Variability in Click-Evoked Potentials in Killer Whales (*Orcinus orca*) and Determination of a Hearing Impairment in a Rehabilitated Killer Whale

Klaus Lucke,[1,2] James J. Finneran,[3] Javier Almunia,[4] and Dorian S. Houser[5]

[1]*Centre for Marine Science & Technology, Curtin University, GPO Box U1987, Perth, WA 6845, Australia*
[2]*IMARES Wageningen UR, Postbus 167, 1790 AD Den Burg, The Netherlands*
E-mail: klaus.lucke@curtin.edu.au
[3]*SSC Pacific, 53560 Hull Street, San Diego, CA 92152, USA*
[4]*Loro Parque Foundation, Puerto de la Cruz, 38400 Santa Cruz de Tenerife, Islas Canarias, Spain*
[5]*National Marine Mammal Foundation, 2240 Shelter Island Drive, Suite 200, San Diego, CA 92106, USA*

Abstract

An immature female killer whale (*Orcinus orca*) stranded in the Wadden Sea in 2010 and was later transferred to Loro Parque, Tenerife, Spain, for rehabilitation. The killer whale, named "Morgan," was suspected to have a hearing impairment. To test whether Morgan has a hearing deficit, auditory brainstem responses to short-duration, broadband click stimuli were recorded. The same procedure was conducted with five other killer whales at Loro Parque for comparative purposes. Stereotypical click-evoked responses were recorded in all of the killer whales except Morgan, even at the highest click level that could be projected. Reductions in the amplitude of the click-evoked response paralleled reductions in the stimulus amplitude of the clicks presented to all of the other whales. The lack of a click-evoked response in Morgan indicates that she suffers from a hearing deficit. The magnitude and frequency range over which the hearing deficit occurs cannot be specified with the techniques used here. Nevertheless, it can be concluded that Morgan's hearing sensitivity to broadband signals is at least 20 to 30 dB worse than the hearing sensitivity of the other killer whales tested. Morgan potentially suffers from a profound hearing deficit or even a complete loss of hearing, but this cannot be determined through the electrophysiological tests used in this experiment.

Key Words: killer whale, *Orcinus orca*, marine mammal, audiometry, auditory evoked potentials, hearing deficit

Introduction

In June 2010, a single female killer whale (*Orcinus orca*) was found drifting in the shallow waters of the Dutch Wadden Sea near the island of Schiermonnikoog. Considered to be in imminent danger of stranding, the whale was caught and transported to the Dolfinarium Harderwijk, the Netherlands, where she was diagnosed with dehydration and severe malnutrition, and subsequently rehabilitated over a period of more than a year (Trouwborst et al., 2013). In November 2011, the animal, named "Morgan," was deemed healthy and was transported to Loro Parque, Tenerife, Spain, which provided an environment with several conspecifics and larger pools.

No concerns were noted regarding the hearing ability of Morgan while she was rehabilitating at the much smaller pool at Dolfinarium Harderwijk. However, once moved to the larger pools at Loro Parque where acoustic cues were more commonly used for calling Morgan to a trainer, Morgan showed inconsistent response to those cues. This gave rise to the speculation that her hearing might be compromised. As with other delphinids, killer whales produce a wide variety of clicks, whistles, and pulsed calls for echolocation and communication (Ford, 1989, 1991). As killer whales rely upon echolocation for navigation and foraging (Diercks et al., 1971; Hall & Johnson, 1972; Barrett-Lennard et al., 1996) and use sounds intensively in social contexts (Ford, 1991), it was speculated that compromised hearing could significantly impact Morgan's training, husbandry procedures, and interactions with conspecifics. Moreover, the presence of a hearing impairment would be an important consideration in the assessment of her release prospects.

Hearing in killer whales can be tested through behavioural methods or through the use of auditory evoked potentials (AEPs), an electrophysiological method that can be used for the rapid determination of hearing sensitivity but which

has received little benchmarking in killer whales. The first hearing thresholds measured in a killer whale were obtained through behavioral methods, but the subject whale demonstrated no sensitivity to sound above 32 kHz (Hall & Johnson, 1972). Greatest sensitivity was observed at 15 kHz, with a threshold of 30 dB re 1 μPa (± 5 dB). Work conducted over two decades later utilizing behavioral and AEP methods found two adult female killer whales with upper frequency limits to hearing between 100 and 120 kHz (Szymanski et al., 1999). The two killer whales showed the greatest hearing sensitivity at 20 kHz. Although audiograms were obtained from each of the whales, the data remain insufficient to determine normal hearing thresholds in this species or to quantify the typical variation in hearing range and sensitivity as a function of age and gender. Additional subjects are required of both genders and across a range of ages to determine population-level variability in hearing within this species as has been demonstrated for the bottlenose dolphin (*Tursiops truncatus*) (Houser & Finneran, 2006b; Houser et al., 2008).

The purpose of the study reported herein was to establish audiometric baseline information on Morgan and to compare it to other killer whales. The acquisition of information from whales of different gender and age contributes to our understanding of variability in killer whales and provides an opportunity to test the hypothesis that Morgan is hearing impaired. The objectives were only partially achieved. The results revealed information about the hearing of Morgan but also demonstrated limitations on the utility of AEP methods in testing the hearing of killer whales and brought into question the results of prior evoked potential audiometry studies utilizing frequency-specific acoustic stimuli.

