HEARING

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Animals use their sense of hearing for communication, navigation, and detection of prey and predators. Cetaceans have superb aquatic hearing and their ears have become the most important sense organ for life underwater. Sirenians have functional aquatic hearing, and marine carnivores rely on their auditory systems in both air and water. Adaptations for hearing in air differ from those for hearing in water; this has resulted in evolutionary compromises for those marine mammals that need to hear in both, and for the ancestors of those that are now fully aquatic.

I. Acoustics

Critical variables regarding hearing for mammals are frequency, loudness, and duration of sound. For pure tones, sound velocity (v) is the product of sound frequency (f) and sound wavelength (l) = v/f. Sound velocity in air is 340 m/s, whereas in water, sound velocity is 1500 m/s. Therefore, for a given frequency, the wavelength is almost five times longer in water than in air.

Sound velocity and wavelengths play an important role in sound localization. Animals determine the direction of a sound by measuring...
of one of the two methods (Heffner and Heffner, 1992). The first is based on the difference in arrival of sounds at the two ears: The interaural time difference. If the distance between the ears is relatively large, the interaural time difference can be used to determine sound direction because sounds arrive earlier at the ear closer to the sound source. However, when the head is small, the time difference of arrival may be too small for the brain to detect. In those cases, a second method to determine direction is used: the intensity difference between sounds at the two ears. The interaural intensity difference is particularly useful for higher frequencies, which attenuate rapidly and increase the shadowing effect of the head (Fig. 1). Thus, in echolocation, using high-frequency hearing gives both better spatial resolution (due to shorter wavelengths) and directional hearing than using low frequencies.

Sound intensity is a measure of incident sound energy and is the most relevant parameter to assess the sensitivity of an animal’s ear at the cochlea (where the ear’s neural receptors are). However, our biosonar instruments measure sound pressure. For practical purposes, we use the sound pressure level ($L_p$): a logarithmic function that relates sound pressure ($p$) to a chosen reference pressure ($p_0$). $L_p = 20 \log \frac{p}{p_0}$, and is expressed in decibels (dB). When the pressure increases 10-fold, $L_p$ increases 20dB. $L_p$ can be used to compare hearing sensitivity of terrestrial and aquatic animals.

With the conventional reference pressure ($p_0$) values of 20 μPa (air) and 1 μPa (water), incident sound waves in air and water have equal intensities when the sound pressure level ($L_p$) of an aquatic sound is 61.6 dB higher than sound pressure level ($L_p$) of the sound in air. Sensitivities of an ear are often expressed as thresholds. The minimum sound pressure level ($L_{p0}$) that still produces an audible sound, hence, a terrestrial animal and an aquatic animal have equal sensitivities if the threshold $L_{p0}$ value of the aquatic animal is 61.6 dB higher than the threshold $L_{p0}$ of the terrestrial animal.

In addition to sound frequency, loudness, and direction, another important factor is acoustic impedance. Sound is attenuated by reflection as it crosses the interface between different media, and the acoustic impedance of the media determines the level of attenuation. The characteristic acoustic impedance of a medium is $Z = p/v$, where $p$ is the sound pressure and $v$ is the particle velocity. A given sound pressure gives air molecules a much larger particle velocity than water molecules, leading to the much lower impedance of air ($Z_{air} = 0.4$ kPa/s/m) than of water ($Z_{water} = 1500$ kPa/s/m). The specific acoustic impedance of the fluid-filled cochlea is approximately one-tenth of the characteristic acoustic impedance of water ($Z_{cochlea} = 150$ kPa/s/m). Hence in hearing, airborne sounds travel from a medium of very low impedance to one with much higher impedance in the ear, and much of the sound intensity is attenuated. In contrast, waterborne sounds travel from a medium with higher impedance to one with slightly lower impedance. Both of these cases are problematic because impedance mismatch causes a reflection of sounds at the interface. To overcome this, an impedance matching device is needed that adjusts either the pressure or particle velocity between the outer medium and the cochlea. In mammals, this is accomplished by the middle ear.

II. Hearing in Air

In a land mammal ear, sound is collected by the pinna and guided through the external auditory meatus to the tympanic membrane, which begins to vibrate (Fig. 2A). The pinna and external auditory meatus are components of the outer ear; the middle ear starts at the tympanic membrane. The vibrations of the tympanic membrane are carried through the middle ear by a chain of three small bones (ossicles): (1) malleus (hammer), (2) incus (anvil), and (3) stapes (stirrup). The malleus is attached to the tympanic membrane by means of a process called the manubrium. The ossicles together form a swing which vibrates between the tympanic membrane and the oval window, which is the opening into the fluid-filled cochlea.

The middle ear functions as an impedance matching device between the surrounding air and the inner ear fluid, decreasing the reflection of sound at the tympanic membrane. As discussed earlier, hearing in air requires transmission of sound energy from areas with low impedance to high impedance. To match impedance in this case, the pressure can be increased and/or particle velocity decreased (as $Z = p/v$), and this is in fact what happens. The pressure is increased by transmitting sound from a larger area (tympanic membrane) to a smaller area (the oval window), and the...
particle velocity is decreased by the lever system: The malleus lever arm is longer than the incus lever arm. These two arrangements together, the area ratio and the lever ratio, contribute to the sound energy transmission in the middle ear.

