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Effect of a Bubble Screen on the Behavioral Responses of Captive Harbor Porpoises (*Phocoena phocoena*) Exposed to Airgun Sounds

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Abstract

In seismic surveys, underwater sounds from airguns are used to detect rocks that may contain gas and oil below the sea floor. Airguns produce broadband high-amplitude impulsive sounds with most energy below 100 Hz. Captive harbor porpoises (*Phocoena phocoena*) respond strongly to firing down-scaled airguns. To reduce porpoises' exposure to airgun sounds, a plastic and aluminum screen with encapsulated air bubbles was placed between the airgun and the harbor porpoises in a pool. The bubble screen reduced the energy of the broadband sounds above 250 Hz, but the broadband single-shot sound exposure level (SELss) was reduced by only 3 dB. The bubble screen was very effective in reducing the behavioral responses of the porpoises to the airgun sounds, even when the broadband SELss experienced was 157 dB re 1 μPa^{2}s. This study provides qualitative support for the hypothesis that frequency content matters in the assessment of the responsiveness of harbor porpoises to impulsive broadband sounds. New airgun designs with reduced high-frequency components (> 1 kHz) may be effective in reducing the behavioral responses of harbor porpoises, but a more systematic and quantitative study is required to address the frequency-dependence of their responses to underwater sounds.

Key Words: anthropogenic noise, airgun, audiogram, behavior, captivity study, odontocete, hearing, impulsive sound, seismic survey

Introduction

The harbor porpoise (*Phocoena phocoena*) is a common marine mammal species found in coastal waters in the temperate zone of the Northern Hemisphere. Due to its sensitive hearing, it is of particular interest for assessing effects of underwater sound (e.g., Finneran, 2016; Bundesamt für Seeschifffahrt und Hydrographie (BSH), 2014; Dekeling et al., 2014). Harbor porpoises respond strongly to high-amplitude broadband sound (with most of its energy below 250 Hz) produced by sources such as seismic airgun arrays (Thompson et al., 2013; Pirotta et al., 2014) and pile driving (Tougaard et al., 2009; Dähne et al., 2013; Brandt et al., 2018), and to low-frequency (1 to 2 kHz) active sonar (Kastelein et al., 2014). Typical responses observed in harbor porpoises include diving (van Beest et al., 2018), cessation of echolocation (Tougaard et al., 2009; Thompson et al., 2013; Pirotta et al., 2014; van Beest et al., 2018), and avoidance of the sound sources (Tougaard et al., 2009; Dähne et al., 2013; Thompson et al., 2013; Stone et al., 2017; van Beest et al., 2018). Captive harbor porpoises exposed to impulsive sounds may increase their respiration rates, jump out of the water (Kastelein et al., 2013), and avoid the exposure location (Lucke et al., 2009). Due to the high metabolic rate of harbor porpoises (Read & Hohn, 1995; Kastelein et al., 1997; Wisniewska et al., 2016), concerns have been raised about long-term, large-scale responses affecting individual animals' fitness and potentially translating into population-level effects (Nabe-Nielsen et al., 2014, 2018; King et al., 2015; van Beest et al., 2018).

To avoid behavioral disturbance, some government regulators have set criteria for the levels of underwater sound that correspond to significant behavioral effects (Southall et al., 2007; Daly & Harrison, 2012; BSH, 2013; Dekeling et al., 2014). Studies of harbor porpoises exposed to impulse sound provide information about the levels at which porpoises are disturbed. Single-shot (or single-pulse) sound exposure levels (SELss) for which responses are observed in harbor porpoises are typically in the range of 135 to 151 dB re 1 µPa^{2}s (Tougaard et al., 2009; Kastelein et al., 2013; Thompson et al., 2013; Brandt et al., 2018; van Beest et al., 2018), but several studies suggest variability in responsiveness within the harbor porpoise population, which may be individual or context-dependent (e.g., Ellison et al., 2012; Brandt et al., 2018; van Beest et al., 2018).