Methods

Subjects
Auditory measurements were conducted at Loro Parque in Tenerife, Spain, in November 2012 as part of the medical diagnostic procedures conducted with Loro Parque's permission. The measurements are in accordance with the ARRIVE (Animal Research: Reporting of In Vivo Experiments) guidelines (Kilkenny et al., 2010). Seven killer whales between 3 mo and 17 y of age, representing both sexes, were held at this facility in four interconnected pools. Six of the animals were born in captivity, with only Morgan coming from the wild. She had been introduced into the group about 1 y prior to testing and interacted normally with all of the killer whales at the facility. All of the animals were healthy at the time of the auditory tests.

Auditory evoked potential methods were utilized to characterize the hearing of four killer whales at the Loro Parque facility (Table 1). Subject whales ranged in age from 6 to 17 y and varied in weight from 1,500 to 3,500 kg. Data collection occurred with the whales both under water and while resting on a platform, in air. Underwater measurements were made in a 10,000 m³ irregularly shaped, concrete pool with a depth of 8 m. The two approaches were taken in order to emulate natural hearing conditions (underwater) and to maximize the signal-to-noise ratio of the evoked response (in air). All tests were performed with the voluntary participation of the killer whales using standard conditioning techniques.

Stimulus Presentation
Stimulus transmissions and AEP recordings were performed using the *EVREST* system (Finneran, 2009), which is custom software interfaced with a data acquisition board (NI PCI-6251; National Instruments, Austin, TX, USA) in a rugged notebook computer. Stimuli consisted of acoustic "clicks," "tone pips," and sinusoidal amplitude modulated (SAM) tones. As tone pips and SAM tones did not produce sufficiently robust or detectable evoked responses, respectively, they were not pursued for determining frequency-specific hearing thresholds (see "Discussion"). Clicks consisted of rectangular pulses with durations of 50 μs. Clicks were presented at a rate of ~30 clicks/s, and the polarity of the click was reversed on each successive presentation. Stimuli were digitally generated, converted to analog with a 1 MHz update rate and 16-bit resolution, low-pass filtered at 200 kHz (8-pole Butterworth, 3C module; Krohn-Hite Corporation, Brockton, MA,

Table 1. List of killer whales (*Orcinus orca*) used for auditory measurements within the different experimental configurations

Name	Sex	Age	Under water	In air
Morgan	F	6-10*	x	x
Keto	M	17	x	x
Skyla	F	8	x	x
Tekoa	M	12		x

*Morgan's age range was estimated from her length at rescue and at hearing test using a published growth curve for Atlantic killer whales (Duffield & Miller, 1988).

USA), and attenuated (custom, 0 to 70 dB range) before being applied to the sound projector. Clicks were presented at sufficient levels to produce a robust evoked response and then attenuated at 10 dB steps when changed. The step size was selected to allow the change in click-evoked response amplitude as a function of stimulus amplitude to be determined within the constraints of the session time permitted by the training staff.

For underwater measurements, a piezoelectric sound projector (ITC 1001; International Transducer Corporation, Santa Barbara, CA, USA) was placed in front of the killer whale, approximately 1.5 m away from the pan region of the lower jaw. The killer whales were positioned near the water surface at the side of the test pool such that the dorsal surface was above the water but the lower jaw was completely submerged. Underwater stimuli were calibrated at the location of the killer whale's ears (at the location of the external acoustic meatus, respectively) while on station but without the whale present. The variation in the acoustic field was relatively low (± 3 dB) around the subject's head. A representative example of the underwater click stimulus frequency spectrum can be found in Figure 1. The center frequency of the click was 18 kHz, and it had a -10 dB bandwidth from 2.9 to 20 kHz.

In-air measurements were conducted while the killer whales voluntarily beached on a concrete platform in the main pool, a behavior which was trained for husbandry purposes. The projector for in-air testing consisted of an underwater sound projector (ITC 1042) embedded in a silicone rubber suction cup (a *jawphone*) which was
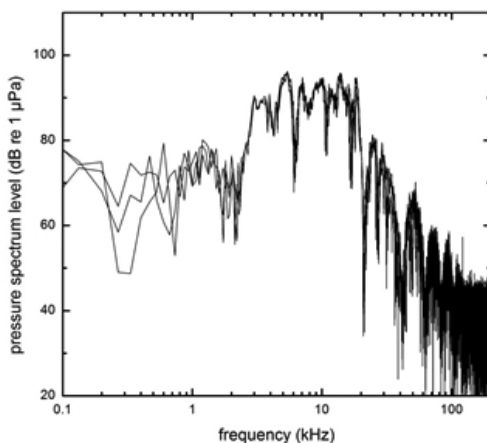
coupled to the whale's lower jaw over the region of the pan (the thinnest region of the lower jaw associated with the medially positioned acoustic fats and considered to be the most sensitive area to sound returning from echoes generated during echolocation) (Brill, 1991; Møhl et al., 1999). The jawphone was calibrated according to distances between the pan region and the auditory bulla of the bottlenose dolphin (Finneran & Houser, 2006); it has not been calibrated against a killer whale, and received sound pressure levels (SPLs) from jawphone-generated signals should only be considered estimates at this time. Clicks produced with the jawphone transducer had a center frequency of 85 kHz and a -10 dB bandwidth from 55 to 110 kHz when measured in the direct field.

