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Aerial hearing sensitivity tests with a male Pacific walrus (*Odobenus rosmarus divergens*), in the free field and with headphones

R. A. Kastelein, P. Mosterd, C. L. van Ligtenberg* and W. C. Verboom**

Harderwijk Marine Mammal Park, Strandboulevard-oost 1, 3841 AB Harderwijk, The Netherlands
**Audiological Centre, Prof. J. J. Groen Foundation, Zangvogelweg 150, 3815 DP Amersfoort, The Netherlands*
***TNO-Institute of Applied Physics (TPD), P.O. Box 155, 2600 AD Delft, The Netherlands*

Summary

The aerial hearing of a 10-year-old male Pacific walrus was tested from 0.125 to 8 kHz, the frequency range covering the ranges of human speech, industrial noise and most walrus vocalizations. Two behavioral audiometric test methods were used in a study area with a fluctuating background noise level of 52 ± 4 dB(A) re 20 µPa. The go/no-go paradigm was used in both tests.

Test 1. Headphones were used to investigate the aerial hearing sensitivity of each ear for pure tones of 0.125, 0.25, 0.5, 1.0, 2.0, 4.0 and 8.0 kHz. A modification of the descending staircase psychometric technique was used (Levitt, 1970). Both ears were equally sensitive. Between 0.125 and 0.25 kHz, the detection thresholds dropped from 105 dB to 80 dB and between 0.25 and 2.0 kHz from 80 to 60 dB re 20 µPa. Between 2.0 kHz and 8.0 kHz the thresholds increased to around 65 dB. The hearing thresholds obtained with headphones suggest very poor hearing in this walrus compared to other tested pinnipeds. However, this does not agree with the day-to-day experiences at the Harderwijk Marine Mammal Park where many behavioral commands are given orally to the study animal. Maybe the outer ear canal was closed off by the auricular muscles due to the presence of headphones.

Test 2. 'Free field' (not a true free field in the acoustical sense of the word, because the room was echoic and not sound isolated) measurements were carried out on the same walrus, in which the aerial hearing sensitivity was tested for 2 types of sound signals (frequency modulated tones and filtered band noise) with centre frequencies of 0.25, 0.5, 1.0, 2.0 and 4.0 kHz. The walrus responded to signals that were 3 to 13 dB above the 1/3-octave background noise levels, which suggests that the hearing thresholds reported were masked thresholds.

The same 'free field' hearing test was done with a human with his head in the same location as the walrus'. The human heard the signals between 0 and 12 dB below the lowest level of the background noise. Comparison of the walrus and the human hearing curves suggests that the walrus' hearing is less acute than that of the human for the tested frequencies.

Tests were conducted to determine which stimulus instigates the closure of the external auditory meatal orifice. The stimulus that causes closure was not discovered, but certain possibilities were ruled out. Closure was not triggered by pressure on the outer ear canal or mechanical stimulation of the skin immediately around the meatal orifice. Perhaps the change in sound field when diving, instigates closure. It is also possible that closure is under voluntary control.

Introduction

Walruses are pinnipeds which live in the Arctic. Both the Atlantic (*Odobenus rosmarus rosmarus*) and Pacific (*Odobenus rosmarus divergens*) subspecies presently occur in smaller numbers than before occupation and exploitation of their distribution areas by humans from industrialized countries (Born, 1992). Conservation measures are needed to protect both subspecies. To establish a rational management strategy, it is necessary, among other things, to know how walruses experience their environment. Knowledge is therefore needed about the sensitivity of walrus' sensory systems, and about their roles in walrus ecology.

One of the senses is hearing. Walruses produce a variety of low-frequency sounds (up to 4 kHz), which seem to have mainly social functions (Schevill *et al.*, 1966; Ray & Watkins, 1975; Miller & Boness, 1983; Stirling *et al.*, 1987; Verboom & Kastelein, 1995; Kastelein *et al.*, 1995). To predict the influence of man-made noise on walruses, such as that described by Salter (1979) and Severinsen

(1990), information on their aerial and underwater hearing sensitivity is needed. Industrial noise consists mainly of low-frequency sounds, and includes sounds produced by vessels (including ice-breakers and fishing ships), air traffic, snow-mobiles, and oil and gas exploration and extraction. So far, only one study on the hearing sensitivity of walruses has been carried out. This was an aerial free field hearing test on Atlantic walruses on Svalbard, Norway (Kastelein *et al.*, 1993). It was a pilot study in which only limited data could be obtained due to field conditions. The aim of the present study was to determine the aerial hearing sensitivity of a male Pacific walrus in the frequency range of its own vocalizations, manmade noise and human speech and to determine which stimulus instigates the closure of the external meatal orifice, or whether closure is under voluntary control.

Materials and Methods

Study animal

The in-air hearing sensitivity of a healthy male Pacific walrus (*Odobenus rosmarus divergens*, code OrZH003) was tested. He was born in Alaska, USA, in 1982 and was found without his mother that same year, after which he was transported to a Sea World park in the USA. In February 1985 the animal arrived at the Harderwijk Marine Mammal Park, and he has been trained to perform in educational shows and psychophysical research projects since May 1986. During the present study, the animal's weight increased from 1014–1250 kg.

