrane, a characteristic profile or envelope develops for the signal.

Basilar membrane dimensions vary inversely, and generally regularly, with cochlear dimensions. The highest frequency each animal hears is encoded at the base of the cochlear spiral (near the oval window), where the membrane is narrow, thick, and stiff. Moving toward the apex of the spiral, as the membrane becomes broader and more pliant, progressively lower frequencies are encoded. Therefore, mammalian basilar membranes are essentially tonotopically arranged resonator arrays, ranging high to low from base to apex, rather like a guitar with densely packed strings graded to cover multiple octaves.⁴ The ear, however, is a reverse instrument in that sound energy is the primary input rather than a product, and it is the differential tuning based on the construction of the inner ear membrane "string" array that forms the basis of hearing range differences among species.

Recall from the earlier discussion of animal size in relation to hearing that, in general, small mammals have good high frequency hearing characteristics and large mammals have comparatively low hearing ranges. Early inner ear models were based on the assumption that all mammalian basilar membranes were constructed of similar components that had a constant gradient with length and that length

scaled with animal size. On average, smaller animals were assumed to have shorter, narrower, stiffer membranes, whereas larger animals had longer, broader, less stiff membranes (von Békésy 1960; Greenwood 1961, 1990). Given that assumption, frequency distributions in the inner ear of any species could be derived by comparing one parameter, basilar membrane length, with an arbitrary standard, the average human membrane length. For many land mammals, this assumption is correct, but only because length is an indirect correlate of other key features for basilar membrane resonance. For these ears, now termed generalists (Fay 1992, Echteler et al. 1994), basilar membrane thickness and width covary regularly with length; therefore, length can proportionately represent stiffness.

Only recently has it become clear that some species, termed specialists (Echteler et al. 1994), do not have the same thickness-width-length relationship as do generalist land mammals (Manley 1972; Ketten 1984, 1997). Most specialist animals have retuned their inner ears to fit an atypical tuning for their body size by either increasing mass to improve low frequency sensitivity in small ears (as in mole rats) or adding stiffening components to increase resonant frequencies in larger inner ears (as in dolphins) (Hinchcliffe and Pye 1969, Sales and Pye 1974, Webster and Webster 1975, Ketten 1984). The most extreme case of specialization is to be found in some bats, which have relatively constant basilar membrane dimensions for about 30% of the cochlea and thereby devote a disproportionate amount of the membrane to encoding very narrow bands of frequencies related to a component of their echolocation signal (Brunns and Schmieszek 1980, Vater 1988a, Kössl and Vater 1995).

Marine mammal ears fall into both categories and some species have a mix of generalist and specialist traits. Like land mammals, pinnipeds and cetaceans have basilar membranes that scale with animal size. Consequently, because marine mammals are relatively large, most have basilar membranes longer than the human average. If marine mammal ears followed the generalist land mammal pattern, most would have relatively poor ultrasonic hearing. For example, standard land mammal length-derived hearing models (Greenwood 1961, 1990; Fay 1992) predict an upper limit of hearing of approximately 16 kHz for bottlenose dolphins (*Tursiops truncatus*), which actually have a functional high frequency hearing limit of 160 kHz (Au 1993). Before the discovery of dolphin echolocation, it was assumed that these large animals had predominately low functional hearing ranges similar to cows. Hearing is not constrained to low frequencies in marine mammals, because they have radically different inner ear thickness-width gradients than generalist land mammals. In odontocetes, very high ultrasonic hearing is related also to the presence of extensive stiffening additions to the inner ear. These features, discussed in detail later, demonstrate the usefulness of comparative audiometric and anatomical studies for teasing apart sensory mechanisms. In fact, one important outgrowth of marine mammal hearing studies has been the development of multifeature hearing models that are better predictors of hearing characteristics for all mammals than traditional, single-dimension models (Ketten 1994).

Marine Mammal Sound Production

Recordings of naturally produced sounds are available for most marine mammal species (Watkins and Wartzok 1985), and they provide the broadest acoustic framework for hearing comparisons. Sound production data obtained in a wide variety of background noise conditions cannot be used to infer hearing thresholds because it is likely that produced sound levels are elevated over minimum audible levels to override background noise. For example, some recordings of odontocete and mysticete sounds have source levels estimated to be as high as 180 to 230 dB re 1 μ Pa (Richardson et al. 1991, Au 1993, Würsig and Clark 1993). However, because mammalian vocalizations typically have peak spectra at or near the best frequency for that species, they are generally good indirect indicators of frequencies the animal normally hears well (Sales and Pye 1974, Popper 1980, Watkins and Wartzok 1985, Henson et al. 1990, Ketten and Wartzok 1990, Popov and Supin 1990a). A classic example is the discovery of ultrasonic signal use by dolphins (Kellogg 1959, Norris et al. 1961), which prompted several decades of investigations into

echolocation and ultrasonic hearing abilities in marine mammals.

Cetaceans

Cetaceans can be divided into high and low frequency sound producers, which are coincident with the two suborders (Table 4-1). Sound production data for odontocetes are consistent with the audiometric data (i.e., ultrasonic use is common and differences in peak spectra of produced sounds are consistent with best frequency of hearing in species that have been tested) (compare Table 4-1 and Fig. 4-5A). Mysticete sound production data imply they are primarily low frequency animals, and it is likely that many baleen species hear well at infrasonic frequencies.

Odontocetes produce species-stereotypic broadband clicks with peak energy between 10 and 200 kHz, individually variable burst pulse click trains, and constant frequency (CF) or frequency modulated (FM) whistles ranging from 4 to 16 kHz (see Tyack, Chapter 7, this volume). Ultrasonic signals are highly species specific and have been recorded from 21 species, although echolocation (or "biosonar") has been demonstrated in only 11 species of smaller odontocetes (Au 1993). All modern odontocetes are assumed, like bats, to be true echolocators, not simply ultrasonic receptors. That is, they "image" their environment by analyzing echoes from a self-generated ultrasonic signal (Kellogg 1959, Norris et al. 1961, Popper 1980, Wood and Evans 1980, Pilleri 1983, Watkins and Wartzok 1985). Echolocation is a two-way function; to be an effective echolocator, an animal must have a coordinated means of generating a highly directional signal and receiving its echo. For this reason, evidence for high frequency ears alone is not sufficient to determine whether any marine mammal (or fossil species) is an echolocator.

Captive odontocetes routinely vary pulse repetition rate, interpulse interval, intensity, and click spectra, particularly in response to high ambient noise (Schevill 1964, Norris 1969, Au et al. 1974, Popper 1980, Thomas et al. 1988, Moore 1990, Popov and Supin 1990a). Normally, however, each species has a characteristic echolocation frequency spectrum (Schevill 1964, Norris 1969, Popper 1980). Well-documented peak spectra of odontocete sonar signals range from approximately 20 kHz up to 160 kHz with source levels as high as 228 dB, but more commonly in range of 120 to 180 dB (Table 4-1).

