

Review

A false killer whale adjusts its hearing when it echolocates

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Accepted 31 January 2008

Summary

The use of auditory evoked potential (AEP) measurements has added considerably to knowledge of the hearing mechanisms of marine mammals. We have recently measured the hearing of a stranded infant Risso's dolphin, the audiograms of white-beaked dolphins temporarily caught and released, and the hearing of anaesthetized polar bears. Most small toothed whales echolocate and hear very high frequency sounds underwater. While much has previously been learned about the echolocation performance and characteristics of the outgoing signals of echolocating dolphins and small whales, the hearing processes occurring while these animals actively echolocate have not previously been examined. Working with a well-trained echolocating false killer whale (*Pseudorca crassidens*) wearing latex surface suction cup electrodes, we have measured echolocation hearing AEPs in response to outgoing echolocation clicks, returning echoes, and comparable simulated whale clicks and echoes in a variety of situations. We have found that: (1) the whale may hear her loud outgoing clicks and much quieter returning echoes at comparable levels, (2) the whale has protective mechanisms that dampen the intensity of her outgoing signals – she hears her outgoing signals at a level about 40dB lower than similar signals presented directly in front of her, (3) when echo return levels are lowered either by making the targets smaller or by placing the targets farther away – without changing the levels of her outgoing signals – the hearing of these echoes remains at almost the same level, (4) if targets are made much smaller and harder to echolocate, the animal will modify what she hears of her outgoing signal – as if to heighten overall hearing sensitivity to keep the echo level hearable, (5) the animal has an active 'automatic gain control' mechanism in her hearing based on both forward masking that balances outgoing pulse intensity and time between pulse and echo, and active hearing control. Overall, hearing during echolocation appears to be a very active process.

Introduction

While there were proponents of the direct comparison of electrophysiological and behaviourally obtained psychophysical (Stevens, 1970) sensory thresholds, only recently, due to the expense, time and difficulty of obtaining experimental subjects, has the use of auditory evoked potential (AEP) threshold measurement in dolphins and whales been emphasized and shown to be directly comparable to behaviourally obtained audiometrics (Yuen et al., 2005; Houser and Finneran, 2006). The direct comparison of physiological and behavioural measurements was made possible through the use of the envelope following response method of obtaining toothed whale hearing thresholds. The toothed whales and dolphins appear especially adapted for following fast changing sounds, as observed with modulation rate measurements, and this makes the technique particularly useful for odontocetes (Dolphin et al., 1995; Supin and Popov, 1995; Mooney et al., 2006). Thresholds can be obtained by modulating the carrier frequency of interest at rates near one-thousand times per second, transforming the responses to various carrier frequency levels *via* fast Fourier transforms, performing a linear regression on the peaks, and determining thresholds where the regression line crosses zero (Nachtigall et al., 2007a).

The use of AEP has allowed a rapid increase in data on marine mammal hearing. Rather than having to rely on a single animal's audiogram to represent the species, there are now good measurements of population variability in the audiograms of

bottlenosed dolphins (Popov et al., 2007) from newly captured groups. There have been attempts to obtain measurements from grey whales (Ridgway and Carder, 2001), sperm whales (Ridgway and Carder, 2001; Nachtigall et al., 2007) and beaked whales (Cook et al., 2006). The hearing of an infant stranded Risso's dolphin has been measured (Nachtigall et al., 2005). The AEP measurement in response to tone pips has been used to examine the hearing of anaesthetized polar bears (Nachtigall et al., 2007b).

Generally, as well as being able to follow modulated sound very fast, the dolphins and small toothed whales hear very high frequency sound under water (Johnson, 1966; Nachtigall et al., 2000). High frequency hearing appears to have evolved along with the ability to echolocate. Echolocation involves the ability to send signals and listen for the returning echoes from the environment. While there has been a good amount published on the characteristics of the outgoing signals of odontocetes (Nachtigall and Moore, 1988; Au, 1993; Thomas et al., 2004), the direct measurement of odontocete hearing during actual echolocation required the development of a technique to measure the AEPs in response to both the outgoing clicks and the returning echoes during an active echolocation task (Supin et al., 2003). This ability to measure what a whale hears of its outgoing echolocation click and its returning echoes has allowed the opportunity to ask very basic questions about odontocete echolocation.

