Testing Hearing in Baleen Whales

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Despite increasing evidence that underwater anthropogenic noise has negative consequences on baleen whale hearing and behaviour, currently there are no direct data available on mysticete hearing in noise. Baleen whale hearing sensitivity can be assessed in several ways: (1) assessment of the frequency of their vocalisations; (2) functional models based upon auditory anatomy; (3) the performance of electrophysiological hearing tests and (4) using behavioural responses to sound exposures. This paper summarises three ongoing, and relatively new, techniques. These techniques complement each other, with the end goal of generating hearing audiograms for baleen whales. The first uses a three-dimensional computer model of a fin whale head (*Balaenoptera physalus*), where simulated sound waves are passed through the model to see how each component vibrates in response. The second is an electrophysical study on restrained minke whales (*Balaenoptera acutorostrata*). Electrophysiological studies measure neural activity when the auditory system is stimulated by sound. The third is a behavioural observation audiometry study on humpback whales (*Megaptera novaeangliae*). Here whales are exposed to a range of frequencies and a significant change of behaviour implies they heard, and responded to, the sound. Each method has advantages and disadvantages but taken together, are likely soon to produce the first baleen whale hearing audiograms.

INTRODUCTION

To accurately predict the effects of increasing level of man-made noise on animal communication, it is necessary to understand their hearing, especially in the presence of noise. There have been several studies on hearing in toothed whales (including several on dolphins). However, no measures of hearing exist for any species of baleen whale despite the fact their hearing is likely to be in the frequency range of the loudest and most pervasive sources of anthropogenic noise.

Audiometry studies, largely based in the US, have culminated in a reasonable understanding of hearing in toothed whales. These studies determined the minimum level of sound that can be “detected” by an animal for a particular frequency, often in the presence of natural or experimentally derived noise. In some instances, this has allowed the critical ratio (CR) of hearing to be determined. The CR is the signal-to-noise ratio (SNR; ANSI/ASA S3.20) for a tone in broadband noise at the threshold of detection and is much more relevant to real-world environments where background noise is spatially and temporally variable, than is the absolute threshold, which is measured in quiet conditions. There are two types of audiometry studies; behavioural audiometry, which involves training an animal to respond if it hears a sound. (e.g., Finneran et al., 2005; Kastelein et al., 2010; Houser et al., 2013; Branstetter et al., 2017), and electrophysiological audiometry, which measures neural activity when the auditory system is stimulated by sound (e.g., Ruser et al., 2016; Houser et al., 2008; Szymanski et al., 1999). Both behavioural (e.g., Finneran et al., 2005; Kastelein et al., 2010; Houser et al., 2013; Branstetter et al., 2017) and electrophysiological (e.g., Houser et al., 2008; Finneran et al., 2009; Ruser et al., 2016) studies are now regularly performed in small, toothed whales (dolphins and porpoises). However, neither technique has been successfully applied to any species of baleen whale; none are kept in captivity and their size largely precludes them from electrophysiological work. Up until recently, only one experiment in a baleen whale, a grey whale (*Eschrictius robustus*), has ever been undertaken (Ridgway & Carder, 2001) and the results were ‘equivocal’.

TECHNIQUES TO ESTIMATE HEARING

Finite element modelling is where three-dimensional computer models of a whale head is built from scans of its skull. Simulated sound waves are then passed through the model to see how each component vibrates in response, i.e., how sounds are conducted and amplified through the hearing apparatus. An incident acoustic wave, of a given pressure amplitude in the sea water surrounding an animal, is transformed into a measure of input to the cochlea. The cochlear input can then be transformed into an approximation of an audiogram. Models have shown that sound likely travels to the whale's tympanoperiotic complex (i.e., ear bones) through both the soft tissue and the bone (Cranford and Krysl 2015). This study concluded that bone conduction was the primary mechanism, and results in the best hearing sensitivity for low-frequency sounds. Using their model, the peak frequency of fin whale hearing was predicted to be 1 kHz, with 'best' hearing between 20 Hz and 10 kHz. Work is underway to use the technique to predict hearing in other baleen whale species.

Scientists have made a major leap forward in minke whale hearing. Here, adolescent minke whales have been successfully captured, held (Kleivane et al., 2024), and auditory evoked potential hearing tests performed, where the neural response of the brain to sound stimuli is measured using small surface electrodes. Animals could only be tested for a small amount of time, limiting the researchers to testing a small range frequencies, but results are promising. Electrophysiological studies are regularly performed in small, toothed whales, given these species can be maintained in captivity. These experiments are obviously more challenging to perform in baleen whales, given they cannot be kept in captivity and animals must be caught and restrained. The advantage of these approach is that species-specific unmasked hearing audiograms. The disadvantage is that hearing thresholds produced from auditory evoked potential hearing tests are higher than hearing thresholds obtained using behavioural audiometry.

