Auditory Evoked Potential Measurement of Hearing Sensitivity in Pinnipeds

Jason Mulsow, Colleen Reichmuth, Dorian Houser, and James J. Finneran

1 Background

The majority of research on marine mammal hearing sensitivity has focused on the odontocete cetaceans (dolphins and porpoises) who possess morphological and neural adaptations that support sensitive passive hearing and a refined echolocation system. Fewer studies have examined the hearing sensitivity of the amphibious pinnipeds (sea lions, seals, and the walrus) who do not possess a sophisticated echolocation system. Passive hearing in pinnipeds is, nonetheless, important in behaviors related to reproduction, foraging, and predator avoidance. Many of these studies have used behavioral psychophysical methods to directly measure an animal's perceptual experience. Although the high-quality data provided by psychophysical methods are the most accurate description of hearing sensitivity, the methods are limited because they require trained subjects tested in captive environments. As a result, psychophysically measured profiles describing hearing sensitivity as a function of frequency (audiograms) are available for a small proportion of pinniped and odontocete species, and each examined species is usually represented by only a few individuals.

Auditory evoked potential (AEP) audiometric methods offer the most promising supplement to psychophysical procedures for measuring hearing sensitivity in a larger number of marine mammals. AEP procedures use electrodes to measure the voltages generated by the auditory system in response to acoustic stimuli and do not require the active participation of a subject. Auditory threshold can be assessed by determining the acoustic stimulus levels at which an electrophysiological response disappears. The relatively large voltages generated by hypertrophic structures in the odontocete auditory nervous system, in addition to research interest in echolocation, have facilitated the

J. Mulsow (✉) • J.J. Finneran
US Navy Marine Mammal Program, Space and Naval Warfare Systems Center Pacific,
San Diego, CA 92152, USA
e-mail: jason.mulsow@gmail.com; james.finneran@navy.mil

C. Reichmuth
Long Marine Laboratory, Institute of Marine Sciences, University of California,
Santa Cruz, Santa Cruz, CA 95060, USA
e-mail: coll@ucsc.edu

D. Houser
National Marine Mammal Foundation, San Diego, CA 92106, USA
e-mail: dorian.houser@nmmfoundation.org

A.N. Popper and A. Hawkins (eds.), *The Effects of Noise on Aquatic Life*,
Advances in Experimental Medicine and Biology 730, DOI 10.1007/978-1-4419-7311-5_16,

refinement of AEP audiometric methods with odontocetes (see Supin et al. 2001). AEP audiometric methods for assessing hearing sensitivity in pinnipeds are comparatively underdeveloped despite a similar need for data outside of existing psychophysical audiograms.

2 Amphibious Hearing Sensitivity in Pinnipeds

Pinnipeds, with a few exceptions such as *Mirounga angustirostris* (northern elephant seal), are sensitive to aerial sound over a wide range of frequencies. Aerial audiograms for both otariids (sea lions and fur seals) and phocids (true seals) usually have a characteristic mammalian "U-shape," with a shallow roll-off in sensitivity at low frequencies below 1 kHz and a sharp high-frequency hearing limit that occurs in the ultrasonic range between 20 and 40 kHz. Thresholds are commonly less than 10 dB re 20 μPa in the region of best sensitivity for many species. Underwater audiograms for pinnipeds, like their aerial audiograms, typically display a U-shape with a shallow low-frequency roll-off and a sharp high-frequency hearing limit. Although their lowest absolute detection thresholds are higher than those reported for odontocetes, thresholds for pinnipeds in the range of best hearing are generally between 50 and 70 dB re 1 μPa. One of the most striking features of the underwater hearing of pinnipeds is the difference between the underwater audiograms of otariid and phocid species: whereas the otariid underwater audiogram is essentially similar to the aerial audiogram in terms of frequency range of hearing, the underwater high-frequency limit for many phocid species is in the region of 70 to 100 kHz, markedly higher than the aerial high-frequency limit (see Hemilä et al. 2006).