Study area

The experiments were not conducted in a sound-isolated anechoic room. Because walruses can produce strong suction orally (Kastelein *et al.*, 1994), it was feared that the study animal would suck sound absorbing material off the walls and swallow it. The study was conducted in the sleeping area of the walrus. It was an indoor room (5 m × 3.5 m) with a door towards a pool. The walrus did not feel at ease when the door was closed. The door was kept open and the background noise level fluctuated much, as outdoor noise sources could not be controlled.

The background noise level in the study area was measured after each session with a sound pressure level meter (Bruel and Kjaer 2235) and a filter (B & K 1625). Filter bandwidth: 1/3-octave and meter settings at RMS/slow. It fluctuated: 52 ± 4 dB(A) re 20 μPa (Table 1 and Fig. 7). Hearing tests were not conducted on days when the background noise level was exceptionally high due to rain, construction noises, continuous gull calls, or wind speeds in excess of Beaufort 4.

Training

Before audiometric testing could begin, the walrus was trained to indicate to the researchers when he heard a sound using the go/no-go paradigm. The animal was trained to station his nose against a spot on a wall. When he heard a sound, he had to break station and move his head about one metre towards the hand of the trainer after which he received a reward. The trainer stood out of sight beside the animal's head. The rewards given were herring (*Clupea harengus*) and mackerel (*Scomber scombrus*). At first the trainer used a dog whistle to produce a test sound. Later, the animal was trained to accept headphones over his auditory meatal orifices. For training, the headphones were connected to a small sound generator which produced one signal (noise with most of the energy between 2 and 4 kHz). The amplitude could be varied by the trainer (Fig. 1). The animal was trained between February and June 1991.

Experiment 1: headphones

The walrus's aerial hearing sensitivity for individual ears was tested for pure tones of 0.125, 0.25, 0.5, 1.0, 2.0, 4.0, and 8.0 kHz, using headphones. An advantage of the headphone technique is that the animal cannot select a more advantageous listening posture, as it can during hearing tests with a loud-speaker. With headphones the position of the auditory meatal orifice relative to the sound source is always similar. Headphones do not block the background noise, but only reduce sound between 0.125–0.25 kHz by about 20 dB, between 0.5 and 1.0 kHz by about 30 dB, and between 2.0 and 8.0 kHz by about 36 dB. During the tests the equipment operator was out of sight of the trainer and the animal, behind the door of an indoor enclosure (Fig. 2). He could see the trainer and the walrus through a 2-way mirror in the door. The equipment operator controlled an audiometer (Peters AP-5, 213), which was linked by a 4 m long cable to the headphones. The audiometer was set to produce pure tones (sinusoid signals) for 2.5 s. The system was calibrated according to ISO standard R389 (1964), the hearing threshold for humans, using an amplifier (Bruel and Kjaer 2113, meter response at RMS/fast, filter dB (linear) 22.4 Hz–22.4 kHz), artificial ear (B & K 4152), microphone (B & K 4144), microphone calibrator (B & K 4230), coupling rubber between headphones and artificial ear (Telephonics) and frequency meter (Thandar TF 1000). When a signal was produced, a small red lamp lit up on the headphone. This indicated to the trainer that a sound was being produced, but could not be seen by the walrus.

Figure 1. The sound generator and headphones used during training (Photo: Henk Merjenburgh).

When the walrus was wearing the headphones and stationed calmly (Fig. 3 A), one of two trial types occurred:

(1) Signal trial

The operator waited for a random time period of up to 15 s before pressing a switch to produce a pure tone in one of the walrus' ears.

The animal could react in three ways:

(a) Correct response. (i) A hit: the animal left his station during or immediately (within 1 s) after sound projection and was rewarded with a fish (Fig. 3B). (ii) A miss: the animal did not respond to a tone. In such a case the trainer loudly called the walrus' name after a random time interval of

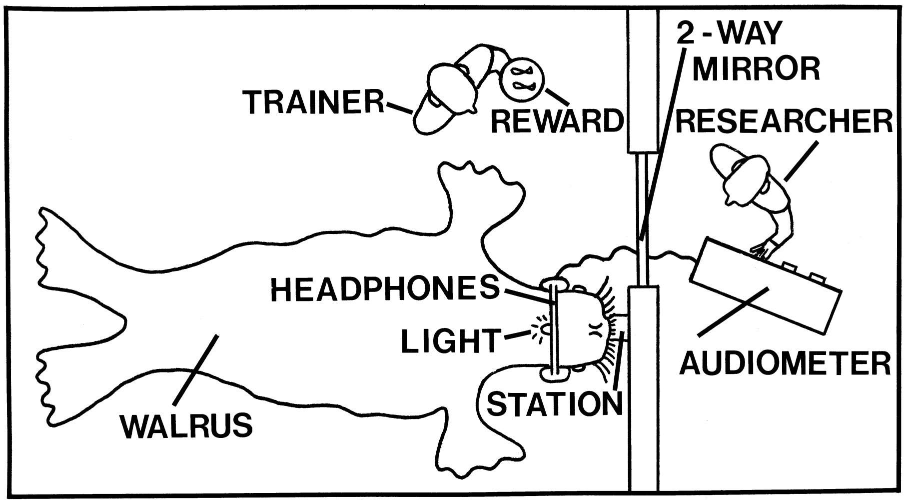

Figure 2. Experiment 1: The study area, showing the walrus and the trainer on one side of the wall, and the equipment operator with the audiometer on the other side (Drawing: Ron Kastelein).