Recent comparative studies of behavioral responses of harbor porpoises to sound stimuli over a wide range of frequencies suggest that they are most susceptible to high-frequency sounds, possibly because these sounds are perceived as being louder than sounds with lower frequencies (at similar sound pressure levels) at which porpoise hearing is less sensitive (Dyndo et al., 2015; Tougaard et al., 2015; Wensveen, 2016; Tougaard & Dähne, 2017). Such frequency-dependence is commonly considered in human noise nuisance assessments, although whether responses to sound in marine mammals are frequency-dependent is still under debate (Houser et al., 2017). The effect of high-frequency (> 10 kHz) sonar sound components on the behavioral responses of harbor porpoises has already been studied. Harbor porpoises responded less strongly to 25 kHz sounds without high-frequency side bands than to the same sounds with high-frequency side bands (Kastelein et al., 2015), and less strongly to 1 to 2 kHz sweeps without harmonics than to the same sounds with harmonics (Kastelein et al., 2012).

Sounds produced by seismic and pile-driving activities have their main energy at low frequencies (< 250 Hz), although the sounds can contain significant energy at higher frequencies (Goold & Fish, 1998). The relative contribution of high frequencies to the total energy in these sounds is influenced by the sound source type used, the way the source is operated, and the presence of mitigation measures such as bubble screens or cofferdams (i.e., watertight tubes around piles from which the water is pumped to create air spaces between the piles and the surrounding water). The distance from the source also affects the frequency content, as higher frequencies (> 1 kHz) attenuate more than lower frequencies (< 1 kHz), and very low-frequency sound (< 100 Hz) cannot propagate effectively in shallow waters. The varying frequency content raises the question whether the presence of high frequencies in short impulsive broadband sounds has an effect on the potential of these sounds to cause disturbance in harbor porpoises. Bubble screens may reduce the energy in the high-frequency components of broadband sounds. Therefore, the goals of the present study are to quantify the effect of a bubble screen on airgun sounds, qualify the effects of the airgun sounds on the harbor porpoises with and without the bubble screen, and evaluate the use of a bubble screen in a practical way so as to protect the welfare of captive porpoises.

Methods

Study Animals and Study Area

The study was conducted with two rehabilitated stranded harbor porpoises. At the time of the study, the female (identified as Porpoise F05) was 6 years old, her body mass was around 42 kg, her body length was 152 cm, and her girth at the axilla was approximately 80 cm. The male (Porpoise M06) was 3 years old, his body mass was around 33 kg, his body length was 127 cm, and his girth at the axilla was approximately 80 cm; he was the subject of a study of temporary hearing threshold shift (TTS) due to exposure to airgun sounds during which the data for the present study were collected (Kastelein et al., 2017c, and an unpublished follow-up project). The hearing of both porpoises had been tested and was representative for animals of their age and species (Kastelein et al., 2017a).

The study was conducted at the SEAMARCO Research Institute, the Netherlands. Its location is remote (no busy roads nearby that would cause changes in the ambient noise) and quiet (very few transient sounds), and it was specifically selected for acoustic research. The animals were kept in a pool complex designed and built for acoustic research, consisting of an outdoor pool (12 m × 8 m; 2 m deep) in which the airgun sounds were produced, connected via a channel (4 m × 3 m; 1.4 m deep) to an indoor pool (8 m × 7 m; 2 m deep) where Porpoise F05 was kept during the airgun exposure sessions and where both animals were kept during the sound calibration sessions (Figure 1). During exposure and calibration sessions, a bubble screen was placed in the outdoor pool, blocking the entrance to the channel leading to the indoor pool to reduce the effect of the airgun sounds on the harbor porpoises in the indoor pool (Figure 2).

The bubble screen was composed of a tough six-layer symmetrical sandwich structure (professional insulation). Each half of the sandwich was composed of an outer plastic layer, a thin aluminum layer, and a plastic layer covering the 3-mm thick bubbles of 10 mm diameter (80 bubbles/100 cm^2). The total thickness of the bubble screen was 7 mm. The volume of each bubble was ~236 mm^3 ($\pi \cdot 5^2 \cdot 3$), which corresponds with a sphere of radius 3.8 mm $(236/(4\pi/3))^{1/3}$. The Minnaert resonance frequency (Minnaert, 1933) was therefore ~0.9 kHz, which meant that the theoretical maximum effectiveness of the bubble screen in preventing sound propagation was expected to occur at around 1 kHz.

