Morphometric Analyses of Ears in Two Families of Pinnipeds

By

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Abstract

Pinniped (seal and sea lion) auditory systems operate in two acoustically distinct environments, air and water. Pinniped species differ in how much time they typically spend in water. They therefore offer an exceptional opportunity to investigate aquatic versus terrestrial hearing mechanisms. The Otariidae (sea lions and fur seals) generally divide their time evenly between land and water and have several adaptations; *e.g.* external pinnae, related to this lifestyle. Phocidae (true seals) spend the majority of their time in water; they lack external pinnae and have well developed ear canal valves.

Differences in hearing ranges and sensitivities have been reported recently for members of both of these families [Kastak, D., Schusterman, R.J., 1998. Low frequency amphibious hearing in pinnipeds. J. Acoust. Soc. Am. 1303, 2216-2228.; Moore, P.W.B., Schusterman, R.J., 1987. Audiometric assessment of northern fur seals, *Callorhinus ursinus*. Mar. Mamm. Sci. 3, 31-53.]. In this project, the ear anatomy of three species of pinnipeds: an otariid, the California sea lion (*Zalophus californianus*), and two phocids, the northern elephant seal (*Mirounga angustirostris*) and the harbor seal (*Phoca vitulina*), was examined using computerized tomography (CT scans) and gross dissection. Three-dimensional reconstructions of the heads and ears from CT data were used to determine interaural dimensions and ossicular chain morphometrics. Ossicular weights and densities were measured conventionally. Results strongly support a canal-centric system for pinniped sound reception and localization. Further, true seals show adaptations for aquatic high frequency specialization.

Key Words: Middle ear; Binaural hearing; Pinnipeds; Marine mammals; Seals;

1. Introduction

Thirty-four species of pinnipeds (eighteen true seals, ten fur seals, five sea lions and one walrus) inhabit the earth today (King 1983). These mammals divide their time between land and water; breathing air yet spending much of their lives underwater. Seals and sea lions belonging to two closely related families (phocids and otariids) which arose from a common terrestrial carnivore (Bininda-Emonds *et al.* 1999; Flynn and Nedbal 1998; Ledje and Arnason 1996a, 1996b; Lento *et al.* 1995; Wyss 1987) approximately 25 million years ago (Barnes *et al.* 1985). When the ancestor of modern seals and sea lions started venturing into water, its ears began the transition to an amphibious structure. However, despite their common ancestry, each pinniped group differs in how much time is spent in water or in air. Consequently, these pinniped families offer an excellent opportunity to investigate the continuum of aerial vs. aquatic adaptations for hearing in mammals.

Pinnipeds utilize many of their senses both in air and underwater, including hearing, vision and tactile (Renouf 1991). In both phocids (true seals) and otariids (sea lions and fur seals), vocalizations are associated with social interactions including territorial behavior, mating, and pup recognition (Thomson and Richardson 1995). Passive localization using acoustic cues is hypothesized to play an important role in numerous activities including foraging, predator avoidance, and navigation (Richardson 1995, Schusterman *et al.* 2000).

Pinnipeds are protected under the United States Marine Mammal Protection Act. This act is designed to protect marine mammals from human interference. It prohibits pinnipeds from being hunted. The law is designed also to defend marine mammals from harmful anthropogenic influences such as chemical and noise pollution. The more scientists know about species sensitivities, the better basis for governmental regulations that implement this act. For example, knowledge of a species hearing abilities allows the government to set reasonable limits on sound sources used in the ocean that will avoid or minimize impacts.

As a group, little is known about pinniped hearing capabilities. This thesis investigates correlations between pinniped head and ear anatomy and hearing abilities. By examining the relationship between anatomy and behavior, the thesis will generate relationships useful for estimating hearing abilities from anatomy in the 25 untested pinniped species. In addition, these relationships will provide independent verification for hearing curves generated by individual animals; lending confidence to behavioral hearing ability measures often based on a single subject.