The basic experimental method

Investigation of hearing during echolocation requires that an active echolocation task be underway. An over 20 year old, 523 kg, false killer whale *Pseudorca crassidens* (Owen 1846) was taught to wear rubber suction cup skin surface electrodes, swim into a stationing hoop 1 m underwater, echolocate, and report the presence or absence of a 12.7 cm long, 3.8 cm diameter hollow aluminium cylinder by pressing a response ball. The whale was 97% correct on the task with 70 target absent and 147 target present trials (Supin et al., 2003). Thus we were able to record AEP responses to both outgoing echolocation clicks and responses to echoes during a functional echolocation task.

As can be seen in Fig. 1, AEPs (auditory brainstem responses, ABRs) were picked up keyed from the individual outgoing echolocation clicks. The outgoing click triggered the opening of a 10 ms window (sweep) of evoked potential recording. ABRs were found at the exact time predicted for the arrival of the click at the animal's ears and at the exact time expected for the echo to arrive as well (when the 5 ms time lag of the neural system is taken into account). Perhaps the most interesting finding of this initial experiment (Supin et al., 2003) was that the ABR responses to the emitted click and the echo were of comparable amplitude in spite of the intensity difference between these two sounds. So the whale heard its outgoing click and the much quieter returning echo at about the same level even though the click (in front of the animal's head) was probably 40 dB louder than the returning echo. There are a number of potential explanations for why an animal might hear these two sounds at different levels but the most straightforward is that there are protective mechanisms that keep the whale from hearing her very loud outgoing clicks at full strength.

Forward masking?

If a rifle were to be fired next to your ear it would take a while for your hearing to recover. You would be forward masked by the noise from the rifle so that quiet sounds like echoes would be hard to hear immediately. The source levels of sperm whale clicks (Møhl et al., 2003) can exceed 235 dB re. 1 μ Pa (peak to peak, p/p) having the same intensity as the sound produced by a powerful rifle shot 0.05 m away from your ear. Bottlenosed dolphins produce intense echolocation clicks exceeding 227 dB re. 1 μ Pa (p/p) (Au, 1980) and wild false killer whales have similarly demonstrated clicks with source levels reaching 225 dB re. 1 μ Pa (p/p) (Madsen et al., 2004). This high power of odontocete clicks has been proposed by some to stun prey (Norris and Møhl, 1983). When echolocation was first discovered in bats, the loud sounds that they produced caused many to wonder whether echolocation was possible based on the belief that the hearing of echoes might be impossible because of the loud outgoing signals (Kick and Simmons, 1984). Echolocation was of course proven (Griffin, 1958) and a mechanism for direct neural stimulation of the stapedial muscles of the middle ear to inhibit hearing during vocalization was demonstrated (Suga and Jen, 1975). An obvious question arises as to whether the echolocating whale has a similar protective mechanism.

Given that invasive investigations are not feasible while working with whales and dolphins, if one can measure hearing during echolocation, one of the first questions to be asked about the effects of short, loud echolocation sounds on a whale is: does a whale hear outgoing signals at the same level as similar signals presented directly in front of it? If there were no protective mechanisms, the whale should hear its own signals at the same level as those presented. If there are protective mechanisms then its own signals should be heard at a much lower level. Supin et al. (Supin et al.,

