

HEARING IN CETACEANS: FROM NATURAL HISTORY TO EXPERIMENTAL BIOLOGY

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Abstract

Sound is a primary sensory cue for most marine mammals, and this is especially true for cetaceans. To passively and actively acquire information about

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their environment, cetaceans have some of the most derived ears of all mammals, capable of sophisticated, sensitive hearing and auditory processing. These capabilities have developed for survival in an underwater world where sound travels five times faster than in air, and where light is quickly attenuated and often limited at depth, at night, and in murky waters. Cetacean auditory evolution has capitalized on the ubiquity of sound cues and the efficiency of underwater acoustic communication. The sense of hearing is central to cetacean sensory ecology, enabling vital behaviours such as locating prey, detecting predators, identifying conspecifics, and navigating. Increasing levels of anthropogenic ocean noise appears to influence many of these activities.

Here, we describe the historical progress of investigations on cetacean hearing, with a particular focus on odontocetes and recent advancements. While this broad topic has been studied for several centuries, new technologies in the past two decades have been leveraged to improve our understanding of a wide range of taxa, including some of the most elusive species. This chapter addresses topics including how sounds are received, what sounds are detected, hearing mechanisms for complex acoustic scenes, recent anatomical and physiological studies, the potential impacts of noise, and mysticete hearing. We conclude by identifying emerging research topics and areas which require greater focus.

Key Words: aural; acoustics; dolphin; whale; soundscape; sensory physiology



1. INTRODUCTION

Hearing in cetaceans is an impressive process resulting from various adaptations to life underwater. Some components of the auditory system of mysticetes (baleen whales) are among the largest of all mammals, and some species are likely to hear infrasonic frequencies. Odontocetes (toothed whales, dolphins, and porpoises) hear extraordinarily high frequencies, extending up to 180 kHz in some species. Most odontocete species have fine-scale frequency discrimination abilities. They can process sounds rapidly, compensating for both the faster underwater sound speed and complex requirements for echolocation. Furthermore, odontocetes have developed a novel mechanism to receive sounds through specialized acoustic fats associated with their lower jaws.

Past investigations of cetacean hearing, particularly those conducted on odontocetes in the past 50 years, have revealed a significant amount of information about the impressive hearing abilities of cetaceans. Because cetaceans are primarily offshore, pelagic animals which are difficult to maintain in captivity, audiometric studies typically involve small sample sizes for a limited subset of species. Consequently, there is still a substantial

amount of knowledge to be gained for most species and within the subject of cetacean hearing.

This review addresses what has been learned regarding cetacean hearing, presenting it within a historical context while incorporating more recent, novel investigations. The review focuses on odontocetes because the majority of information available examines this suborder. We also address what little is known about mysticete hearing and suggest future research areas.

2. EARLY INVESTIGATIONS

The study of cetacean hearing started as an observational inquiry, centred on natural history. One of the notable earlier studies was published by John Hunter in 1787 (Hunter, 1787). In his lengthy work titled “Observations on the Structure and Oeconomy of Whales”, Hunter noted that cetacean ears are made of the same structures as quadruped ears including an external opening, a tympanic membrane, the Eustachian tube, ossicles, cochlea, and semicircular canals. However, there is no pinna and the ear canal is a long tube taking a “serpentine course” through the tissues of the head. The bony portion of the ear, composed of the “tympanum” (tympanic) and the “round, bony process” (periotic), is very hard and is not as integrated into the skull as in other quadrupeds. Regarding how the organ functions, Hunter speculated that the tympanic cavity amplifies sound through the vibration of bone and these vibrations are directly transferred to the inner ear.

In 1812, Everard Home published an account of the ears of bowhead whales (*Balaena mysticetus*). He noticed the peculiarity of the tympanic membrane in these animals, which is convex unlike in any other animal and projects into the ear canal (Home, 1812). This derived tympanic membrane, which is common to mysticetes but not found in odontocetes, is now called the “glove finger”. Home hypothesized that the bowhead whale hears through vibrations of the tympanic bone, which are transmitted via another “membrane” stretched across the tympanic cavity and attaching to the malleus.

Remington Kellogg studied the evolution of whales in the 1920s, comparing currently existing species to fossil cetaceans and examining various modifications to the skull as cetaceans evolved to live under water (Kellogg, 1928). In the process, Kellogg elaborated upon previous descriptions of the auditory anatomy. He noted that the attachment of the tympanic and periotic bones (housing the middle and inner ears) to the skull differs between toothed whales and baleen whales: the bones are only attached to the skull by ligaments in toothed whales, while the periotic bones of all living and fossil baleen whales have a long posterior process that

is wedged between the exoccipital and squamosal bones. Kellogg speculated that the dense, heavy, air-filled tympanic bulla serves as a resonating sounding box, vibrating somewhat independently of the periotic and transmitting sound along the ossicles. This “resonance theory” seems to have been a popular viewpoint at this time, as the same mechanism was also described by [Claudius \(1858\)](#) and [Denker \(1902\)](#)¹ even though they disagreed about the involvement of the ossicles.

Various other theories on cetacean sound reception also existed during this time period. [Camper \(1762\)](#)¹ thought that sperm whales heard through the ear canal. [Buchanan \(1828\)](#) stated that bowhead whales heard through the Eustachian tube. An unnamed scientist (described in [Kernan, 1919](#)) thought that sound reaches the cochlea directly through vibrations of the periotic bone, but this was dismissed by Kernan because he thought that the cochlear fluid needs to receive an orderly succession of waves from the ossicles for sensitivity to different frequencies. [Kernan \(1919\)](#) supported bone conduction, where vibrations from the entire skull are transmitted to the tympano-periotic complex through a bony outgrowth of the tympanum that may contact the skull. [Yamada \(1953\)](#) also supported the bone conduction theory, arguing that even if the tympano-periotic complex lacks bony connections to the skull, fibrous connections prevent acoustic isolation of the ears. He reasoned that resonance of air in the middle ear cavity cannot be essential to auditory function because the cavity often fills up with parasites.

Yamada also provided a summary of conflicting theories of the time, including [Boenninghaus’s \(1904\)](#) “sound-funnel” theory. [Boenninghaus](#)¹ proposed a soft-tissue pathway which ends at the tympanic bulla, putting the malleus into motion and thus transferring sounds via the ossicles to the inner ear. This seems to be the theory closest to the current view of odontocete sound reception described by [Norris \(1968; see below\)](#). However, Yamada noted that [Boenninghaus’s](#) work was “really so hard to understand that. . . a serious confusion was brought into our field”. Yamada concluded his discussion by stating that the experiments necessary to settle the dispute of how cetaceans receive sound are not yet feasible, but the field will greatly benefit from technical advances in the future.

While the mechanism of hearing remained unclear, the anatomic potential for acute hearing in cetaceans was becoming evident. [Hunter \(1787\)](#) had noted the well-developed cochlea relative to the semicircular canals, an observation repeated by [Fraser \(1952\)](#). [Langworthy’s \(1931\)](#) study of the central nervous system revealed that the acoustic nerves and acoustic components of the brain are exceptionally well developed in odontocetes. He commented that the highly developed odontocete cerebral cortex may have

¹ These works are unavailable in English. Therefore, the content was obtained from [Yamada’s \(1953\)](#) descriptions of the theories.

been driven by very acute hearing and need for acoustic processing, analogous to the rapid growth and differentiation of the primate cortex as a response to its complex optic structures and binocular stereoscopic vision. Indeed, researchers began suspecting that odontocetes might echolocate and “see” through their hearing in 1947 (Schevill and McBride, 1956).

The first underwater recordings of cetacean vocalizations were made in the 1940s, which greatly advanced our understanding of the sounds used by cetaceans (Schevill and Lawrence, 1949). In 1952, Kellogg and Kohler borrowed a transducer from the U.S. Navy for a primitive behavioural hearing experiment on captive dolphins (Kellogg and Kohler, 1952). Based on the results, they surmised that dolphins can hear ultrasonic sounds of up to 50 kHz. High-frequency hearing in odontocetes was also supported by the histological examination of their cochlea (Yamada and Yoshizaki, 1959).

Meanwhile, the controversy on *how* cetaceans received sounds was not yet settled. Reysenbach De Haan (1957) argued that the cetacean ear canal was vestigial based on experiments using tissue from blue whales (*Balaenoptera musculus*). He took a section of blubber which contained the ear canal, immersed it in water, and used hydrophones to show that sound conductivity was not significantly different through water compared to blubber. Furthermore, the orientation of the ear canal relative to the sound source made no difference in sound propagation. Therefore, he concluded that the ear canal could not be a preferential pathway for sound. Dudok Van Heel (1962) supported this view as well. Fraser and Purves (1960) came to the opposite conclusion by measuring sound waves travelling through a dissected ear canal compared to the surrounding tissue in fin whales. Because sound was attenuated the least through the ear canal, they surmised that it is a preferential sound reception pathway. Regarding the alternate theories, Fraser and Purves stated, “The adaptation of the sound path in normal terrestrial mammals is, on the face of it, more acceptable than any *de novo* method of sound conduction in mammals”.

3. NORRIS AND THE “JAW HEARING” HYPOTHESIS

The major breakthrough in the field came in the mid-1960s. Norris was walking on a beach in Mexico when he came across a dolphin skeleton. He noticed a region of the lower jaw which was so thin that it was translucent (Fig. 4.1A). Norris termed this region the “pan bone” and observed that this is a common feature to all odontocetes. This thin area of bone was overlain with an oval fatty area which he called the “acoustic window”. Norris hypothesized that sound enters the odontocete head through this oval fat body and goes through the thinnest part of the mandible to the “acoustic fat” filling the mandibular canal (Fig. 4.1B). While the precise role of the pan bone is still under debate and the existence

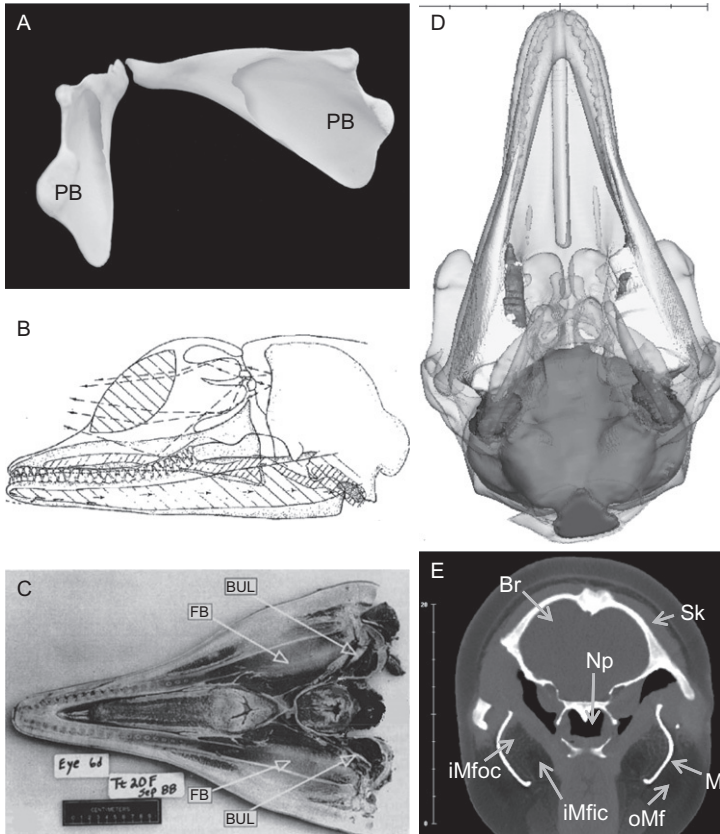


Figure 4.1 The lower jaws of a harbor porpoise (MH416Pp), posterior view. Note the enlarged mandibular foramen on the medial side, which is a common feature to all odontocetes and is filled with fats associated with sound reception. The thin “pan bone” area which Norris proposed as the acoustic window is labeled PB. (B) Proposed sound pathways in a porpoise head showing incoming sounds traveling through the lower jaw (modified from Norris, 1964). (C) Coronal slice of a dolphin head, modified from Ridgeway (1999). FB, fat body in the lower jaw; BUL, tympanic bulla. (D) A 3D reconstruction of peripheral auditory system of *Feresa attenuata*, pygmy killer whale, based on computerized tomography (CT). Ventral view illustrating the tympano-periotic complex (blue), the inner mandibular acoustic fat bodies including the outer (yellow) and inner core (orange). The bones of the mandibles and skull are transparent and grey. (E) Anatomically labeled CT image in the transaxial plane of the peripheral hearing apparatus of a live pygmy killer whale. Br, brain; iMfic, inner mandibular fat body inner core; iMfoc, inner mandibular fat body outer core; M, mandible; Np, nasal passages; oMf outer mandibular fat body; Sk, skull (D-E were adapted with permission from Montie *et al.*, 2011).

of these mandibular fat bodies was known since the 1800s, Norris was the first one to associate them with the auditory system. Norris observed that the fats lead directly to the tympanic bulla and hypothesized that they may provide a low impedance pathway to the ears (Fig. 4.1; Norris, 1964, 1968).