The best position in terms of signal presentation (i.e., resulting in the highest AEP amplitude) was identified by presenting a click at a constant stimulus level and moving the jawphone to different positions along the lower jaw. The best position for stimulus presentation was just ventral and slightly anterior to the corner of the mouth, over the pan region, as has been observed in bottlenose dolphins (Finneran & Houser, 2006). Once the location corresponding to the maximum AEP amplitude was located, acoustic stimuli were presented to the killer whales in a series of attenuating amplitudes, starting at levels that clearly produced an AEP and reducing it to the point that the AEP was no longer visible in the electrophysiological recordings. The application of the jawphone was consistent with previous uses in other odontocetes (Cook et al., 2006; Houser et al., 2008; Mooney et al., 2008; Finneran et al., 2009). In-air testing improved the signal-to-noise ratio of the evoked potentials and permitted data collection from an additional killer whale ("Tekoa").

AEP Recordings
Three electrodes—inverting, non-inverting, and ground—were positioned along the dorsal midline of the killer whales in order to acquire the AEPs as is common for testing of other odontocetes in water (Yuen et al., 2005; Finneran et al., 2009). The non-inverting electrode was placed approximately 17 cm behind the whale's blowhole, slightly lateral to the dorsal midline and over the assumed location of the auditory brainstem. The inverting electrode was placed approximately midway between the non-inverting electrode and the dorsal fin to provide a stable voltage recording to which the non-inverting electrode could be referenced. The ground electrode was placed near the dorsal fin. The electrodes consisted of 10-mm diameter gold cup-electrodes embedded in a suction cup made of silicon rubber. Electrodes were coupled to the skin of the whales with conductive
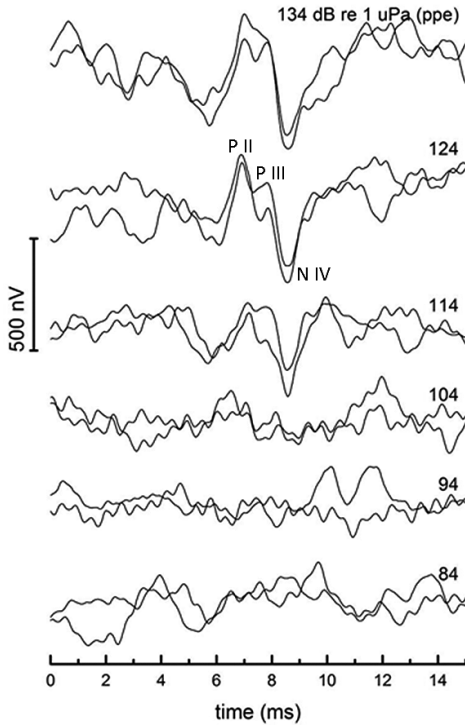

Figure 1. Frequency spectrum of the click stimulus measured under water at the location of the killer whales near the side of the pool at Loro Parque; data for three independent measurements are superimposed.

Figure 2. Click-evoked potentials measured in an adult male killer whale ("Keto") while he rested at the side of the pool; clicks were presented across a range of amplitudes (SPL$_{ppe}$), which are presented above and to the right of each AEP waveform. Multiple waveforms represent the repeated AEP measurements collected at the same click level. The peaks P II, P III, and N IV are labelled for the click-evoked AEP records obtained at an amplitude of 124 dB SPL$_{ppe}$.

Figure 3. Click-evoked potentials measured in an adult female killer whale ("Skyla") while she rested at the side of the pool; clicks were presented across a range of amplitudes (SPL$_{ppe}$), which are located to the right and above each AEP waveform. Multiple waveforms represent the repeated AEP measurements collected at the same click level.

paste. The potential difference between the invert-ing and non-inverting electrodes was amplified (94 dB) and bandpass filtered (100 Hz to 1 kHz) with a biopotential amplifier (ICP511; Grass Technologies, Rockland, MA, USA) before being digitized using a multifunction data acquisition card (NI PCI-6251) and stored on a laptop com-puter. Evoked responses were digitized at a rate of 20 kHz with 16-bit resolution over a 30-ms sweep duration. The differential electrode signal was syn-chronously averaged using a weighted averag-ing method (Elberling & Wahlgreen, 1985), with a total of 1,024 epochs contained in each grand average. During the measurements, the pumps of the filtration system were switched off to reduce the ambient noise in the pools and to eliminate electrical artifacts in the AEP measurements.
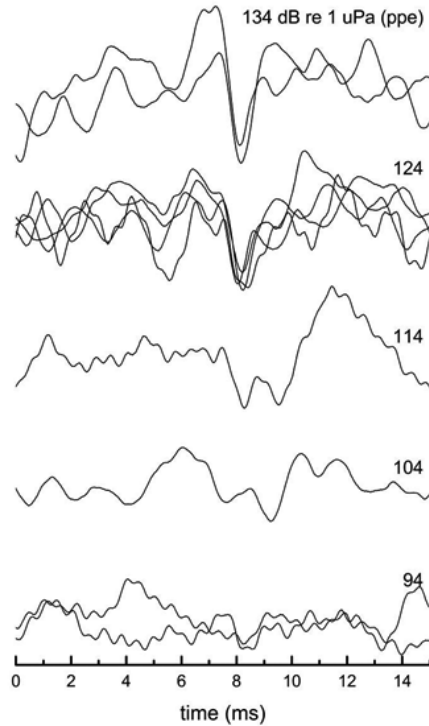
Results