3 Development of Noninvasive Audiometric Methods

The first evoked potential measurements of hearing sensitivity with pinnipeds were conducted using intracranial electrodes, allowing for the reduction of extraneous electrical noise levels relative to AEP voltages (Bullock et al. 1971; Ridgway and Joyce 1975). These studies demonstrated that the electrophysiological responses evoked by frequency-specific acoustic stimuli could be used to estimate the audiogram of pinnipeds.

Recent AEP studies with pinnipeds have recorded AEPs using small needle electrodes that are placed superficially under a subject's skin. The ratio of AEP signal to extraneous noise that is provided by these surface electrodes is significantly lower that those obtained with intracranial electrodes. Despite this, studies with a phocid, *Phoca vitulina* (harbor seal; Wolski et al. 2003), and an otariid, *Eumetopias jubatus* (Steller sea lion; Mulsow and Reichmuth 2010)], have demonstrated that these noninvasive recordings can provide a rapid estimate of a subject's psychophysical aerial audiogram. Most notably, relative sensitivity and the high-frequency hearing limit of the audiogram are accurately reproduced using AEP methods. The subjects of both studies were chemically sedated or anesthetized for the duration of data collection. The AEPs of interest were not markedly affected by the chemical agents and electrical artifacts related to subject movement during testing were largely eliminated, resulting in signal-to-noise conditions favorable for detecting the presence of an electrophysiological response. The stimuli used to elicit responses in *Phoca vitulina* were tone bursts, and the experimenters visually determined the presence or absence of an AEP in the electrophysiological record. For testing with *Eumetopias jubatus*, sinusoidally amplitude-modulated (SAM) tones were used to elicit rhythmic AEPs that were phase-locked to the rate of amplitude modulation imposed on the stimulus. This phase locking allows for frequency-domain analysis of the AEP as opposed to traditional time-domain analysis. After Fourier analysis of the time-domain

AEP waveform, the response is detectable as a spectral peak at the stimulus amplitude-modulation rate. The low-level AEPs (on the order of tens of nanovolts) that persist at near-threshold stimulus levels can then be objectively detected using frequency-domain signal-to-noise statistics.

Although AEP procedures with pinnipeds do not yet possess the same level of refinement as those with odontocetes, procedures using SAM tone stimuli with anesthetized subjects can provide an estimate of a subject's aerial audiogram in less than an hour. The AEP audiograms obtained for numerous untrained *Eumetopias jubatus* and *Zalophus californianus* (California sea lion) individuals have been similar to previously reported psychophysical audiograms in terms of relative sensitivity and high-frequency hearing limit. These results suggest that psychophysical audiograms obtained for a few individuals are representative of larger populations and reinforce the idea that the otariids form a functional hearing group. Profoundly elevated thresholds have been detected in a few subjects of both species, demonstrating that AEP methods can provide a tool for the rapid detection of hearing loss.

4 Limitations of AEP Measurements

Thresholds obtained with AEP methods are almost uniformly elevated relative to psychophysical thresholds. This relative elevation is normally largest at the low-frequency end of the audiogram, the frequency range in which anthropogenic noise predominantly occurs. There is a high degree of intersubject variability in AEP thresholds; standard deviations of 10–20 dB at each frequency are common. This is quite large compared with the level of intersubject variability in existing psychophysical data, and it is not yet known whether this is inherent to the AEP methods or due to actual variability in the hearing sensitivities of the individuals that have been tested thus far using these methods.

All noninvasive AEP studies with pinnipeds have been limited to measuring the aerial hearing sensitivity of subjects. Although concerns regarding the negative effects of aerial anthropogenic noise have to some extent motivated AEP studies with pinnipeds, primary interests lie in understanding the potential effects of underwater noise. The use of chemical sedation or anesthesia during pinniped AEP studies unfortunately makes the submersion of a subject a difficult prospect. Some conclusions regarding underwater sensitivity can, however, be based aerial audiograms obtained during AEP procedures (see below). Direct measurements of underwater hearing will likely continue to be one of the main challenges facing AEP hearing sensitivity measurements with pinnipeds.