Not everyone accepted Norris' hypothesis immediately. However, Norris' stimulating idea led to a series of validation studies, enabled by technological advances of the time. Bullock *et al.* (1968) conducted physiological recordings from anaesthetized dolphins and found the greatest response when sound was played to the lower jaw. Norris and Harvey (1974) implanted small hydrophones in various locations of a dead bottlenose dolphin head and found sound to be concentrated in the proposed sound channel of the jaws. Brill *et al.* (1988) found that a bottlenose dolphin's echolocation abilities were greatly reduced when its lower jaws were covered by an acoustically opaque hood. The authors suggested that the hood prevented the animal from hearing the returning echoes, thus behaviourally supporting the notion of jaw hearing. A behavioural hearing test also supported these observations in which sound was presented via a "jawphone", or a transducer implanted in a suction cup (Brill *et al.*, 2001). The tests showed that high frequencies were best detected when sounds were presented along the lower jaw (e.g. Fig. 4.1C). However, the dolphin detected lower frequencies better when they were presented near the opening to the ear canal. These reports were supported with similar electrophysiological hearing tests (Møhl *et al.*, 1999; Mooney *et al.*, 2008).

Scientists from other fields also made significant contributions. For example, biochemical studies showed that "acoustic fats" are incredibly specialized, comprising endogenously synthesized shorter, branch-chained fatty acids and wax esters not typically found in mammalian adipose tissues (Varansi and Malins, 1972; Litchfield *et al.*, 1975; Morris, 1975; Varansi *et al.*, 1975). Recent work by Koopman *et al.* (2006) has revealed a complex and consistent topographical distribution of lipids within odontocete perimandibular fats, with the highest relative wax ester concentrations for each species all occurring in the caudal-most portions of the inner mandibular fat bodies, which connect to the tympano-periotic complex. This new study confirmed early suggestions of heterogeneity in lipid composition of odontocete perimandibular fats (Malins and Varanasi, 1975).

Koopman *et al.* (2006) also found that the distribution of fatty acids shows consistent patterns, where the shortest and branched-chain compounds were concentrated in the middle of the inner fat body and around the tympano-periotic complex. It has been shown that sound velocity in lipids is a function of their molecular weight and that sound also travels faster through triacylglycerols than through wax esters (Gouw and Vlughter, 1967; Hustad, 1971; Flewellen and Morris, 1978). Therefore, the study hypothesized that the topographical arrangement of lipids within perimandibular fat bodies of odontocetes is arranged so that sound is directed to the ears as it bends towards the inner low-velocity centre of the mandibular fat body, which has a higher concentration of wax esters and short, branched-chain lipids. Such an acoustic channel has also been proposed for odontocete melons in previous studies which have found compositional heterogeneity

within the melon (Varanasi and Malins, 1972; Litchfield *et al.*, 1973; Wedmid *et al.*, 1973; Blomberg and Lindholm, 1976; Scano *et al.*, 2005).

Interestingly, Zahorodny *et al.* (2009) found that the perimandibular fats of the bottlenose dolphin do not display the same pattern of having an inner low-velocity channel, although the fats closest to the tympano-periotic complex do follow the pattern of having the highest wax ester content and shortest, branched-chained fatty acids and fatty alcohols. These differences between species, as well as differences in lipid composition found between age classes, may reflect the complexity, development, and niche-related adaptations of the fat “channels” (Koopman and Zahorodny, 2008). Together, these studies helped establish the validity of Norris’ unconventional theory, leading to a paradigm shift by uncovering a whole new mechanism for mammalian hearing.

4. WHAT ODONTOCETES HEAR

4.1. Basic hearing abilities

An audiogram provides a plot of frequency versus detection limit (hearing threshold, e.g. Fig. 4.2). The first odontocete audiogram was published by Johnson (1966, 1967). Using operant-conditioned and a go/no-go procedure, an 8- to 9-year-old male bottlenose dolphin was trained to press a lever

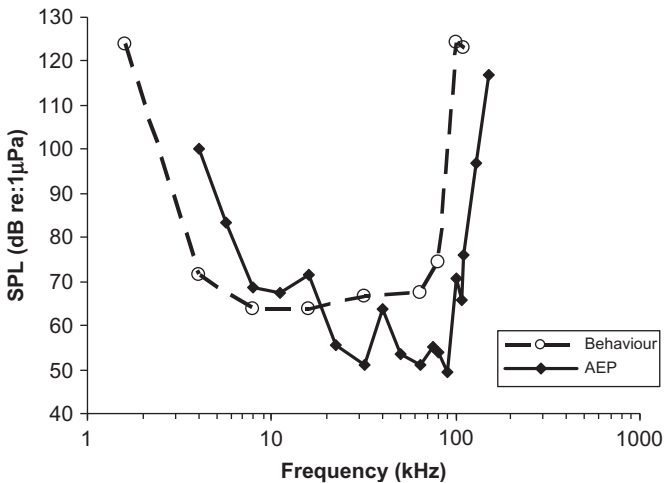


Figure 4.2 Audiograms of two Risso’s dolphins. One was collected behaviourally and the other using AEP methods. The dashed audiogram was measured from an older animal with high-frequency hearing loss. The solid audiogram was measured for a neonate animal which presumably had more “normal” hearing (adapted with permission from Nachtigall *et al.*, 2005).

when a sound was detected (a “go” or positive response). If the animal did not detect a sound, it would remain still (a “no-go”). A staircase method, which steps sound levels up or down based on correct and incorrect responses, was used to vary sound levels. The animal was given a 90-s time out for incorrect responses. This work described an auditory range of 75 Hz to 150 kHz and thresholds at or below 50 dB re 1 μ Pa from approximately 10 to 115 kHz. Maximal sensitivity was 40.8 dB at 65 kHz (Table 4.1). This broad and sensitive audiogram set a benchmark to which all other odontocete audiograms have been, and continue to be, compared.

This bottlenose dolphin audiogram was soon succeeded by comparative hearing tests in several other odontocete species including one harbour porpoise (*Phocoena phocoena*), one killer whale (*Orcinus orca*), and one Amazon river dolphin (*Inia geoffrensis*) (Andersen, 1970; Hall and Johnson, 1972; Jacobs and Hall, 1972). The hearing tests from each of these animals produced different audiograms. The harbour porpoise had slightly less sensitive hearing compared to the bottlenose dolphin, and its best hearing was found at slightly lower frequencies (8–32 kHz). The killer whale was most sensitive at even lower frequencies and had a high-frequency cut-off of only 32 kHz. The Amazon river dolphin had a narrow range of “best sensitivity” (10–50 kHz) and a high-frequency limit of 105 kHz. (Note that the meaning of “best sensitivity” can vary between studies; in this case, it refers to 20 dB above the lowest threshold.) At the time, it was not clear whether the large variations between these audiograms were due to species or individual differences.

Since these early audiograms, there have been several additions to the roster of species with hearing tests (Table 4.1). These now include the Chinese river dolphin *vexillifer* (Wang *et al.*, 1992), beluga (*Delphinapterus leucas*) (White *et al.*, 1978; Awbrey *et al.*, 1988; Klishin *et al.*, 2000; Mooney *et al.*, 2008), false killer whale (*Pseudorca crassidens*) (Thomas *et al.*, 1988; Yuen *et al.*, 2005), tucuxi (*Sotalia fluviatilis guianensis*) (Sauerland and Dehnhardt, 1998), Risso’s dolphin (*Grampus griseus*) (Nachtigall *et al.*, 1995, 2005), striped dolphin (*Stenella coeruleoalba*) (Kastelein *et al.*, 2003), finless porpoise (*Neophocoena phocanoides*) (Popov *et al.*, 2005), Gervais’ beaked whale (*Mesoplodon europaeus*) (Cook *et al.*, 2006; Finneran *et al.*, 2009), Pacific bottlenose dolphins (*Tursiops truncatus gilli*) (Ljungblad *et al.*, 1982; Houser *et al.*, 2008), white-beaked dolphin (*Lagenorhynchus albirostris*) (Nachtigall *et al.*, 2008), long-finned pilot whale (*Globicephala melas*) (Pacini *et al.*, 2010), Blainville’s beaked whale (*Mesoplodon densirostris*) (Pacini *et al.*, 2011), and the pygmy killer whale (*Feresa attenuata*) (Montie *et al.*, 2011). These audiograms have yielded a substantial amount of information on odontocete hearing sensitivity.

One conclusion that can be derived from the above studies is that there is a huge diversity in hearing ranges and sensitivities among odontocetes. These disparities appear to be a combination of species differences and individual variation. Increasing sample sizes within a species has shown that there are

Table 4.1 Odontocete audiograms chronologically from initial tests on the species

Species	<i>n</i>	Hearing range (kHz)	Best sensitivity (kHz)	Method	References
<i>T. truncatus</i>	1	0.75–150	7–130	Behaviour	Johnson (1966, 1967)
	42	10–150	10–80 ^a	Physiology	Houser and Finneran (2006b)
<i>P. phocoena</i>	1	1–150	2–140	Behaviour	Andersen (1970)
	1	0.250–180	4–150	Behaviour	Kastelein <i>et al.</i> (2002)
<i>O. orca</i>	1	0.5–31	5–30	Behaviour	Hall and Johnson (1972)
	2	4–100	12–52	Behaviour	Szymanski <i>et al.</i> (1999)
	2 ^b	1–100	16–45	Physiology	Szymanski <i>et al.</i> (1999)
<i>I. geoffrensis</i>	1	1–105	10–50	Behaviour	Jacobs and Hall (1972)
<i>D. leucas</i>	2	1–130	15–110	Behaviour	White <i>et al.</i> (1978)
	4	0.125–8 ^c	4–8	Behaviour	Awbrey <i>et al.</i> (1988)
	1	8–128	27–107	Physiology	Klishin <i>et al.</i> (2000)
	2	2–130	14–90	Behaviour	Finneran <i>et al.</i> (2005)
	1	8–128	22–90	Physiology	Mooney <i>et al.</i> (2008)
<i>T. truncatus gilli</i>	1	2–135	25–110	Behaviour	Ljungblad <i>et al.</i> (1982)
	13	10–150	20–130 ^a	Physiology	Houser <i>et al.</i> (2008)
<i>P. crassidens</i>	1	2–115	16–64	Behaviour	Thomas <i>et al.</i> (1988)
	1	4–45	7–27	Behaviour	Yuen <i>et al.</i> (2005)
	1 ^b	4–45	6.7–27	Physiology	Yuen <i>et al.</i> (2005)
<i>L. vexillifer</i>	1	1–200	10–65	Behaviour	Wang <i>et al.</i> (1992)

<i>G. griseus</i>	1	1.6–110	4–80	Behaviour	Nachtigall et al. (1995)
	1	4–150	8–108	Physiology	Nachtigall et al. (2005)
<i>S. fluviatilis guianensis</i>	1	4–135	16–105	Behaviour	Sauerland and Dehnhardt (1998)
<i>S. coerulealba</i>	1	32–120	0.5–160	Behaviour	Kastelein et al. (2003)
<i>N. phoccanoides</i>	2	8–152	32–139	Physiology	Popov et al. (2005)
<i>M. europaeus</i>	1	10–80	40–80	Physiology	Cook et al. (2006)
	1	20–90	20–80	Physiology	Finneran et al. (2009)
<i>L. albirostris</i>	2	16–181	32–128	Physiology	Nachtigall et al. (2008)
<i>G. melas</i>	1	22.5–50	4–100	Physiology	Pacini et al. (2010)
<i>S. bredanensis</i>	14	10–120	Unclear	Physiology	Mann et al. (2010)
<i>M. densirostris</i>	1	5.6–160	40–50	Physiology	Pacini et al. (2011)
<i>F. attenuata</i>	2	5–120	20–60	Physiology	Montie et al. (2011)

Note: [Bullock et al. \(1968\)](#) published hearing ranges and relative responses, but not calibrated audiograms.