Acoustics

Acoustical terminology follows *ISO 18405 Underwater Acoustics – Terminology* (International Organization for Standardization [ISO], 2017a) and *ISO 18406 Underwater Acoustics – Measurement of Radiated Underwater Sound from Percussive Pile Driving* (ISO, 2017b). Where symbols for non-SI units are needed, IEEE Standard 260.1 (Institute of Electrical and Electronics Engineers [IEEE], 2004) is followed. The SELss are not frequency-weighted unless explicitly stated.

Sensation Levels of Airgun Exposures—SnLs (Ellison et al., 2012; Houser et al., 2017) of the airgun exposures were estimated in the indoor and outdoor pools at the location of the hydrophones (Figure 1). SnL was estimated from the level difference of the sound exposure L_E and duration-corrected hearing threshold $L_{E,\mathrm{ht}}$ in decidecade (one-tenth decade) frequency bands, as with the reference value for sound exposure:

$$\mathrm{SnL} = 10\log_{10}\left(\sum_{10\ \mathrm{Hz}}^{40\ \mathrm{kHz}} 10^{\frac{\left(L_{E,\mathrm{ddec},ss}(f)-L_{E,\mathrm{ddec,ht}}(f)\right)}{10\ \mathrm{dB}}} / E_{p,0}\right)\ \mathrm{dB}$$

The composite audiogram for cetaceans echolocating at very high-frequency (VHF) proposed by Southall et al. (2019) was adopted for the hearing threshold, and a hearing integration time, $\tau = 125$ ms, was used to correct that hearing threshold to an equivalent SEL hearing threshold (Kastelein et al., 2010) by adding $10\log_{10}(\tau/1s)$ dB.

Background Noise and Stimulus Measurements—The impulsive airgun sounds and ambient noise were measured with equipment consisting of a hydrophone (Brüel & Kjaer [B&K] – 8106; sensitivity -173 dB re 1 V/µPa) in the indoor pool and another (B&K – 8105) in the outdoor pool (1 m in front of the airgun; Figure 1), with a multichannel high-frequency analyzer (B&K Lan-XI type 3161-A-1/1) and a laptop computer with B&K PULSE software (*Labshop*, Version 20.0.0.455; high-pass filter: 22.4 Hz; sample frequency: 131,072 Hz). The system was calibrated with a pistonphone (B&K – 4223). Measurements of background noise conditions in the indoor pool showed that ambient noise levels were around or below those of Sea State 0, in agreement with earlier studies (see Kastelein et al., 2012).

Airguns—The data used for this study were collected during experiments aimed at investigating TTSs due to airgun exposures (Kastelein et al., 2017c, and an unpublished follow-up project). For this purpose, two down-scaled airguns were designed and built: (1) a smaller airgun with volume 82 cm^3 (5 in^3 [cubic inches]) and (2) a larger airgun with volume 164 cm^3 (10 in^3). The trigger required to fire the airgun was generated by a firing controller (electronic pulse generator) which controlled a solenoid valve. The operating pressure ranged from 2 to 8 bar (200 to 800 kPa).

Measuring the Reduction in Sound Level Due to the Bubble Screen for Airgun Sound—For the airgun sound spectrum measurements on both sides of the bubble screen, the smaller airgun was placed in the outdoor pool at mid-water depth (1 m), slightly off-center (Figure 1). While the airgun sound calibration measurements were made in the outdoor pool, both animals were housed in the indoor pool, and the bubble screen was deployed (Figure 2b). For the indoor pool, a single measurement at the location of the hydrophone (Figure 1) was made to quantify the effect of deploying the