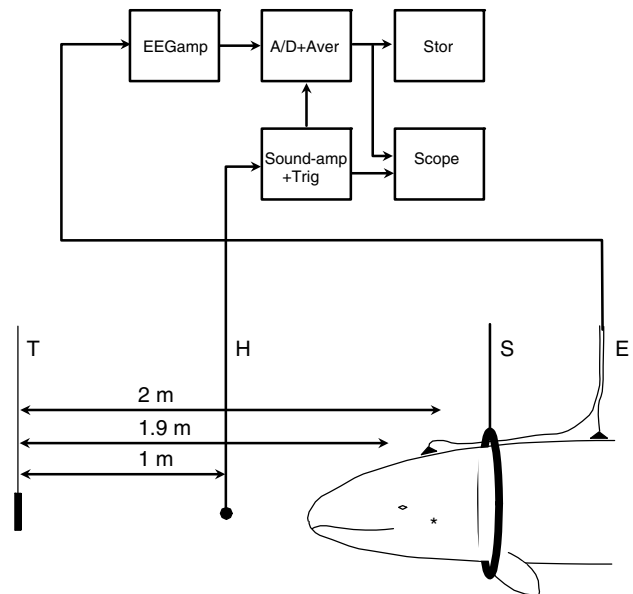


Fig. 1. Relative positions of the animal and equipment during experiments and block diagram of data acquisition during echolocation trials. T, target; H, hydrophone; S, hoop station; E, electrodes; EEGamp, EEG amplifier; A/D+Aver, analog-to-digital converter and averager; Store, data storage; Sound-amp+Trig, sound amplifier and trigger; and Scope, monitoring oscilloscope. Distance from target to the animal's ears (*), 2.0 m; distance to the expected sound-production region, 1.9 m; distance to the triggering hydrophone, 1 m.

2006) tested the hearing of the false killer whale in these two situations: (1) to her own outgoing clicks while she was actually echolocating one of two aluminium cylinders presented 3 m away, and (2) to simulated false killer whale clicks presented directly in front of her at a variety of levels comparable to her own clicks. The data in Fig. 2 show that when targets were present, the whale heard her own clicks almost 40 dB less sensitively than she heard simulated false killer whale clicks of equal intensity presented directly in front of her.

So, there obviously is some sort of protective system that allows the whale to hear her outgoing signal but protects her from its full intensity by 40 dB. The nature of this protective system at this general level could be simply from the anatomical structures of the head (Ketten, 2000; Cranford, 2000) due to sound protection and channelling or it could be more complex. A further look at the data presented in Fig. 2 suggests that the protection mechanisms may be more much more complex. Note that there was a large difference in how the whale heard her own outgoing signals depending on whether targets were present or absent. When targets were not presented the animal heard her own clicks about 15 dB better than when targets were there. It would appear that the whale's hearing was changed by whether or not targets were present.

Varying intensity and time of target echoes

In our first experiment (Supin et al., 2003), there was an initial lack of difference between the whale's hearing of outgoing clicks and much quieter echoes and so the question arose as to whether echoes from various sized targets at various distances would be heard differently. Large targets nearby produce intense echoes while small targets farther away produce much less intense echoes. Once again the whale was presented with the standard task of echolocating and indicating whether or not cylinders were present.

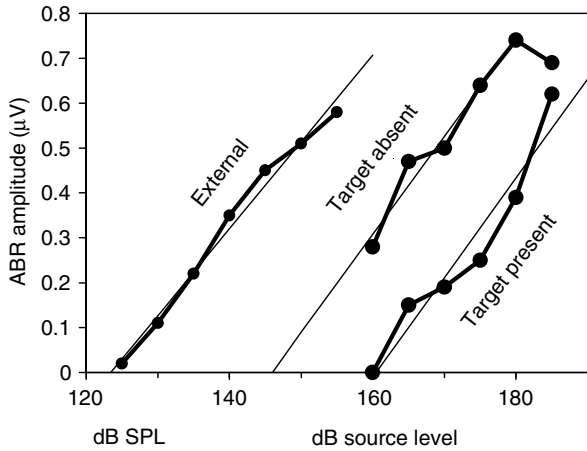


Fig. 2. Thresholds for passive false killer whale-like clicks presented 2 m in front of the whale (specified in sound-pressure level, SPL) and thresholds for clicks produced by the whale (specified in source level). Note that (with targets present) the whale is about 40 dB less sensitive to clicks that it produces as compared with passively presented clicks. ABR, auditory brainstem response.