^a Greatly varied depending on sex and age.

^b Same animal tested as preceding study.

^c Did not establish upper limit.

many instances of hearing loss. For example, [Ridgway and Carder \(1997\)](#) demonstrated that hearing loss in bottlenose dolphins appears to be correlated with age and sex. Older animals were more likely to have high-frequency hearing loss compared to younger individuals. Males had a greater incidence and extent of high-frequency hearing loss compared to females. These results implied that the relatively narrower audiograms in species such as the killer whale and Risso's dolphin reflected incidences of individual high-frequency hearing loss rather than a species-wide phenomenon ([Hall and Johnson, 1972](#); [Nachtigall *et al.*, 1995](#)). This hypothesis was supported by subsequent tests of both species ([Szymanski *et al.*, 1999](#); [Nachtigall *et al.*, 2005](#)). For the killer whale, [Szymanski *et al.*](#) showed a substantially greater high-frequency limit of 120 kHz, as opposed to 32 kHz ([Hall and Johnson, 1972](#)), while the frequency of best hearing was similar to the previous study (18 and 20 kHz). [Nachtigall *et al.*'s \(2005\)](#) work examined the hearing of a neonate Risso's dolphin ([Fig. 4.2](#)). This animal had a high-frequency limit of 150 kHz, instead of 100 kHz, and good sensitivity (<80 dB) over a wider range, from 8 to 110 kHz. Lowest thresholds were 49.5 dB at 90 kHz, instead of the previously reported threshold of 67 dB at 64 kHz, although these elevated thresholds from [Nachtigall *et al.*, 1995](#) were likely masked by the noisy test conditions of Kaneohe Bay.

While the above studies established that intra-species variation existed, these differences were examined in greater detail for two subspecies of bottlenose dolphins (*T. truncatus* and *T. truncatus gilli*) ([Houser and Finneran, 2006b](#); [Houser *et al.*, 2008](#)). Variability in the range of hearing and age-related reductions in sensitivity were consistent between the two bottlenose dolphin subspecies. However, areas of best sensitivity differed between the two subspecies. The authors suggested that both genetic differences between the subspecies and the background noise conditions of the populations could be causing these differences.

4.2. Functional explanations for diversity in audiograms

These species differences, and the consistencies in audiogram shape between closely related species, suggest that there is a genetic component to odontocete hearing ([Houser and Finneran, 2006b](#); [Houser *et al.*, 2008](#)), which has been observed in other mammals ([Vanke, 1980](#)). In general, these differences are often attributed to correlations with the sounds produced, such as the frequencies of the echolocation clicks of the species.

Compared to the average bottlenose dolphin audiogram, the range of best sensitivity (20 dB within the lowest threshold in this case) for killer whales was centred around much lower frequencies of 12–52 kHz ([Szymanski *et al.*, 1999](#)). The best sensitivities were also comparatively lower, in the range of 40–50 kHz, for the two beaked whale species measured ([Finneran *et al.*, 2009](#); [Pacini *et al.*, 2011](#)). Correspondingly,

beaked and killer whale echolocation click signals are centred at lower frequencies than for clicks produced by bottlenose dolphins (20–50 vs. 80–130 kHz) (Au *et al.*, 1974, 2004; Johnson *et al.*, 2007).

Harbour porpoises show a broad range of good sensitivity between 16–140 kHz which included relatively high frequencies (Kastelein *et al.*, 2002). They are also sensitive up to 180 kHz. Compared to the bottlenose dolphin, porpoise echolocation pulses are narrow band, high-frequency signals, consistent with their high-frequency hearing (Au *et al.*, 1999). This is exceptional for odontocetes with only one other species, white-beaked dolphins, detecting signals at such high frequencies (Nachtigall *et al.*, 2008).

Whistles are presumably just as important, at least to the species that produce them. For the bottlenose and *Stenella* spp., whistle fundamental frequencies often do not overlap with the regions of best sensitivity (Johnson, 1967; Kastelein *et al.*, 2003; Lammers *et al.*, 2003). However, whistle harmonics can overlap with “best” hearing ranges, suggesting that their auditory system is well adapted to detect these components of the communication signals (Lammers *et al.*, 2003). Notably, echolocation signals can change with hearing abilities (Ibsen *et al.*, 2007; Klopper *et al.*, 2010). As high-frequency hearing is lost, animals seem to alter their echolocation centroid frequencies to match regions of maximal auditory sensitivity. Thus, there is substantial evidence that hearing sensitivities match the acoustic signals produced. Echolocation clicks with substantial sound energies at frequencies beyond the range of best hearing have been found only in the white-beaked dolphin (Rasmussen and Miller, 2002; Nachtigall *et al.*, 2008). While somewhat unexpected, this is probably a function of slight differences in the animals’ auditory anatomy or physiology. There are several examples of terrestrial animals producing sounds beyond their hearing range (Pytte *et al.*, 2004).

4.3. The auditory evoked potential method

Increased audiogram sample sizes, even across different methods and experimental conditions (Fig. 4.3), have greatly broadened our understanding of odontocete hearing sensitivity. Many of these audiograms were made possible by applying electrophysiological methods to study hearing. The primary electrophysiological method that has been used is called the auditory evoked potential (AEP) method. AEPs provide a non-invasive and rapid way to test hearing by measuring the small voltages generated by neurons in the auditory system in response to acoustic stimuli (Fig. 4.4). Voltages in response to sound are often generated in the brainstem and are sometimes referred to as auditory brainstem responses (ABRs). Louder acoustic stimuli lead to larger amplitudes in the AEP signals. As the stimulus is reduced in intensity, the resulting AEP signals also become reduced. The intensity at which the AEP signal is no longer detectable is defined as the

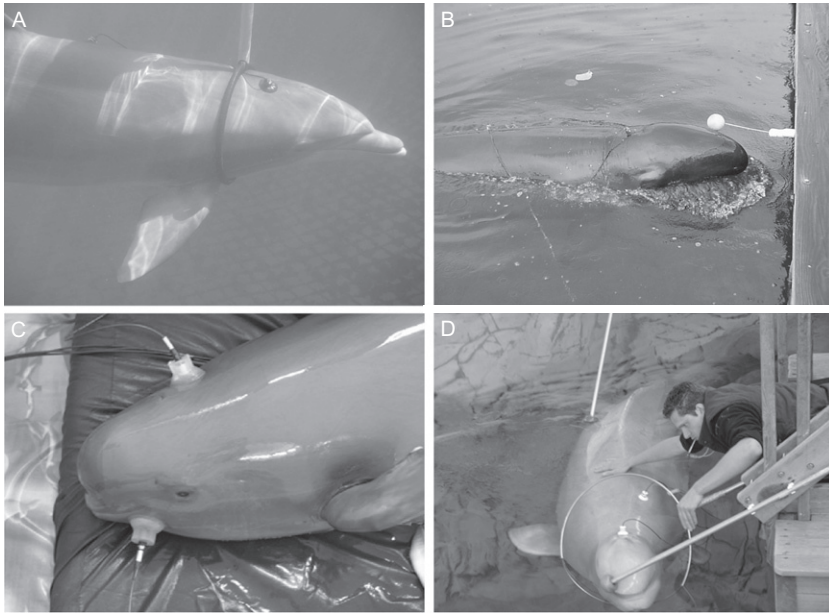


Figure 4.3 Various hearing test studies and animal examinations. (A) A bottlenose dolphin during an auditory evoked potential (AEP) hearing test in the free field. The dolphin is stationed in a hoop 1 m below the surface and 2 m from the sound generator. Note the AEP electrodes on the head and back of the dolphin. (B) A false killer whale responding positively during a combined psychoacoustic and electrophysiological task. The animal responds that it detects an object by touching a yellow ball with its rostrum. The stimulus in this case was the echolocation detection of cylinder target. In hearing test tasks, reporting the detection of a tone would generate a similar response. (C) Measuring the hearing of a finless porpoise out of water using a suction cup jawphone transducer placed on the pan bone region of the lower jaw. Responses are measured using AEPs. A suction cup electrode is visible on top of the head, just behind the blowhole. (D) Beluga whale during an AEP hearing test to examine directional sensitivity. Pictures A-D are from respective research presented in: Mooney *et al.*, 2009a,b; Supin *et al.*, 2003; Mooney *et al.*, 2011; Mooney *et al.*, 2008.

hearing threshold. Actual threshold determinations can be conducted in several ways (Finneran *et al.*, 2007a; Nachtigall *et al.*, 2007; Supin and Popov, 2007). The AEP method requires no training of the subject and is used to assess hearing in a variety of taxa including other mammals, such as humans (Hecox and Galambos, 1974; Dolphin and Mountain, 1992), birds (Brittan-Powell *et al.*, 2002), teleost fish (Ladich and Yan, 1998), cartilaginous fish (Casper *et al.*, 2003), and invertebrates (Lovell *et al.*, 2005).

Electrophysiological auditory measurement techniques have been established for several decades in marine mammals. Initially, the methods varied, electrophysiological tools adapted for marine mammals were not widely

available, the experiments were often invasive, and the methods were not widely applied (Bullock *et al.*, 1968; Ridgway *et al.*, 1981; Popov and Supin 1990b). Early studies initially required anaesthesia, a major accomplishment for animals which respire voluntarily (Ridgway and McCormick, 1967). Bullock *et al.* (1968) followed this work with the first acoustically stimulated electrophysiological auditory recordings from 29 odontocetes among 4 species. This was a comprehensive study that addressed waveform characteristics, temporal resolution, electrode placement, frequency tuning, masking using background noise, and pure tones versus modulated stimuli. The study produced an “audiogram” similar in frequency responses and sound levels to Johnson’s audiogram for the bottlenose dolphin. Evoked potentials were measured using tungsten and stainless steel electrodes inserted in several locations, with reliable responses originating from the inferior colliculus.

McCormick *et al.* (1970) followed with an integrative anatomical and electrophysiological study of the mechanisms of the dolphin middle ear using dissections and physiological recordings from the inner ear’s round window. They concluded that sound will induce the movement of the ossicles (thus a functional middle ear) and be conducted to the inner ear through the oval window. While still a novel study, the results were slightly limited by the inevitable surgery and the necessity to make measurements with the animal at the water surface. Odontocete middle ear mechanisms are still debated today.