The click-evoked auditory brainstem response (ABR) for the largest animal ("Keto") during ses-sions in which he rested at the surface near the side of the pool are shown in Figure 2. The peaks of the click-evoked ABR were labelled accord-ing to the nomenclature presented by Szymanski et al. (1998). At the maximum click level pro-duced (134 dB re 1 µPa peak-to-peak equivalent sound pressure level [SPL$_{ppe}$]), the peak-to-peak amplitudes of the evoked response were greater than 500 nV. The amplitude of the AEP declined with decreasing stimulus level and is not observed at 94 dB re 1 µPa SPL$_{ppe}$. Figure 3 shows a simi-lar series for the smaller female killer whale "Skyla." The AEP amplitude was slightly larger than that of Keto for the same stimulus level. In some instances, only a single AEP measurement at a particular click level was conducted for Skyla;
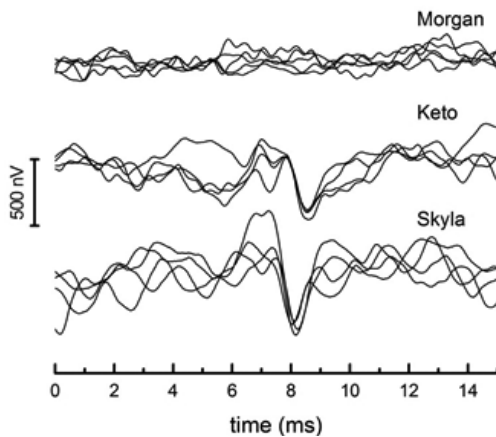
Figure 4. Click-evoked potentials measured in three killer whales while resting at the side of the pool; click levels were 134 dB SPL$_{ppe}$ for all of the whales. No click-evoked response was observed in Morgan. Multiple waveforms represent repeated measurements of the same subject under constant measurement conditions.
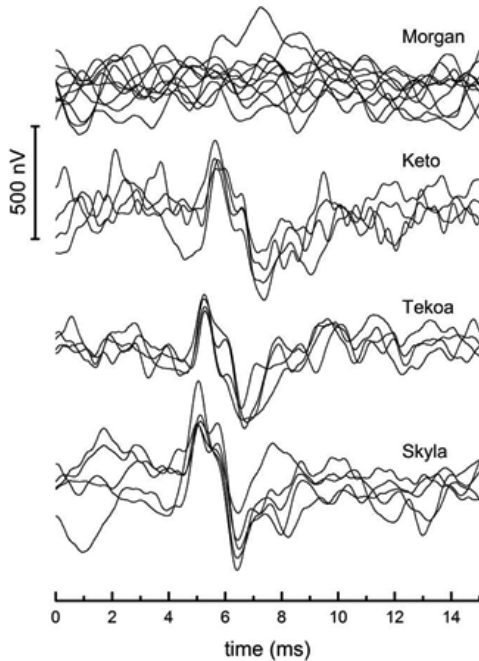

Figure 5. Waveforms showing the click-evoked potentials measured in four killer whales that voluntarily beached themselves for testing. The maximum possible click level was used for Morgan, Keto, and Tekoa; click levels for Skyla were 10 dB lower. Multiple waveforms represent repeated measurements in the same subject under constant measurement conditions. Note that no click-evoked AEP is observed in the killer whale Morgan.

however, the trend of decreasing AEP amplitude with click level remained apparent.

Figure 4 compares the AEP produced in response to a click stimulus across three different whales. The click stimulus was approximately 134 dB SPL$_{ppe}$ for Morgan, Keto, and Skyla. Of considerable note is the fact that no click-evoked AEP was found in Morgan, even though it would be reasonably expected that the click-evoked response would occur as was observed in the larger and older animals. Figure 5 shows a similar comparison for animals that were tested while voluntarily beaching themselves out of the water. This test condition provided the greatest signal-to-noise ratio for the AEPs, yet no click-evoked AEP was observed in Morgan for the highest click level tested. Click-evoked responses were observed in each of the other killer whales tested using the same or lower click levels.

The ambient noise pressure spectral density of the main pool with the music turned off and on is shown in Figure 6. For comparison, typical sound levels of ocean background noises at different frequencies, adapted from Wenz (1962) and National Research Council (NRC) (2003), are shown.