Sound enters the cochlea of the inner ear at the oval window. The mammalian cochlea is a fluid-filled coiled structure through which extends the long and narrow basilar membrane. The basilar membrane supports the organ of Corti, which contains the auditory sensory cells (hair cells). The vibrations of the stapes at the oval window set up waves in the inner ear fluid, and these waves cause the basilar membrane to vibrate. These vibrations bend short hairlike structures (stereocilia) implanted on the sensory cells, leading to nerve impulses in the cranial nerve VIII. The basilar membrane is organized tonotopically. The base of the membrane is sensitive to high frequencies, and the apex to low frequencies.

The hearing range of a species is largely determined by the anatomy of the outer, middle, and inner ear structures (Ruggiero and Temchin, 2002). In the middle ear, low-frequency transmission is constrained by the elasticity of the system: A large tympanic membrane, high middle ear volume, and a flaccid (nonstiff) ossicular chain improve low-frequency hearing. High-frequency transmission is constrained by the mass of the system: Light ossicles and a small middle ear characterize high-frequency ears. Cochlear dimensions, especially basilar membrane length, can also be used to predict the high- and low-frequency limits for most mammals.

III. Bone Conduction Hearing

The term "bone conduction" is used to describe a particular kind of sound perception that differs from the land mammal mechanism described above. Bone conduction occurs when sound energy is transmitted from a surrounding medium to the cochlea through vibrations of the bony parts of the head without passing through the outer ear and the moving ear ossicles as described. Functionally, there are two types of bone conduction: (1) Compressional and (2) inertial. In the compressional type, a pressure differential develops across the cochlear partition of the inner ear. In the inertial type, relative motion between the ossicular chain and the temporal bone leads to cochlear stimulation, similar to how land mammals usually hear airborne sound. Both types lead to displacement of the basilar membrane and neural impulses of the hair cells. Directional hearing is not possible with bone-conducted hearing.

The terrestrial mammal ear is not acoustically isolated from the skull as the bones that house the middle and inner ears are in close contact with each other and with the rest of the skull. Whereas most airborne sound is reflected at the air-tissue interface, this is not the case if sounds travel through a dense medium (such as soil) and the body is in extensive contact with this medium. This tight connection between substrate, the animal's body, and its ear makes bone conduction possible, and thus, some terrestrial mammals have bone conduction as a second hearing mechanism in addition to the mammal mammal mechanism described above. However, bone conduction may interfere with airborne sounds entering the ear, and many land mammals show adaptations to minimize bone conduction. Bone conduction is more common in aquatic animals because the density of water is similar to the density of the body tissues and allows for efficient transfer of energy (Nummela, 2002).

IV. Odontocete Cetaceans

Odontocetes are the only group of marine mammals that have developed the capability for sophisticated echolocation, enabled by their excellent underwater hearing, and compromising airborne sound reception. Some species can hear very high frequencies, exceeding even 150 kHz, and have great hearing sensitivity. Additionally, odontocetes have developed rapid auditory temporal processing, which facilitates sound localization.

The ears of modern odontocetes are adapted for underwater hearing (Fig. 4B). Odontocetes lack an outer ear pinna, and their external auditory meatus is very narrow, partly occluded, and not functional in hearing. The tympanic membrane has also lost its function in hearing, and has become a long, conical structure referred to as the tympanic ligament. The tympanic ligament attaches with its medial tip to a small remnant of the manubrium of the malleus and plays a role in the pressure regulation of the middle ear cavity.

Another major difference between the ears of terrestrial mammals and the ears of cetaceans is that cetacean ears are acoustically isolated from the skull. The tympanic and periotic bones, which
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The middle and inner ears, are separated from the skull by air spaces that prevent bone conduction. In most odontocete species, the bony connection between this tympanosinotic complex and the skull is very small. Exceptions are the sperm whales (physeterids) and beaked whales (ziphiids), where the tympanosinotic complex has larger contact with the skull.

The tympanic bone of odontocetes is bowl-shaped, and houses the middle ear cavity. The lateral wall of the tympanic bone is thin, like in mammals in general; in odontocetes, this wall is called the tympanic plate. The medial part of the tympanic (the involucrum) is thick and bulky, a massive counterpart to the thin lateral part. The three middle ear ossicles are situated between the tympanic plate and the oval window. The malleus has a long, thin process which is fixed to the anterior rim of the tympanic bone. As in land mammals, the ossicular chain consists of malleus, incus, and stapes, and the first two of these form most of the mass of the chain. In water, but not in air, heavy ossicles can transmit high frequencies. Thus, killer whales and mice can hear equally high frequencies, but the ossicles differ hugely in size.