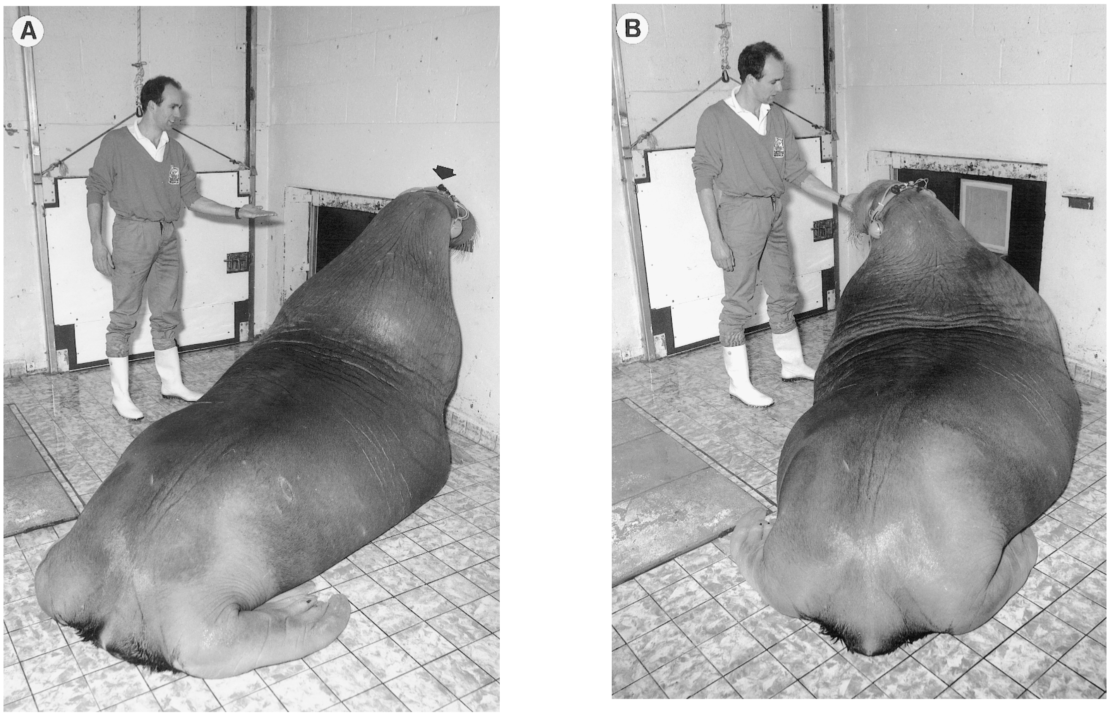

Figure 3. Experiment 1: (A) The walrus at his station, waiting for a sound (pure tone) from one side of the headphones. The trainer is out of the walrus' sight. Note the small light (arrow) on the top of the headphones which, when it was on, indicated to the trainer that a sound signal was being produced. (B) The walrus' correct response after he heard a sound. After this he received a reward (Photos: Henk Merjenburgh).

between 2 and 10 s after the sound signal was produced. The trainer gave a reward and sent the animal back to the station for the following trial.

(b) Incorrect response (iii) (false alarm). The animal responded before a signal had been produced. The trainer would say 'no', and send the animal back to the station for the next trial.

(2) Control (or 'catch') trial (no sound produced) The operator told the trainer after a random time period of up to 15 s after the walrus had stationed to end the trial. The animal could respond in two ways:

(a) Correct response. The animal stayed at the station until the trainer acoustically indicated the end of the trial. Then the walrus would move his head towards the trainer and receive a reward.

(b) Incorrect response (false alarm). The walrus left his station during the up to 15 s interval. In such a case, the operator told the trainer it was a false alarm and the trainer would send the animal back to the station for the next trial.

Thresholds were obtained by a modification of the descending staircase psychometric technique. Before detailed testing began, the levels of the thresholds were bracketed in 5 dB descending steps. During testing, the initial level was set 10 dB above the bracketed thresholds. When the animal detected (hit) a sound in three consecutive signal trials ($P_x=0.794$), the amplitude was lowered in the next trial by 2 dB. If the animal did not detect (miss) a sound in three consecutive signal trials the amplitude was increased by 2 dB in the following trial. The turning point from miss to hit is called a reversal.

Daily, one approximately ten-minute session was held between 11.00 and 14.00 hrs. A session consisted of about 25 trials. Twenty percent of all trials in a session were control trials during which no sound was produced. This percentage of control trials was enough to make the animal stay calm at station until he heard a sound. Each day only one frequency was tested, so the animal could 'tune in' to a particular frequency. Sessions contained around 4 reversals. Each frequency was tested four times randomly distributed during the study.

The detection thresholds of the left ear were calculated as the mean levels of 16 reversals for each frequency. Testing the hearing of the walrus' left ear was done during a period of 7 months between June and December 1991.

After testing the left ear, the right ear was tested using the same procedure. The start amplitude of a signal was chosen to be 5 dB above the threshold of the left ear. The detection thresholds of the right ear were calculated as the mean of 12 reversals for each frequency. Testing the hearing of the right ear was done during a period of 1 month in January 1992.