There are strong correlations between habitat types, societal differences, and peak spectra (Gaskin 1976, Wood and Evans 1980, Ketten 1984). Considering that frequency and wavelength are inversely related, there is an inverse relationship between frequency and the size of the object or detail that can be detected with echolocation. On the basis of their

Table 4-1. Marine Mammal Sound Production Characteristics

Scientific Name	Common Name	Signal Type	Frequency Range (kHz)	Frequency Near Maximum Energy (kHz)	Source Level (dB re 1 μ Pa)	References (Partial references only for some species)
Cetacea						
Odontoceti						
Delphinidae						
<i>Cephalorhynchus commersonii</i>	Commerson's dolphin	Pulsed sounds	< 10	0.2-5	—	Watkins and Schevill 1980, Dziedzic and de Buffrenil 1989
		Clicks	—	6	—	Dziedzic and de Buffrenil 1989
		Click	—	116-134	160	Kamminga and Wiersma 1981, Shochi et al. 1982, Evans et al. 1988, Au 1993
<i>C. heavisidii</i>	Heaviside's dolphin	Pulsed sounds	0.8-5 ^a	0.8-4.5 ^a	—	Watkins et al. 1977
		Click	—	2-5	—	Watkins et al. 1977
<i>C. hectori</i>	Hector's dolphin	Click	—	112-135	150-163	Dawson 1988, Dawson and Thorpe 1990, Au 1993
<i>Delphinus delphis</i>	Common dolphin	Whistles, chirps, Barks	—	0.5-18	—	Caldwell and Caldwell 1968, Moore and Ridgway 1995
		Whistles	4-16	—	—	Busnel and Dziedzic 1966a
		Click	0.2-150	30-60	—	Busnel and Dziedzic 1966a
		Click	—	23-67	—	Dziedzic 1978
<i>Feresa attenuata</i>	Pygmy killer whale	Growls, Blats	—	—	—	Pryor et al. 1965
<i>Globicephala macrorhynchus</i>	Short-finned pilot whale	Whistles	0.5-> 20	2-14	180	Caldwell and Caldwell 1969, Fish and Turl 1976
		Click	—	30-60	180	Evans 1973
<i>G. melaena</i>	Long-finned pilot whale	Whistles	1-8	1.6-6.7 ^b	—	Busnel and Dziedzic 1966a
		Clicks	1-18	—	—	Taruski 1979, Steiner 1981
		Click	—	6-11	—	McLeod 1986
<i>Grampus griseus</i>	Risso's dolphin	Whistles	—	3.5-4.5	—	Caldwell et al. 1969
		Rasp/pulse burst	0.1-> 8 ^c	2-5	—	Watkins 1967
		Click	—	65	~120	Au 1993
<i>Lagenodelphis hosei</i>	Fraser's dolphin	Whistles	7.6-13.4	—	—	Leatherwood et al. 1993
<i>Lagenorhynchus acutus</i>	Atlantic white-sided dolphin	Whistles	—	6-15 ^b	—	Steiner 1981
<i>L. albirostris</i>	White-beaked dolphin	Squeals	—	8-12	—	Watkins and Schevill 1972
<i>L. australis</i>	Peale's dolphin	Pulses (buzz)	0.3-5	0.3	—	Shevill and Watkins 1971
		Clicks	to 12	to 5	Low	Shevill and Watkins 1971
<i>L. obliquidens</i>	Pacific white-sided dolphin	Whistles	2-20	4-12	—	Caldwell and Caldwell 1971
		Click	—	60-80	180	Evans 1973
<i>L. obscurus</i>	Dusky dolphin	Whistles	1.0-27.3	6.4-19.2 ^b	—	Wang Ding et al. 1995
<i>Lissodelphis borealis</i>	Northern right whale dolphin	Whistles, tones	1-16	1.8, 3	—	Leatherwood and Walker 1979
<i>Orcinus orca</i>	Killer whale	Whistles	1.5-18	6-12	—	Steiner et al. 1979, Ford and Fisher 1983, Morton et al. 1986
		Click	0.25-0.5	—	—	Shevill and Watkins 1966
		Scream	2	—	—	Shevill and Watkins 1966
		Click	0.1-35	12-25	180	Diercks et al. 1971, Diercks 1972
		Pulsed calls	0.5-25	1-6	160	Shevill and Watkins 1966, Awbrey et al. 1982, Ford and Fisher 1983, Moore et al. 1988
<i>Pseudorca crassidens</i>	False killer whale	Whistles	—	4-9.5	—	Busnel and Dziedzic 1968, Kamminga and van Velden 1987
		Click	—	25-30, 95-130	220-228	Kamminga and van Velden 1987, Thomas and Turl 1990

Table 4-1 continued

Scientific Name	Common Name	Signal Type	Frequency Range (kHz)	Frequency Near Maximum Energy (kHz)	Source Level (dB re 1 μ Pa)	References (Partial references only for some species)
<i>Sotalia fluviatilis</i>	Tucuxi	Whistles	3.6–23.9	7.1–18.5 ^b	—	Wang Ding et al. 1995
		Click	—	80–100	High	Caldwell and Caldwell 1970, Norris et al. 1972, Kamminga et al. 1993
<i>Sousa chinensis</i>	Humpback dolphin	Whistles	1.2–>16	—	—	Schultz and Corkeron 1994
<i>Stenella attenuata</i>	Spotted dolphin	Whistles	3.1–21.4	6.7–17.8 ^b	—	Wang Ding et al. 1995
		Whistles	—	—	—	Evans 1967
		Pulse	to 150	—	—	Diercks 1972
<i>S. clymene</i>	Clymene dolphin	Whistles	6.3–19.2	—	—	Mullin et al. 1994
<i>S. coeruleoalba</i>	Spinner dolphin	Whistles	1–22.5	6.8–16.9 ^b	109–125	Watkins and Schevill 1974, Steiner 1981, Norris et al. 1994, Wang Ding et al. 1995
		Pulse bursts	Wide band	5–60	108–115	Watkins and Schevill 1974, Norris et al. 1994
		Screams	—	—	—	Norris et al. 1994
<i>S. longirostris</i>	Long-snouted spinner dolphin	Pulse	1–160	5–60	—	Brownlee 1983
		Whistle	1–20	8–12	—	Brownlee 1983
		Click	—	low– 65	—	Watkins and Schevill 1974, Norris et al. 1994
<i>S. plagiodon</i>	Spotted dolphin	Click	1–160	60	—	Ketten 1984
		Whistles	5.0–19.8	6.7–17.9 ^b	—	Caldwell et al. 1973, Steiner 1981
		Clicks	1–8	—	—	Caldwell and Caldwell 1971b
<i>S. styx</i>	Gray's porpoise	Squawks, barks, growls, chirps	0.1–8	—	—	Caldwell et al. 1973
		Whistles	6–> 24	8–12.5	—	Busnel et al. 1968
<i>Steno bredanensis</i>	Rough-toothed dolphin	Whistles	—	4–7	—	Busnel and Dziedzic 1966b
		Click	—	5–32	—	Norris and Evans 1967
<i>Tursiops truncatus</i>	Bottlenosed dolphin	Whistles	0.8–24	3.5–14.5 ^b	125–173	Lilly and Miller 1961, Tyack 1985, Caldwell et al. 1990, Schultz and Corkeron 1994, Wang Ding et al. 1995
		Rasp, grate, mew, bark, yelp	—	—	—	Wood 1953
		Click	0.2–150	30–60	—	Diercks et al. 1971, Evans 1973
		Bark	0.2–16	—	—	Evans and Prescott 1962
		Whistle	4–20	—	—	Caldwell and Caldwell 1967, Evans and Prescott 1962
		Click ^d	—	110–130	218–228	Au et al. 1974, Au 1993
Monodontidae	<i>Delphinapterus leucas</i>	Whistles	0.26–20	2–5.9	—	Shevill and Lawrence 1949, Sjare and Smith 1986a,b
		Pulsed tones	0.4–12	1–8	—	Shevill and Lawrence 1949, Sjare and Smith 1986a,b
		Noisy vocalizations	0.5–16	4.2–8.3	—	Shevill and Lawrence 1949, Sjare and Smith 1986a,b
		Echolocation click	—	40–60, 100–120	206–225	Au et al. 1985, 1987, Au 1993
<i>Monodon monoceros</i>	Narwhal	Pulsed tones	0.5–5	—	—	Ford and Fisher 1978
		Whistles	0.3–18	0.3–10	—	Ford and Fisher 1978
		Click	—	40	218	Møhl et al. 1990
Phocoenidae	<i>Neophocaena phocaenoides</i>	Clicks	1.6–2.2	2	—	Pilleri et al. 1980
		Click	—	128	—	Kamminga et al. 1986, Kamminga 1988