In odontocetes, sound does not arrive at the middle ear by passing through the ear canal. Instead, sounds are transmitted to the odontocete ear by passing through specialized fatty tissues associated with their lower jaws. This fat pad fills a cavity inside the lower jaw and passes to the ear through the greatly enlarged mandibular foramen (Figs 3 and 4). The fat is composed of lipids that transmit sounds at very low sound speeds. The fat pad reaches the tympanic plate, and a cone-shaped feature that has been called an acoustic funnel on the lateral side of the tympanosinotic complex (see Cranford et al., 2010; Yamato and Pyenson, 2015). The tympanic plate vibrations, along with vibrations of the entire tympanosinotic complex, are passed through the ossicular chain and to the cochlea.

Experimental evidence has shown that the odontocete lower jaw is very sensitive to sound. Mohl et al. (1986) found that the best auditory sensitivity is at the middle of the lower jaw of a dolphin, and Popov et al. (2008) presented evidence indicating that there may actually be more than one "acoustic window." They were able to identify at least two different sound-receiving areas with different frequency sensitivities. The significance of these multireceiving areas is not clear yet but it is possible that they provide cues for localization of sound sources and sound pattern recognition, because the best-sensitivity axis direction may be frequency-dependent. Furthermore, subsequent investigations suggest that there are slight differences in sound reception pathways among different odontocete taxa (Mooney et al., 2014).

As noted in the previous sections, hearing underwater requires transmission of sound energy from areas with high impedance to somewhat lower impedance. Thus in order to match impedances, the pressure can be decreased, and/or the particle velocity increased (as Z = p/υ). However, when the vibrations move from the larger tympanic plate to the smaller oval window, pressure is increased, not decreased, causing an impedance mismatch and leading to reflection of sounds at the interface. In odontocetes, two lever mechanisms exist to address the impedance mismatch, by increasing particle velocity. First, the lateral wall of the tympanic bone (the tympanic plate) vibrates more than the thick involucrum, which stays practically immovable. Second, the malleus and incus move very little in the epitympanic recess, and the incus long arm moves much more, in the rotation of the ossicular chain. Together, these two levers greatly increase the particle velocity and serve as impedance matching devices (Hemila et al., 2010).

In addition to impedance matching, another challenge of underwater hearing is that the sound travels in water nearly five times faster than in air; this means that the wavelength at a given frequency is much longer in water, reducing considerably the usefulness of the interaural time difference. The high frequencies together with a large head of odontocetes compensate for the higher sound velocity in water, resulting in good directional hearing.

Audiograms for odontocetes are presented in the article on Echolocation. Comparisons of behavioral and evoked electrophysiological measuring techniques show that the thresholds using these methods are similar, but that the evoked potential methods had consistently higher thresholds, especially at the lowest frequencies (Supin et al., 2001; Mooney et al., 2012). Remarkably, recent work has revealed that odontocete-hearing sensitivities are also situation-dependent. Odontocetes engage in short-term passive and long-term active control of hearing sensitivities (Supin and Nachtigall, 2015; Nachtigall et al., 2016).

Figure 3  Medial view of lower jaws of deer (A, right jaw, Odocoileus) and dolphin (B, left jaw, Lagenorhynchus) showing the mandibular foramen. Scale bar = 5 cm. From Nummela, S., Thevissen, J.G.M., Bijleveld, T., Hussain, T., and Kamar, K. (2007). Sound transmission in archaic and modern whales: Anatomical adaptations for underwater hearing. Anl. Rec. 390(1): 716-733, with permission.

Figure 4  Odontocete (bottlenose dolphin) and mysticete (minke whale) skulls, right lateral view, showing the mandibular fat tissue. The images are not to scale (Illustration by M. Yamato from CT scan data. Courtesy of Darlene R. Reitner, Chief Scientist, WHOI Computerized Scanning and Imaging Facility).
V. Mysticete Cetaceans

Mysticetes (baleen whales) do not echolocate and they are specialized to produce and hear low frequencies. Low-frequency sounds propagate over longer distances and are suitable for long-distance communication. Mysticetes can communicate with each other over hundreds or even thousands of kilometers; the lowest frequencies used are approximately 10–15 Hz.

Mysticetes lack an outer ear pinna. Furthermore, their external auditory meatus is totally occluded and unlikely to be functional for hearing. The medial end of the meatus is filled by earwax (wax plug). A part of the tympanic membrane, the glove finger, bulges into the external auditory meatus, and another part is attached to the malleus. The malleus is fused to the bony wall of the tympanic ring by means of a long and strong rod-like process, instead of the thin and elastic process of odontocetes. The tympanoperiosteal complex is partly isolated from the skull with sinuses, but a long posterior process makes a broad contact with the skull.

The mysticete ear and its ossicles are very large, but the relative size of the parts is similar to that of odontocetes, and these ears may function similarly at some level. It remains unclear how sound reaches the middle ear in mysticetes, since they do not have a fat-filled mandibular canal, like odontocetes have, nor the open external auditory meatus of terrestrial mammals. However, there are large masses of fatty tissues associated with the ears of at least some mysticete taxa, including balaenopterids and balaenids (Fig. 4). Yamato et al., 2012, 2014. A recent modeling study suggests that baleen whales perceive low-frequency sound via bone conduction (Cranford and Krysl, 2015). No behavioral or reliable evoked potential measurements on mysticete hearing exist, but their hearing frequency ranges have been modeled based on middle and inner ear morphologies (Ketten, 2000; Parks et al., 2007; Tubelli et al., 2012; Cranford and Krysl, 2015).