Experiment 2: 'free field' presentation

The walrus' aerial hearing sensitivity was tested in the 'free field' (not a true free field in the acoustical sense of the word, because the room was echoic and not sound isolated. It was the same room as used in experiment 1), using a custom-built portable sound generator. Its built-in loud-speaker produced two types of signals: (a) Filtered band noise. Centre frequencies: 0.25, 0.5, 1.0, 2.0 and 4.0 kHz, slope: 24 dB/octave, bandwidth: 1/1-octave; (b) Frequency modulated tones. Centre frequencies: 0.5, 1.0, 2.0 and 4.0 kHz. The centre frequencies were modulated according to the 'frequency shift keying' method. Switching frequency: 12 Hz, by square wave, modulation depth: ± 4%, creating sweeps in the following discrete frequency ranges: 480–520, 960–1040, 1920–2080, 3840–4160 Hz. Abrupt signal onset/offset transients were prevented by gating the signals with 200 ms rise and fall times. Because of the small modulation, the sound had a tonal character. The signals produced negligible harmonics. These signals were chosen because in non-cooperative humans, such as children, they are more arousing than pure sinusoid signals.

The sound pressure level could be varied in nine calibrated (± 2 dB accuracy) steps between 20 and 100 dB re 20 μPa by three amplitude settings (around 30 dB difference between each, depending on the frequency) and by varying the distance between the loud-speaker and the walrus' meatal orifice in three stages (10, 33 and 100 cm), giving 10 dB attenuation steps. The loud-speaker was positioned in a horizontal plane with the head, at an angle of about 110 degrees to the sagittal plane of the head measured from the nose (Fig. 4). To determine the distance between the loud-speaker and the meatal orifice, flexible wires of 9 and 32 cm were attached to the apparatus. The trainer estimated the distance of 1 cm between the tip of the wire and the animal's meatal orifice. The flexibility of the wires ensured that the walrus was not irritated or injured when it turned its head to respond to the sounds.

Bracketed levels of the thresholds were determined during two pre-test sessions. During the actual experiments the sound level of the first trial of a session was set 10 dB above the roughly determined threshold. When the animal detected a sound (a hit) in two consecutive signal trials ($P_x = 0.707$), the amplitude was lowered in the next trial by about 10 dB (depending on the frequency). If the animal did not detect a sound in two consecutive signal trials the amplitude was increased by about 10 dB (the exact amount depended on the frequency) in the following trial. A session contained approximately 20 trials of which 30% were control trials. Two or three frequencies were tested during a session.

Data were collected between January 1992 and November 1994. Each frequency was tested 6 times randomly distributed during the study. The detection thresholds were calculated by taking the average of the minimum levels the animal responded to in the six sessions. Because only large amplitude steps were feasible with the available equipment, the animal either never, or always detected a signal at a particular level.

Experiment 3: 'free field' measurements with open headphones

To determine whether the pressure of the headphones in experiment 1 instigated the closure of the meatal orifice or made the outer ear canal collapse, 'free field' hearing measurements were conducted while the walrus was wearing headphones (same metal spring as during experiment 1) and ear pads from a hearing protector (David Clark, model 10 A) from which the ear pads had been partly removed (Fig. 5). During these hearing tests there was pressure on the skin in a 6 cm diameter circle around the meatal orifice, but sound could still directly reach the orifice. The same data collection method was used as in experiment 2.

Frequency modulated tones with centre frequencies of 500, 1000 and 2000 Hz were tested during one session in June 1992.

Experiment 4: 'free field' measurements with open headphones with grids

To determine whether mechanical irritation of the skin immediately around the meatal orifice instigated the closure of the orifice, an aluminum grid was glued to the open headphone cups used in experiment 3 (Fig. 6) which ensured that mechanical contact was made with the skin immediately surrounding the meatal orifice, without completely blocking the orifice. The same data collection method was used as in experiment 2.

Filtered band noise signals with centre frequencies of 250 and 500 Hz were tested during one session in June 1992.