5 Future Research Directions

AEP audiometric techniques for pinnipeds currently possess a level of refinement that is likely sufficient for testing with any of the otariids, a family for which audiometric data is available for only 3 of 14 species. The signal-to-noise ratios in AEP recordings with phocids are, however, generally much smaller than those for otariids. Modifications of the objective audiometric techniques that have proven useful for otariids should be a focus of future research aimed at measuring hearing sensitivity in phocids.

Some of the results of aerial AEP procedures can probably be extrapolated to describe certain features of underwater hearing. For example, both the aerial and underwater high-frequency hearing limits of otariids are limited by cochlear sensitivity and are therefore very similar (Hemilä et al. 2006). The aerial high-frequency hearing limit is accurately represented using AEP methods, and it most likely can provide a rapid estimate of underwater frequency range of hearing. Other auditory processes that primarily involve the cochlea (e.g., energetic masking, temporary threshold shift) are likely to have similarities in air and underwater. Future studies may therefore be able to simultaneously predict the effects of aerial and underwater noise on the pinniped auditory system using a large sample size of untrained subjects.

6 Conclusions

Although AEP audiometric methods for pinnipeds still do not possess the level of sophistication of those for odontocetes, they are currently providing a useful supplement to traditional behavioral psychophysics for measuring hearing sensitivity. Within-subject comparisons of electrophysiological and psychophysical methods have demonstrated that AEP thresholds obtained from sedated or anesthetized pinnipeds provide a rapid estimation of a subject's aerial audiogram. The features of relative sensitivity and high-frequency hearing limit have been similar in psychophysical and AEP audiograms for *Eumetopias jubatus* and *Zalophus californianus*, suggesting that the high-quality psychophysical data from a few individuals are representative of larger populations of animals. Drawbacks of AEP audiometric methods include a tendency for a high degree of intersubject variability in frequency-specific thresholds and a near-uniform elevation of thresholds relative to psychophysical data.

Future studies of pinniped hearing should focus on the further development of AEP audiometric methods, especially those that will help to resolve the challenge of testing underwater hearing sensitivity and promote testing with phocid species. In the absence of AEP methods that can examine underwater hearing, some features of aerial hearing, such as the high-frequency hearing limit of otariid subjects, can likely be used to predict underwater hearing capabilities. The generalization of results from aerial AEP procedures to underwater function may also be a promising means of investigating noise effects such as masking and temporary threshold shift.

References

Bullock TH, Ridgway SH, Nobuo S (1971) Acoustically evoked potentials in midbrain auditory structures in sea lions (pinnipedia). Z Vergl Physiol 74:372–387.

Hemilä S, Nummela S, Berta A, Reuter T (2006) High-frequency hearing in phocid and otariid pinnipeds: An interpretation based on inertial and cochlear constraints. J Acoust Soc Am 120:3463–3466.

Mulsow J, Reichmuth C (2010) Psychophysical and electrophysiological aerial audiograms of a Steller sea lion (*Eumetopias jubatus*). J Acoust Soc Am 127:2692–2701.

Ridgway SH, Joyce PL (1975) Studies on seal brain by radiotelemetry. Rapp P-V Reun Cons Int Explor Mer 169:81–91.

Supin AY, Popov VV, Mass AM (2001) The sensory physiology of aquatic mammals. Kluwer Academic Publishers, Boston, MA.

Wolski LF, Anderson RC, Bowles AE, Yochem PK (2003) Measuring hearing in the harbor seal (*Phoca vitulina*): Comparison of behavioral and auditory brainstem response techniques. J Acoust Soc Am 113:629–637.