VI. Sireniens

Sireniens have been reported to have good high-frequency hearing, although their hearing sensitivity and high-frequency hearing limit is much lower than that of odontocetes. Manatees have relatively good localization abilities as well. The ear anatomy of sireniens is very different from that of any other mammals (Ketten et al., 1999; Chapla et al., 2007).

Sireniens have no outer ear pinna, and their external auditory meatus ends in a blind sac, where fatty tissue separates the meatus and the tympanic membrane. The tympanoperiosteal complex is not fused to the skull bones. The tympanic membrane is large and bulges outward due to a cartilaginous keel of the malleus. The middle ear ossicles are massive and pachyostotic and their density is the highest known among mammals (2.9 g/cm³, Chapla et al., 2007, even higher than the dense ear bones of cetaceans, 2.6–2.7 g/cm³). The sirenian ossicles are much denser than the periosteal bone, which houses the cochlea.

The sound path to the ear of sireniens is unclear. It is possible that sound passes through the very fatty zygomatic process to the ear, like the mandibular fat of odontocetes. It is also possible that sireniens use bone conduction, or that sound waves pass directly through the soft tissues of the head to the ears.

Evoked potential studies on the West Indian manatee (Trichechus manatus) showed an in-air response of up to 35 kHz, with the largest peaks in response to stimuli from 1 kHz to 1.5 kHz. Auditory evoked potential measurements on the Amazonian manatee (T. inunguis) in a water-filled bath showed response to stimuli up to 60 kHz. An underwater behavioral audiogram for the West Indian manatee was U-shaped, as is common for mammals, and the hearing range extended from 0.4 kHz to 46 kHz, with peak sensitivity at 161 Hz and 18 kHz. The range of best hearing was 8–20 kHz (Fig. 5, Gerstein et al., 1999). Florida manatees (T. manatus latirostris) have

![Figure 5](https://example.com/figure5.png)

been found to have surprisingly good temporal resolution, roughly 10 times that of humans and half that of dolphins.

Manatees vocalizations range from 4 kHz to above 25 kHz. Many of these vocalizations are harmonic, and it is possible that the high temporal resolution of the auditory system provides a useful system for detecting the harmonics. Selective pressures to localize sound underwater might also be responsible for the high-frequency sensitivity of the manatee. Higher-frequency sounds will produce larger interaural intensity differences than low-frequency sounds because they are more effectively shadowed by the head.

VII. Pinnipeds

Pinnipeds are amphibious and need to hear in both air and water. All pinnipeds have retained the land mammal sound transmission mechanism: Airborne sound is transmitted through the tympanic membrane and ossicular chain. As in most carnivores, the middle ear cavity is large and the periotic bone is fused to the other skull bones. Unlike terrestrial carnivores, the middle ear cavity is lined with cavernous tissue, which equalizes middle ear pressure while diving. It is hypothesized that pinnipeds rely on bone conduction underwater.

All otariids have a small outer ear pinna, and middle ear ossicles similar in size to those of terrestrial carnivores. In contrast, phocids and odobenids do not have pinnae, and have inflated, pachyostotic ossicles, with elephant seal ossicles being the most extreme (Kastelein et al., 1996). The mass of phocid and odobenid ossicles is further increased by their high density (2.2–2.5 g/cm³ vs. ~2.0 g/cm³ in land mammals). The enlarged ossicular mass limits the high-frequency hearing in air, but may enhance bone conduction by creating a larger phase difference between parts of the ossicular chain that vibrate differently. The inflated incus has moved the mass center point of the ossicular chain away from the rotational axis, increasing the different phases of vibration between the stapes and cochlear capsule.

The hearing sensitivity of pinnipeds in air is generally similar to that of terrestrial mammals, and their underwater hearing sensitivity is worse than that of fully aquatic mammals (Fig. 5; Hemila et al., 2006; Reichmuth et al., 2013). The high-frequency hearing limits of otariids and odobenids are similar in air and water, and are constrained by the shape of the cochlea. The high-frequency hearing limits of phocids are lower in air than water (Fig. 6), and are limited by the mass inertia of the heavy phocid ossicles. However, recent work suggests that seals and sea lions can detect very high-frequency underwater sounds, at 50–180 kHz; the mechanism for this is not yet clear (Cunningham and Reichmuth, 2016).

Pinnipeds are large mammals, and their head size and head movement behaviors assist in sound localization (Holt et al., 2004). Pinniped aerial sound localization is similar to that of land mammals, and they also have good underwater sound localization ability (Bodson et al., 2006). With their amphibious lifestyle, pinnipeds will need the ability to hear in air; thus their ears are not as specialized for underwater hearing compared to the fully aquatic species (Figs 5 and 7). Pinnipeds use hearing in combination with alternative senses that are possibly equally prominent (Schusterman et al., 2006; see articles on Vision and Sensory Biology).

