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Measuring Hearing in Odontocete Cetaceans

Messung des Hörvermögens bei Zahnwalen

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Abstract

The initial measurements of odontocete hearing were obtained using captive trained animals and established psychophysical procedures that revealed very sensitive hearing at very high frequencies. However, these procedures tend to take a long time and require dedicated animals. New procedures using brain wave auditory evoked potential measurements in response to sound allowed for faster hearing tests and quick measurement of the hearing of untrained animals, including animals that stranded on beaches. As a result, knowledge of hearing in odontocetes rapidly expanded. The development of new procedures continued, including the possible inclusion of hearing measurements gathered via startle responses and via Evoked Auditory Potentials gathered from free-swimming wild animals with temporary tags attached with suction cups. Understanding hearing in marine mammals remains a priority to ensure that proper management decisions are made to minimize the impact of man-made underwater noise on these species

Keywords: Hearing, dolphins, whales, AEP

C. Scott Johnson's (1966) measurement of the original audiogram of the bottlenose dolphin (*Tursiops truncatus*, Montague) was the first true measurement of hearing in a whale or dolphin. However, it took over two years to complete, and he used young trained animals and developed the psychophysical method and training as he went along. The animals were trained in the laboratory with the help of professional animal trainers who learned their craft based on the principles devised with pigeons by B.F. Skinner and techniques used by dolphin trainers in oceanaria. Johnson's techniques were logical and produced outstanding data, demonstrating very high frequency underwater hearing with relatively good detection of sounds with frequencies up to 150 kHz. The techniques that Johnson developed became the 'gold standard' for measuring ma-

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rine mammal hearing. If one followed his methods, a researcher was assured of administering accurate hearing tests. Most psychophysical behavioral tests of hearing have taken a long time to complete, but true measures of hearing, which require an animal to report the presence and absence of sound, require that the animal be trained. Once a baseline for a species is established with multiple animals, Auditory Evoked Potential (AEP) measures, which are much quicker, can be used to measure the hearing of individuals (Yuen et al., 2005). AEP measurements of hearing are not based on the animal's reports of experiencing sound, but on measurements of brainwave patterns produced in response to sound. Suction cups containing passive electrode sensors are normally placed on the whale or dolphin's skin (see Fig. 1). Typically, sounds to be measured are presented in patterns that are replicated in the brain so that they can be easily distinguished. This hearing measurement technique is now used for most human babies born in hospitals during their first couple of days of life. The technique applied to whales and dolphins was developed within the laboratory and in marine zoological parks. Animal hearing had to be tested using both behavioral psychophysical and evoked auditory potential testing procedures,