1.1 The history of pinniped hearing research

Early published accounts of the pinniped auditory system focused on descriptive anatomy (Rosenthal 1825, Hyrtl 1845, Doran 1878, Zuckerkandl 1896, Denker 1899, Tandler 1899). Thirty years ago, the publication of the first seal behavioral audiogram (Møhl 1968a) changed the emphasis from anatomy to behavior for studying these systems. Additional audiograms followed representing both aerial and underwater thresholds of numerous seal and sea lion species including the harp seal, *Phoca groenlandicus,* (Terhune and Ronald 1971, 1972), the ringed seal, *Phoca hispida,* (Ronald and Terhune 1975), the California sea lion, *Zalophus californianus,* (Schusterman *et al.* 1972; Schusterman 1974), the northern fur seal, *Callorhinus ursinus,* (Moore and Schusterman 1987), the Hawaiian monk seal, *Monachus schauinslandi*, (Thomas *et al.* 1990), the Pacific walrus, *Odobenus rosmarus*, (Kastelein *et al.* 1996), and the northern elephant seal, *Mirounga angustirostris*, (Kastak and Schusterman 1997). Recent papers (Kastak and Schusterman 1998; Kastak and Schusterman 1999; Kastak *et al.* 1999) have used behavioral techniques to show significant hearing differences between largely aquatic seals (phocids) and largely terrestrial sea lions (otariids). During the last 30 years, some research appeared also on how anatomical and physiological differences among pinnipeds relate to differences seen among the behavioral audiograms. Early work in this area was invasive, including acute investigations of cortical and midbrain responses from implanted electrodes (Bullock *et al.* 1971, Ridgway and Joyce 1975) and cochlear microphonics (Møhl and Ronald 1975, Lipatov 1992). This work was limited to very few species. Consequently, at this time, our knowledge of the anatomy underlying hearing differences among pinnipeds remains limited. This thesis addresses the anatomical issues of air- versus water-adapted ears by utilizing several techniques novel to this field, including tomography (CT scan imaging) and broad species comparisons.

1.2 Mammalian Hearing

Scientists have divided the mammalian ear into three parts: the outer ear, the middle ear and the inner ear (Fig 1). The outer ear functions as a sound collector. In most terrestrial mammals this portion of the ear is an external pinna. Its shape and location play important roles in amplifying certain frequencies of sound while attenuating others. In addition, the positioning of the sound reception point in the head, commonly the pinna, is critical for localization. The outer ear also includes the external auditory canal, which funnels sound waves to the tympanic membrane. This membrane designates the transition point to the middle ear.