Finally, a project based on Australia, is focussing on humpback whales This project builds upon a prior experiment, which exposed migrating humpback whales to 2 kHz tones (Dunlop et al., 2013). Groups consistently displayed an avoidance reaction to the tones stimulus, at received levels assumed to be close to their detection threshold in noise. The Australian project aims to estimate the frequency range of hearing, and relatively sensitivity, in a wild population of humpback whales using a similar experimental design. Behavioural response experiments do not rely on restraining and training the animal but instead rely on the natural responses of animals to noise sources. In a sense, acoustic behavioural response studies in whales are like behavioural observation audiometry in humans. The work uses a behavioural observation audiometry (BOA) technique typically used in infants or small children incapable of fulfilling or comprehending instructions (Limberger 2009). It relies on the observation of behavioural responses synchronized with the transmission of an acoustic stimulus. The "minimum response level" (MRL) indicates the lowest level of sound to which a subject is responsive (Gans 1987; Norrix 2015). Though not equivalent to the hearing threshold obtained through behavioural audiometry, it is a useful estimate of hearing sensitivity when other options are not available. One disadvantage of this approach is that subjects may not respond at detection threshold but at some level above detection. The other disadvantage, with regards to whales, is that these experiments are carried out in the open ocean, a noisy environment, meaning signals across the frequency range of good hearing sensitivity are likely to be masked.

AUSTRALIAN AUDIOMETRY STUDY

This work is being conducted over five field seasons (2020 to 2024) at Peregian Beach, 100 km north of Brisbane, Queensland, Australia, during September and October, when whales are migrating from breeding to feeding grounds. The field site is unusual in that it is a near-shore migratory corridor for a large population of humpback whales (>30,000), at least half of which pass within 10 km of shore. Major benefits of using this site are: 1) much lower noise levels than in many ocean sites, 2) the predictable movement of the whales allows them to be targeted and tagged and responses can be detected reliably, 3) group responses can be measured from land leading to a robust sample size with minimal interference, 4) the social context of the target group (location and behaviours of whales within several kilometers of the focal group) can also be measured from land as this has been demonstrated to affect behaviour, 5) new groups are available every day (low risk of resampling), 6) 11 previous field seasons at this site provide a wealth of background data on whale movements, behaviour and abundance, and 7) the study area has been extensively characterized acoustically with many measurements of transmission loss leading to validated empirical sound transmission models.

Six tone frequencies are being tested: 62 Hz, 250 Hz, 1 kHz, 4 kHz, 16 kHz, 22 kHz. Each group of whales is exposed to one frequency, with eight to ten groups exposed per frequency. These frequencies were chosen to provide data for areas of likely best sensitivity (models suggest 1 to 6 kHz) as well as testing whether there is significantly less sensitivity at lower frequencies (62 Hz; predicted by Houser et al.'s 2001 cochlear model and Tubelli et al.'s 2018 tympanic bone model). The tones are 2 seconds in duration with a third-octave upsweep (e.g., the 1 kHz tone was an upsweep from 1 – 1.25 kHz). The tone is repeated every 4 seconds, hence a 50% duty cycle. Although the upsweep reduces the precision of the test in terms of it being a single, discreet frequency, the third-octave bandwidth is much less than that between experimental frequencies (two octave spacing). Tones are transmitted using a Lubell VC2C, Lubell LL916 or GeoSpectrum M18C-4 depending on frequency. Whale behaviours are measured using a combination of suction cup tags (which included a pressure sensor, accelerometers and magnetometers as well as hydrophones), boat-based focal follows, and land-based focal follows (Fig. 1). Responses are defined as a significant change in movement, speed and dive behaviour within the exposed groups at some point during the experiment.

Figure 1 – A series of photos showing the behavioural data collection methodologies during the humpback behavioural audiometry experiment (tagging – top photo, boat-based focal follow – middle photo, and land-based surveys – bottom photo).

CONCLUSIONS

The Australian humpback study demonstrates that behavioural audiometry studies on hearing in free-swimming, wild cetaceans are possible under certain conditions. Already, this work has confirmed that humpback whales are likely to have critical ratios comparable to other marine mammals and suggest that these large whales can hear up to at least 22 kHz. The whales routinely appeared to detect signals that were not evident using single hydrophone recordings (audibly or spectrographically), and in conditions of high conspecific noise (song chorusing, showing mysticetes likely have considerable processing gains in hearing. Combined with evidence from finite element modelling and the electrophysiological study, we are likely to be underestimating the acoustic information available to mysticetes under natural conditions.

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