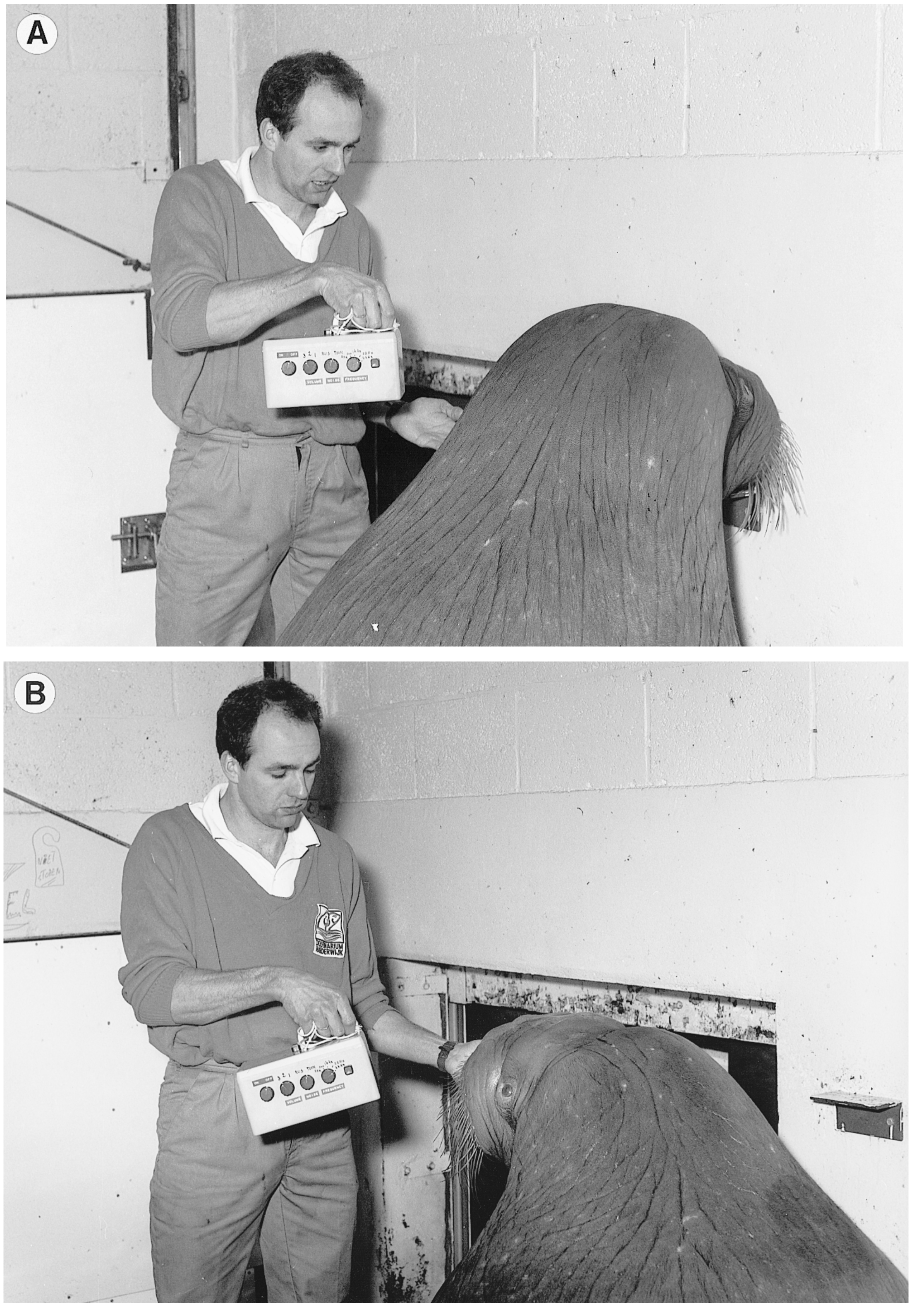

Figure 4. Experiment 2: (A) The walrus stationed and waiting for a sound signal (frequency modulated tones or filtered band noise signals) from the portable sound generator. (B) The walrus' correct response after he heard a sound. After this he received a reward (Photos: Henk Merjenburgh).

Experiment 5: a frequency modulated tone produced in a headphone

To determine whether the difference in hearing thresholds found in experiments 1 and 2 were caused by a difference in signal types, or were due to the presence or absence of headphones, the 1000 Hz frequency modulated tone, produced by the sound generator in experiments 2 and 3, was presented

Figure 5. Experiment 3: Open headphones which were used during 'free field' hearing tests to determine whether the auricular muscles, which can close off the outer ear canal, were triggered by the pressure of headphones or that the pressure of the headphones made the outer ear canal collapse (Photo: Henk Merjenburgh).

through one side of a pair of consumer headphones (Altai, HVS 22; frequency range 30–18 000 Hz). The hearing sensitivity of the left ear was tested. An attenuator on the headphones allowed adjustment of the sound pressure level.

The same data collection method was used as in experiment 2. The sound pressure level was first set at a level that was audible to the walrus (70 dB re 20 µPa, 1/1-octave). During each 10-min session the sound pressure level was reduced in uncalibrated (approximately 2 dB) steps until the animal no longer responded. This was done during eight sessions between July and December, 1993.

Experiment 6: 'free field' presentation to a human

The same 'free field' hearing test as in experiment 2 was done with a human (a healthy 36-year-old man) with his head in the same location as the walrus'.

Results

Experiment 1: headphones

The detection threshold levels for pure tones of the left and right ear are shown in Table 1 and Figure 7. Both ears were similarly sensitive. Between 125 and 250 Hz the thresholds dropped from 105 to 80 dB re 20 µPa. Between 0.25 and 2.0 kHz the thresholds dropped from 80 to 60 dB re 20 µPa. Between 2.0 and 8.0 kHz the thresholds increased to around 65 dB.

When the sound pressure level was 10 dB above the thresholds described here, the animal reacted to the onset of the signal very decisively, and rarely had false alarms. Nearer to the threshold, the animal's reaction time increased. He frequently responded around 1 s after the tone onset, and sometimes as the sound ceased, which was 2.5 s after the onset. When sounds near the threshold were tested, the animal usually moved his head slowly towards the trainer and often did not break station, but moved his mystacial vibrissae, or repositioned his head against the wall, closed his eyes or rolled his eyes dorsally at the time that the sound was produced. The overall false alarm rate was around 10% of all trials.

The animal was very cooperative, and often waited near the station while the audiometer was being installed in the adjacent room. No sessions had to be cancelled due to the animal's behaviour.