Continued on next page

Table 4-1 continued

Scientific Name	Common Name	Signal Type	Frequency Range (kHz)	Frequency Near Maximum Energy (kHz)	Source Level (dB re 1 μ Pa)	References (Partial references only for some species)
<i>Phocoenoides dalli</i>	Dall's porpoise	Clicks	0.04-12	—	120-148	Evans 1973, Evans and Awbrey 1984
		Click	—	135-149	165-175	Evans and Awbrey 1984, Hatakeyama and Soeda 1990, Hatakeyama et al. 1994
<i>Phocoena phocoena</i>	Harbor porpoise	Clicks	2	—	100	Busnel and Dziedzic 1966a, Schevill et al. 1969
		Pulse	100-160	110-150	—	Møhl and Anderson 1973
		Click	—	110-150	135-177	Busnel et al. 1965, Møhl and Anderson 1973, Kamminga and Wiersma 1981, Akamatsu et al. 1994
<i>P. sinus</i>	Vaquita	Click	—	128-139	—	Silber 1991
Physeteridae						
<i>Kogia breviceps</i>	Pygmy sperm whale	Clicks	60-200	120	—	Santoro et al. 1989, Caldwell and Caldwell 1987
<i>Physeter catodon</i>	Sperm whale	Clicks	0.1-30	2-4, 10-16	160-180	Backus and Schevill 1966, Levenson 1974, Watkins 1980a,b
		Clicks in coda	16-30	—	—	Watkins 1980a,b
Platanistoidea						
Iniidae						
<i>Inia geoffrensis</i>	Boutu	Squeals	< 1-12	1-2	—	Caldwell and Caldwell 1970
		Whistle	0.2-5.2	1.8-3.8 ^b	—	Wang Ding et al. 1995
		Click	25-200	100	—	Norris et al. 1972
		Click	—	95-105	—	Kamminga et al. 1989
		Click	—	85-105	—	Diercks et al. 1971, Evans 1973, Kamminga et al. 1993
<i>Inia geoffrensis</i>	Boutu	Click	20-120	—	156	Xiao and Jing 1989
		Click	—	—	—	—
Platanistidae						
<i>Platanista minor</i>	Indus susu	Clicks	0.8-16	—	Low	Andersen and Pilleri 1970, Pilleri et al. 1971
		Click	—	15-100	—	Herald et al. 1969
Pontoporiidae						
<i>Lipotes vexillifer</i>	Baiji	Whistles	3-18.4	6	156	Jing et al. 1981, Xiao and Jing 1989
<i>Pontoporia blainvilliei</i>	Franciscana	Click	0.3-24	—	—	Busnel et al. 1974
Ziphiidae						
<i>Hyperoodon ampullatus</i>	Northern bottle-nose whale	Whistles	3-16	—	—	Winn et al. 1970
		Clicks	0.5-26	—	—	Winn et al. 1970
<i>Hyperoodon</i> spp.	Bottlenose whale	Click	—	8-12	—	Winn et al. 1970
<i>Mesoplodon carlhubbsi</i>	Hubb's beaked whale	Pulses	0.3-80	0.3-2	—	Buerki et al. 1989, Lynn and Reiss 1992
<i>M. densirostris</i>	Blainville's beaked whale	Whistles, chirps	<1-6	—	—	Caldwell and Caldwell 1971a
		Whistles	2.6-10.7	—	—	Buerki et al. 1989, Lynn and Reiss 1992
Mysticeti						
Balaenidae						
<i>Balaena mysticetus</i>	Bowhead whale	Calls	0.100-0.580	0.14-0.16	128-190	Thompson et al. 1979, Ljungblad et al. 1980, Norris and Leatherwood 1981, Würsig and Clark 1993
		Tonal moans	0.025-0.900	0.10-0.40	128-178	Ljungblad et al. 1982, Cummings and Holliday 1987, Clark et al. 1986