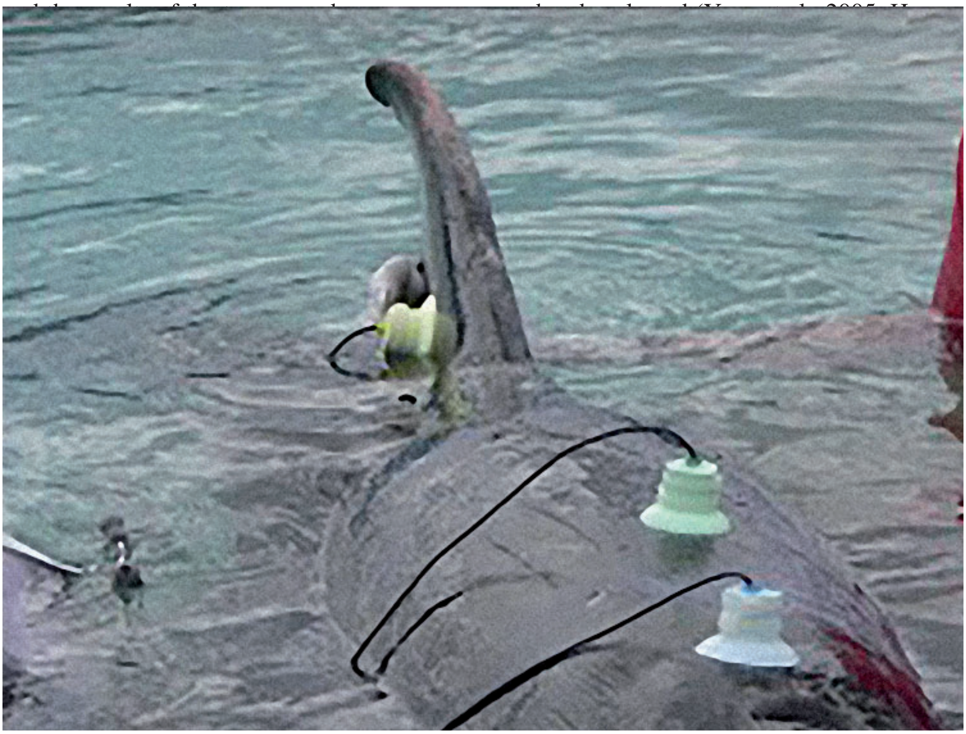

Fig. 1: Suction cups containing surface electrodes attached to a beached cetacean. Photo: Marine Mammal Research Program, University of Hawaii

Establishing a baseline for a species requires measuring the hearing of multiple animals within that species. If the hearing of only one individual is tested, the resulting audiogram should be interpreted with caution as hearing abilities can vary among individuals of the same species. The initial hearing measurements published by Hall & Johnson (1972) for killer whales (*Orcinus orca*) were very different from those of bottlenose dolphins, not due to a species difference, but due to intraspecific variations. The early studies showed an upper frequency cutoff at 30 kHz, which was much lower than the 150 kHz frequency cutoff measured by Johnson for bottlenose dolphins (*Tursiops truncatus*). Because of the amount of time required for behavioral tests and the scarcity of available subjects, the 30 kHz upper frequency cutoff for *O. orca* remained the only representative data for this species for over 25 years. However, when Szymanski et al. (1999) tested the hearing of two killer whales at the Marine World Park in California, they found that the high-frequency hearing cutoff was closer to 100 kHz, which more closely resembles the higher thresholds found in other odontocete cetaceans. These thresholds were further confirmed with „gold standard" psychophysical behavioral measures conducted by Branstetter et al. (2017) on eight different killer whales from two different marine parks within the last five years.

The development of rapid hearing testing procedures and their validation with psychophysical behavioral measures has provided valuable scientific information about dolphin and small whale hearing. It has also laid the foundation for evaluating the effects of loud sounds on cetaceans and for conserving groups and individual animals exposed to excessive anthropogenic noise. Early measures of auditory brain responses primarily relied on responses to clicks and showed promise for measuring audiograms but were not refined for precise hearing measurements to specific frequencies (Bullock & Ridgway, 1972; Ridgway et al., 1981). Shortly after the development of the Auditory Evoked Potential envelope following response procedure for measuring cetacean hearing (Supin & Popov, 1995; Dolphin et al., 1995), conservationists and animal welfare advocates began seeking ways to rapidly assess cetacean hearing.

When a group of Risso's dolphins (*Grampus griseus*) stranded on a beach in Southern Portugal,

Fig. 2: Stranded neonate Risso's dolphin (*Grampus griseus*) at Mundo Aquatico Rehabilitation Facility of ZooMarine in Guia. Photo: Marine Mammal Research Program, University of Hawaii

a neonate *G. griseus*, so young that it still had fetal fold creases visible on its side, was rescued and taken to the rehabilitation facility at the ZooMarine marine park in Guia, Albufeira, Portugal (see Fig. 2). During the rehabilitation, the staff and veterinarians observed that the animal had difficulty maintaining horizontal stability and suspected that the ears and vestibular system (responsible for balance) may have been damaged by overexposure to anthropogenic noise. A behavioral psychophysical audiogram had been previously measured for one adult *G. griseus* (Nachtigall, Au, Pawloski & Moore, 1995). The management at ZooMarine Park in Portugal's Algarve requested that the hearing of the stranded calf be quickly tested. The stranded infant's hearing was tested at night when veterinarians were not administering medical care. The data showed (Nachtigall, Yuen, Mooney & Taylor, 2005) that compared to the audiogram obtained using behavioral methods for the older Risso's dolphin, the hearing threshold values at upper frequencies were much lower (i.e., better sensitivity) for this neonate animal. This means that this neonate whale heard well at much higher frequencies. The results redefined hearing sensitivity for the *G. griseus* species, with peak sensitivity near 100 kHz and the ability to hear sounds above 150 kHz. The experiment also demonstrated that, like human infants in hospitals, infant cetacean hearing could be rapidly assessed for diagnostic purposes and assistance in medical care.