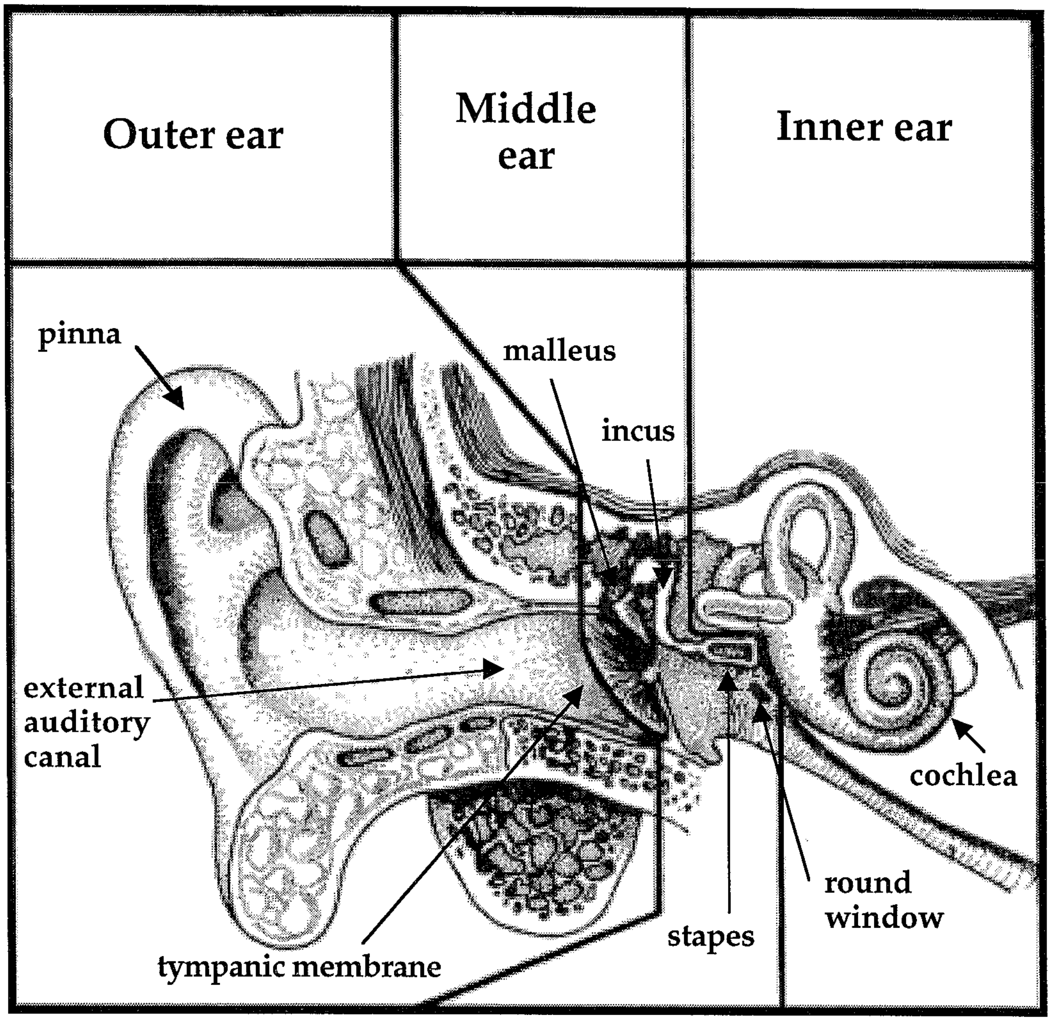

Figure 1. Schematic diagram of the human ear (adapted from Yost 1994).

The middle ear transduces airborne sound waves into mechanical movements. When sound waves reach the tympanic membrane they cause it to vibrate. These vibrations are transmitted to the ossicular chain, which consists of three bones, the malleus, incus and stapes. The malleus is connected directly to the tympanic membrane. It conducts energy to the incus, which connects to the stapes. The stapes vibrates the oval window membrane, which is the boundary with the inner ear.

Movement of the oval window membrane transmits vibrations representing acoustic energy to the fluid filled cochlea. Vibrations in the cochlear fluid cause the basilar membrane inside the cochlea to undulate. The portion of the basilar membrane which experiences the largest motion depends upon the input frequencies. These movements of the membrane bend cilia on hair cells connected to the membrane, that trigger the release of electrical signals sent by the auditory nerve to the brain. Final information processing steps takes place in the central auditory nervous system.

The description above (see Yost 1994 for further details) illustrates the most common sequence of events in mammalian hearing. However, there are alternative pathways for sound reception in addition to the canal route described above including bone condition and air space conduction. In bone conduction, sound is transmitted directly to the cochlea through skeletal and cranial bones, bypassing the outer and middle ears. In air space conduction, sound energy is transmitted to the cochlea through direct vibration of air spaces in the middle ear rather than the ossicular chain (Yost 1994). The mechanisms pinnipeds use are a matter of contention (Møhl 1968b, Ramprashad *et al.* 1972, Repenning 1972, Terhune 1974, Lipatov 1992, Renouf 1991). Understanding and clarifying the sound conduction paths used in pinnipeds is a major goal of this thesis.

1.3 Comparative studies

Comparative studies are often useful for illuminating broad evolutionary patterns. This study continues this comparative trend, investigating the anatomy behind the hearing differences in pinnipeds by combining tomography (CT scans) with traditional dissection. This pairing of digital with gross dissection gives unique insight into the pinniped auditory system.