The click-evoked I/O function for Keto (peak-to-peak amplitude of the P II wave, raw AEP data shown in Figure 2) is shown in Figure 7. The
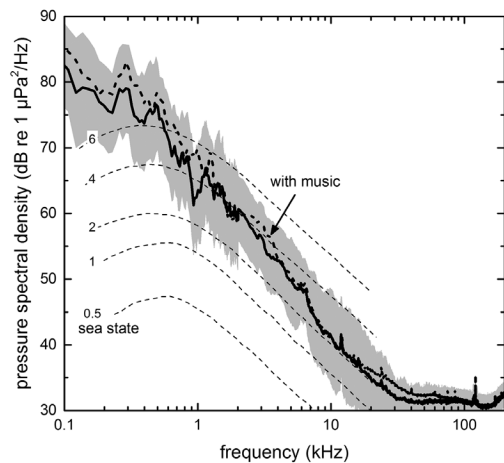

Figure 6. Ambient noise pressure spectral density of the main pool. The thick solid line shows the mean pressure spectral density with the music of the facility turned off, the gray region shows the mean noise spectral density +/- SD with the music turned off, and the thick dashed line shows the mean noise spectral density with music turned on. Ambient noise measurements did not significantly vary at different sites within the facility. The thin dashed lines show the typical sound levels of ocean background noises at different frequencies (adapted from Wenz, 1962, and NRC, 2003).
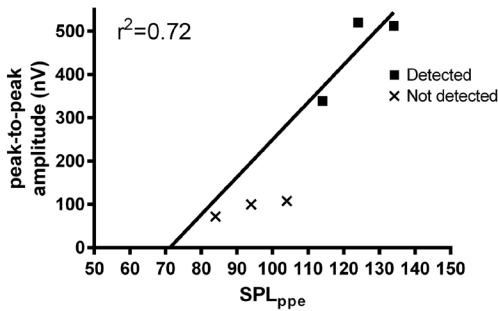
Figure 7. The click-evoked input/output (I/O) function for Keto (raw AEP data shown in Figure 2). Data show the peak-to-peak amplitude of the P II wave. The regression line is extrapolated to the 0-crossing to obtain a threshold consistent with the approach used by Szymanski et al. (1999).

regression line is extrapolated to the 0-crossing to obtain a threshold consistent with the approach used by Szymanski et al. (1999).

Discussion

The click-evoked AEPs measured in most of the killer whales resemble the expected pattern of evoked responses to clicks and tone bursts previously reported for this species and, for in-air measurements conducted herein, using the same transducer (ITC 1042) for signal transmission (Szymanski et al., 1998, 1999). The lack of a click-evoked response in Morgan attests to the fact that this animal suffers from a hearing deficit. The magnitude and frequency range of the hearing deficit cannot be specified with the techniques used herein as the click stimulus lacks the necessary frequency specificity. Nevertheless, it can be concluded based upon the recording of click-evoked responses at varying click levels in other killer whales that Morgan's hearing ability within the frequency bandwidth of the click stimulus is at least 20 to 30 dB worse than the hearing sensitivity of the other killer whales tested. To determine the exact frequency range and magnitude of hearing loss, the use of more frequency-specific stimuli would be required. The failure to observe a click-evoked AEP is consistent with behavioral observations indicating that Morgan does not react to purely acoustic cues. Only when paired with visual cues by the trainers or visually observable movements of other animals would Morgan reliably show a behavioral reaction.

The specific cause of Morgan's hearing impairment is unknown. However, acoustic recordings made to characterize the ambient noise levels in the pools at Loro Parque indicate that noise at

the facility can be ruled out as a potential cause for her hearing impairment (Figure 6). The sound levels measured under water were only slightly elevated during shows. Moreover, AEP measurements in the other killer whales, which have been held in this facility and have been participating in shows for years, did not indicate hearing impairment. There is no indication of any antibiotic use that could have contributed to ototoxicity while at Loro Parque or during the rehabilitation as has been speculated in other odontocetes with profound hearing loss (Finneran et al., 2005). Thus, it is reasonable to conclude that Morgan's hearing impairment occurred prior to her arrival at Loro Parque. However, it can only be speculated at which point in life Morgan developed the hearing impairment; it might be congenital, could have been acquired as a juvenile, or may have occurred at any other point prior to her stranding (Ridgway & Carder, 1997; André et al., 2003; Mann et al., 2010; Wright, 2011).

Usually, killer whale society is based on matrilineal descent where close and prolonged associations of mothers and offspring are commonly seen (Ford, 2009). A solitary female killer whale in the southern North Sea is, therefore, surprising and gives rise to the speculation that Morgan's hearing deficit might have caused her separation from a social group. The inability to perceive acoustic cues might also have contributed to her emaciated state when she stranded as a significant loss in hearing could detrimentally affect foraging success by limiting echolocation capabilities. Accumulating evidence suggests that hearing loss is not atypical in odontocetes and that stranding has co-occurred with hearing loss in a number of stranding cases (Mann et al., 2010; Schlundt et al., 2011). In each of the cases where rehabilitation was attempted, the presence of significant hearing deficits has been a critical piece of information in determining whether animals should be released back to the wild.

The latency and relative amplitude of peaks P II, P III, and N IV can be observed in the click-evoked AEP records obtained from Skyla and Keto for received levels ranging from 104 to 134 dB SPL$_{ppe}$. The magnitude and latencies of the click-evoked AEP are similar to what has been previously reported (Szymanski et al., 1995, 1998). Below 104 dB SPL$_{ppe}$, the responses are either non-existent, masked by biological noise (e.g., myogenic noise), or lost due to attenuation of the signal as it travels to the skin surface. The dimensions of the killer whale head make it impossible, at least in adult animals, to record ABRs close to the signal generator as the distance between the recording location and dipole source is directly related to the attenuation of the far field potential

(Supin et al., 2001). This finding, which is related to the brain-to-body mass ratio, is consistent with both the amplitude and latencies of click-evoked responses in other odontocete species of varying size (Popov & Supin, 1990a, 1990b; Finneran et al., 2009; Schlundt et al., 2011).