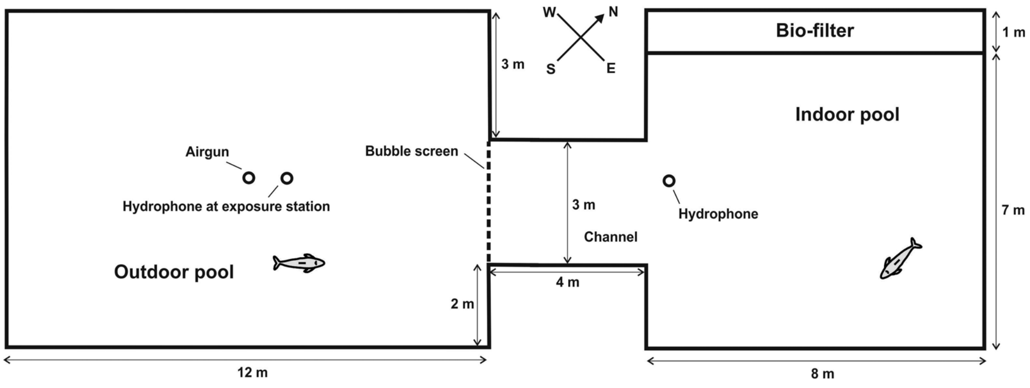

Figure 1. Top view of the pool complex consisting of an outdoor pool in which the airgun sounds were produced and where Porpoise M06 was exposed to them, and the indoor pool where Porpoise F05 was kept during exposure sessions and where both study animals were kept during sound calibration sessions. The hydrophone in the outdoor pool is at the same location as the exposure station on which Porpoise M06 stationed during exposures. The bubble screen was placed in the outdoor pool in front of the entrance to the channel (see Figure 2).

bubble screen. The measurement location was chosen such that it was aligned with the outdoor hydrophone, it was positioned in the deeper part of the indoor pool that was the preferred swimming location of the animals, and it was also more towards the entrance of the pool where we expected the highest SEL of airgun sounds in the indoor pool to occur. This measurement was used to obtain an estimate of the sound level experienced by the animal(s) in the indoor pool. The broadband SELss in the indoor pool were 144.7 dB re 1 µPa^{2}s without the screen and 141.6 dB 1 µPa^{2}s with the screen, averaged over 10 shots. Most of the energy of the airgun sounds' spectrum was below 1 kHz; peaks occurred at 50 and 500 Hz (Figure 3a). The difference in SELss measured in the indoor pool with and without the bubble screen (i.e., the insertion loss) was measured in one-third octave (base 10) bands (Figure 3).

Airgun Sounds During Behavioral Response Observations—The sound levels to which the animals were exposed varied in Exposure Condition 2 (see the next section). The sound levels at the exposure station in the outdoor pool (Figure 1)were measured in replicated sessions of single-airgun series of 10 single-airgun shots, and double-airgun series of 10 airgun shots, 20 airgun shots, and 40 shots, all carried out at 8 bar (800 kPa) operating pressure.

Maximum and minimum broadband SELs during the free-swimming exposure sessions in the outdoor pool (Exposure Conditions 1 & 3; see the

Figure 2. (a) The bubble screen rolled up above the water, and (b) the bubble screen deployed in front of the channel leading to the indoor pool