Table 4-1 continued

Scientific Name	Common Name	Signal Type	Frequency Range (kHz)	Frequency Near Maximum Energy (kHz)	Source Level (dB re 1 μ Pa)	References (Partial references only for some species)
<i>Balaena mysticetus</i>	Bowhead whale	Pulsive	0.025–3.500	—	152–185	Clark and Johnson 1984, Würsig et al. 1985, Cummings and Holliday 1987
		Song	0.02–0.50	< 4	158–189	Ljungblad et al. 1982, Cummings and Holliday 1987, Würsig and Clark 1993
<i>Eubalaena australis</i>	Southern right whale	Tonal	0.03–1.25	0.16–0.50	—	Cummings et al. 1972, Clark 1982, 1983
		Pulsive	0.03–2.20	0.05–0.50	172–187 181–186	Cummings et al. 1972, Clark 1982, 1983 Clark (in Würsig et al. 1982)
<i>E. glacialis</i>	Northern right whale	Call	< 0.400	< 0.200	—	Watkins and Schevill 1972, Clark 1990
		Moans	< 0.400	—	—	Watkins and Schevill 1972, Thompson et al. 1979, Spero 1981
Neobalaenidae						
<i>Caperea marginata</i>	Pygmy right whale	Thumps in pairs	<0.300	0.060–0.135	165–179	Dawbin and Cato 1992
Balaenopteridae						
<i>Balaenoptera acutorostrata</i>	Minke whale	Sweeps, moans	0.06–0.14	—	151–175	Winn and Perkins 1976, Schevill and Watkins 1972
		Down sweeps	0.06–0.13	—	165	Schevill and Watkins 1972
		Moans, grunts	0.06–0.14	0.06–0.14	151–175	Schevill and Watkins 1972, Winn and Perkins 1976
		Ratchet	0.85–6	0.85	—	Winn and Perkins 1976
<i>B. borealis</i>	Sei whale	Thump trains	0.10–2	0.10–0.20	—	Winn and Perkins 1976
		Fm sweeps	1.5–3.5	—	—	Thompson et al. 1979, Knowlton et al. 1991
<i>B. edeni</i>	Bryde's whale	Moans	0.070–0.245	0.124–0.132	152–174	Cummings et al. 1986
		Pulsed moans	0.10–0.93	0.165–0.900	—	Edds et al. 1993
		Discrete pulses	0.70–0.95	0.700–0.900	—	Edds et al. 1993
<i>B. musculus</i>	Blue whale	Moans	0.012–0.400	0.012–0.025	188	Cummings and Thompson 1971, 1994, Edds 1982, Stafford et al. 1994
<i>B. physalus</i>	Fin whale	Moans	0.016–0.750	0.020	160–190	Thompson et al. 1979, Edds 1988
		Pulse	0.040–0.075	—	—	Clark 1990
		Pulse	0.018–0.025	0.020	—	Watkins 1981
		Ragged pulse	< 0.030	—	—	Watkins 1981
		Rumble	—	< 0.030	—	Watkins 1981
		Moans, down-sweeps	0.014–0.118	0.020	160–186	Watkins 1981, Watkins et al. 1987, Edds 1988, Cummings and Thompson 1994
		Constant call	0.02–0.04	—	—	Edds 1988
		Moans, tones, upsweeps	0.03–0.75	—	155–165	Watkins 1981, Cummings et al. 1986, Edds 1988
		Rumble	0.01–0.03	—	—	Watkins 1981, Edds 1988
		Whistles ^f , chirps ^f	1.5–5	1.5–2.5	—	Thompson et al. 1979
		Clicks ^f	16–28	—	—	Thompson et al. 1979
<i>Megaptera novaeangliae</i>	Humpback whale	Songs	0.03–8	0.1–4	144–186	Thompson et al. 1979, Watkins 1981, Edds 1982, 1988, Payne et al. 1983, Silber 1986, Clark 1990
		Social	0.05–10	< 3	—	Thompson et al. 1979
		Song components	0.03–8	0.120–4	144–174	Thompson et al. 1979, Payne and Payne 1985
		Shrieks	—	0.750–1.8	179–181	Thompson et al. 1986
		Horn blasts	—	0.410–0.420	181–185	Thompson et al. 1986
		Moans	0.02–1.8	0.035–0.360	175	Thompson et al. 1986
		Grunts	0.025–1.9	—	190	Thompson et al. 1986

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Table 4-1 continued

Scientific Name	Common Name	Signal Type	Frequency Range (kHz)	Frequency Near Maximum Energy (kHz)	Source Level (dB re 1 μ Pa)	References (Partial references only for some species)
<i>Megaptera novaeangliae</i>	Humpback whale	Pulse trains	0.025-1.25	0.025-0.080	179-181	Thompson et al. 1986
		Slap	0.03-1.2	—	183-192	Thompson et al. 1986
Eschrichtiidae						
<i>Eschrichtius robustus</i>	Gray whale	Call	0.2-2.5	1-1.5	—	Dahlheim and Ljungblad 1990
		Moans	0.02-1.20	0.020-0.200, 0.700-1.2	185	Cummings et al. 1968, Fish et al. 1974, Swartz and Cummings 1978
		Modulated pulse	0.08-1.8	0.225-0.600	—	Dahlheim et al. 1984, Moore and Ljungblad 1984
		FM sweep	0.10-0.35	0.300	—	Dahlheim et al. 1984, Moore and Ljungblad 1984
		Pulses	0.10-2	0.300-0.825	—	Dahlheim et al. 1984, Moore and Ljungblad 1984
		Clicks (calves)	0.10-20	3.4-4	—	Fish et al. 1974, Norris et al. 1977
Fissipedia Mustelidae						
<i>Enhydra lutris</i>	Sea otter	Growls ^c , whine	3-5	—	—	Kenyon 1981, Richardson et al. 1995
Pinnipedia Odobenidae						
<i>Odobenus rosmarus</i>	Walrus	Bell tone	—	0.4-1.2	—	Schevill et al. 1966, Ray and Watkins 1975, Stirling et al. 1983
		Clicks, taps, knocks	0.1-10	< 2	—	Schevill et al. 1966, Ray and Watkins 1975, Stirling et al. 1983
		Rasps	0.2-0.6	0.4-0.6	—	Schevill et al. 1966
		Grunts	≤ 1	$\leq L$	—	Stirling et al. 1983
Otariidae						
<i>Arctocephalus philippii</i>	Juan Fernandez fur seal	Clicks	0.1-0.2	0.1-0.2	—	Norris and Watkins 1971
<i>Callorhinus ursinus</i>	Northern fur seal	Clicks, bleats	—	—	—	Poulter 1968
<i>Eumetopias jubatus</i>	Northern sea lion	Clicks, growls	—	—	—	Poulter 1968
<i>Zalophus californianus</i>	California sea lion	Barks	<8	<3.5	—	Schusterman et al. 1967
		Whinny	<1-3	—	—	Schusterman et al. 1967
		Clicks	—	0.5-4	—	Schusterman et al. 1967
		Buzzing	< 1-4	< 1	—	Schusterman et al. 1967
Phocidae						
<i>Cystophora cristata</i>	Hooded seal	Grunt	—	0.2-0.4	—	Terhune and Ronald 1973
		Snort	—	0.1-1	—	Terhune and Ronald 1973
		Buzz, click	to 6	1.2	—	Terhune and Ronald 1973
<i>Erignathus barbatus</i>	Bearded seal	Song	0.02-6	1-2	178	Ray et al. 1969, Stirling et al. 1983, Cummings et al. 1983
<i>Halichoerus grypus</i>	Gray seal	Clicks, hiss	0-30, 0-40	—	—	Schevill et al. 1963, Oliver 1978
		6 Calls	0.1-5	0.1-3	—	Asselin et al. 1993
		Knocks	to 16	To 10	—	Asselin et al. 1993
<i>Hydrurga leptonyx</i>	Leopard seal	Pulses, trills	0.1-5.9	—	—	Ray 1970, Stirling and Siniff 1979, Rogers et al. 1995
		Thump, blast	0.04-7	—	—	Rogers et al. 1995
		Ultrasonic	up to 164	50-60	Low	Thomas et al. 1983a