VIII. Polar Bears and Sea Otters

Polar bears and sea otters have ears similar to those of land carnivores. Both species use the general land mammal sound transmission in air, and presumably rely on bone conduction underwater. Whether there are morphological adaptations that enhance bone conduction is currently unknown. Nachigali et al. (2007) measured auditory evoked potentials for the polar bear in air, and found that they are sensitive to a wide frequency range of sounds, with the best sensitivity between 11.5 kHz and 22.5 kHz. In behavioral psychoacoustic studies, Owen and Bowles (2011) found the best hearing sensitivity to be between 8 kHz and 14 kHz, with a sharp decline between 14 kHz and 25 kHz, suggesting that the upper limit of hearing in polar bears is 10–20 kHz below that of small carnivores.

Behavioral measurements on sea otter hearing have shown that the aerial audiogram resembles that of sea lions and shows a reduction in low-frequency sensitivity relative to terrestrial mustelids, with best sensitivity being ~1 dB re 20 μPa at 8 kHz. Underwater, hearing sensitivity was significantly reduced when compared with any pinniped species, indicating that sea otters are primarily adapted to receiving airborne sounds (Ghoul and Reichmuth, 2014).

IX. Evolution of Cetacean Hearing

Since much of the sound transmission in mammals involves bones and the fossil record of cetaceans is well documented, the ear offers an opportunity to study the acquisition of specific adaptations in cetacean evolution. The first important evolutionary event in cetacean hearing evolution is the origin of the modern generalized

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**Figure 5** Audiograms for (A) phocids and (B) otariids. All threshold intensities are given in decibels relative to 1 μW/m², for comparison of thresholds in water and air. Open symbols in-air; filled symbols underwater. O: ● Phoca vitulina; Δ: ▲ Mirounga angustirostris; ■: Zalophus californianus; △: ▼ Callorhinus ursinus. From Hemila, S., Nunn, N., S., Bert, A., and Reuter, T. (2006). High frequency hearing in phocid and otarid pinnipeds: An interpretation based on inertial and cochlear constraints. J. Acoust. Soc. Am. 120, 3463–3486, with permission.
whale underwater hearing, which occurred during the Eocene in less than 10 million years (Nummela et al., 2004, 2007).

Pakicetids, the earliest whales (Fig. 8A), had an outer ear canal leading to the tympanic membrane, a small mandibular foramen in their lower jaw indicating that no mandibular fat pad was present, and a tympanoperostric complex that was in close contact with the skull. In these features of the outer and middle ears, pakicetids resembled terrestrial mammals. A fossil incus of Pakicetus, resembling the incus of artiodactyls, indicates that pakicetids still had a land mammal ear with a normal malleus and a tympanic membrane. Unlike land mammals, pakicetids had an involucrum, a thick medial lip to the tympanic bone that is not attached to the skull. This allows the involucrum to vibrate independently of the surrounding bones and can assist in bone-conducted sound transmission. While absent in nearly all representatives of the cetacean sister group (artiodactyls), a pachyostotic involucrum does occur in the small, mousedeer-like Indobala, a close relative of cetaceans (Thewissen et al., 2007). In air, pakicetids used the land mammal sound transmission mechanism, and underwater hearing was rooted in bone conduction.

The next step in cetacean evolution is represented by ambulocetids, whose ear structures are poorly known. These whales had a massive lower jaw with a large mandibular foramen, suggesting that a mandibular fat pad was present. The tympanic bone was large, with a thick involucrum, and was in anatomical proximity to the lower jaw. It is likely that ambulocetids used bone-conducted hearing, in both water and land. On land, they may have kept their lower jaw on the ground, similar to modern crocodiles. However,
The mechanism did not provide good sensitivity or a wide frequency range for ambulocetid hearing. The ears of remingtonocetid and protocetid cetaceans were more specialized than those of the ambulocetid. Remingtonocetids and protocetids (Fig. 8b) had a large mandibular foramen, a small contact between the tympanic and periotic, a conical tympanic membrane similar to modern cetaceans, and a malleus which lacked the process for attachment of the tympanic membrane. This morphology suggests that the modern generalized whale hearing mechanism originated with these families: Underwater sound vibrations arrived at the lower jaw were carried through the mandibular fat pad to the tympanoperiotic complex, and transmitted through the ossicles to the cochlea. The lateral auditory meatus was still present and could channel airborne sound to the tympanic membrane; however, the shape of tympanic membrane and malleus would have made this sound path inefficient.

There were no air-filled sinuses that could isolate the ear acoustically, suggesting these animals also had poor directional hearing (Fig. 8).

The protocetid middle ear was followed by the functionally modern late Eocene basilosaurid ear. The very large mandibular foramen of Zygorhiza indicates that sound passed through the mandibular fat pad, even though an external auditory meatus was still present. The tympanoperiotic complex was partly isolated from the skull by air sinuses, and the ossicles resembled those of modern dolphins. There are some similarities between the basilosaurid archarchocet Zygorhiza and modern mysticetes, and it is possible that basilosaurids were sensitive to low-frequency sounds. Therefore, the mysticete low-frequency hearing may have had its antecedents already among late archarchocetes.

Among extinct mysticetes from the Miocene, the cochlear morphology indicates low-frequency sensitivity. But in these, the lateral mandibular wall was thick, and the fat pad was reduced or absent. It is unlikely that the ear of these whales transmitted high-frequency sounds well. The reduction of the mandibular fat pad in mysticetes may have been the result of a shift toward low-frequency sounds (Steeman, 2009).