Prior work by Szymanski et al. (1998) showed that ~100 µs clicks presented at comparable stimulus amplitudes typically produced click-evoked AEP peak-to-peak amplitudes < 1 µV. This is comparable to the average peak-to-peak AEP amplitudes of 512 nV for Keto and 740 nV for Skyla obtained under similar test conditions in this study (Figures 2 & 3). However, later work by Szymanski and colleagues (1999) utilized tone pips to estimate frequency-specific thresholds in two killer whales. The AEP thresholds were reported to be comparable to, and sometimes lower than, behavioral thresholds measured in the same animals, with AEP thresholds as low as 37 dB re 1 µPa SPL$_{ppe}$. This result contrasts sharply with results reported herein in which quality AEPs could not be obtained at higher SPLs using click stimuli, which are expected to produce more robust AEPs compared to tone pips of equivalent SPL. The noise floor between the Szymanski et al. (1999) study and this study are comparable, but performing the same regression procedure as Szymanski et al. with click-evoked AEPs produces a threshold of ~72 dB SPL$_{ppe}$ (Figure 7), which is 35 dB higher than the lowest threshold estimated by Szymanski et al. That Szymanski et al. were able to obtain AEP thresholds at levels comparable to or below behavioral thresholds in such large animals, which have a relatively small brain-to-body mass ratio for odontocetes, is counter to expectation since AEP thresholds are typically higher than behavioral thresholds even in the smaller odontocetes for which the brain-to-body mass is much more favorable (Yuen et al., 2005; Finneran & Houser, 2006; Houser & Finneran, 2006a).

The exact reasons for the discrepancy between the present results and those of Szymanski et al. (1999) are unknown; however, close inspection of the previously published data (Szymanski et al., 1996, 1998, 1999) reveals a number of potential issues. First, the input/output (I/O) functions utilized for linear extrapolation to threshold values are nonmonotonic (see Szymanski et al., 1999, Figure 4). They show considerable variability and deviate from the types of I/O functions typically observed for odontocete-evoked potential audiometry using various stimulus types (Popov & Supin, 1987, 1990a; Finneran et al., 2005; Nachtigall et al., 2005, 2007; Yuen et al., 2005). Second, the range of stimulus peak-to-peak SPLs reported for the tone bursts used by Szymanski et al. (1999) was from 10 to 150 dB re 1 µPa. It is not clear how this dynamic range was achieved given the transmitting voltage responses of the various projectors since there is no mention of a hardware attenuator and the D/A converters possessed only 12-bit resolution. Finally, the ability to obtain evoked responses from an adult killer whale at tone burst levels < 60 dB re 1 µPa peak-to-peak seems unlikely due to the size of the subject. As a rule, even though odontocetes possess a favorable brain-to-body mass ratio, the evoked response must travel a greater distance to the surface of an animal as it gets larger in size. In odontocetes, this is compounded by an increasing blubber depth with an increase in the overall size of the killer whale. Blubber is a poor conductor of electricity, and an increase in blubber depth should enhance the attenuation of the evoked responses measured in the far field. Thus, significant questions exist regarding the AEP threshold estimates in killer whales using tone burst stimuli, and additional work should be conducted to replicate the studies of Szymanski et al. (1999). Audiometric testing should be performed in other killer whales so that comparisons between individuals can be made and an estimate of the variability in the hearing sensitivity of this species determined. Both psychoacoustic and electrophysiological approaches should be undertaken to address both the small sample size currently available for killer whales (Hall & Johnson, 1972; Szymanski et al., 1999) and the discrepancies in the compared results of the two methods reported to date.

Conclusions

The lack of a click-evoked response in Morgan indicates that she suffers from a hearing deficit. To date, it can be concluded that her hearing ability is at least 20 to 30 dB worse than the hearing sensitivity of the other killer whales tested in the same facility. Psychophysical procedures may be useful in quantifying her hearing deficit, provided she is not completely deaf. Although AEP measurements allow a rapid assessment of hearing capabilities due to the size-dependent loss of the electrophysiological signal in large mammals, hearing thresholds at any particular frequency are unlikely to be quickly obtained with current AEP methods. Continued exploration of AEP methods and hardware development is required to determine what sorts of modifications are needed to better record evoked responses from large mammals without significant loss of the AEP to distance attenuation.

Acknowledgments

Literature Cited

André, M., Supin, A., Delory, E., Kamminga, C., Degollada, E., & Alonso, J. M. (2003). Evidence of deafness in a striped dolphin, *Stenella coeruleoalba*. *Aquatic Mammals*, *29*(1), 3-8.