Table 4-1 continued

Scientific Name	Common Name	Signal Type	Frequency Range (kHz)	Frequency Near Maximum Energy (kHz)	Source Level (dB re 1 μ Pa)	References (Partial references only for some species)
<i>Leptonychotes weddellii</i>	Weddell seal	>34 Calls	0.1–12.8	—	153–193	Thomas and Kuechle 1982, Thomas et al. 1983b, Thomas and Stirling 1983
<i>Lobodon carcinophagus</i>	Crabeater seal	Groan	<0.1–8	0.1–1.5	High	Stirling and Siniff 1979
<i>Ommatophoca rossii</i>	Ross seal	Pulses	0.25–1	—	—	Watkins and Ray 1985
<i>Phoca fasciata</i>	Ribbon seal	Siren	4–1–4	—	—	Watkins and Ray 1985
		Frequency sweeps	0.1–7.1	—	160	Watkins and Ray 1977
<i>P. groenlandica</i>	Harp seal	15 sounds	<0.1–16	0.1–3	130–140	Møhl et al. 1975, Watkins and Schevill 1979, Terhune and Ronald 1986, Terhune 1994
<i>P. hispida</i>	Ringed seal	Clicks	—	30	131–164	Møhl et al. 1975
		Barks, clicks, yelps	0.4–16	<5	95–130	Stirling 1973, Cummings et al. 1984
<i>P. largha</i>	Spotted seal	Social sounds	0.5–3.5	—	—	Beier and Wartzok 1979
<i>P. vitulina</i>	Harbor seal	Clicks	8–150	12–40	—	Schevill et al. 1963, Cummings and Fish 1971, Renouf et al. 1980, Noseworthy et al. 1989
		Roar	0.4–4	0.4–0.8	—	Hanggi and Schusterman 1992, 1994
		Growl, grunt, groan	< 0.1–0.4	< 0.1–0.25	—	Hanggi and Schusterman 1992, 1994
		Creak	0.7–4	0.7–2	—	Hanggi and Schusterman 1992, 1994
Sirenia						
Dugongidae						
<i>Dugong dugon</i>	Dugong	Chirp-squeak ^d	3–8	—	Low	Nair and Lal Mohan 1975
		Sound 1 ^e	1–2	—	—	Marsh et al. 1978
		Chirp ^e	2–4	—	—	Marsh et al. 1978
		All sounds	0.5–18	1–8	—	Nishiwaki and Marsh 1985, Anderson and Barclay 1995
Trichechidae						
<i>Trichechus inunguis</i>	Amazonian manatee	Squeaks, pulses	6–16	6–16	—	Evans and Herald 1970
<i>T. manatus</i>	West Indian manatee	Squeaks	0.6–16	0.6–5	Low	Schevill and Watkins 1965

Data compiled from Popper 1980, Watkins and Wartzok 1985, Ketten 1992, Au 1993, Richardson *et al.* 1995, Ketten 1997.

^aEquipment capable of recording to 10 kHz only.

^bFrequency determined as "mean minimum frequency minus 1 sd . . . to . . . mean maximum frequency plus 1 sd." (*sensu* Richardson *et al.* 1995).

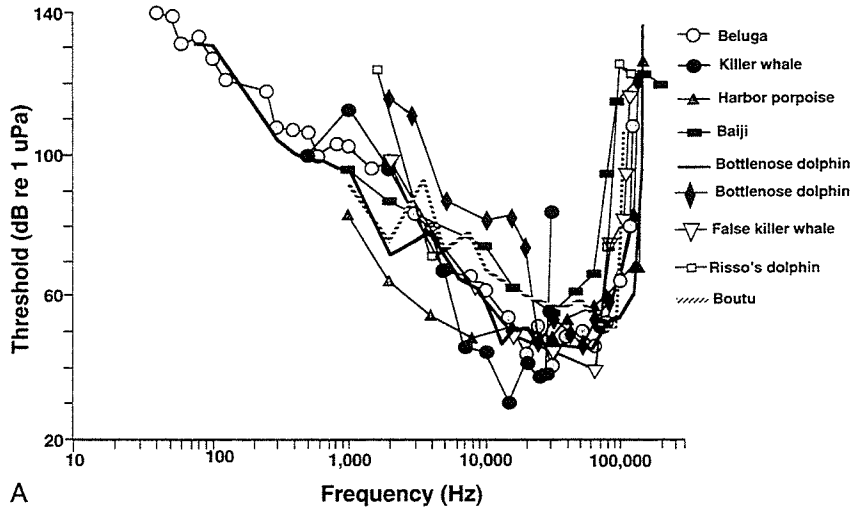
^cRecorded in air.

^dPerformance in high background noise (Au 1993)

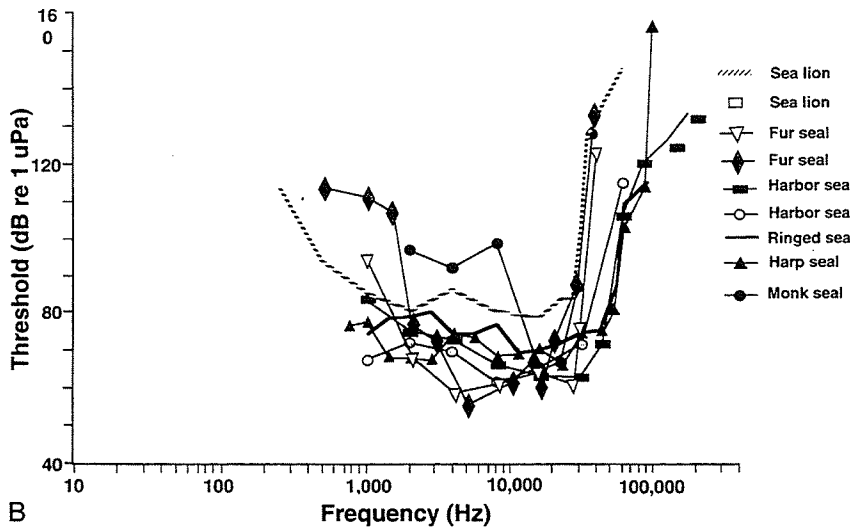
^eFew recordings or uncertain verification of sound for species.

ultrasonic signals, odontocetes fall into two acoustic groups: Type I, with peak spectra (frequencies at maximum energy) above 100 kHz, and Type II, with peak spectra below 80 kHz (Ketten 1984, Ketten and Wartzok 1990) (Table 4-1). Type I echolocators are inshore and riverine dolphins that operate in acoustically complex waters. Amazonian bottlenose (*Inia geoffrensis*) routinely hunt small fish amid the roots and stems choking silted "varzea" lakes created by seasonal flooding. These animals produce signals up to 200 kHz (Norris *et al.* 1972). Harbor porpoises typically use 110 to 140 kHz signals

(Kamminga 1988). Communication signals are rare (or are rarely observed) in most type I species (Watkins and Wartzok 1985); their auditory systems are characterized primarily by ultra-high frequency adaptations consistent with short wavelength signals. Type II species are nearshore and offshore animals that inhabit low object density environments, travel in large pods, and, acoustically, are concerned with both communication with conspecifics and detection of relatively large, distant objects. They may use ultra high frequency signals in high background noise, but typically



A



B

Figure 4-5. Underwater audiograms for (A) odontocetes and (B) pinnipeds. For some species, more than one curve is shown because data reported in different studies were not consistent. Note that for both the bottlenose dolphin and the sea lion, thresholds are distinctly higher for one of the two animals tested. These differences may reflect different test conditions or a hearing deficit in one of the animals. (Data compiled from Popper 1980, Fay 1988, Au 1993, Richardson et al. 1995.)

they use lower ultrasonic frequencies with longer wavelengths that are consistent with detecting larger objects over greater distances and devote more acoustic effort to communication signals than Type I species.