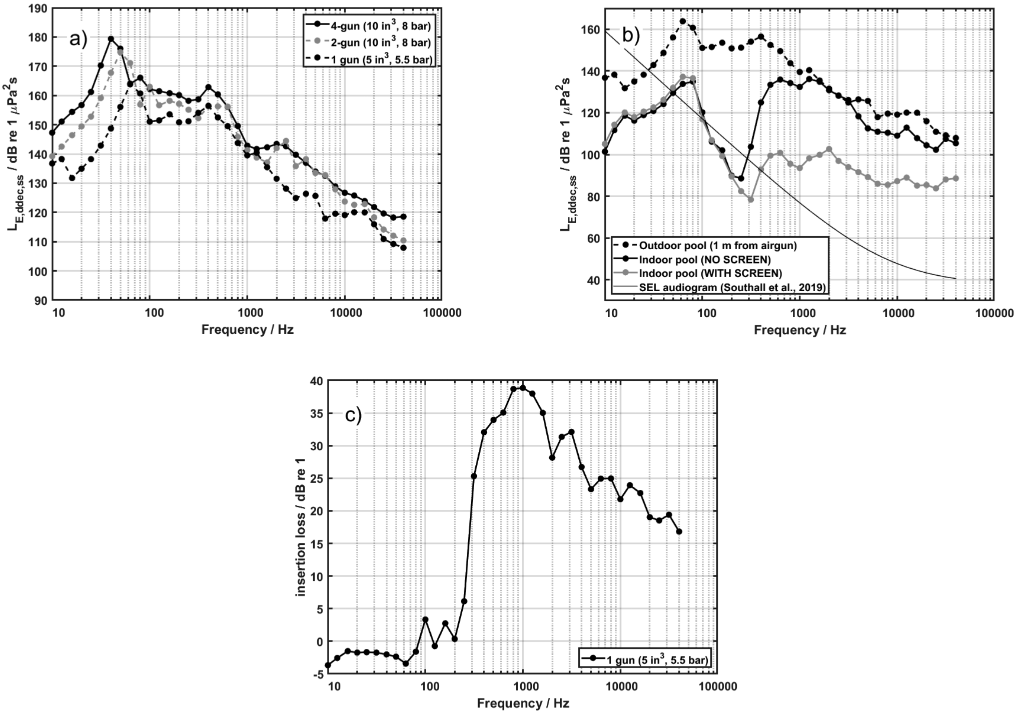

Figure 3. (a) The levels at the exposure station in the outdoor pool (recorded 1 m in front of the airgun) for three airgun set-ups (single smaller airgun fired at 5.5 bar [550 kPa], and two and four larger airguns fired at 8 bar [800 kPa]); (b) the single smaller airgun sound (averaged over five shots) measured at 1 m from the source in the outdoor pool and at the indoor measurement location with and without the bubble screen (see Figure 1); also shown is the harbor porpoises' (*Phocoena phocoena*) SEL audiogram (derived from the composite harbor porpoise audiogram in Southall et al., 2019); and (c) the insertion loss: the difference between the two indoor pool spectra shown in (b).

next section) were estimated using measurements of a single larger airgun fired at an operating pressure ranging from 2 to 8 bar and measured in the outdoor pool on a grid of locations with horizontal spacing of 1 m and at 0.5, 1, and 1.5 m depth. The mean SELss was obtained by taking the arithmetic mean over all measurement locations.

Measurements in the indoor pool of the two- and four-airgun array set-ups were not carried out. Because of slight misalignments of the two- and four-airgun array acoustic centers relative to the single-airgun exposures, estimates of the maximum levels in the indoor pool could not be made for Exposure Conditions with two- and four-airgun exposures. A comparison of the measured spectra near the source (Figure 3a) resulted in 13 to 15 dB higher sensation levels (SnLs) for the four-airgun exposure than for the single-airgun exposure. This suggests that the SnLs resulting from the four-airgun exposure in the indoor pool were also approximately 13 to 15 dB higher (SELss = 155 to 157 dB re 1 μPa²s; SnL ~58 to 60 dB) than the single-airgun exposure. Therefore, the SnLs of the four-airgun exposures with the bubble screen (Exposure Conditions 2 & 4) were lower in the indoor pool than those for the single-airgun exposure when it was fired at lower pressure without the bubble screen (Exposure Condition 1).

Behavior

As part of the exposure protocol used in the TTS study (Kastelein et al., 2017c), the animals in the indoor pool were monitored routinely to ensure that they showed no response (e.g., abnormal swimming speed, jumps, or restless behavior) to the airguns firing in the outdoor pool. An experienced observer watched the harbor porpoise(s) in the indoor pool continuously while the airguns were being fired in the outdoor pool. The experiments were designed to investigate TTS in Porpoise M06 in the outdoor pool, so only qualitative measures of response can be reported for the animal(s) in the indoor pool; no quantitative measures of behavior (e.g., respiration rate, swimming speed, or jumps; Kastelein et al., 2015) are available. In this study, a behavioral response to the airgun sound was considered to have taken place when the observer (who had experience with behavioral response studies with this animal and other harbor porpoises; Kastelein et al., 2013, 2015, 2017b, 2018a, 2018b) saw an increase in the number of jumps, respiration rate, respiration force, increasing distance to the sound source, or swimming speed (causing waves in the pool).

Exposure Conditions
The behavior of the harbor porpoises in the indoor pool was observed under four Exposure Conditions (summarized in Table 1); the data for this study were collected between June 2016 and January 2017:

1. The SEL was increased in the hope of eliciting TTS (Kastelein et al., 2017c) during 10 airgun exposure sessions (10 shots; one shot every 4 s) with Porpoise F05 in the indoor pool and Porpoise M06 in the outdoor pool swimming freely (no bubble screen). The behavioral responses observed under this condition led to the construction of the bubble screen in an attempt to reduce unnecessary exposure to sound for Porpoise F05.

2. TTS in Porpoise M06 could not be elicited in Exposure Condition 1, so he was trained to approach the airguns during the exposures (in Kastelein et al., 2017c, there were one to two airguns; in a follow-up study, four airguns were used). This resulted in 233 airgun exposure sessions (various airgun volumes and pressures) with Porpoise F05 in the indoor pool behind the bubble screen and Porpoise M06 at the exposure station during airgun shots in the outdoor pool. The average session shot interval range was 13 to 17 s.