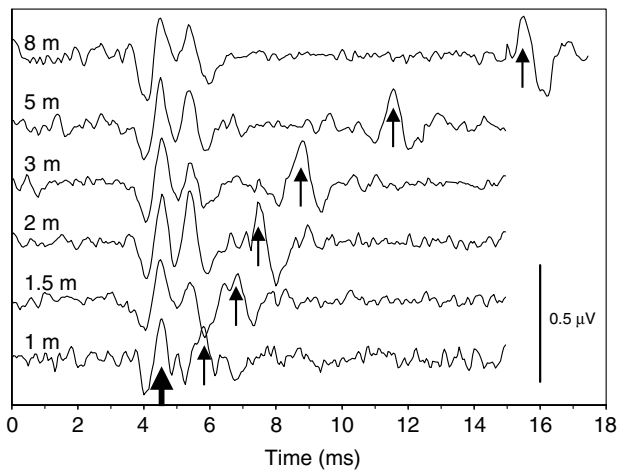


Fig. 3. Averaged auditory evoked potential (AEP) records. Echolocation-related evoked potential records at target distances of 1, 1.5, 2, 3, 5 and 8 m. The initial bold arrow marks the outgoing pulse-related ABR while other arrows indicate the echo-related ABRs. The active electrode negativity is upward.

Echoes and AEPs were recorded. Targets were presented at distances from the animal varying from 1 to 8 m. Fig. 3 shows the actual averaged brain response records from the whale. The first response at a standard lag between 4 and 6 ms is the whale's response to her outgoing click. The second response in each line that is shown to vary with increasing distance (and therefore time because the sound takes more time to go from the animal to the target and return) is the response to the echo from the cylinder. These results indicate that the size of the AEPs relating to the echoes (although perhaps very slightly less than the AEPs to the outgoing clicks) was nevertheless very comparable in amplitude to AEPs produced in response to the much more intense outgoing clicks. Secondly, even though there was a 36 dB physical difference in the echo returns between this target at 1 m as compared with 8 m, there was almost no difference in the size of the echo ABR responses. The animal heard the signals at the same level even