Use of deep ocean stationary arrays has substantially increased our database of mysticete sounds. Recent analyses suggest that mysticetes have multiple, distinct sound production groups, but habitat and functional relationships for the potential groupings are not yet clear (Würsig and Clark 1993; for review, see Edds-Walton 1997). In general, mysticete vocalizations are significantly lower in frequency than those of odontocetes (Table 4-1). Most mysticete signals are characterized as low frequency moans (0.4–40 sec; funda-

mental frequency well below 200 Hz); simple calls (impulsive, narrow band, peak frequency < 1 kHz); complex calls (broadband pulsatile AM or FM signals); and complex “songs” with seasonal variations in phrasing and spectra (Thompson et al. 1979; Watkins 1981; Edds 1982, 1988; Payne et al. 1983; Watkins and Wartzok 1985; Silber 1986; Clark 1990; Dahlheim and Ljungblad 1990). Infrasonic signals, typically in the 10- to 16-Hz range, are well-documented in at least two species, the blue whale (*Balaenoptera musculus*) (Cummings and Thompson 1971, Edds 1982), and the fin whale (*Balaenoptera physalus*) (Watkins 1981; Edds 1982, 1988; Watkins et al. 1987). Suggestions that these low frequency signals are used for long-distance

communication and for topological imaging are intriguing but have not been definitively demonstrated.

Pinnipeds

The majority of pinniped sounds are in the sonic range (20 Hz – 20 kHz), but their signal characteristics are extremely diverse (compare Table 4-1 with Fig. 4-5B). Some species are nearly silent, others have broad ranges and repertoires, and the form and rate of production vary seasonally, by sex, and whether the animal is in water or air (Watkins and Wartzok 1985, Richardson et al. 1995). Calls have been described as grunts, barks, rasps, rattles, growls, creaky doors, and warbles in addition to the more conventional whistles, clicks, and pulses (Beier and Wartzok 1979, Ralls et al. 1985, Watkins and Wartzok 1985, Miller and Job 1992). Although clicks are produced, there is no clear evidence for echolocation in pinnipeds (Renouf et al. 1980, Schusterman 1981, Wartzok et al. 1984).

Phocid calls are commonly between 100 Hz and 15 kHz, with peak spectra less than 5 kHz, but can range as high as 40 kHz. Typical source levels in water are estimated to be near 130 dB re 1 μ Pa, but levels as high as 193 dB re 1 μ Pa have been reported (Richardson et al. 1995). Infrasonic to seismic level vibrations are produced by northern elephant seals (*Mirounga angustirostris*) while vocalizing in air (Shipley et al. 1992).

Otariid calls are similarly variable in type, but most are in the 1 to 4 kHz range. The majority of sounds that have been analyzed are associated with social behaviors. Barks in water have slightly higher peak spectra than in air, although both center near 1.5 kHz. In-air harmonics that may be important in communication range up to 6 kHz. Schusterman et al. (1972), in their investigation of female California sea lion (*Zalophus californianus*) signature calls, found important interindividual variations in call structure and showed that the calls have fundamental range characteristics consistent with peak in-air hearing sensitivities.

Odobenid sounds are generally in the low sonic range (fundamentals near 500 Hz; peak < 2 kHz), and are commonly described as bell-like although whistles are also reported (Schevill et al. 1966, Ray and Watkins 1975, Verboom and Kastelein 1995).

Sirenians

Manatee (*Trichechus manatus* and *T. inunguis*) and dugong (*Dugong dugon*) underwater sounds have been described as squeals, whistles, chirps, barks, trills, squeaks, and froglike calls (Sonoda and Takemura 1973, Anderson and Barclay 1995, Richardson et al. 1995) (Table 4-1). West Indian manatee (*Trichechus manatus*) calls typically range from 0.6 to 5

kHz (Schevill and Watkins 1965). Calls of Amazonian manatees (*Trichechus inunguis*), a smaller species than the Florida manatee (a subspecies of *T. manatus*), are slightly higher with peak spectra near 10 kHz, although distress calls have been reported to have harmonics up to 35 kHz (Bullock et al. 1980). Dugong calls range from 0.5 to 18 kHz with peak spectra between 1 and 8 kHz (Nishiwaki and Marsh 1985, Anderson and Barclay 1995).

Fissipeds

Descriptions of otter sounds are similar to those for pinnipeds and for terrestrial carnivores (Table 4-1) (i.e., growls, whines, snarls, and chuckles) (Kenyon 1981). Richardson et al. (1995) state that underwater sound production analyses are not available but that in-air calls are in the 3- to 5-kHz range and are relatively intense.

In Vivo Marine Mammal Hearing Data

As indicated in the introductory sections, hearing capacity is usually expressed as an audiogram, a plot of sensitivity (threshold level in dB SPL in air and dB re 1 μ Pa in water) versus frequency (Figs. 4-2 and 4-5), which is obtained by behavioral or electrophysiological measures of hearing.

Mammals typically have a U-shaped hearing curve. Sensitivity decreases on either side of a relatively narrow band of frequencies at which hearing is significantly more acute. The rate of decrease in sensitivity is generally steeper above this best frequency or peak sensitivity region than below. Behavioral and neurophysiological hearing curves are generally similar, although behavioral audiograms typically have lower thresholds for peak sensitivities (Dallos et al. 1978). Interindividual and intertrial differences in audiograms may be related to variety of sources, including ear health, anesthesia, masking by other sounds, timing, and anticipation by the subject.

Hearing curves are available for approximately 12 species of marine mammals. All have the same basic U-shaped pattern as land mammal curves (compare Fig. 4-5A,B with Fig. 4-2). As noted earlier, peak sensitivities are generally consistent with the vocalization data in those species for which both data sets are available (compare Table 4-1 with Fig. 4-5A,B). Detailed reviews of data for specific marine mammal groups are available in Bullock and Gurevich (1979), McCormick et al. (1980), Popper (1980), Schusterman (1981), Watkins and Wartzok (1985), Fay (1988), Awbrey (1990), Au (1993), and Richardson et al. (1995). Data discussed here for cetaceans and sirenians are limited to underwater measures. Most pinnipeds are in effect "amphibious" hearers in that they operate and presumably use sound in both air and

water; therefore, data are included from both media where available. No published audiometric data are available for mysticetes, marine otters (*Lutra felina* and *Enhydra lutris*), or polar bears (*Ursus maritimus*).