The origin of echolocation occurred around the time of divergence of odontocetes and mysticetes, or possibly within the earliest odontocetes, based on anatomical features of the cranium and the ear (Geisler et al., 2014) and cochlear anatomy (Park et al., 2010) in basal odontocetes from the Oligocene.

See Also the Following Articles

Archaeocetes, Baleen Whales, Evolution, Basiosaurids, and Kelenkenodontids, Cetacean Evolution, Echolocation, Sensory Biology, Sound Transmission, Vision

References


HINDLIMB ANATOMY

PETER J. ADAM

With the development of tail flukes for producing propulsion in cetaceans and sirensians, the pelvises and hindlimbs became vestigial structures that now associate only loosely with the spine. The major role of the pelvic apparatus in these forms, when present, is to serve as attachment points for muscles acting on the genitalia and the abdominal body wall. Aquatic carnivores (pinnipeds, some otters) maintain some ties to the terrestrial environment and have not had such a dramatic reduction in the pelvis and hindlimb structures. Both pinnipeds and the sea otter (Enhydra lutris) have embedded the toes in a flipper to aid aquatic locomotion.

I. Cetaceans

The known fossil record documenting cetacean evolution shows a progressive reduction and loss of hindlimb skeletal elements and the association of the pelvic girdle from the vertebral column as whales became less dependent on near-shore environments and developed tail flukes to generate swimming thrust (Thewissen, 2001). This trend is most marked with the origin of the basilosaurids, in which the tibia and fibula became fused with each other and other hindlimb elements co-ossified into a single immobile mass, and where this mass is not attached to the vertebral column by a joint (Uhen, 1991). Among modern forms, only vestiges of the hindlimb skeleton can be found, and these are contained within the body wall. Mammals may possess fragments of pelvis, femur, and tibia (Fig. 1), whereas the occurrence of hindlimb and pelvic elements is more varied among both individuals and species of odontocetes. When present, the pelvises bear little resemblance to those of terrestrial mammals and may exist only as a band of connective tissue connecting the spinal musculature to the remainder of the body. In males, the pelvis is typically a simple bar-shaped bone. Articulated femora and occasional tibiae have been described from several mysticete and odontocete taxa, although occurrence of these elements is infrequent. Hindlimb buds are present during early embryogenesis of all whale species documented so far, although the mesodermal cells that usually form the internal limb structures die or are reallocated to other functions as limb buds are resorbed later in ontogeny (Seddon et al., 1997; Thewissen et al., 2006). Retention of a rudimentary pelvis is associated with the attachment of numerous muscles acting on the reproductive organs of both sexes. In males, the pelvis is usually much larger than that of females. It serves as the site of origin of muscles acting on the genitalia and anal region (e.g., the penis retractor and levator ani muscles) and may also serve as a site of attachment for posterior fibers of the rectus abdominis muscle. In these modern cetaceans, the pelvis is not connected to the vertebral column by means of a joint, and there is no sacrum consisting of multiple vertebrae (Moran et al., 2015). The hindlimb bones are embedded in the hypaxial spinal musculature. Rearrangements of spinal and pelvic muscles in association with tail-based locomotion have led to considerable controversy over specific identities of muscles in these regions.

II. Sirensians

The evolutionary loss of the hindlimb in sirensians closely parallels that of cetaceans (Fig. 1), with modern forms possessing only a vestigial pelvis composed of ischium and ilium bones. In dugongs.

Figure 1 Line drawing of the right pelvis of a cetacean (left) and sirenian (right) in lateral view (anterior toward the right). Position and orientation of the pelvis are indicated by boxes on the skeletal outlines.
Male sea otters defend small (2-8km²) territories, which overlap with those of several females. The occupants of the best territories—containing much kelp, which protects females and pups—have access to high density of females, inducing mild polygyny. The reproduction cycle of females is not strongly synchronized, thus males try to defend territories year-round. Those who can maintain a territory over several seasons experience the highest lifetime reproductive success.

Polar bears live at low densities, thus a roam-and-search system becomes the most effective strategy for male reproductive success. Males search for dispersed females in estrus during the reproductive season (February-May). Females may incite male competition by leaving olfactory signals. Only full-sized males can successfully defend females during consortship (~14 days). Searching and mating with maximally 4–5 females keeps males occupied in late spring. Because they fast and fight during this time, they may incur mortality costs of reproduction.

V. Concluding Remarks

Marine mammal sociobiology has advanced significantly in recent years, yet remains at an early stage. This is in part due to a lack of detailed knowledge on the distribution of resources and predators of marine mammals in ocean environments. Coupling observation, comparative, and experimental work with new instrumentation and molecular tools remains a challenging agenda to unravel the social lives of marine mammals.