The pace of invasive electrophysiological studies in the United States slowed after the passage of the Marine Mammal Protection Act of 1972. However, substantial AEP work was continued by Soviet scientists (see review by Ridgway, 1980). Advancements included using AEPs to identify response-generating regions within the cortex and identifying how AEP onset and offset responses were impacted by frequency and duration (Ladygina and Supin, 1970, 1977; Popov and Supin, 1976, 1978). The thresholds produced were similar to prior psychophysical (behavioural) tests (Johnson, 1966). Classical conditioning was used to measure hearing physiologically by pairing tones with electric shocks, while monitoring changes in heart rate, respiration, and galvanic skin response (Supin and Sukhoruchenko, 1970; Sukhoruchenko, 1971, 1973). The experiments detected the upper limit of hearing and showed that both bottlenose dolphins and porpoises have precise frequency discrimination abilities across their hearing range. Using operant conditioning, Thompson and Herman (1975) demonstrated that dolphins can distinguish two sounds that differ in frequency by only 0.2–0.3%, displaying remarkably precise frequency analyses.

Some of the early AEP studies pioneered the development of non-invasive methods which recorded responses from the surface of the skin (Seeley *et al.*, 1976). This method was similar to those used on humans and set the stage for rapid advances in odontocete AEP recordings (Hecox and Galambos, 1974). Within the past two decades, an emphasis on relatively simple, non-invasive AEP techniques has been developed, providing insights

into the auditory systems of odontocetes (Dolphin *et al.*, 1995; Supin and Popov 1995; Supin *et al.*, 2001; Nachtigall *et al.*, 2007).

Early non-invasive dolphin AEP measurements were stimulated with tone pips and revealed dolphin AEP responses involving a series of five to seven neurophysiological “wave” responses (Popov and Supin, 1985, 1990b). An efficient and reliable method to obtain AEP hearing thresholds has used the envelope-following response (EFR) or auditory steady-state response (ASSR; Supin and Popov, 1995). In this method, the stimulus is a sinusoidally amplitude-modulated tone or a series of clicks (Fig. 4.4). The series of resulting AEP waves are all visible at the onset of an EFR, but if a stimulus is played at a rapid enough rate, most of the waves blend together in a sinusoidal fashion. The animal’s EFR is a consequent sinusoidal “following” of the envelope of the carrier signal; when the animal is able to detect the stimulus, the AEP recordings contain a sinusoidal signal at the frequency with which the amplitude of the stimulus is modulated. The results of this method compare favourably to those from behavioural psychometric audiograms (Szymanski *et al.*, 1999; Yuen *et al.*, 2005; Houser and Finneran, 2006a). Other aspects of odontocete AEPs are well reviewed elsewhere (Supin *et al.*, 2001; Nachtigall *et al.*, 2007).

5. HEARING MECHANISMS FOR COMPLEX AUDITORY SCENES

While the increasing number and quality of audiograms provide insights into what odontocetes hear, substantial progress has also been made regarding how odontocete hearing works. For hearing to provide any advantage to an individual listener, an animal must not only detect, discriminate, and recognize sounds but also know the sound source location. These abilities are complicated by the presence of multiple sounds occurring simultaneously in Euclidean space. An excellent example of a fundamental, but complex auditory task, occurs during cooperative nocturnal feeding by Hawaiian spinner dolphins (*Stenella longirostris*). These animals are tasked with cooperatively herding a low-density mesopelagic biomass into a dense group that is more conducive to feeding (Benoit-Bird and Au, 2009). Behaviourally, the group spreads out in a horizontal line and swims towards the low-density layer forcing the fish to coalesce for protection. To accomplish this task, the dolphins must acoustically monitor the position of group members and coordinate their herding behaviour, acoustically monitor the position and density of their prey, and still remain vigilant for potential predators. Monitoring the position and direction of the movement in group members is likely accomplished by both directly echolocating on group members and passively listening to specific acoustic cues associated with other group member’s directional phonations. Foraging groups in Hawaii

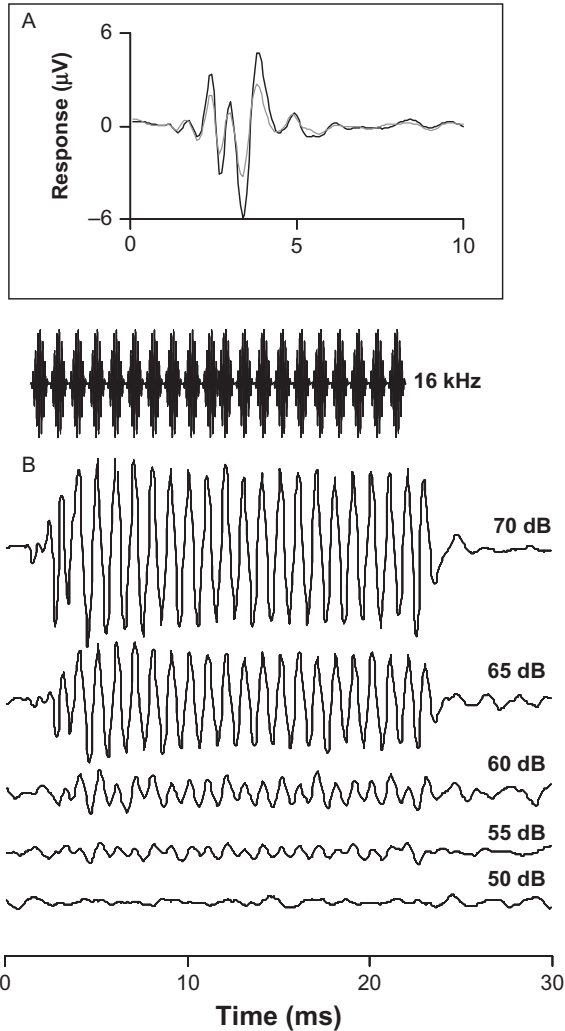


Figure 4.4 (A) Finless porpoise AEP waveforms to a click stimulus. Two responses are overlaid on top of each other. Note the series of wave responses generated from the multiple generators of the auditory system, from the eighth nerve up through the brainstem. (B) Bottlenose dolphin EFRs or ASSRs to 16 kHz amplitude-modulated stimuli (top trace). The EFRs decrease in amplitude as stimulus amplitude correspondingly decreases.

typically range from 16 to 28 individuals (Benoit-Bird and Au, 2009), meaning that there will be a cacophony of clicks and echoes coming from many different sources and targets that the dolphin auditory system must make sense of. Understanding how this is accomplished requires an

understanding of how the dolphin's auditory system segregates and recognizes sounds in complex auditory scenes.

5.1. Basic hearing model

The dolphin auditory pathway can be modelled as a series of transfer functions that convert the environmental pressure fluctuations into perception. The primary stages are the head-related transfer function (HRTF), amplification by the middle ear ossicles, spectral decomposition at the basilar membrane (BM), transduction and amplitude compression at the hair cells, low-pass filtering by the eighth nerve and higher auditory areas, and reintegration of the information from both ears to form a percept. What follows is a review on some of the stages that have been studied.

5.2. Head-related transfer function

In terrestrial mammals, the primary purpose of the outer ear (i.e. the pinna and meatus) is to focus sound towards the middle and inner ear. In addition, the complex ridges and folds of the pinna, as well as the head and torso, also differentially filter sound depending on the source's location. This is known as a position-dependent spectral filter or an HRTF and aids a listener in determining the location of a sound source, especially in the vertical plane (Branstetter and Mercado, 2006). A feature often found in auditory predators (e.g. the barn owl, *Tyto alba*; Knudsen, 1981) is pronounced asymmetry in external auditory anatomy that results in an HRTF with salient localization cues. In water, the terrestrial pinna loses its reflective and filtering capabilities due to the density similarity with water. As a result, natural selection has sacrificed the archetypal odontocete pinna to provide a more streamlined shape for locomotion. To compensate for the loss of the pinna, the reflective and refractive properties of internal anatomical structures may function as a pinna analogue (Ketten, 1997; Aroyan, 2001). Like other auditory predators, odontocetes exhibit pronounced asymmetry in anatomical structures including the skull (Ness, 1967; Fahlke *et al.*, 2011), soft tissue (Cranford *et al.*, 1996), and cranial air sacks (Cranford *et al.*, 1996; Houser *et al.*, 2004). To date, a detailed HRTF of any cetacean has not been measured. However, data from behavioural experiments (Brill *et al.*, 2001), electrophysiological experiments (Supin and Popov, 1993), and computer models (Aroyan, 2001) all suggest that odontocetes possess a salient and complex HRTF.

5.3. Middle ear transfer function

The function of the middle ear in terrestrial animals is to amplify sounds to overcome impedance mismatch between air and the fluid-filled cochlea. Impedance mismatch between an ocean environment and the fluid-filled

cochlea is minimal, which calls into question the function of the middle ear in odontocetes. The ossicles of odontocetes are rigid and calcified, lacking the mobility of their terrestrial ancestors (Ketten, 1997). Nevertheless, mechanical models based on the anatomy of the tympano-periotic complex suggest the odontocete middle ear functions as a velocity amplification device using a lever mechanism (Nummela *et al.*, 1999). The rigidity of the system may be a specialization for high-frequency hearing associated with echolocation, and the computer models are able to provide reasonable fits to odontocete audiograms (Hemilä *et al.*, 2001).

5.4. Frequency and temporal resolution at the auditory periphery

Sound enters the cochlea at the oval window and displaces the differentially stiff BM. The odontocete BM functions on the same principles as terrestrial mammals. The basal end is stiffer and maximally displaced by shorter wavelength, high-frequency sounds. The apical end responds to long wavelength, lower frequency sounds (Ketten and Wartzok, 1990). The basal end of the odontocete BM is especially thick (25 μm), narrow (30 μm), and rigid, consistent with their sensitivities to ultrasonic sounds. Towards the apex, the thickness decreases (5 μm) and the width increases ninefold to increase sensitivity to lower frequencies (Ketten and Wartzok, 1990). Because of the frequency-dependent displacement of the BM, hair cells at specific locations will fire best for a characteristic frequency. Odontocete hair cell density along the BM appears to be uniform (Ketten and Wartzok, 1990) as in most terrestrial mammals. Each site along the BM is tuned to a specific frequency. Because there is a uniform distribution of hair cells on the BM, but not a uniform displacement (i.e. lower frequencies have longer wavelengths and thus displace a larger surface area of the BM), more hair cells are allocated to lower frequencies resulting in finer frequency resolution.