Cetaceans

Electrophysiological and behavioral audiograms are available for seven odontocete species (Au 1993), most of which are Type II delphinids with peak sensitivity in the 40- to 80-kHz range. Data, generally from one individual, are available also for beluga whales (*Delphinapterus leucas*), bottlenose, and harbor porpoise. There are no published audiograms for adult physeterids or ziphiids, or any mysticete. The available data indicate that odontocetes tend to have at least a 10-octave functional hearing range, compared with 8 to 9 octaves in the majority of mammals. Best sensitivities range from 12 kHz in killer whales (Schevill and Watkins 1966, Hall and Johnson 1971) to more than 100 kHz in bottlenose and harbor porpoise (Møhl and Andersen 1973, Voronov and Stosman 1977, Supin and Popov 1990).

Until recently, most odontocete audiometric work was directed at understanding echolocation abilities rather than underwater hearing per se. Therefore, much of what is known about odontocete hearing is related to ultrasonic abilities. Acuity measures commonly used in these studies include operational signal strength, angular resolution, and difference limens. The first two are self explanatory. Difference limens (DL) are a measure of frequency discrimination based on the ability to differentiate between two frequencies or whether a single frequency is modulated. Difference limens are usually reported simply in terms of Hz or as relative difference limens (rdl), which are calculated as a percent equal to 100 times the DL in Hz/frequency. Au (1990) found that echolocation performance in bottlenose dolphins was 6 to 8 dB poorer than that expected from an optimal receiver. Target detection thresholds as small as 5 cm at 5 m have been reported, implying an auditory angular resolution ability of 0.5°, although most data suggest 1° to 4° for horizontal and vertical resolutions are more common (Bullock and Gurevich 1979, Popper 1980, Au 1990). Minimal intensity discrimination in bottlenose dolphins (1 dB) is equal to human values; temporal discrimination (≈8% of signal duration) is superior to human abilities. Frequency discrimination in bottlenose dolphins varies from 0.28% to 1.4% rdl for frequencies between 1 and 140 kHz; best values are found between 5 and 60 kHz (Popper 1980). These values are similar to those of microchiropteran bats and superior to the human average (Grinnell 1963, Simmons 1973, Sales and Pye 1974, Long 1980, Pollack 1980, Popper 1980, Watkins and Wartzok 1985). Frequency discrimination and angular resolutions in harbor porpoises (0.1% to 0.2% rdl; 0.5° to 1°

are on average better than those for bottlenose dolphins (Popper 1980).

An important aspect of any sensory system for survival is the ability to detect relevant signals amidst background noise. Critical bands and critical ratios are two measures of the ability to detect signals embedded in noise. In hearing studies, the term masking refers to the phenomenon in which one sound eliminates or degrades the perception of another (for a detailed discussion, see Yost 1994). To measure a critical band, a test signal, the target (usually a pure tone), and a competing signal, the masker, are presented simultaneously. Fletcher (1940) showed that as the bandwidth of the masker narrows, the target suddenly becomes easier to detect. The critical band (CB) is the bandwidth at that point expressed as a percent of the center frequency. If the ear's frequency resolution is relatively poor, there is a broad skirt of frequencies around the target tone that can mask it, and the CB is large. If the ear has relatively good frequency resolution, the CB is relatively narrow. Critical ratios (CR) are a comparison of the signal power required for target detection versus noise power, and are simply calculated as the threshold level of the target in noise (in dB) minus the masker level (dB). Critical bands tend to be a constant function of the CRs throughout an animal's functional hearing range. Consequently, CR measures with white noise, which are easier to obtain than CBs, have been used to calculate masking bandwidths based on the assumption that the noise power integrated over the critical band equals the power of the target at its detection threshold, or,

$$CB \text{ (in Hz)} = 10^{(CR/10)} \quad (\text{equation 7})$$

(Fletcher 1940, Fay 1992). This implies that the target strength is at least equal to that of the noise; however, there are exceptions. Although uncommon, *negative* CRs, meaning the signal is detected at levels below the noise, have been reported for human detection of speech signals⁵ and for some bats near their echolocation frequencies (Schuknecht 1993, Kössl and Vater 1995). Critical bands are thought to depend on stiffness variations in the inner ear. In generalist ears, the critical bandwidths are relatively constant at about 0.25 to 0.35 octaves/mm of basilar membrane (Ketten 1984, 1992; West 1985; Allen and Neeley 1992). Although hearing ranges vary widely in terms of frequency, most mammals have a hearing range of 8 to 9 octaves, which is consistent with earlier findings that the number of CBs was approximately equal to basilar membrane length in millimeters (Pickles 1982, Greenwood 1990).

Based on CR and CB data, odontocetes are better than most mammals at detecting signals in noise. Odontocetes have more CBs and the CRs are generally smaller than in humans. Furthermore, odontocete critical bandwidths ap-

proach zero and are not a constant factor of the critical ratio at different frequencies. The bottlenose dolphin has 40 CBs, which vary from 10 times the CR at 30 kHz to 8 times the CR at 120 kHz (Johnson 1968, 1971; Moore and Au 1983; Watkins and Wartzok 1985; Thomas et al. 1988, 1990b). Critical ratios for bottlenose dolphins (20 to 40 dB) are, however, generally higher than in other odontocetes measured. The best CRs to date (8 to 40 dB) are for the false killer whale (*Pseudorca crassidens*) (Thomas et al. 1990b), which is also the species that has performed best in echolocation discrimination tasks (Nachtigall et al. 1996).

Sound localization is an important aspect of hearing in which the medium has a profound effect. In land mammals, two cues are important for localizing sound: differences in arrival time (interaural time) and in sound level (interaural intensity). 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 (Dudok van Heel 1962, Gentry 1967, Renaud and Popper 1975, Moore et al. 1995); however, because of sound speed differences, small or absent pinna, and ear canal adaptations in marine mammals, localization mechanisms may be somewhat different from those of land mammals.

In mammals, the high frequency limit of functional hearing in each species is correlated with its interaural time distance (IATD = the distance sound travels from one ear to the other divided by the speed of sound; Heffner and Masterton 1990). The narrower the head, the smaller the IATD, the higher the frequency an animal must perceive with good sensitivity to detect arrival time through phase differences. For example, consider a pure tone, which has the form of a sine wave, arriving at the head. If the sound is directly in front of the head, the sound will arrive at the same time and with the same phase at each ear. As the animal's head turns away from the source, each ear receives a different phase, given that the inter-ear distance is different from an even multiple of the wavelength of the sound. Therefore, IATD cues involve comparing time of arrival versus phase differences at different frequencies in each ear. Phase cues are useful primarily at frequencies below the functional limit; however, the higher the frequency an animal can hear, the more likely it is to have good sensitivity at the upper end of frequency range for phase cues.