Ears from three species of pinnipeds, divided among the Otariidae and Phocidae families, were included in this study. Otariids (sea lions and fur seals) are adapted to a nearly equi-amphibious lifestyle, spending approximately half their time in water and half on land. They are more streamlined than most terrestrial mammals and have reduced pinnae, but this group is agile on land (King 1983). Phocids, however, spend very little time on land. They are even more streamlined and have no external pinnae. This family swims gracefully but moves awkwardly on land. For this study, the otariids were represented by the California sea lion (*Zalophus californianus*); the phocids or true seals were represented by the northern elephant seal (*Mirounga angustirostris*) and the harbor seal (*Phoca vitulina*).

These species were good candidates for anatomical work for two reasons. There is a relatively large body of behavioral work on their hearing abilities (Møhl 1968a, 1968b; Schusterman *et al.* 1972; Schusterman 1974; Moore and Schusterman 1987; Kastak and Schusterman 1998, 1999; Kastak *et al.* 1999; Southall *et al.* 2000). In addition, specimens for dissection are not generally difficult to obtain.

This thesis compares seal and sea lion outer and middle ear anatomy and hearing ability, particularly in the context of pinnipeds as amphibious mammals within larger mammalian data sets. One section focuses on correlations of interaural distances with upper frequency hearing limits (Heffner and Heffner 1992; Ketten 2000). This component addresses the question of which hearing mechanisms are functionally important in pinnipeds. Another section focuses on the correlation of a function of ossicular weight with upper frequency hearing limit. This component concentrates on verifying the functional anatomical basis for middle ear transduction from earlier work by Hemilä *et al.* (1995). A final section examines correlations of upper functional hearing limit with ossicular density. This component also expands on techniques and data from previous studies (Parnell and Dreher 1963, Lees et al 2001).

2. Materials and Methods

2.1 Specimens

This study focused on three species from two families. Live animal measurements were obtained through the New England Aquarium, the Woods Hole Aquarium and SeaWorld of Florida. Specimens for dissection were obtained through the California Marine Mammal Stranding Network, courtesy of National Marine Fisheries Service permit F/SWR3:JGC. Study animals included eight live and thirteen postmortem California sea lions (*Zalophus californianus*), nine postmortem northern elephant seals (*Mirounga angustirostris*), and six live and twenty postmortem harbor seals (*Phoca vitulina*). In general, a broad range of sex-age class combinations was represented in the data set. It was not possible to obtain an adult male northern elephant seal for dissection; therefore in comparison to the other specimens studied only a limited set of measurements from a museum collection skull were obtained for males of this species. Tables 1, 2 and 3 summarize the data for the specimens examined in this study, including age class, sex, and condition.

2.2 External Measures

In vivo measures of external features were taken from animals at the New England Aquarium (Guthrie, PV 18-Lana, Chacoda, Reggae, Rigel) and the Woods Hole Aquarium (PV15-Sandy, PV16-Coco). Parallel measures on postmortem specimens were obtained prior to dissection. Intermeatal distance was measured in two ways: as the straight line distance between the meatus and

Table 1
California sea lion (*Zalophus californianus*) specimens

ID	Age class	Sex	Condition	Place of origin	Procedure/ Measures
ZaC11	NA	NA	Skull	HMCZ	CT
ZaC19	Adult	F	Head	MMC	EM,CT,D,O
ZaC21	Adult	F	Head	MMC	EM,CT,D,O
ZaC22	Adult	F	Head	MMC	EM,CT,D,O
SW1	Adult	M	Live	SeaWorld	EM
SW2	Adult	M	Live	SeaWorld	EM
SW3	Adult	M	Live	SeaWorld	EM
SW4	Adult	M	Live	SeaWorld	EM
SW5	Adult	M	Live	SeaWorld	EM
SW6	Adult	M	Live	SeaWorld	EM
SW7	Adult	M	Live	SeaWorld	EM
SW8	Adult	M	Live	SeaWorld	EM
Guthrie	Adult	M	Live	NEAQ	EM
ZaC23	Adult	M	Head	MMC	EM,CT,D,O
ZaC12	Juvenile	M	Head	MMC	EM,CT,D,O
ZaC15	Yearling	M	Head	MMC	EM,CT,D,O
ZaC01	Yearling	F	Right ear	MMC	O
ZaC02	Yearling	M	Right ear	MMC	O
ZaClit 01	NA	NA	Information	Møhl 1968b	OW
ZaC17	Subadult	M	Head	MMC	EM,CT,D,O
ZaC18	Subadult	M	Head	MMC	EM,CT,D,O
ZaC20	Subadult	M	Head	MMC	EM,CT,D,O