Frequency selectivity has been measured in odontocetes using both electrophysiological (Popov *et al.*, 1997) and behavioural methods (Au and Moore, 1990; Lemonds, 1999; Finneran *et al.*, 2002a) in different masking paradigms. One of the most common methods for measuring frequency selectivity is a band-widening, masking paradigm resulting in a metric known as the critical band (CB). Listeners are required to detect the presence of a sinusoidal tone masked by a narrow band of noise centred on the signal frequency. Thresholds are estimated as a function of increasing bandwidth. A result replicated across many animal species is that thresholds increase as a function of bandwidth, but only up to a specific bandwidth known as the CB. Masking noise beyond this CB no longer contributes to the masking of the signal. To account for this result, Fletcher (1940) suggested that the auditory periphery behaves as a series of overlapping band-pass filters. Each filter processes frequency energy within a limited

range while attenuating peripheral frequency energy. A related metric known as the critical ratio (CR) is based on the idea that since only a small band of noise contributes to the masking of the signal, the auditory filter bandwidth can be estimated by measuring tonal thresholds in wide-band noise. This assumes that the amount of energy in the noise band that masks the signal is equivalent to the signal at thresholds. If the pressure spectral density of the noise (N) and the signal at threshold (S_{th}) are known, the CB can be estimated by

$$\Delta F_{CB} = \frac{S_{th}}{KN}, \quad (4.1)$$

where ΔF_{CB} is the CB and K is a constant. If K is assumed to be equal to 1, the equation simplifies to

$$\Delta F_{CR} = \frac{S_{th}}{N}, \quad (4.2)$$

where ΔF_{CR} is the critical ratio. If CR is expressed in dB re 1 Hz, the CR can be simplified by subtracting the pressure spectral density level (L_N , in dB re $1 \mu\text{Pa}^2/\text{Hz}$) from the signal SPL at threshold (L_S , in dB re $1 \mu\text{Pa}$):

$$L_{CR} = L_S - L_N, \quad (4.3)$$

where L_{CR} is the critical ratio. The CR is the most widely used masking metric for marine mammals due to the relative ease of data collection (i.e. only one noise bandwidth is required compared to CBs which require several noise bandwidths). Figure 4.5 displays CRs for several odontocete

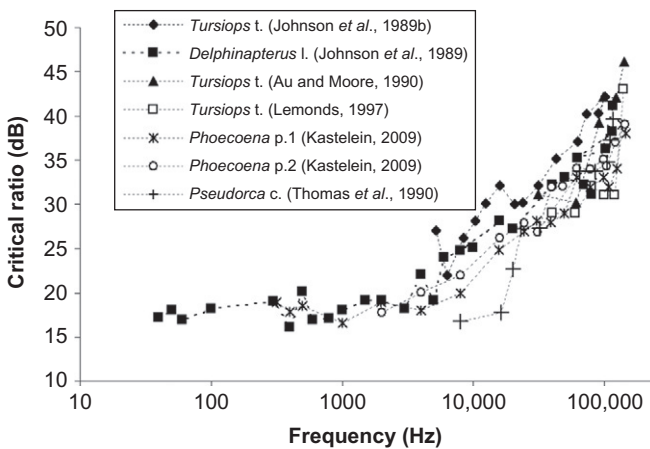


Figure 4.5 Critical ratios for several odontocete species as a function of frequency.

species. A common feature among terrestrial mammals is that CRs increase as a function of frequency due to increasing bandwidths of auditory filters. The relationship between the centre frequency of a filter and the bandwidth of a filter can be described as a quality factor, Q :

$$Q = \frac{f_0}{\Delta f}, \quad (4.4)$$

where f_0 is the frequency of the signal and Δf is the filter bandwidth. Q values for bottlenose dolphins have been estimated to be 12.3 for CRs and 2.2 for CBs (Au and Moore, 1990). A consequence of a constant- Q filter bank is that higher frequencies associated with wider filters will have a reduced spectral resolution compared to lower frequencies (see Fig. 4.6). The trade-off, however, is that wide, high-frequency filters will have excellent temporal resolution (see Fig. 4.7). A recent re-evaluation of Q values for the bottlenose dolphin suggests that these animals have a constant- Q filter bank for lower frequencies (< 40 kHz) and a constant bandwidth filter bank for frequencies above 40 kHz (Lemonds *et al.*, 2011). Similar constant bandwidth filters have been measured in harbour porpoises (Popov *et al.*, 2006).

Auditory filter shapes have been measured using a notched-noise methodology for bottlenose dolphins and belugas (Lemonds, 1999; Finneran *et al.*, 2002a). Equation (4.1) can be rewritten as

$$P_s = K \int_{-\infty}^{\infty} N(f) W(f) df, \quad (4.5)$$

where P_s is the power of the signal at threshold, $N(f)$ is the noise power spectral density, and $W(f)$ is a weighting function described by the shape of the auditory filter. $W(f)$ is often estimated using a rounded-exponential (roex) function:

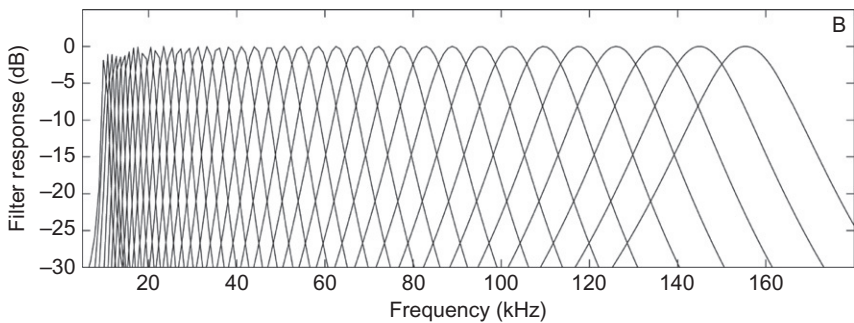


Figure 4.6 Frequency response of a gamma-tone filter bank (adapted from Branstetter *et al.*, 2007b) that was fit from notched-noise masking data (Lemonds, 1999). Frequency resolution is sharper for lower frequencies.

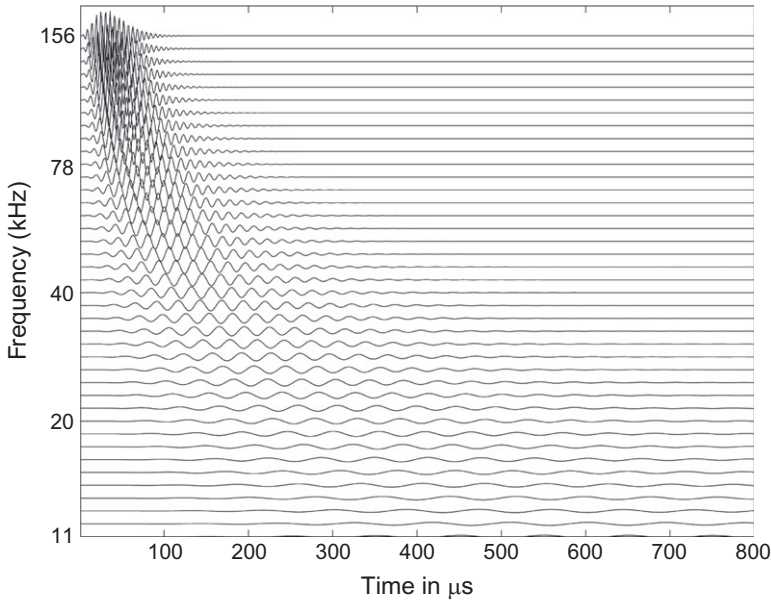


Figure 4.7 Impulse response of the gamma-tone filter bank (from Fig. 4.6) which illustrates the high degree of temporal resolution at the higher frequencies and the “ringing” at the lower frequencies (adapted from Branstetter *et al.*, 2007b).

$$W(g) = (1 - r)(1 + pg)e^{-pg} + r, \quad (4.6)$$

where g is a normalized frequency deviation ($g = |f - f_o|/f_o$, where f is frequency and f_o is the signal frequency), and p and r are adjustable parameters.

Biomimetic models using simulated auditory filters derived from empirical measurements have proven useful for investigating what time–frequency information is available to dolphins during echolocation discrimination tasks for artificial targets (Roitblat *et al.*, 1993b; Branstetter *et al.*, 2007b) as well as natural fish targets (Au *et al.*, 2009) and as inputs into neural network classifiers (Roitblat *et al.*, 1993a; Au *et al.*, 1995; Branstetter and Mercado, 2006). These models attempt to incorporate limitations of the dolphin auditory system with respect to both frequency and temporal resolution and mimic how this information might be organized and utilized for classification purposes.

5.5. Transduction and low-pass filtering

In addition to resolving characteristics of the auditory filters, hair cell transduction and low-pass filtering of the eighth nerve (and beyond) will also affect how sounds are perceived. Little is known about hair cell transduction in any marine mammal. However, hair cell anatomy appears to be similar to

terrestrial mammals. One striking difference is that odontocetes have a high density of afferent innervations with up to 2900 ganglion cells, 100 inner hair cells (IC), and 300 outer hair cells/mm (Ketten, 1997). There are about three times as many ganglion cells/IC in some odontocetes compared to humans (Ketten, 1997). Hair cells behave as non-linear, half-wave rectifiers (Berg, 1996; Branstetter *et al.*, 2007b) that can be described by a simple model:

$$f_{\text{rect}}(t) = \frac{f(t) + \sqrt{f(t)^2}}{2} \quad (4.7)$$

where t is the instantaneous amplitude of the time domain waveform. Another characteristic of hair cell response is amplitude compression, which is partially responsible for the broad range in amplitude sensitivity of mammalian listeners (Regan, 1994). Input–output functions describing amplitude compression have not been estimated in cetaceans. Unlike typical neurons, hair cells do not have refractory periods, which make them extremely fast. However, ganglion cells are much more sluggish and behave as low-pass filters which can be described with an exponential decay function:

$$h(t) = ke^{-t/\tau}, \quad (4.8)$$

where k is a constant, t is units of time, and τ is the critical interval or integration time constant (Berg, 1996). The critical interval (τ) for transient signals appears to be around 264 μs (Vel'min and Dubrovskii, 1976; Moore *et al.*, 1984). For tonal signals, the integration time constant appears to be governed by a different mechanism than transient signals. Time constant is frequency dependent and much longer in duration. For example, the integration time constants are approximately 200 and 100 ms for a 10- and 20-kHz tone, respectively. The time constant for a 100-kHz tone is less than 10 ms. Differences in integration times for tonal signals and transient signals may be the result of compartmentalized hearing abilities for communication signals and echolocation signals, respectively.

5.6. Auditory masking with complex stimuli

The auditory masking experiments previously described (CBs, CRs, and filter shape measurements) were all conducted with Gaussian noise maskers. The primary finding of these studies is that only noise within a single auditory filter centred on the signal frequency contributes to the masking of the signal. This finding is a special case of masking that applies to Gaussian noise but fails to generalize to more complex sounds animals might encounter in the ocean. In natural auditory scenes, sounds are often amplitude and frequency modulated, and the auditory system can use common modulation patterns to segregate sound sources (Bregman, 1990). This has been

demonstrated in dolphins in what is called comodulation masking release or CMR (Branstetter and Finneran, 2008). When broadband noise is coherently amplitude modulated across frequency regions, a release from masking as large as 17 dB has been reported, compared to Gaussian noise of equal pressure spectral density (Fig. 4.8). An important feature of CMR is that the effect is most salient when noise bandwidths exceed an auditory filter bandwidth (Hall and Grose, 1990; Branstetter and Finneran, 2008). In other words, more total noise power equals less masking. Several acoustic variables contribute to CMR. Wide-band noise (i.e. greater than an auditory filter bandwidth) produces a systematic decrease in masking. In addition, lower AM rates produce greater amounts of CMR (Branstetter and Finneran, 2008). A similar release from masking has been demonstrated for natural sounds including ice-cracking noise (Erbe, 2008) and snapping shrimp noise (Trickey *et al.*, 2011), both of which are also coherently amplitude modulated across frequency regions (Fig. 4.9).