Experiment 2: 'free field' presentation

The walrus' hearing sensitivity to the frequency modulated tones and the filtered 1/1-octave band noise signals of a particular frequency was similar

Figure 6. Experiment 4: Open headphones with a grid which were used during 'free field' hearing tests to determine whether the auricular muscles, which can close of the outer ear canal, were triggered by mechanical irritation of the skin immediately around the meatal orifice (Photo: Henk Merjenburgh).

(Table 1 and Fig. 7, in which the filtered band noise is presented as 1/3-octave band levels). He detected signals that were 3 to 13 dB above the background noise level (filter bandwidth: 1/3-octave).

Experiment 3: 'free field' measurements with open headphones

The lowest signal amplitude the walrus detected when wearing open headphones for the 500 Hz frequency modulated tone was 50 dB, for the 1.0 kHz frequency modulated tone 53 dB and for the 2.0 kHz frequency modulated tone 56 dB. Comparison of these values with the 'free field' thresholds derived without headphones in experiment 2 (Table 1 and Fig. 7), shows that the walrus' hearing with and without the open headphones was similar for the tested frequencies.

Experiment 4: 'free field' measurements with open headphones with grids

The lowest signal amplitude the walrus detected the 250 Hz filtered band noise signal was 48 dB, and for the 500 Hz filtered band noise signal 52 dB (1/3-octave band levels). Comparison of these numbers with the 'free field' thresholds derived without headphones in experiment 2 (Table 1 and Fig. 7), shows that the walrus' hearing with and without the open headphones with grids was similar for the tested frequencies.

Experiment 5: a frequency modulated tone produced in a headphone

In all eight sessions the animal detected the 1.0 kHz frequency modulated tone until the amplitude was reduced to below 62 dB re 20 μPa (Table 1 and Fig. 7).

Experiment 6: 'free field' presentation to a human

The human heard the signals between 0 and 12 dB below the lowest level of the background noise (Table 1 and Fig. 7).

Discussion and Conclusions

Differences among thresholds

The hearing thresholds derived with headphones of the left and the right ear are similar. This means that both ears had a similar hearing sensitivity, which is a natural phenomenon in most healthy mammals. This finding also serves as an argument against pathological ears in the study animal.

The fact that the detection thresholds derived with headphones were higher than those derived

Table 1. Aerial hearing thresholds (SPL in dB re 20 µPa) of a male Pacific walrus and a man and the background noise level range (filter bandwidth: 1/3-octave)

		Walrus					Man	
		Headphones			Free field (masked)		Free field (masked)	
		Pure tone						
Frequency (Hz)	Background noise level range	Left ear	Right ear	Freq. mod. tone Left ear	Modulated tones	Filtered band noise	Modulated tones	Filtered band noise
125	39–47	105	106		—	—	—	—
200	39–47							
250	40–48	78	79		—	51	—	40
315	39–47							
400	39–47							
500	37–45	77	80		56	55	32	36
630	40–48							
800	39–47							
1000	39–47	64	67	62	53	54	34	36
1250	38–46							
1600	37–45							
2000	37–45	61	59		58	54	25	32
2500	37–45							
3150	38–46							
4000	35–43	69	66		49	51	22	23
5000	34–42							
6300	30–38							
8000	30–38	67	63		—	—	—	—

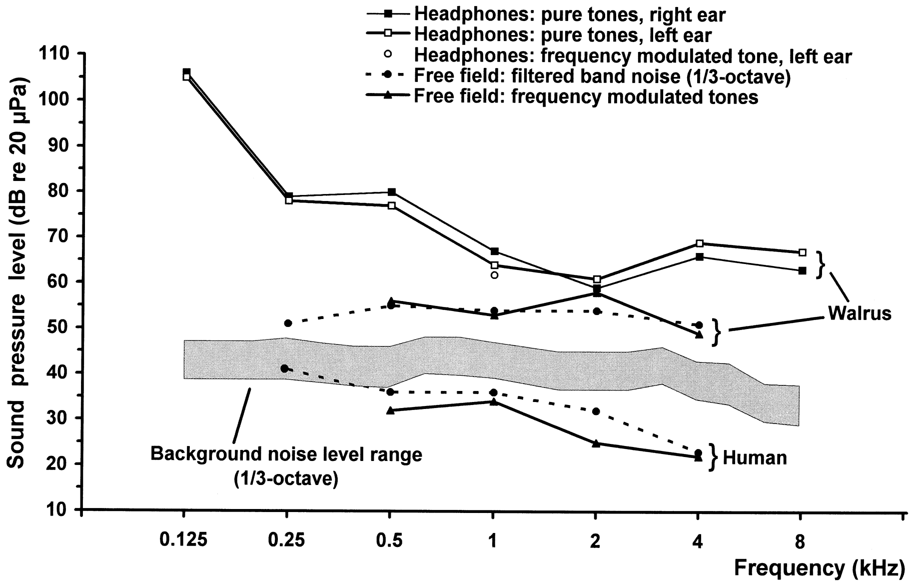

Figure 7. Aerial hearing thresholds (SPL in dB re 20 µPa) of a male Pacific walrus for several sound signals during experiments with headphones and in the 'free field', the 'free field' threshold of a man, and the background noise level range (1/3-octave band levels).

during 'free field' tests is very surprising, since the background noise level in headphones is lower (about 20 to 36 dB depending on the frequency) than outside and therefore, the derived hearing thresholds were expected to be lower than those obtained in 'free field' tests. The difference between the headphones and 'free field' measurements could be caused by contributions of the following phenomena.