See Also the Following Articles

Energetics ■ Feeding Strategies and Tactics ■ Group Behavior ■ Mating Systems ■ Parental Behavior ■ Predator–Prey Relationships ■ Thermoregulation

References


B. Song Structure

Humpback whale song is composed of a sequence of varied sounds ranging from high-pitched squeaks to midrange trumpeting and screeches, to lower frequency ratchets and roars, and combinations of all these. This sequence is typically about 10–15 min in duration, although it may range from 5 to 90 min. It is then repeated without a break (Payne and McVay, 1971; Winn and Winn, 1978).

The song has a predictable structure or framework. Discrete sounds are termed units. Several different sounds or units are arranged in a phrase. The phrase is then repeated some variable number of times (e.g., 10 times), and this series of the same phrase is called a theme, say, “Theme 1.” After several minutes of singing Theme 1, the singer changes to “Theme 2,” a different phrase (arrangement of sounds), repeating it until moving on to the next theme. A typical song may contain six themes, sung in order 1–2–3–4–5–6, and then the singer starts at 1 again. The number of themes in a song varies from population to population and from year to year. A song session may continue without a break for hours (Payne and McVay, 1971).

Several characteristics of song display are notable. First is the precision by which a singer repeats its complex song in any song session. An undisturbed singer may repeat the same themes, phrases, and units faithfully for hours as if on a continuous loop. The second characteristic is that all the singers in a humpback assembly, and there may be hundreds, follow the same structural rules and broadcast essentially the same song at any one time (Payne et al., 1985; Noad et al., 2000). There is some variation in song presentation and some songs are exceptional to the point that they have been termed “aberrant” by investigators. The significance of this variability is not yet understood.

C. Song Progression

One of the more striking characteristics of humpback song is that it progressively changes. Different sounds, and arrangements of sounds, form to create new phrases and themes, whereas older patterns are lost. The rate of song change varies. Gradual changes may be incorporated over 5 or more years before full replacement of the “original” version (Payne and Payne, 1965); or, a song can change entirely from one season to the next (Noad et al., 2000).

At any one time, however, all the singers in a population sing fundamentally the same version of this ever-changing song (Payne et al., 1985; Cerchio et al., 2001). The mechanism by which this occurs is not known. Presumably, the innovations are spread when individual whales introduce a change, copied collectively. This was emphasized by a discovery that, over a 9-year period, all the humpback whales off eastern Australia essentially adopted the western Australian humpback song, apparently introduced to that region by the mixing of whales (Noad et al., 2000).
D. Song Characteristics and Population Definition

Researchers have considered use of humpback whales’ song to define “stocks” or study population-scale interactions (Payne and Guiney, 1983). That is, if separate populations sing the same song the presumption is they must mix at some point in their migratory cycle, whereas different songs indicate isolated populations. However, recent studies indicate this is not necessarily as simple as it sounds.

On the one hand, humpback populations throughout the entire North Pacific basin sing a very similar song clearly indicating some degree of mixing occurs (Payne and Guiney, 1983; Cerchio et al., 2001; Darling et al., 2014). And as expected, Pacific and Atlantic humpback songs are entirely different from each other as the populations are clearly separate. However, eastern South Pacific humpback songs may be entirely different from one island archipelago to the next, despite relatively close proximity. Further, the predominant song type may shift, for example, from Tonga 1 year to French Polynesia the next, and so on. This pattern has been dubbed “dynamic horizontal cultural transmission” of song—its mechanism not understood (Garland et al., 2011). Song comparison becomes even more complicated when songs are only partially similar, i.e., two populations have some themes or phrases in common, with others unique. For example, a song comparison Madagascar and Western Australia found one of five themes in common (Murray et al., 2012), or a song comparison between Asia and Hawaii found 9 of 18 phrases in common (Darling et al., 2014). Some song components may be more sensitive to change than others. Until factors determining the type, degree, and rate of song change are better understood, the full potential for using song to define population units is unknown.

II. Singing Behavior

A. Seasonality

Singing is a seasonal behavior pattern. It occurs primarily during the winter half of the year, through the peak of humpback whale breeding season. Songs become increasingly common on the feeding grounds as fall progresses into winter, are heard regularly during migrations, and predominate on warm water winter breeding grounds. It is not clear when singing activity declines in spring, but songs have occasionally been recorded during midsummer, and even during active feeding (Clark and Clapham, 2004; Stimpert et al., 2012).

B. A Male Communication

A singer on the breeding ground is typically a lone adult male. However, it is not unusual for an “escort,” the adult male accompanying a cow with calf, to be singing. Also, occasionally a singer has a companion adult, male or female, or a juvenile in the close vicinity (Darling et al., 2006; Smith et al., 2006). A singer may remain stationary for many hours, adopting a motionless, head-down, tail-up posture approximately 50–100 feet beneath the surface, interrupted only when it surfaces to breathe. At other times, a singer travels steadily during a song session and may move tens if not hundreds of kilometers across the breeding ground or along a migratory route.

C. Interactions of Singers

Humpback songs are loud and can be heard underwater for at least several kilometers and, in some circumstances in deep ocean basins, possibly hundreds of kilometers. A collection of dozens of singing humpbacks produces a substantial noise, clearly designating the location—on an oceanic scale—of an assembly of humpbacks during breeding season. It is likely that individual humpbacks interact with the collective singing herd over distances.