5.7. Sound localization

Due to limited visibility, locating prey, predators, conspecifics, or any other biologically relevant object or event is often accomplished through sound. To localize sounds in the horizontal plane, humans and animals have been shown to exploit binaural stimulus differences related to loudness, temporal onset, and phase. Because the cetacean auditory system evolved from the

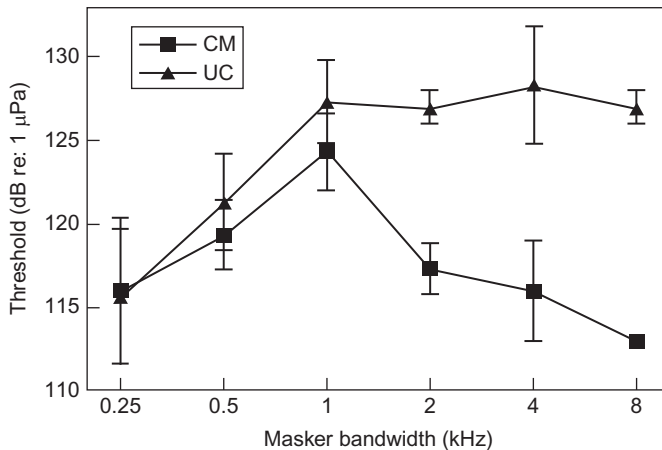


Figure 4.8 Thresholds for a 10-kHz tone as a function of masker bandwidth for comodulated noise (CM) and uncomodulated (UC) or Gaussian noise. Both noise types had a flat noise spectral density of 95 dB re 1 μ Pa²/Hz. A processing transition can be seen at 1 kHz (the critical bandwidth for a 10-kHz tone) where thresholds asymptote for UC noise while thresholds decrease for CM noise (adapted from Branstetter and Finneran, 2008).

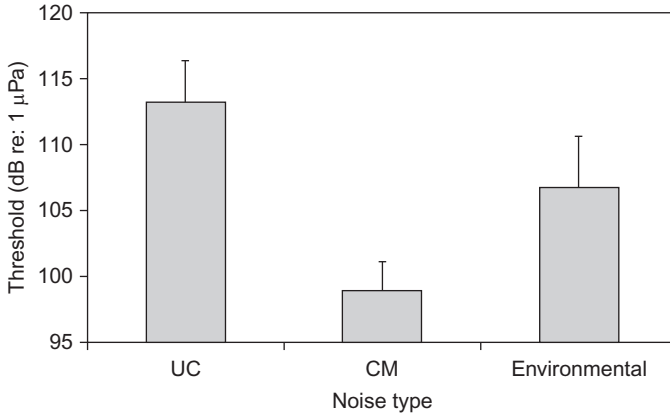


Figure 4.9 Thresholds for a 10-kHz tone masked by three broadband noise types (UC, Gaussian; CM, comodulated; environmental, snapping shrimp). A release from masking is present for CM and environmental noise (adapted from [Trickey et al., 2011](#)).

archetypal terrestrial auditory system, changes in anatomy and physiology occurred to compensate for a dense aquatic medium where sound travels almost five times faster than in air. For terrestrial animals, interaural loudness differences (ILDs) are created by sound shadowing due to the impedance mismatch between the air medium and an animal's head. In water, terrestrial animals lose ILDs due to the density similarity of the head and water. For odontocetes, ILDs are created not by external anatomy, but by internal structures of varying density. The dense tympano-periotic complex, which houses the middle and inner ear, is completely separated from the skull by a matrix of air sinuses, lipids, and vascularization collectively called the albuminous foam ([Ketten, 1992](#)). The foam, along with additional structures such as cranial air sacks and mandibular fats, collectively functions to acoustically isolate each ear and produces ILDs in excess of 20 dB ([Supin and Popov, 1993](#)). Sensitivity to ILDs has been measured in the bottlenose dolphin to be less than 1 dB ([Moore et al., 1995](#)). Interaural time differences (ITDs) will be five times smaller in aquatic environments due to increased sound speed in water relative to air. However, dolphins are still capable of exploiting ITDs and have demonstrated sensitivity to ITDs as small as 7 μ s ([Moore et al., 1995](#)). In terrestrial mammals, the use of interaural phase differences (IPDs) decreases with an increase in frequency because the wavelengths get smaller. While it is unlikely that odontocetes use IPDs for higher frequencies, it has not been tested. IPDs could be exploited by mysticetes, which have large heads and use low-frequency sounds.

ILDs and ITDs only provide source information in the horizontal plane. However, dolphins have excellent localization abilities not only in the horizontal plane but also in the vertical plane. The minimum audible

angle (MAA) for the bottlenose dolphin is 0.9 and 0.7 in the horizontal and vertical planes, respectively (Renaud and Popper, 1975). The fact that the bottlenose dolphins can localize as well (if not slightly better) in the vertical plane despite the lack of ITDs and ILDs is remarkable and suggests an additional mechanism exists for vertical localization. As mentioned previously, dolphins likely have a salient HRTF due to the pronounced asymmetry of cranial structures. Position-dependent spectral cues related to the dolphin's HRTF may be providing the dolphin with fine vertical localization abilities. Although a detailed HRTF for an odontocete has not been measured, receiving beam patterns have been measured for the bottlenose dolphin for a few frequencies, resulting in a complex pattern. The 3-dB beam widths for 30, 60, and 120 kHz were measured to be 59.1°, 32.0°, and 13.7°, respectively, in the horizontal plane and 30.4°, 22.7°, and 17.0° in the vertical plane (Au and Moore, 1984). Receiving beam patterns are more directional for higher frequencies, which likely aid the animal in localizing sounds during echolocation. The ability of the bottlenose dolphins to echoically discriminate horizontal angular differences has been measured to be about 0.9–1.5° (Branstetter *et al.*, 2003, 2007a) which is significantly smaller than the receiving 3 dB beam width, but similar to the dolphin's MAA. The receiver beam width likely aids in gross localization as well as attenuating off-axis signals during echolocation.



6. ADVANCED ANATOMICAL AND PHYSIOLOGICAL STUDIES

6.1. Anatomy

The recent use of computerized tomography (CT) has proven useful to study *in situ* auditory anatomy of odontocetes (Ketten and Wartzok, 1990; Ketten, 1994, 1997, 2000; Houser *et al.*, 2004; Soldevilla *et al.*, 2005; Cranford *et al.*, 2008; Montie *et al.*, 2011). These imaging techniques are particularly valuable for studying fatty sound reception pathways since these unique fats have a low melting temperature, are soft at room temperature, and are liquid at body temperatures for at least some species (Norris, 1968), making them difficult to study via dissection. Dissection also prevents the study of the *in situ* geometries of these fats. In fact, a magnetic resonance imaging (MRI) study by Ketten (1994) led to the finding of a new fat channel lateral to the tympano-periotic complex in some odontocetes (*Delphinus delphis*, *Lagenorhynchus acutus*, and *T. truncatus*) that may be a better sound reception pathway for lower frequency sounds (Bullock *et al.*, 1968; Renaud and Popper, 1975; Popov and Supin, 1990a; Popov *et al.*, 2008).

Live cetaceans were CT scanned for the first time by Houser *et al.* (2004) using bottlenose dolphins trained by the U.S. Navy's Marine Mammal

Program. The use of live animals eliminated issues associated with post-mortem changes in air space volumes and tissue characteristics potentially affecting the data. This study also incorporated functional investigations of auditory and sound production tissues through single-photon emission computed tomography and positron emission tomography, identifying extensive blood flow in the lower jaw and melon fats. Since these tissues are relatively metabolically inert, the authors hypothesized that the blood flow served as a thermoregulatory control of lipid density, optimizing the acoustic fats for sound reception and propagation. The application of such advanced functional imaging techniques to fully aquatic, live mammals may have seemed inconceivable to most researchers before this study.

An equally challenging and exciting idea for the future was presented by Moore *et al.* (2011b), who developed a hyperbaric computed tomography technique for investigating the effect of pressure on lung compression in post-mortem marine mammals. The paper concludes with potential modifications of the system for application to live animals in the future. If this technique can actually be used on live animals, it may enable investigations on changes in middle ear air volumes and tissues relevant to the auditory system with simulated depth.

Applying biomedical imaging techniques to cetaceans has also enabled the modelling of sound reception pathways in odontocete heads. One type of modelling technique that is often used is called the finite element method (FEM). In FEM, a model is constructed by defining a set of mathematical equations in a continuous domain. For example, to model sound propagation through a dolphin head, the mathematical model is the wave equation together with a set of boundary conditions. The domain, which in this case corresponds to the dolphin head and the surrounding medium, is discretized into small connected “elements” creating what is called the finite element mesh. By employing structural data from CT and material properties from different types of tissues like bone, muscle, and fats, the acoustical power flow of both isolated anatomical structures and whole multi-tissue systems can be modelled to estimate optimal impedance paths for sounds from internal or external sources. While computer models of odontocete sound production had been developed earlier (Aroyan *et al.*, 1992), the application of FEM and related methods to odontocete sound reception has seen much progress over the past decade (Aroyan, 2001; Krysl *et al.*, 2006; Cranford *et al.*, 2008, 2010).

6.2. Advancements in AEPs

As described above, there are many types of studies which address hearing in odontocetes. However, a large proportion of them now involve AEP measurements (Fig. 4.4). AEP is an appealing method because data can be gathered rapidly with minimal or no animal training investment.

A complete audiogram can be obtained in an untrained animal in less than 20 min, enabling hearing tests even during situations where time is severely limited (Nachtigall *et al.*, 2004, 2005). Recording times can be dramatically decreased by simultaneously recording responses to multiple frequencies (Finneran and Houser, 2007) and using automated methods of response detection (Finneran *et al.*, 2007a).

One advantage of AEP-related methodology has been to opportunistically measure the hearing of stranded animals, thus broadening the number of individuals and species tested (Ridgway and Carder, 2001; André *et al.*, 2007). Early attempts at recording AEPs from stranded animals were conducted at rehabilitation facilities and produced mixed results (Ridgway and Carder, 2001). The animals tested were large and included a pygmy sperm whale (*Kogia breviceps*), a grey whale (*Eschrichtius robustus*) calf, and a neonate sperm whale (*Physeter macrocephalus*). The response records were somewhat noisy and full audiograms were not acquired, perhaps because the large size of animals reduced signal-to-noise ratios of the AEP (Szymanski *et al.*, 1999; Houser *et al.*, 2007). However, the study produced novel records, showed the efficacy of the technique, and laid substantial groundwork for future research.

Improvements in methods and equipment between 2001 and 2005 led to successful AEP recordings from a stranded neonate Risso's dolphin (*G. griseus*), producing a full audiogram and an estimate of temporal resolution (Nachtigall *et al.*, 2005; Mooney *et al.*, 2006). This animal had sensitive and broadband hearing, discounting suggestions that there may have been permanent auditory damage due to a potential noise-induced stranding event (Fig. 4.2). However, "profound" hearing loss has been found in other stranded odontocetes including pilot whales, bottlenose dolphins, and rough-toothed dolphins (Mann *et al.*, 2010). The authors speculated that the causes of hearing loss vary and could include congenital defects, chemical contaminants, and normal presbycusis.

A major advance in AEP technology is the development of portable systems which can be applied in field situations (Ridgway and Carder, 2001; Delory *et al.*, 2007; Taylor *et al.*, 2007; Finneran, 2009). The AEP test on the stranded Risso's dolphin involved flying a desktop computer from Hawaii to Portugal and was conducted over 5 days. Since these tests, AEP systems have been reduced in size to laptop-based systems, and audiograms are collected much more rapidly. To date, AEP recordings in the field have been made with catch-and-release procedures on white-beaked dolphins (Nachtigall *et al.*, 2008) and beach-stranded delphinids (Moore *et al.*, 2011a), showing promising results despite logistical challenges.