Barrett-Lennard, L. G., Ford, J. K. B., & Heise, K. (1996). The mixed blessing of echolocation: Differences in sonar use by fish-eating and mammal-eating killer whales. *Animal Behaviour*, *51*, 553-565. http://dx.doi.org/10.1006/anbe.1996.0059

Brill, R. L. (1991). The effects of attenuating returning echolocation signals at the lower jaw of a dolphin (*Tursiops truncatus*). *The Journal of the Acoustical Society of America*, *89*, 2851-2857. http://dx.doi.org/10.1121/1.400723

Cook, M. L. H., Verela, R. A., Goldstein, J. D., McCulloch, S. D., Bossart, G. D., Finneran, J. J., . . . Mann, D. A. (2006). Beaked whale auditory evoked potential hearing measurements. *Journal of Comparative Physiology A*, *192*, 489-495. http://dx.doi.org/10.1007/s00359-005-0086-1

Diercks, K. J., Trochta, R. T., Greenlaw, C. F., & Evans, W. E. (1971). Recording and analysis of dolphin echolocation signals. *The Journal of the Acoustical Society of America*, *49*, 1729-1732. http://dx.doi.org/10.1121/1.1912569

Duffield, D. A., & Miller, K. W. (1988). Demographic features of killer whales in oceanaria in the United States and Canada 1965-1987. *Rit Fiskideildar*, *11*, 297-306.

Elberling, C., & Wahlgreen, O. (1985). Estimation of auditory brainstem response, ABR, by means of Bayesian inference. *Scandinavian Audiology*, *14*, 89-96. http://dx.doi.org/10.3109/01050398509045928

Finneran, J. J. (2009). Evoked response study tool: A portable, rugged system for single and multiple auditory evoked potential measurements. *The Journal of the Acoustical Society of America*, *126*, 491-500. http://dx.doi.org/10.1121/1.3148214

Finneran, J. J., & Houser, D. S. (2006). Comparison of in-air evoked potential and underwater behavioral hearing thresholds in four bottlenose dolphins (*Tursiops truncatus*). *The Journal of the Acoustical Society of America*, *119*, 3181-3192. http://dx.doi.org/10.1121/1.2180208

Finneran, J. J., Houser, D. S., Mase-Guthrie, B., Ewing, R. Y., & Lingenfelser, R. G. (2009). Auditory evoked potentials in a stranded Gervais' beaked whale (*Mesoplodon europaeus*). *The Journal of the Acoustical Society of America*, *126*, 484-490. http://dx.doi.org/10.1121/1.3133241

Finneran, J. J., Dear, R., Carder, D. A., Belting, T., McBain, J., Dalton, L., & Ridgway, S. H. (2005). Pure tone audiograms and possible aminoglycoside-induced hearing loss in belugas (*Delphinapterus leucas*). *The Journal of the Acoustical Society of America*, *117*, 3936-3943. http://dx.doi.org/10.1121/1.1893354

Ford, J. K. B. (1989). Acoustic behaviour of resident killer whales (*Orcinus orca*) in British Columbia. *Canadian Journal of Zoology*, *67*, 727-745. http://dx.doi.org/10.1139/z89-105

Ford, J. K. B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Canadian Journal of Zoology*, *69*, 1454-1483. http://dx.doi.org/10.1139/z91-206

Ford, J. K. B. (2009). Killer whale – *Orcinus orca*. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 650-657). San Diego: Elsevier Academic Press. http://dx.doi.org/10.1016/B978-0-12-373553-9.00150-4

Hall, J. D., & Johnson, C. S., (1972). Auditory thresholds of a killer whale *Orcinus orca* Linnaeus. *The Journal of the Acoustical Society of America*, *51*, 515-517. http://dx.doi.org/10.1121/1.1912871

Houser, D. S., & Finneran, J. J. (2006a). A comparison of underwater hearing sensitivity in bottlenose dolphins (*Tursiops truncatus*) determined by electrophysiological and behavioral methods. *The Journal of the Acoustical Society of America*, *120*, 1713-1722. http://dx.doi.org/10.1121/1.2229286

Houser, D. S., & Finneran, J. J. (2006b). Variation in the hearing sensitivity of a dolphin population obtained through the use of evoked potential audiometry. *The Journal of the Acoustical Society of America*, *120*, 4090-4099. http://dx.doi.org/10.1121/1.2357993

Houser, D. S., Gomez-Rubio, A., & Finneran, J. J. (2008). Evoked potential audiometry of 13 Pacific bottlenose dolphins (*Tursiops truncatus gilli*). *Marine Mammal Science*, *24*(1), 28-41. http://dx.doi.org/10.1111/j.1748-7692.2007.00148.x

Kilkenny, C., Browne, W. J., Cuthill, I. C., Emerson, M., & Altman, D. G. (2010). Improving bioscience research reporting: The ARRIVE guidelines for reporting animal research. *PLOS Biology*, *8*(6), e1000412. http://dx.doi.org/10.1371/journal.pbio.1000412

Mann, D., Hill-Cook, M., Manire, C., Greenhow, D., Montie, E., Powell, J., . . . Hoetjes, P. (2010). Hearing loss

in stranded odontocete dolphins and whales. *PLOS ONE*, *5*, 1-5. http://dx.doi.org/10.1371/journal.pone.0013824