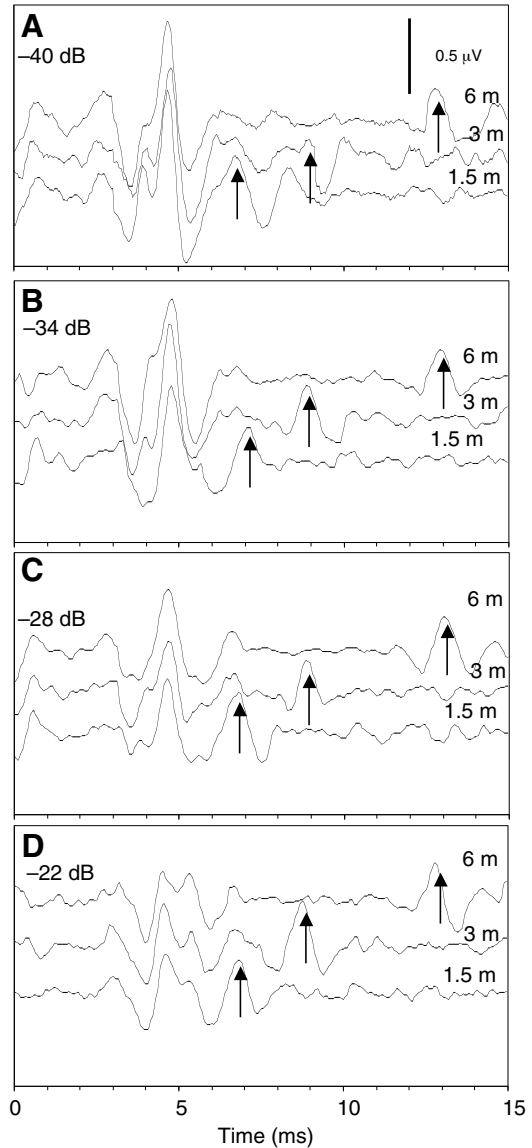


Fig. 4. Echolocation-related AEPs recorded at different target strengths (-40 to -22 dB, as designated in panels A-D) and different target distances (1.5, 3 and 6 m) as indicated on the records in each panel. The arrows indicate the AEP complex as echo related.

though there was a 36 dB difference. It is important to note that the intensity of the animal's outgoing signals barely changed at all.

The echoes from 1 m and those from 8 m were certainly different in intensity but they also varied in time. While the animal's hearing may have been somewhat protected, the outgoing pulses were still probably very intense sounds. Given the short interval between the outgoing signal and the returning echo, the whale would have been forward masked by the outgoing signal. Any intense sound (remember the rifle shot analogy) temporarily reduces the hearing of following sounds for a short time. Popov and Supin (Popov and Supin, 1990), and Supin et al. (Supin et al., 2001) showed that short pulses of sound forward mask the hearing of the second sound pulse in bottlenosed dolphins. Both the intensity and the time influence hearing recovery during forward masking. This phenomenon may help to explain the similarity of responses of the ABRs at two distances. Echoes from targets close by may be forward masked by

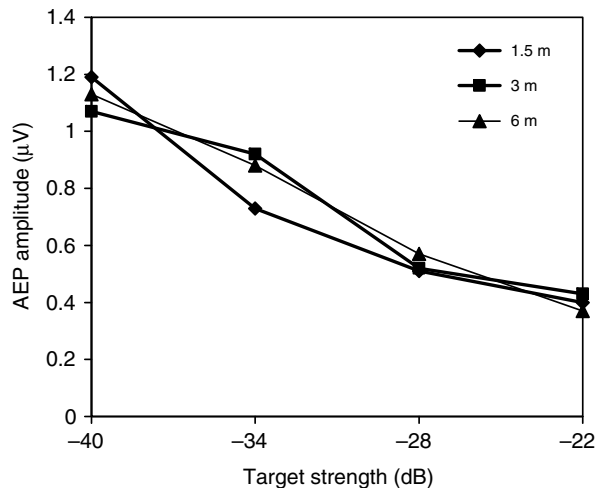


Fig. 5. The AEP related to the outgoing signal is dependent on the target strength (the argument) and distance (the parameter).

the outgoing click. As time passes and the hearing system recovers, target echoes from farther away may no longer be forward masked as a gradual recovery occurs across the milliseconds. Or, when the distance, for example, increases the echo intensity decreases, but the echo response releases from masking to a greater extent due to a longer delay. So these two processes (echo attenuation and recovery) may compensate one another because of similar intensity-to-distance and recovery-to-delay ratios. The same sorts of forward masking data previously shown in the bottlenosed dolphin were recently verified in this false killer whale (Supin et al., 2007)

Other automatic gain control processes

While forward masking may assist in explaining the fact that the echo response is independent of distance, it does not explain the earlier finding that the whale heard outgoing clicks differently in target-present and target-absent situations. Many electronic sonars implement automatic gain control to keep the signal levels within a reasonable range, and while we have measured, but never found, substantial differences in the outgoing signal levels of our false killer whale in the tasks we have completed (for details, see Supin et al., 2004; Supin et al., 2005; Supin et al., 2006), other investigators examining data from odontocetes echolocating at greater ranges in the wild indicate that the animals increase the intensity of their echolocation pulses with target distance (Rasmussen et al., 2002; Au and Benoit-Bird, 2003). Obviously, increasing the intensity of the outgoing pulse for short range targets like those used in the false killer whale experiments presented here would tend to increase the forward-masking effect and thus not benefit the animal in an attempt to hear quieter echoes, unless perhaps, like bats (Kick and Simmons, 1984; Suga and Jen, 1975), whale middle ear stapedial muscles received messages directly from their vocalization systems and attenuated the hearing of the outgoing calls at the middle ear.