Recently, novel AEP experiments have combined AEPs with morphological studies to address form-and-function questions. Montie *et al.* (2011) examined the hearing of two stranded pygmy killer whales. They moved electrode locations and created 3D reconstructions of the brain from CT

images (Fig. 4.1), while concurrently measuring the amplitude of the ABR waves. Their results provided evidence that the neuroanatomical sources of ABR waves I, IV, and VI were the auditory nerve, inferior colliculus, and the medial geniculate body, respectively. Other studies have combined AEP with CT and MRI to examine the hearing pathways of odontocetes (Mooney *et al.*, 2011). Using a jawphone transducer to present stimuli, Mooney *et al.* showed that AEP responses can be generated from multiple locations on the head and body. Jawphones placed at the mandibular fat bodies (identified from MRI and CT) tended to produce higher amplitude AEPs, lower thresholds, and faster responses, although this was somewhat frequency dependent (Fig. 4.3C). Thus, the head receives and guides sound in multiple ways, confirming earlier findings by Möhl *et al.* (1999) which mapped the areas of best sensitivity in the bottlenose dolphin head using AEPs and jawphone-presented stimuli. These areas of best sensitivity differ slightly between the few species examined (bottlenose dolphin, beluga, finless porpoise; Fig. 4.3C and D), suggesting that the diverse morphologies found among odontocete species affect how each of them receives sound (Mooney *et al.*, 2008).

6.3. AEPs during echolocation

Bullock and Ridgway (1972) had discovered that AEP responses varied based on whether they were induced from self-generated clicks or simulated clicks presented by the researchers, laying the groundwork for substantial future developments of hearing protection and auditory gain control. Since then, AEPs have been used to measure hearing during echolocation, addressing auditory gain control and how ears are adapted to hear quiet echoes which occur immediately after loud clicks (Supin *et al.*, 2003; Nachtigall and Supin, 2008). These studies methodically addressed this issue by training a false killer whale to echolocate on cylinder targets while AEPs were concurrently measured (Fig. 4.3B). The earliest work established that far-field evoked potential methods can be used to record AEPs in response to both outgoing clicks and returning echoes (Supin *et al.*, 2003). The click and echo AEPs had similar amplitudes, despite substantial (40 dB) differences in the relative stimulus intensity levels. Impressively, these results suggested an “attenuation of sound transmission from the sound generator to the ears and/or a neurophysiological mechanism of releasing responses to echoes from masking by loud emitted clicks”.

In two succeeding experiments, the authors varied the target distance and length (i.e. the target strength), thus varying the intensity of the returning echoes. The amplitudes of echo-generated AEPs were independent of the variables. The click-generated AEPs were dependent on target strength, but not distance (Supin *et al.*, 2004, 2005). The sound pressure levels of the outgoing clicks did not vary based on target strength, which

suggested that the differences in AEP amplitude were due to changing hearing sensitivities as the animal echolocated—a fascinating finding. Supin *et al.* (2006) sorted AEPs relative to the SPL of the outgoing click and compared these responses from simulated clicks of varying amplitude. Evoked potential amplitudes, and thus hearing of these clicks, were dependent on whether or not a target was present, and whether the animal was passively hearing or actively echolocating. Thus, this whale adjusted its hearing based on the context of the experiment (Supin *et al.*, 2006).

Adjustments and recovery from auditory dampening of loud echolocation clicks appeared to be based on both the distance of a target (i.e. the time interval between the outgoing click and the incoming echo) and the intensity of the click (Supin *et al.*, 2007). The use of electronically simulated phantom echoes allowed the “echo” amplitude and distance to be adjusted. In both behavioural and electrophysiological studies, echo thresholds or response levels appear dependent on distance of the target. As the time between click and echo increased, hearing ability improved, suggesting that the protection of ears during echolocation may somewhat mask the hearing of clicks; however, this forward masking was released as time increased (Supin *et al.*, 2008, 2009). Follow-up studies in a standard echolocation task showed that while echo-generated AEPs were constant with target distance, click-generated AEPs increased. The results indicated that control of hearing during echolocation served as a way to keep sensitivities to echoes constant, perhaps as a means to compensate for natural echo attentions and to improve hearing abilities of quiet echoes at greater distances (Supin *et al.*, 2010). These hypotheses were confirmed by subsequent phantom echo studies (Supin *et al.*, 2011). Overall, these novel investigations revealed much information regarding the active process of odontocete hearing and their impressive echolocation capabilities. While few studies have addressed parallel investigations in “standard” hearing tests, it is possible that odontocetes may also adjust sound reception or sensitivities when not producing sounds.

This work has expanded recently with comparative studies in the bottlenose dolphin and the harbour porpoise. The porpoise showed that it alters its outgoing click amplitudes as well as its click AEP levels (Linnenschidt *et al.*, 2012). Like Supin, the authors supposed that these gain controls maximized detection of quiet echoes. In similar experiments, Li *et al.* found that the bottlenose dolphin may enact direct control over both the click and echo (Li *et al.*, 2010). Echo-generated AEP amplitudes increased with target distance, suggesting an “overcompensation” of echo hearing. This was unlike the porpoise and false killer whale studies, but it was not clear whether these were species, individual or physiological differences. It is also notable that these mechanisms are not only a means to improve echo detection but also a way to protect sensitive ears from repeated, intense echolocation clicks (Li *et al.*, 2011).



7. THE IMPACTS OF NOISE

As discussed above, odontocetes may have a mechanism to protect their sensitive ears from their own loud echolocation clicks. However, these mechanisms may not be sufficient to overcome the constant exposure to human-made sound. The effects of noise on marine mammals have been a substantial topic of concern for researchers, policy makers, and the public. Much of these interests stem from beaked whale strandings that were associated with high-amplitude naval sonar (Frantzis, 1998; Balcomb and Claridge, 2001; Evans *et al.*, 2001). The actual sonar-induced physiological or behavioural effects on the stranded animals have been extensively debated (Jepson *et al.*, 2003; Fernandez *et al.*, 2005; Cox *et al.*, 2006; Southall *et al.*, 2006; Brownell *et al.*, 2009). Furthermore, the reality is that ocean noise is diverse, including shipping and vessel traffic, construction of wind farms, air guns related to seismic exploration, and construction and scientific surveys. These sounds can be broadly grouped into noise categories of (i) continuous (or near-continuous) such as shipping, (ii) impulse sounds such as seismic air guns or military munitions, and (iii) intermittent noise such as construction or sonar. Behavioural changes in response to elevated noise conditions from these various sources have caused alarm (e.g. Miller *et al.*, 2000; Holt *et al.*, 2009; Parks *et al.*, 2009).

In terrestrial mammals, a well-established and primary concern of noise exposure is noise-induced hearing loss (Ward *et al.*, 1958; Kryter, 1994). Over-exposure to noise can induce both temporary and permanent hearing loss, also referred to as temporary or permanent threshold shifts. For marine mammals, a wide array of data are needed to predict potential occurrences of noise impacts. The necessary research efforts to address noise impacts on marine mammals have been addressed by four National Research Council reports and a more recent report by Southall *et al.* to establish a science-based noise exposure criterion (National Academy of Sciences, 1994, 2000, 2003, 2005; Southall *et al.*, 2007). Hearing-related recommendations include establishing baseline hearing sensitivities in a greater number of species and individuals, investigating auditory scene analyses in regards to how cetaceans process and evaluate multiple acoustic cues simultaneously, determining the levels and effects of auditory masking, and the sounds and conditions which induce temporary and permanent threshold shifts (i.e. temporary and permanent hearing loss). These previous documents provide comprehensive reviews of this specific subject, addressing behavioural, physiological, and anatomical noise impacts; thus we will only briefly address hearing and noise exposures to provide an update on the data since these reports and to place these data in the context of past results and conclusions.

Temporary threshold shifts (TTSs) have received substantial experimental attention in recent years. It was first established in cetaceans (five

bottlenose dolphins and two belugas) using 1 s pure tones across a range of frequencies (0.4–75 kHz) (Schlundt *et al.*, 2000). Shifts of 6–17 dB re 1 μPa were measured at exposure levels generally between 192 and 201 dB, but TTS was also documented for fatiguing stimuli as low as 182 dB. Shortly thereafter, intense impulse sounds (226 dB_(peak–peak) re 1 μPa and a sound exposure level (SEL) of 186 dB re 1 $\mu\text{Pa}^2 \text{ s}$) from a seismic watergun were used as the fatiguing noise to induce TTS (Finneran *et al.*, 2002b). The SEL can be calculated by

$$\text{SEL} = 10 \log_{10} \left(\int_0^T \frac{p^2(t)}{p_0^2 t_0} dt \right), \quad (4.9)$$

where t_0 is the reference time of 1 s, $p(t)$ is the instantaneous sound pressure of the signal, and p_0 is the reference pressure of 1 μPa . This metric is useful because it integrates the squared pressure over the total duration of the signal and is often used to predict TTS due to multiple exposures of varying duration. Threshold shifts were induced in the beluga tested, but not in the bottlenose dolphin. A subsequent study used increased duration, lower amplitude, broadband noise (4–11 kHz, 179 dB re 1 μPa and 55 min) to induce TTS in a bottlenose dolphin. (Nachtigall *et al.*, 2003). Shifts were variable between sessions from -1 to 18 dB. These early studies were pivotal in multiple respects. First, They established that TTS can occur by multiple types of noise exposure. Second, there were substantial differences regarding the occurrence and levels of TTS that were actually induced within replicate conditions. Thus, amount of TTS induced varied across the species and individuals, but also within individuals. The variations and covariates revealed the mountainous task of predicting auditory noise impacts.

Subsequent work has improved the methods for measuring TTS, addressed means to bridge some of these variables, and filled in key data gaps. Since the 2007 Southall *et al.* publication, Finneran and colleagues used AEP technology to measure TTS at multiple frequencies simultaneously, making it possible to rapidly determine at which frequencies TTS is induced (Finneran *et al.*, 2007b). Several research groups have also addressed how best to predict situations that may induce TTS (Finneran *et al.*, 2005; Mooney *et al.*, 2009a). Recent work has shown that if the fatiguing noise type is constant, but duration and amplitude are varied, TTS onset is well predicted by SEL (Mooney *et al.*, 2009a; Finneran *et al.*, 2010). In other words, shorter duration sounds require greater energy to induce TTS compared to longer duration signals. It should be noted that these studies did not investigate impulse sounds such as seismic air guns, which may have entirely different effects (Ward, 1997). The TTS growth in dolphins was also correlated with SEL, and TTS exposure duration continued to play a greater influence in generating TTS compared to SPL (Finneran *et al.*, 2010). These results have several implications. First, TTS

onset and growth data are better represented as functions of SPL and duration rather than SEL alone. Second, short duration signals such as most sonar must be of very high received intensity to induce TTS (Mooney *et al.*, 2009b). These situations are probably rare because they would usually require the animal to be close to the sound source. Third, longer duration sounds such as constant shipping or snapping shrimp noise may induce TTS at much lower intensity and sensation levels (the SPL relative to threshold). These chronic exposures, such as shipping noise, may induce quite different impacts compared to the brief, intense exposures. The impacts of these chronic exposures are a growing area of concern.

Hearing thresholds were comparatively examined using noise exposures with a mid and a higher frequency tone (3 and 20 kHz) to address the impacts of hearing sensitivities on TTS (Finneran and Schlundt, 2010). The results showed that at 20 kHz TTS not only began at a lower exposure level compared to the 3-kHz exposures but also grew at a faster rate. Repeated exposures also increased noise impact susceptibility (Finneran and Schlundt, 2010). The results clearly demonstrated auditory impact risk criteria must take exposure frequency, hearing sensitivity, and prior experience into account.