The method of rapidly testing hearing through AEP analysis, which was developed within the laboratory and then used as a diagnostic tool during the rehabilitation of animals, has other distinct values. It can quickly test hearing during temporary threshold shift (TTS) experiments and analyze the hearing of dolphins and small whales that have recently stranded on the beach. Cetacean stranding has been demonstrated to be caused by overexposure to anthropogenic noise (Frantzis, 1998; Evans & England, 2001), and determining regulatory sound limits is crucial. Sound limits for humans have been established by the determination of TTS, which determines sound levels that temporarily reduce hearing or cause an upward shift in hearing threshold. Similar levels were sought for cetaceans (Nachtigall et al., 2003; Weilgart, 2007), but reliable TTS measurements could not be obtained without quick measures of hearing. AEP provide quick hearing measurements (Nachtigall et al., 2004), allowing regulatory levels to be established to protect wild animals from overexposure to noise and potential subsequent stranding (National Marine Fisheries Service, 2018).

New and faster behavioral methods were developed by scientists at the Navy Lab in San Diego to measure the recovery of hearing in TTS experiments by training dolphins and beluga whales to whistle immediately when they hear a sound (Schlundt et al., 2000). Although this training procedure works well for threshold shift experiments (Finneran, 2015), the behavioral training method still requires that the animal is adapted to an enclosed environment and receives extensive training (Schlundt et al., 2000), limiting the number of animals that can be tested. On the other hand, AEP measurements of cetacean hearing are less time-consuming and can be conducted without adaptation or any animal training (Supin et al., 2001; Houser & Finneran, 2006; Andre & Nachtigall, 2007). While true hearing tests still rely on behavioral measures of animal reports of hearing, AEP measures can be used in various situations where animals are available for only short periods of time.

Because AEP hearing tests can be done quickly and are part of the veterinary diagnostic routine for stranded animals, their use has allowed for much-needed expansion of the study of hearing in small whales and dolphins. They can now measure the hearing of interesting deep-diving small whales that are rarely held in research facilities or animal display facilities and have stranded on beaches (Pacini et al., 2010). At times this may require taking the animal back to an animal care facility for rehabilitation, but hearing tests can also be conducted right on the beach. AEP hearing tests enable addressing difficult conservation questions and concerns.

Beaked whales (*Mesoplodon densirostris*) are a group of highly elusive small whales that are capable of diving to depths exceeding 3000 meters and holding their breath for close to four hours (Quick et al., 2020). They gained notoriety following an infamous mass stranding in the Bahamas (Evans & England, 2001) that was believed to have been caused by U.S. Navy activities. This incident spurred a strong interest in understanding the hearing abilities of beaked whales. During the rehabilitation of a wild young Blainville's beaked whale that had stranded off the coast of Maui, Hawaii, its hearing was tested, revealing exceptional hearing sensitivity between 40 and 80 kHz (Pacini et al., 2011), the frequency range where its primary echolocation click energy is found. Interestingly, the whale also appeared to hear signals above 100 kHz (see Figure 3), indicating a broader hearing range than previously thought.

Auditory testing was not limited to stranded wild animals. New possibilities emerged to answer lingering questions, including the high-frequency hearing capabilities of white-beaked dolphins (*Lagenorhynchus albirostris*). In a study by Mitson (1990), white-beaked dolphins' echolocation signals were recorded while they were feeding on sand-eels and responding to high-frequency sonars. Mitson reported echolocation click energy with frequencies as high as 305 kHz, well above the typical upper hearing frequency limit for odontocetes of about 150 kHz. However, the question of whether white-beaked dolphins could hear frequencies over 300 kHz remained unanswered. These dolphins are often observed off the coast of Iceland during the summer months, and for several decades, temporary dolphin captures have been taking place for scientific purposes off Tampa Bay, Florida, on an annual basis to monitor a population of bottlenose dolphins. Therefore, it did not seem too much of a reach to attempt to temporarily capture a white-beaked dolphin, place it onboard a boat in a water-filled foam-lined box for a short period of time, and examine its hearing (see Figure 4). A group organized around Lee Miller's lab at the University of Southern Denmark (Nachtigall et al., 2008) accomplished this effort with two white-beaked dolphins. While the animals did not hear over 300 kHz, the dolphins did hear as well as harbor porpoises up to near 180 kHz, and the technique to catch and release and to measure hearing was demonstrated to be viable. Although the effort worked very well for the white-beaked dolphins, a similar attempt organized by the same group to catch the larger mysticete minke whale (*Balaenoptera acutorostrata*)