(1) The headphones tested only one ear at a time, whereas in the free field tests both ears were tested simultaneously. In humans, low-frequency hearing thresholds obtained using headphones tend to be about 6 dB higher than those which rely on a sound field generated by external speakers (Sylvian and White, 1933). This is presumed to result from masking by the amplification of physiological noise as a result of wearing headphones. Experiment 5 supports this phenomenon. It shows that the detection level of the frequency modulated tone of 1000 Hz was 9 dB higher when presented to one ear by headphones than when presented to both ears in free field conditions.

(2) The headphones may have instigated the closure of the auditory meatus.

(3) There may have been a calibration problem. The B & K 4152 artificial ear has a 4 cc coupler, which is made to mimic the characteristics of the human ear, and not the walrus ear. What the characteristics for the walrus ear should be, is unknown.

(4) In experiment 1 (headphones) the animal was tested at the 79.4% level because the sound level was dropped only after 2 consecutive hits, and raised after one miss (Levitt, 1971). In experiment 2 ('free field'), only the low turning points were used, so the threshold should, in theory, be just below the 50% correct point. If the psychometric function has a gentle slope, then there may be a number of dB difference between the 50% and 79% points. In a harbour seal (*Phoca vitulina*) the difference would be between 6 and 7 dB (Terhune & Turnbull, 1995). However, this argument is disproved by experiment 5 (modulated tone presented headphones) in which the 50% detection level is 2 dB below the 79.4% detection level of the left ear derived with headphones.

The 'free field' results show that the hearing thresholds for pure tones and 1/3-octave filtered noise are similar. This would mean that the critical bandwidth for frequencies of 500 Hz and higher are approximately 1/3-octave and similar to the human critical bandwidth in this frequency range. The derived 'free field' thresholds, although somewhat higher than expected with respect to the background noise, should probably be considered as masked hearing thresholds. The present study therefore presents a conservative estimation of the walrus in-air hearing sensitivity. Experiences with the trained walrus in the present study do support these conclusions. Many of the commands used for show and husbandry behaviours are presented by

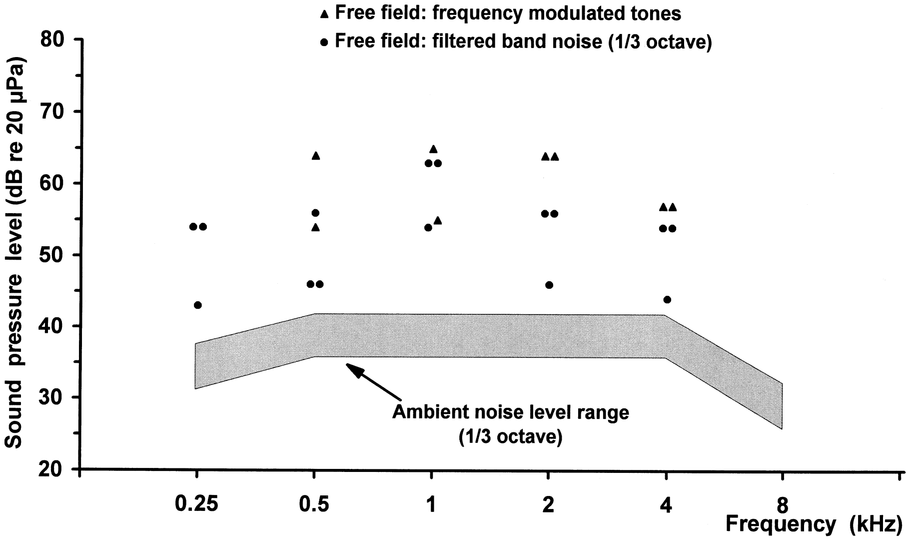

Figure 8. The lowest levels of filtered band noise signals and frequency modulated tones 3 wild Atlantic walruses responded to (by opening their eyelids and rolling their eyes or raising their heads) and the average ambient noise level range (mainly caused by wind and the surf; data converted to 1/3-octave band levels). Adapted from Kastelein *et al.* (1993).

human speech at a distance of 1 m at a level at which humans would communicate at such a distance. The animal performs the correct behaviours even if the commands are given from behind (Piet Mosterd, pers. obs.). It is unlikely that communication sound recognition levels will be less than 20 dB above the threshold (Terhune & Turnbull, 1995). At 1 kHz, the spectrum level of the loudest ambient noise was about 23 dB re 20 µPa. This would result in a critical ratio of 30 dB for the modulated tones. This is high for most mammals, but not impossible.

The 'free field' tests were conducted in an echoic, non-sound isolated room, and were thus not true free field in the acoustic sense of the word. The sound field was quite complicated due to the reflections from the floor, walls, ceiling, trainer and walrus.

Comparison of the walrus and the human hearing curves suggests that the walrus's hearing sensitivity is less than that of humans for the tested frequencies.

Influence of methodology on thresholds

Moore & Schusterman (1987) used 'warm-up' and 'cool-off' trials, in which the intensity of the signal was at least 10–15 dB above the threshold, to assess the degree of stimulus control over otariids before and after a session. In the present study this technique would probably have led to a poorer performance by the walrus. Pre-tests indicated that when a session was started with loud signals, the walrus was so tuned to this intensity, that it would not respond to much (10 dB or more) lower levels afterwards. The best results were obtained when the amplitude of the first trial was close to the threshold, forcing the animal to concentrate on faint sounds. The same phenomenon has been observed in harbour seals (Jack Terhune, pers. comm.). Maybe lower detection thresholds would have been obtained using an ascending staircase method.