In a further attempt to broaden the range of intensities of whale echo returns and to examine hearing of both outgoing signals and small echo returns, target cylinders of varying sizes and distances were presented to the echolocating whale (Supin et al., 2005). Cylinders all had the same diameter and wall thickness but were of various heights: 180, 90, 45 and 23 mm with corresponding target strengths of -22 , -28 , -34 and -44 dB. These targets were presented at three distances to further alter the strength of the returning

echoes: 1.5, 3 and 6 m. The averaged AEP brain wave records are presented in Fig. 4. Looking first at the echo returns from targets at the various distances, it can be seen that the whale heard most of the echoes at about the same level. Once again, the size of the AEP response was relatively uniform and independent of distance to the target. The AEP responses to the target echoes were also relatively uniform independent of the size of the target. The smallest target echo AEP response at the greatest distance seen in the top line of Fig. 4D to the right side is at about the same level as the largest target at the closest distance seen in Fig. 4A nearest the click echo. While the hearing of the echoes was measured at a near-constant level, the hearing (not the level) of the outgoing pulse changed dramatically. Despite the fact that there was negligible difference in the amplitude of the outgoing pulses, the hearing of those outgoing pulses changed as the targets changed. The differences in the relative sizes of the AEPs may be seen numerically in Fig. 5. The AEPs to the outgoing pulses at around $1.2\mu\text{V}$ to the smallest targets were three times the size of the AEPs to the largest targets at around $0.4\mu\text{V}$. It would appear as though the whale uses some other sort of automatic gain control process. While bats control the hearing of the outgoing pulse by attenuating the hearing of the call (Suga and Jen, 1975) when the call is made by the vocal apparatus directly stimulating the stapedial muscles to contract and reduce bat hearing during the call, it seems as though a very different process is going on with the whale. The whale's ability to hear the outgoing pulse is modulated by the size of the target echo. If it were like the bat, all outgoing pulses would essentially be heard at about the same level. They would be equally attenuated by the equal outgoing signal level. The whale, however, hears the outgoing pulses at very different levels depending on how large the echo return is. It is almost as if the whale needs to 'open its ears' to keep the echo level high enough to hear it, and when the whale opens its ears, it also must necessarily hear more of the intense outgoing signal. So, in these experiments, when the animal had a very small echolocation target far away, the AEPs to her outgoing signals were as high as $1.2\mu\text{V}$ but when the targets were larger and nearby, giving larger echoes, the hearing of her outgoing signals was lessened to the $0.4\mu\text{V}$ level. It would appear that there is a true automatic gain control of the whale hearing system during echolocation based on the level of echo. The false killer whale adjusts her hearing to keep the echo level in a hearable range.

Although this may be unusual for an auditory system, it makes very good sense in an evolutionary light. Perhaps the principal functions for echolocation are prey detection, classification and localization (Nachtigall, 1980; Schnitzler and Henson, 1980). Information about fish and other prey is represented in echoes to an echolocating odontocete. It makes sense that an auditory system has evolved to adjust to keep these echoes in the range most easily heard.

The authors gratefully acknowledge funding from the US Office of Naval Research and the Russian Ministry of Science and Education. This is contribution 1309 from the Hawaii Institute of Marine Biology. The whale work was completed under a Marine Mammal Permit issued to P.E.N. from the NMFS office of Protected Species with protocols approved by the University of Hawaii Animal Care and Utilization Committee. All figures were previously published in *The Journal of the Acoustical Society of America*, and are used with permission.

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