3. In the follow-up study with four airguns, TTS could not be elicited in Porpoise M06 at the exposure station after 40 shots (the maximum number that could be achieved with training, as the porpoise had eaten 40 rewards in a session) with a mean shot interval of 13 s. Therefore, the exposure SEL was increased by allowing Porpoise M06 to swim freely in the pool while experiencing shot intervals of 4 s (though the received SPL was reduced by a few dB, the shot interval was decreased from ~13 to 4 s, and the exposure duration was increased from around 9 min to 30, 60, and 90 min). This resulted in 30 sessions in which Porpoise F05 was in the indoor pool behind the bubble screen, and Porpoise M06 was swimming freely in the outdoor pool during airgun shots (every 4 s).

4. During six airgun calibration sessions (1 to 2 h of airgun shots every 10 s), during which the airguns were fired every 10 s in the outdoor pool, both harbor porpoises were in the indoor pool behind the bubble screen.

Table 1. Summary of Exposure Conditions in which two harbor porpoises (*Phocoena phocoena*) were exposed to intermittent airgun sounds, showing the presence or absence of the bubble screen between the outdoor and indoor pools, and the location of the animals during the exposure. Exposure Conditions 1 through 3 were airgun exposure sessions; Exposure Condition 4 was a sound calibration session.

Exposure Condition	Number of airguns	Total airgun volume (in^3)	Airgun pressure (bar)	Shot interval (s)	Number of successive shots	Exposure duration (min)	Bubble screen	Location of harbor porpoises	
								M06	F05
1	1	10	2 to 4	4	10	0.75	Absent	Outdoor pool (swimming freely)	Indoor pool
2	1 to 4	10 to 40	8	Varying (session average range: 13-17)	10 to 40	0.75 to 2.7	Present	Outdoor pool (at exposure station)	Indoor pool
3	1	10	8	4	450 to 1,350	30 to 90	Present	Outdoor pool (swimming freely)	Indoor pool
4	1 to 4	5 to 40	2 to 8	10	360 to 720	60 to 120	Present	Indoor pool	Indoor pool

Results

Effect of Bubble Screen on Sound Spectrum

The bubble screen reduced the transmission of high-frequency airgun sounds from the outdoor pool to the indoor pool by 20 to 40 dB in one-third octave (base 10) bands above 250 Hz (Figure 3b & c). The maximum reducing effect of the bubble screen was found near 1 kHz, which corresponds to the estimated Minnaert resonance frequency of the air bubbles. A slight increase (~3 dB) in the low-frequency range (below 80 Hz) was observed. The broadband SELss in the indoor pool was approximately 3 dB lower when the bubble screen was deployed than when it was not.

Qualitative Observations of Effect of Bubble Screen on Behavior

In Exposure Condition 1, with Porpoise F05 in the indoor pool and Porpoise M06 in the outdoor pool, both swimming freely with no bubble screen (10 sessions), Porpoise F05, in the indoor pool, responded strongly even to the lowest SELss achieved with the single airgun (145 dB re 1 µPa^{2}s). In the outdoor pool, Porpoise M06 did not respond up to SELss of 156 dB re 1 µPa^{2}s but did respond to higher SELss.

In Exposure Condition 2, with Porpoise F05 in the indoor pool during airgun sessions and Porpoise M06 in the outdoor pool with the bubble screen, Porpoise F05 showed no behavioral response to the airgun sounds during all 233 sessions. Porpoise M06 was participating in airgun sound exposure sessions and was trained to swim to the exposure station up to 40 times in quick succession (average session shot interval range: 13 to 17 s). He did not increase his respiration rate, swimming speed, nor number of jumps.

In Exposure Condition 3, with Porpoise F05 in the indoor pool, and with Porpoise M06 swimming freely in the outdoor pool exposed to airgun sound (shot interval: 4 s), with the bubble screen, strong behavioral responses were observed in Porpoise M06 during all 30 sessions: he increased his swimming speed and respiration rate, and he swam around the perimeter of the pool, avoiding the location of the airguns. During these exposure sessions, Porpoise F05 was in the indoor pool on the other side of the bubble screen and showed no response to the airgun sounds.