On a smaller scale, several studies have focused on the interactions of individual singers with other whales. Generally, lone singers sing until one of two things happen. First, most often, they are joined by other lone males (occasionally pairs of males), the singing stops, and a brief, nonaggressive interaction follows that ranges from a single surfacing and crisisscrossing to occasionally a tail blow or a breach. The pair splitting up again after a few minutes (Darling and Berube, 2001). One or the other may start singing again shortly after the interaction. These joiner-singer interactions repeat continually across the breeding assembly with individuals alternating in the singer or joiner role, purpose unknown. Second, the singer stops singing with out any close approach by another whale and then rushes to approach a passing group of whales—often a cow with calf or a competitive group. In these cases, the singer joins a group that includes a potentially breeding female (Darling et al., 2006). Also, as mentioned, on occasion a male escorting a cow with calf, or a male in an adult male-female pair sings—raising the question of whether they are singing to other males while in company of a female, or singing to the female (Darling et al., 2005; Smith et al., 2006).

III. Function

The function of the song has been the subject of much speculation. Much of this has revolved around proposals of the song as a male display to attract females, signal status to other males, or a combination of these (Twyck, 1981; Clapham, 1999; Darling and Berube, 2001). However, other suggestions include that the song serve as a means to synchronize estrus, a spacing mechanism between males, a migratory beacon, and even as sonar by males to find females. One relatively new hypothesis proposes that the song may function as an index of association between males, perhaps as a basis for organizing males during the breeding season (Darling et al., 2006), whereas another speculates singers are “prospecting” for females (Smith et al., 2005). The continual, collective change of the song within a population confounds many simple explanations.

Conservatively, the song is a communication from male humpbacks during breeding season. It provides the location of the singer and by association the entire herd, and signals that breeding activity is underway. The song also likely broadcasts information about the individual singer, but what information, or who the recipients are remains speculative. The song, at the least, plays a role in modulating brief, nonaggressive male-male interactions. The connection between this behavior and actual mating, or other potential functions of the song, is unknown.

IV. Songs of Other Species

Much of our developing knowledge of the songs of other species of whales is the result of recent advances in remote sound recording technology, deployed in locations, seasons, and over time periods not conducive to human presence. This exploration indicates blue, fin, and minke whales emit repetitive series of calls fitting the definition of song, but the structure appears simpler than humpback, phrase, and theme complexity in humpbacks. The songs of bowhead whales, however, are perhaps even more puzzling than those of humpbacks. Compared to humpbacks, the bowhead's repetitive patterns—their songs—are shorter; however, a population produces multiple, entirely different songs in one season. And, remarkably, bowheads can produce two different sounds at the same time.
SOUND


SOUND

ADAM S. FRANKEL

This chapter reviews the basics of marine mammal sounds and mechanisms of sound production. The main focus is on characteristics of internally produced sounds. Nonvocal sounds, such as tail slaps, are not treated in detail here. Certain species that stand out as particularly unusual or particularly well studied get special attention. Other species are treated in taxonomic groups, when their acoustic characteristics are similar or less well known. Odontocetes are organized according to their three main sound types: clicks, pulsed sounds, and whistles.

I. Fundamentals of Sound

Several key terms help describe sound. The frequency of a sound is the number of times a complete sound wave occurs per second, and is reported as Hertz (Hz). Frequency is a physical characteristic of sound. Pitch is the perception of frequency. Sounds below 20 Hz are termed infrasonic, whereas those above 20 kHz are ultrasonic.

We often want to know the amplitude of a sound. Decibels (dB) are defined as 10 times the logarithm of the ratio of measured sound pressure level (SPL) to a reference level (e.g., 1 Pa). Therefore, in-water decibels are expressed as XX dB re 1 Pa. Source level is the level at a standardized distance of 1 m. For example, fin whales have been measured at 171 dB re 1 Pa at 1 m.

Importantly, in-air and in-water decibels are not the same. This is due to different reference levels (90 μPa in air, 1 μPa in water) and the physical characteristics of the transmission media (air or water). The medium can be characterized by its acoustic impedance, which is the sound velocity multiplied by the density of the medium. The difference in acoustic impedance between air and water is quite high, which accounts for most of the difference between air and water decibels. Generally, adding 61.5 dB to an in-air measurement will convert it to an in-water measurement. Furthermore, the difference in acoustic impedance creates a need to couple sound from one media to another, as we shall see in more detail.

Frequency-modulated (FM) sounds change frequency over time. Dolphin whistles are usually frequency modulated. Amplitude-modulated (AM) signals are those that rapidly change loudness, over time. Many mysticete calls are amplitude modulated and sound like whoops.

A record of sound pressure versus time is a waveform. Animal sounds are often represented as a spectrogram with frequency on the y-axis and time on the x-axis. Fig 1 shows the waveform and spectrogram of blue whale calls. The first sound is an AM signal that shows individual amplitude pulses in the waveform. The second signal is an FM signal, with a smooth envelope (or waveform outline). The AM signal has typical sidebands, whereas the FM signal is a downward sweep from about 20 to 15 Hz. This is the lowest or fundamental frequency contour. The additional “lines” above it are harmonics, which are integer multiples of the fundamental frequency.