While these prior studies addressed auditory physiology, they did not address the perception of sound intensity, or loudness. Equal loudness contours provide a comparison of tones that are perceived at the same sound level, providing a means to modify acoustic damage risk criteria by placing greater emphasis on sensitive frequencies. The first of these studies in a non-human animal was conducted with a bottlenose dolphin (Finneran and Schlundt, 2011). The animal was trained to perform a loudness comparison test, where it indicated which of two sequential tones was perceived as louder. The resulting equal loudness contours were similar in shape to the dolphin audiogram. As in humans, the contours became flatter at higher SPLs (Finneran and Schlundt, 2011). Based on these data, the authors were able to provide modified auditory weighting functions which provided greater insight into the frequencies dolphins may be most sensitive. In general, there was an inverse relationship between sensitivity and hearing thresholds, with similar loudness responses (± 2.5 dB) from approximately 6 to 100 kHz. These weighting functions were substantially different from those proposed by Southall *et al.* (2007), reflecting the need for management practices that can adapt to the growing literature of best available data.



8. HEARING IN MYSTICETES

In contrast to the immense amount of progress that has been made on hearing in odontocetes, the study of mysticete hearing has been more stagnant over the past several decades. Mysticetes are large, rarely kept in

captivity, and have never been trained, making them more difficult to study. Therefore, several indirect methods have been applied to gain information about mysticete hearing. One method is based on vocalization data, based on the premise that animals typically vocalize at frequencies audible to conspecifics. Recordings of mysticete vocalizations conducted since 1951 suggest that baleen whales use and hear low-frequency sounds (Watkins and Wartzok, 1985). Vocalizations down to 12 Hz have been recorded in the blue whale (Cummings and Thompson, 1971).

Anatomical studies of middle and inner ear structures afford another way to understand what kinds of sounds mysticetes may hear. Yamada and Yoshizaki (1959) noted the lack of high-frequency specializations in mysticete cochleae, in contrast to the cochleae of odontocetes. Mysticetes also possess massive, loosely joined ossicles and wide BMs, consistent with low-frequency hearing (Ketten, 1994). Parks *et al.* (2007) predicted that the total possible hearing range for the North Atlantic right whale (*Eubalaena glacialis*) is approximately 10 Hz to 22 kHz, based on measurements of their BMs. These anatomical studies are promising for studying hearing in rare and inaccessible species, especially if they can be validated by future physiological studies (Yamato *et al.*, 2008).

A third method for deducing what types of sounds mysticetes may hear is the playback technique, in which a range of naturally recorded or artificially generated sounds are presented to wild animals. An acoustic stimulus that elicits a behavioural response from an animal is presumed to be audible to the animal. While most playback studies on mysticetes are not designed to test their hearing, they support the hypothesis that mysticetes are able to hear and differentiate vocalizations of conspecifics (Clark and Clark, 1980; Tyack, 1983; Mobley *et al.*, 1988; Parks, 2003). In a study of minke (*Balaenoptera acutorostrata*), fin (*Balaenoptera physalus*), humpback (*Megaptera novaeangliae*), and right whales near Cape Cod, Watkins (1986) found that most whales reacted to human-made sounds between 15 Hz and 28 kHz, whereas higher frequency sounds between 36 and 60 kHz elicited no response. These data also support the notion that mysticetes are sensitive to lower frequencies. Yet, an individual may not always respond to an audible sound, and the received levels of the sounds are often unknown, limiting the effectiveness of playback studies as a method for studying hearing.

The ultimate goal for understanding what mysticetes hear is to obtain audiograms showing hearing sensitivity as a function of frequency. Behavioural tests using trained, captive animals are unlikely, as mentioned above. However, AEP testing may be a possibility in the future. As noted earlier, Ridgway and Carder (2001) attempted to record AEPs from a stranded grey whale calf which was rehabilitated at Sea World of San Diego between January 1997 and March 1998. While some preliminary AEPs were recorded, an audiogram could not be produced.

Besides the rarity of opportunities to conduct AEP testing, a major obstacle in applying current AEP methods to mysticetes is that mysticetes are generally larger and also have very different cranial morphologies compared to odontocetes. It is likely that customized equipment needs to be developed based on the auditory anatomy and sound reception mechanisms of mysticetes.

This leads us to the other fundamental question about mysticete hearing: *how* do baleen whales receive sound? There is still no consensus regarding how the auditory system of baleen whales functions, and this question has not received much attention for the past 50 years. Interestingly, Yamato *et al.* recently described a potential fatty sound reception pathway in the minke whale (Yamato *et al.*, 2012). Combining CT, MRI, and dissections, the authors found a well-formed fat body adjacent to the mandibular ramus and lateral to the tympano-periotic complex (Fig. 4.10). This fat body inserts into the tympano-periotic complex at the juncture between the tympanic and periotic bones and is in contact with the ossicles. Preliminary dissections of fin and humpback whales also indicate that they possess fat bodies associated with the ears, suggesting that fatty sound reception pathways may not be a unique feature of odontocete cetaceans.

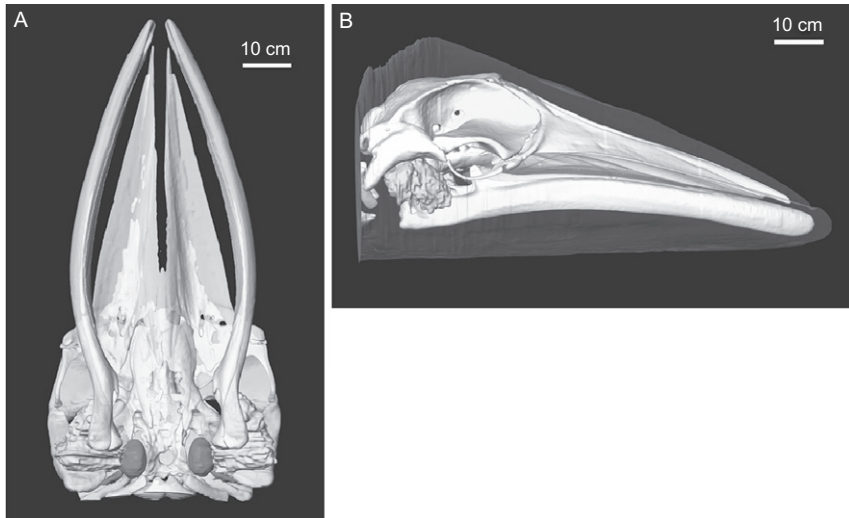


Figure 4.10 Three-dimensional reconstructions of the auditory system of the minke whale based on CT data, showing fat bodies associated with the ears. The fats are shown in yellow, the tympano-periotic complex (ears) in purple, and bone in off-white. (A) Ventral view. (B) Lateral view (adapted from Yamato *et al.*, 2012).

9. CONCLUSIONS AND FUTURE WORK

Our knowledge of cetacean hearing has substantially increased in recent years. Through technological advancements such as AEPs and FEM, there are a greater number of research questions which can be addressed. This provides an improved understanding of how and what many species hear, as well as their sophisticated acoustic processing abilities. Much of this work has been in applied research to determine noise impacts but have also yielded more basic information in auditory scene processing and mammalian hearing. These developments have also made clear several data gaps and research priorities.

Mysticete hearing abilities have been predicted from a variety of studies, but there has yet to be an audiogram established. While AEPs will be difficult to measure for some species, the method has potential for smaller animals such as the minke whale or juvenile whales. Entangled or stranded situations might offer reasonable test scenarios. This would not only establish the sound sensitivity of a “great” whale but also empirically test the current auditory models for future applications to other species.

There are also quite a few odontocete species for which audiograms also need to be established. Measuring the audiogram for these species provides data-based methods to evaluate potential noise impacts. This would also provide much needed information regarding the diversity of auditory capabilities. Acquiring these data likely requires the continual advancement of AEP technologies for field situations, and perhaps even integrating them into non-invasive tagging tools. Such tools would not only produce audiograms but will also enable the study of auditory gain control mechanisms and hearing during echolocation in natural situations. A tag-based technology would also greatly increase study sample sizes, a clear limitation for many cetacean audiometric studies.

Investigations of a greater number of species would also address the subtle differences found between taxa. There are clear morphological and behavioural differences between species, suggesting subtle auditory physiological differences as well. A clear way to investigate this is through research which addresses classic form-and-function questions, combining anatomical studies with physiological and experimental research. We may also find that species adapt to noise impacts in different manners, since some animals seem particularly sensitive to sound. For odontocetes which are high-frequency specialists, high-frequency hearing loss which is typical in mammals may have unique impacts. Physiological investigations of hearing loss and auditory protective mechanisms may further our understanding of how or whether certain animals can reduce the impacts of noise exposure.

Despite the recent advancements, there is continual room for improvements in understanding of basic hearing abilities. As anthropogenic use of

aquatic environments increases, so does the need for empirical studies on sensory ecology. Information regarding the overlap between human and cetacean acoustic habitats is crucial to evaluate the potential impacts on these sound-sensitive marine animals. Ultimately, these studies will further our understanding of the evolution of mammalian hearing and the adaptations acquired for sophisticated auditory systems which process and cope with complex auditory scenes.

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TIMELINE

- 1762: Camper claims that whales hear through the ear canal, as in terrestrial mammals.
- 1787: Hunter speculates that the tympanic cavity amplifies sound through vibration of bone, and these vibrations are directly transferred to the inner ear.
- 1858: Claudius says vibrations in water are accepted by whole head, and air space resonances are transmitted to the inner ear.
- 1904: Boenninghaus proposes a general soft-tissue sound reception pathway in odontocetes (toothed whales).
- 1919: Kernan proposes bone conduction as the hearing mechanism.
- 1957: Reysenbach De Haan supports a soft-tissue sound reception pathway.
- 1958: Kellogg publishes experimental evidence supporting echolocation in odontocetes.
- 1962: Dudok Van Heel argues that the ear canal is vestigial.
- 1964: Norris speculates that odontocetes may receive sounds through “acoustic fats” located within and surrounding the lower jaws.
- 1966: Purves and colleagues still maintain that the ear canal is functional.
- 1968: Evoked potential experiments by Bullock *et al.* support Norris’ hypothesis.
- 1970: McCormick *et al.* record cochlear potentials from anaesthetized dolphins. They argue that the ear canal is not functional and support bone conduction.
- 1974: Norris and Harvey use hydrophones implanted in dead porpoise heads to support the lower jaw acoustic fat theory.

- 1975: The biochemical uniqueness of “acoustic” fats is demonstrated by Varanasi *et al.*
- 1976: Seeley, Ridgway, and colleagues record AEPs from dolphins non-invasively.
- 1988: Brill finds that an acoustically opaque hood on the lower jaw of dolphins decreases hearing ability. Norris’ hypothesis is more widely accepted as evidence accumulates in support of it.
- 1995: Supin *et al.* establish the EFR in dolphin AEPs and are rapidly progressing AEP methods.
- 2000: Schludt *et al.* demonstrate TTS in odontocetes.
- 2001: Navy sonar is correlated with a Bahamas beaked whale stranding event fuelling the growing concern for noise impacts on marine mammals.
- 2001: Ridgway and Carder record AEPs from large, stranded cetaceans showing the techniques possibilities.
- 2003: Supin and Nachtigall initiate their experiments on hearing during echolocation.
- 2005: Nachtigall *et al.* collect an AEP audiogram from a stranded Risso’s dolphin showing the efficacy of the technique in strandings, greater species, and high-frequency hearing loss.
- 2006: Houser and Finneran demonstrate the variation in dolphin audiograms through hearing examinations of a population of bottlenose dolphins.
- 2007: Finneran and Houser record AEPs to multiple simultaneous sinusoidal amplitude-modulated tones.
- 2008: Hearing tests on a beluga whale by Mooney *et al.*, (2008) show hearing pathways between odontocetes may have subtle differences.
- 2009: Sonar can induce temporary hearing loss but exposures must be relatively intense and prolonged. (Mooney *et al.*, 2009b).
- 2011: Finneran and Schuldt produce the first relative loudness curve for marine mammals with a bottlenose dolphin.

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