The walrus in the present study was very calm and cooperative. This was perhaps partly because he was tested in his own living quarters, and not in an unfamiliar acoustic chamber. Psychophysical studies with walruses have indicated that this species' cooperation is less dependent on their appetite than is that of sea lions in similar tests (Kastelein & van Gaalen, 1988; Kastelein *et al.*, 1989).

Comparison with other pinniped audiograms

The 'free field' detection thresholds of the Pacific walrus derived in the present study with a psychophysical technique, correspond to those derived from three wild Atlantic walruses on Svalbard, Norway (Kastelein *et al.*, 1993) in which spontaneous reactions (such as opening and rolling of the eyes and lifting of the head) acted as signs that the animals perceived the sound signals (Fig. 8). The average level of the background noise in the present study was quite similar to that in the field study. However, the ambient noise in the field, caused by waves hitting the beach, resembled white noise, whereas the background noise in the present study did not.

The aerial auditory capabilities of four pinniped species (*Zalophus californianus*, *Callorhinus ursinus*, *Phoca vitulina*, and *Phoca groenlandica*) were summarized by Moore & Schusterman (1987). However, comparison of the auditory thresholds of different species is only valid within certain limits because of discrepancies in ambient noise level, equipment and measuring technique, methodology and definition of the thresholds. In addition, almost all published information on marine mammal hearing sensitivity was obtained from only one or two individuals per species.

The present study was the first in which a pinniped's hearing was tested with headphones. The idea was followed by Kastak & Schusterman (1995) who tested the aerial hearing sensitivity of a California sea lion (*Zalophus californianus*) and a harbour seal (*Phoca vitulina*) for a 100 Hz pure tone. The 50% correct detection levels were 79 and 65 dB re 20 µPa, respectively. In the present study the aerial hearing thresholds derived with headphones for 125 Hz tones were around 105 dB re 20 µPa. This suggests that the hearing of the walrus in the present study was less sensitive to low frequency noise than the California sea lion and harbour seal tested by Kastak & Schusterman (1995).

Ecological significance

Walruses are social animals, and vocalizations play an important role in their social interactions (Miller, 1985). A positive relationship may well exist between the frequency range of the walrus' aerial and underwater social calls and the frequency range of its most sensitive hearing. Aerial sounds produced by walruses are reported to be between 10 and 4000 Hz (Miller & Boness, 1983; Kibal'chich & Lisitsina, 1979; Miller, 1985; Kastelein *et al.*, 1995; Verboom & Kastelein, 1995), and underwater sounds are reported to be between 200 and 4000 Hz (Schevill *et al.*, 1966; Ray & Watkins, 1975; Stirling *et al.*, 1987). The only source level measurement of walrus vocalizations is reported by Verboom & Kastelein (1995). The average source level of the rutting whistles was 120 dB re 1 pW.

The frequency range tested in the present study contains the ranges of human speech, man-made industrial noise and most of the range of walrus vocalizations. Combining the results of the present study with those of a similar experiment in the wild (Kastelein *et al.*, 1993) enables us to give a rough indication of the distance at which a walrus can hear a man-made noise in his natural environment. Based on the average ambient noise on Svalbard (51 dB(A); Kastelein *et al.*, 1993) and the conclusion of the present study that the walrus' critical bandwidth is approximately 1/3-octave, it is expected that a helicopter (MBB Bolkow type 105, source level 130 dB(A) re 1 pW) flying at a height of 30 m above a flat gravel beach, can be detected by a walrus at a distance of roughly 600 m.

Stimulus instigating the closure of the meatal orifice

In a harbour seal it is possible to induce closure of the meatus when the seal is on land by irritating the skin surrounding the orifice (Mohl, 1968). During the hearing tests with headphones in the present study, the auricular muscles (see Kastelein *et al.*, 1996) might have closed the animal's outer ear because of contact with, or pressure from, the headphones on the skin surrounding the meatal orifices. However, experiment 3 ('free field' measurements with open headphones) showed that, because the detection thresholds with the open headphones were similar to the 'free field' measurements without headphones, the outer ear canal was not closed (or collapsed) due to the pressure of the headphones on the cartilaginous outer ear canal. The apparently low hearing sensitivity, compared to that of other tested pinnipeds, measured with the headphones in experiment 1 was therefore not caused by the collapse of the outer ear canal. Experiment 4 ('free field' measurements with the open headphones with grids) showed that a potential reflex of the auricular muscles to close the meatal orifice was not caused by contact between the headphones and the skin in a 3 cm radius around the meatal orifice (i.e. physical stimulation of mechanoreceptors in the skin). This means that another stimulus triggers the closing reflex or that the muscles are under voluntary control. In terrestrial mammals, such as dogs or deer, the movement of the pinnae by the auricular muscles is triggered by acoustic signals. It is possible that the change in ambient acoustic conditions when the walrus submerges induces the auricular muscles to close the meatal orifice. Maybe the headphones mimicked the acoustic conditions found under water, and the meatal orifices were closed during the hearing tests conducted with headphones because of these acoustic conditions.

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