Notes: CT-CT scanned, for internal measures; D-dissection; EM-external measures; F-female; HMCZ-Harvard Museum of Comparative Zoology; M-male; MMC-The Marine Mammal Center, Sausalito, CA; NA-not available; NEAQ-New England Aquarium, Boston, MA; O-ossicles; OW-ossicular weight; SeaWorld-SeaWorld of Florida;

Table 2
Northern elephant seal (*Mirounga angustirostris*) Specimens

ID	Age class	Sex	Condition	Place of origin	Procedure/ Measures
MA21	Adult	M	Head	HMCZ	CT
MA11	Juvenile	F	Head	MMC	EM,CT,D
MA07	Juvenile	NA	Ears	MMC	O
MA14	Yearling	NA	Head	SeaWorld	O
MA13	NA	NA	Head	SeaWorld	EM,CT,D,O
MA23	Adult	F	Head	MMC	EM,CT,D,O
MA24	Juvenile	F	Head	MMC	EM
MA22	Weaner	F	Head	MMC	EM
MA00	NA	NA	Head	MMC	EM, CT,

Notes: CT-CT scanned, for internal measures; D-dissection; EM-external measures; F-female; HMCZ-Harvard Museum of Comparative Zoology; M-male;
MMC--The Marine Mammal Center, Sausalito, CA; NA-Not available; O-ossicles;

Table 3
Harbor seal (*Phoca vitulina*) specimens

ID	Age class	Sex	Condition	Place of origin	Procedure/ Measures
PV18-Lana	Adult	F	Live	NEAQ	EM
Chacoda	Adult	M	Live	NEAQ	EM
Reggae	Adult	M	Live	NEAQ	EM
Rigel	Adult	M	Live	NEAQ	EM
PV14	Juvenile	F	Head	NEAQ	CT,EM
PV15-Sandy	Juvenile	F	Live	WHAQ	EM
PV16-Coco	Juvenile	F	Live	WHAQ	EM
DO6979	Juvenile	M	Whole	NEFSC	EM
DO5476	Juvenile	M	Whole	NEFSC	EM
DO5226	Juvenile	M	Whole	NEFSC	EM
PV10	Juvenile	NA	Head	SeaWorld	CT,EM,D
DO4233	Yearling	F	Whole	NEFSC	EM
DO6976	Yearling	M	Whole	NEFSC	EM
DO5227	Yearling	M	Whole	NEFSC	EM
DO5773	Yearling	M	Whole	NEFSC	EM
DO6977	Yearling	M	Whole	NEFSC	EM
DO6978	Yearling	M	Whole	NEFSC	EM
PV17	Yearling	NA	Head	NEAQ	CT,EM
PVG	Yearling	NA	Whole	NEAQ	CT
PVJ	Yearling	NA	Whole	NEAQ	CT
PV23	Yearling	NA	NA	NEAQ	CT
PV13	Pup	NA	Head	NEAQ	CT
PV22	Pup	NA	Flensed head	NEAQ	CT
Pvlit01	NA	NA	Information	Nummela 1995	OW
Pvlit02	NA	NA	Information	Møhl 1968b	OW
PV06	NA	NA	Flensed head	SeaWorld	CT,O

Notes: CT-CT scanned, for internal measures; D-dissection; EM-external measures; F-female; M-male; NEAQ-New England Aquarium, Boston, MA; NA-not available; NEFSC- Northeast Fisheries Science Center Marine Mammal Archive; OW--ossicular weight; WHAQ-Woods Hole Aquarium, Woods Hole MA;

as the curved distance (shortest external path) over the head between the meatuses (Fig 2). In sea lions, these measurements were taken based on the meatal opening at the base of the pinnae. Other measurements were taken opportunistically. These included head girth, diameter, tip of snout to meatus or base of pinnae, and pinnal or meatal dimensions.