Clearly, IATDs depend on the sound conduction path in the animal and the media through which sound travels. 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 auditory meatus, and therefore the IATD is the intermeatal (IM) distance measured around the head divided by the speed of sound in air. In aquatic ani-

mals, sound can travel in a straight line, by tissue conduction, through the head given that tissue impedances are similar to the impedance of seawater. Experiments with delphinids suggest that intercochlear (IC) or interjaw distances are the most appropriate measure for calculating IATD values in odontocetes (Dudok van Heel 1962, Renaud and Popper 1975, Moore et al. 1995). The IC distances of dolphins are acoustically equivalent to a rat or bat IM distance in air because of the increased speed of sound in water. Supin and Popov (1993) proposed that marine mammals without pinnae were incapable of using IATD cues, given the small interreceptor distances implied by the inner ear as the alternative underwater receptor site. Recently, however, Moore et al. (1995) demonstrated that the bottlenose dolphin has an IATD on the order of 7 μ sec, which is better than the average human value (10 μ sec) and well below that of most land mammals tested. 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 versus high frequency limits follow similar trends.

Intensity differences can be detected monaurally or binaurally, but binaural cues are most important for localizing high frequencies. In land mammals, intensity discrimination thresholds (IDT) tend to 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 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 sound level. Binaural behavioral studies and evoked potential recordings for bottlenose dolphin indicate an approximate IDT limit of 1 to 2 dB (Bullock et al. 1968, Moore et al. 1995). In harbor porpoise, IDTs range 0.5 to 3 dB (Popov et al. 1986). Thresholds in bottlenose range from 3 to 5 dB (Supin and Popov 1993), but again, because of small sample size and methodological differences, it is unclear whether these numbers represent true species differences. Fay (1992) points out that the IDT data for land mammals do not fit Weber's Law, which would predict a flat curve for IDT (i.e., intensity discrimination in dB should be nearly constant). Rather, the IDTs decrease with increasing level and increase slightly with frequency.

In the past decade, auditory evoked potential (AEP) or auditory brainstem response (ABR) procedures have been established for odontocetes (Popov and Supin 1990a, Dolphin 1995). These techniques are highly suitable for studies with marine mammals for the same reasons they are widely

used for measuring hearing in infants or debilitated humans—namely, they are rapid, minimally invasive, and require no training or active response by the subject. An acoustic stimulus is presented by ear or jaw phones and the evoked neural responses are recorded from surface electrodes or mini-electrodes inserted under the skin. The signals recorded reflect synchronous discharges of large populations of auditory neurons. The ABRs consist of a series of 5 to 7 peaks or waves that occur within the first 10 msec after presentation of click or brief tone burst stimuli. Most mammals have similar ABR patterns, but there are clear species-specific differences in both latencies and amplitudes of each wave (Jewett 1970, Dallos et al. 1978, Achor and Starr 1980, Dolan et al. 1985, Shaw 1990). The delay and pattern of the waves are related to the source of the response. For example, wave I in most mammals is thought to derive from synchronous discharges of the auditory nerve; wave II from the auditory nerve or cochlear nucleus. The ABRs from dolphins show clear species dependence. Typical ABRs from harbor porpoise and bottlenose dolphin have three positive peaks with increasing amplitudes, but those in harbor porpoise have longer latencies (Bullock et al. 1968, Ridgway et al. 1981, Bibikov 1992).

Recent work using continuous amplitude modulated stimuli (AMS) at low frequencies in bottlenose dolphins and false killer whales suggest odontocetes can extract envelope features at higher modulation frequencies than other mammals (Kuwada et al. 1986, Dolphin and Mountain 1992, Dolphin 1995). Supin and Popov (1993) also showed that envelope following responses (EFR) are better measures of low frequency auditory activity than ABR. The anatomical correlates of EFRs have not been identified, but the data suggest auditory central nervous system adaptations in dolphins may include regions specialized for low as well as high frequencies.

Pinnipeds

Pinnipeds are particularly interesting because they are faced with two acoustic environments. Different ways for sensory information to be received and processed are required for equivalent air and water hearing in their amphibious lifestyle. One possibility is that pinnipeds have dual systems, operating independently for aquatic and airborne stimuli. If this is the case, 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 neffinlike dual but equal hearing is that pinnipeds are adapted primarily for one environment and have a “compromised” facility in the other. Renouf (1992) argued that there is an “a priori justifi-

cation for expecting otariids and phocids” to operate with different sensory emphases, given that phocids are more wholly aquatic. This question cannot be definitively resolved until more pinniped species have been tested. As with cetaceans, present data are limited to a few individuals from mostly smaller species. However, the most recent data suggest there are significant differences among pinnipeds in both their primary frequency adaptations and in their adaptations to air versus water to warrant more widespread species research.

Underwater behavioral audiograms for phocids are somewhat atypical in that the low frequency tail is relatively flat compared to other mammalian hearing curves (compare Figs. 4-2 and 4-5A with Fig. 4-5B; see also Fay 1988 or Yost 1994 for additional comparisons). In the phocids tested (harbor seal [*Phoca vitulina*], harp seal [*Phoca groenlandica*], ringed seal [*Phoca hispida*], and Hawaiian monk seal [*Monachus schauinslandi*]), peak sensitivities ranged between 10 and 30 kHz, with a functional high frequency limit of about 60 kHz, except for the monk seal which had a high frequency limit of 30 kHz (Schusterman 1981, Fay 1988, Thomas et al. 1990a). Low frequency functional limits are not yet well established for phocids, and it is likely that some of the apparent flatness will disappear as more animals are tested below 1 kHz. However, the fact that all phocid plots have remarkably little decrease in overall sensitivity below peak frequency is notable. Currently available data from an on-going study comparing harbor seal and northern elephant seal hearing suggest that the elephant seal has significantly better underwater low frequency hearing thresholds than other pinnipeds tested to date (Kastak and Schusterman 1995, 1996).

In-air audiograms for phocids have more conventional shapes with peak sensitivities at slightly lower frequencies (3 to 10 kHz) (Fay 1988; Kastak and Schusterman 1995, 1996). In-air evoked potential data on these species are consistent with behavioral results (Bullock et al. 1971, Dallos et al. 1978). In-air and underwater audiograms cannot be compared directly; however, when the data are converted to intensity measures, the thresholds for airborne sounds are poorer, on average (Richardson et al. 1995), implying that phocids are primarily adapted for underwater hearing.

Underwater audiograms and aerial audiograms are available for two species of otariids. Underwater hearing curves for California sea lions and northern fur seals (*Callorhinus ursinus*) have standard mammalian shapes. Functional underwater high frequency hearing limits for both species are between 35 and 40 kHz with peak sensitivities from 15 to 30 kHz (Fay 1988, Richardson et al. 1995). As with phocids, otariid peak sensitivities in air are shifted to lower frequencies (< 10 kHz; functional limit near 25 kHz), but there is rel-