Fig. 3: Beaked whale (*Mesoplodon densirostris*) in a rehabilitation facility. Photo: Aude Pacini

Fig. 4: Testing the hearing of the white-beaked dolphin (*Lagenorhynchus albirostris*) temporarily held aboard ship. Photo: Marine Mammal Research Program, University of Hawaii

was unsuccessful. Unfortunately, no behavioral or evoked potential measures of hearing of mysticete whales are currently available. It is generally believed that the smaller toothed dolphins and whales, the odontocetes, evolved high-frequency hearing and that odontocetes have excelled in echolocation, while the mysticetes have not taken the same evolutionary path. High-frequency directional echolocation type signals are not usually recorded from the larger mysticete whales, while every odontocete recorded has shown echolocation-type signals (Surlykke et al., 2014). Most mysticete vocalizations are of lower frequency compared to those of odontocetes. Measuring hearing at low frequencies using AEP is generally more difficult than measuring high-frequency hearing.

New techniques for measuring hearing are under development so that the basic hearing of healthy wild animals can be tested in the future. Developing these techniques requires access to animals in marine parks and research facilities that have established audiograms. Detectable startle responses to sounds as unexpectedly quiet as 140 dB re 1 (µPa) have been observed in false killer whales (*Pseudorca crassidens*), and startle responses tend to stay at a relatively set level above threshold for mammals (Koch and Schnitzler, 1997). If that is true with cetaceans, then one could obtain thresholds across the auditory spectrum and subtract the set amount to estimate an audiogram. This would be particularly helpful in attempting to estimate the thresholds of large mysticete whales.

Auditory evoked potential measures typically require non-invasive suction cup electrodes to record the small electrical signals from the brain, with wires connected to the recording and processing equipment. So far, animals in human care, recently captured prior to release, or stranded have been the primary sources for new species audiograms. Archival tags attached to wild animals have been used effectively to obtain a great deal of interesting data on the acoustics and behavior of wild animals. The tags attach temporarily to the animals via suction cups and are recovered later. The initial data processing and data storage occur directly on the tag, without the need for wires. Smith et al. (2021) have developed a new tag that can be attached to free-swimming harbor porpoises. Evoked potential responses of sounds presented to the animal were recorded on the attached tag, allowing a „wireless" measure of acoustic thresholds. If this exciting new procedure continues to develop, and the tags can be placed on wild free-swimming animals, the audiograms of many animals, including new species, can be measured. If new techniques for measuring low-frequency hearing are also developed, the hearing of large mysticete whales can finally be measured.

Zusammenfassung

Die ersten Messungen des Gehörsinns von Zahnwalen wurden mit in Menschenobhut trainierten Tieren und etablierten psychophysikalischen Verfahren durchgeführt, die ein sehr empfindliches Gehör bei sehr hohen Frequenzen zeigten. Diese Verfahren sind jedoch in der Regel sehr zeitaufwändig und erfordern speziell trainierte Tiere. Neue Verfahren, bei denen das auditorisch evozierte Potenzial des Gehirns als Reaktion auf Geräusche gemessen wird, ermöglichten schnellere Hörtests und eine rasche Messung des Gehörs von untrainierten Tieren, auch von gestrandeten Tieren. Infolgedessen erweiterte sich das Wissen über das Hörvermögen von Zahnwalen rasch. Die Entwicklung neuer Verfahren wurde fortgesetzt, einschließlich der möglichen Einbeziehung von Hörmessungen, die über Schreckreaktionen und über evozierte Hörpotentiale von freischwimmenden Wildtieren mit temporären, mit Saugnäpfen befestigten Markierungen durchgeführt wurden. Das Verstehen des Hörens von Meeressäugetieren hat nach wie vor Priorität, um sicherzustellen, dass geeignete Managemententscheidungen getroffen werden, um die Auswirkungen des vom Menschen verursachten Unterwasserlärms auf diese Arten zu minimieren.

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