Møhl, B., Au, W. W. L., Pawlowski, J., & Nachtigall, P. E. (1999). Dolphin hearing: Relative sensitivity as a function of point of application of a contact sound source in the jaw and head region. *The Journal of the Acoustical Society of America*, *105*, 3421-3424. http://dx.doi.org/10.1121/1.426959

Mooney, T. A., Nachtigall, P. E., Castellote, M., Taylor, K. A., Pacini, A. F., & Esteban, J-A. (2008). Hearing pathways and directional sensitivity of the beluga whale, *Delphinapterus leucas*. *Journal of Experimental Marine Biology and Ecology*, *362*, 108-116. http://dx.doi.org/10.1016/j.jembe.2008.06.004

Nachtigall, P. E., Mooney, T. A., Taylor, K. A., & Yuen, M. M. L. (2007). Hearing and auditory evoked potential methods applied to odontocete cetaceans. *Aquatic Mammals*, *33*(1), 6-13. http://dx.doi.org/10.1578/AM.33.1.2007.6

Nachtigall, P. E., Yuen, M. M. L., Mooney, T. A., & Taylor, K. A. (2005). Hearing measurements from a stranded infant Risso's dolphin, *Grampus griseus*. *Journal of Experimental Biology*, *208*, 4181-4188. http://dx.doi.org/10.1242/jeb.01876

National Research Council (NRC). (2003). *Ocean noise and marine mammals*. Washington, DC: National Academies Press. 219 pp.

Popov, V. V., & Supin, A. Ya. (1987). Characteristics of hearing in the beluga *Delphinapterus leucas*. *Doklady Akademii Nauk SSSR*, *2945*, 1255-1258.

Popov, V. V., & Supin, A. Ya. (1990a). Electrophysiological studies of hearing in some cetaceans and a manatee. In J. A. Thomas & R. A. Kastelein (Eds.), *Sensory abilities in cetaceans* (pp. 405-415). New York: Plenum Press. http://dx.doi.org/10.1007/978-1-4899-0858-2_27

Popov, V. V., & Supin, A. Ya. (1990b). Auditory brainstem responses in characterization of dolphin hearing. *Journal of Comparative Physiology A*, *166*, 385-393. http://dx.doi.org/10.1007/BF00204811

Ridgway, S. H., & Carder, D. A. (1997). Hearing deficits measured in some *Tursiops truncatus*, and discovery of a deaf/mute dolphin. *The Journal of the Acoustical Society of America*, *101*(1), 590-594. http://dx.doi.org/10.1121/1.418122

Schlundt, C. E., Dear, R. L., Houser, D. S., Bowles, A. E., Reidarson, T., & Finneran, J. J. (2011). Auditory evoked potentials in two short-finned pilot whales (*Globicephala macrorhynchus*). *The Journal of the Acoustical Society of America*, *129*, 1111-1116. http://dx.doi.org/10.1121/1.3531875

Supin, A. Ya., Popov, V. V., & Mass, A. M. (2001). *The sensory physiology of aquatic mammals*. Boston: Kluwer Academic Publishers. http://dx.doi.org/10.1007/978-1-4615-1647-7

Szymanski, M. D. (1996). *Auditory evoked potentials of killer whales (*Orcinus orca*)* (Unpublished doctoral dissertation). University of California, Davis.

Szymanski, M. D., Bain, D. E., & Henry, K. R. (1995). Auditory evoked potentials of a killer whale (*Orcinus orca*). In R. A. Kastelein, J. A. Thomas, & P. E. Nachtigall (Eds.), *Sensory systems of aquatic mammals* (pp. 1-10). Woerden, the Netherlands: De Spil Publishers.

Szymanski, M. D., Supin, A. Ya., Bain, D. E., & Henry, K. R. (1998). Killer whales (*Orcinus orca*) auditory evoked potentials to rhythmic clicks. *Marine Mammal Science*, *14*, 676-691 http://dx.doi.org/10.1111/j.1748-7692.1998.tb00756.x.

Szymanski, M. D., Bain, D. E., Kiehl, K., Pennington, S., Wong, S., & Henry, K. R. (1999). Killer whale (*Orcinus orca*) hearing: Auditory brainstem response and behavioral audiograms. *The Journal of the Acoustical Society of America*, *106*, 1134-1141. http://dx.doi.org/10.1121/1.427121

Trouwborst, A., Caddell, R., & Couzens, E. (2013). To free or not to free? State obligations and the rescue and release of marine mammals: A case study of "Morgan the orca." *Transnational Environmental Law*, *2*, 117-144. http://dx.doi.org/10.1017/S2047102512000222

Wenz, G. M. (1962). Acoustic ambient noise in the ocean: Spectra and sources. *The Journal of the Acoustical Society of America*, *34*, 1936-1956. http://dx.doi.org/10.1121/1.1909155

Wright, K. A. (2011). Decreased ability to acquire food of a captive deaf dolphin (*Tursiops truncatus*): Slower reaction times and lower success rates. *Studies by Undergraduate Researchers at Guelph*, *4*, 63-70.

Yuen, M. M. L., Nachtigall, P. E., Breese, M., & Supin, A. Ya. (2005). Behavioral and auditory evoked potential audiograms of a false killer whale (*Pseudorca crassidens*). *The Journal of the Acoustical Society of America*, *118*, 2688-2695. http://dx.doi.org/10.1121/1.2010350