In Exposure Condition 4, with Porpoises F05 and M06 both swimming freely in the indoor pool during six calibration sessions (lasting 1 to 2 h) in which the airgun SELss distribution in the outdoor pool was measured with the bubble screen in place (one shot every 10 s), neither animal responded to the sounds.

Discussion

The observations reported herein support the idea that the frequency content of impulsive sounds is an important driver for the behavioral responses of harbor porpoises to the sounds (Tougaard et al., 2015; Wensveen, 2016). Although the broadband SELss in the indoor pool with and without the bubble screen differed by only ~3 dB, the reduction in the sound energy above 250 Hz when the

Table 2. Summary of responses observed under four airgun Exposure Conditions for harbor porpoises in the outdoor pool (where the airgun was firing) and in the indoor pool (with and without the bubble screen). Ranges of unweighted broadband SELss are indicated. Exposure Conditions 1 through 3 were airgun exposure sessions; Exposure Condition 4 was a sound calibration session.

Exposure Condition	Observed responses in outdoor pool	Outdoor pool SELss (dB re 1 µPa^{2}s)	Observed responses in indoor pool	Indoor pool SELss (dB re 1 µPa^{2}s)
1 (no screen)	M06 swimming freely; no behavioral response up to SELss 156 dB SEL	156-160[1]	F05 swimming freely; strong behavioral response to all SELss	145-149[2]
2 (screen)	M06 at exposure station; trained to participate in repeated exposures	175-183[3]	F05 swimming freely; no behavioral response to all SELss	149-157[2]
3 (screen)	M06 swimming freely; increased swimming speed, increased respiration, and avoidance of airgun location	164[1]	F05 swimming freely; no behavioral response to all SELss	149[2]
4 (screen)	--	--	F05 and M06 swimming freely; no behavioral response to all SELss	143[4]-157[2]

[1] Arithmetic mean of measured levels in the outdoor pool

[2] Prediction at indoor pool hydrophone location (see "Methods" section for details)

[3] Measured level at the exposure station in the outdoor pool (i.e., location of the hydrophone)

[4] Measured level at the indoor pool hydrophone location

screen was deployed had a marked effect on the behavioral response of the harbor porpoises.

The two study animals responded differently to the airgun sounds (Exposure Condition 1; Table 2): Porpoise M06 showed no response up to a mean received SELss of 156 dB re 1 µPa^{2}s, whereas Porpoise F05 increased he r swimming speed, respiration rate, exhalation force, and number of jumps (typical responses to sound; Kastelein et al., 2013) already at a mean received SELss of 145 dB re 1 µPa^{2}s. When the bubble screen was deployed, Porpoise F05, the more responsive of the two harbor porpoises, did not react to the airgun sounds at any level used in the TTS study.

Porpoise M06 cooperated willingly during the TTS study (Kastelein et al., 2017c) and allowed himself to be exposed to up to 40 airgun shots per session of SELss = 182 dB re 1 µPa^{2}s (SnL ~81 dB). However, during the free-swimming exposures (Exposure Condition 3), Porpoise M06 did respond to the airgun sounds at SELss of 164 dB re 1 µPa^{2}s. He may have learned to cope with high airgun sound levels at the exposure station due to positive reinforcement during training. Also, an analysis of changes in Porpoise M06's susceptibility to TTS during the study suggests that he may have learned to suppress his hearing sensitivity to reduce the loudness of the sound (unpub. research). Therefore, it is unlikely that his response to the airgun sounds at the exposure station in the pool reflects the response of a naïve animal in the wild. Individual differences in responsiveness have been demonstrated in other marine mammal species (e.g., Houser et al., 2013a, 2013b) and in wild harbor porpoises exposed to airguns (van Beest et al., 2018). These individual differences may be related to many factors such as age, sex, personality, history, and body condition. The availability of only two animals prevents us from drawing conclusions on what factors were prevailing here.

Based on their reviews of data on harbor porpoises exposed to sound, Tougaard et al. (2015) and Wensveen (2016) suggested that responsiveness increases for SnLs above ~45 to 50 dB. Recent measurements of responses of harbor porpoises in the field suggest a response threshold audiogram-weighted SELss of 112 to 116 dB re 1 µPa^{2}s (van Beest et al., 2018), which corresponds to SnLs of ~67 to 71 dB. The broadband SnLs reported by van Beest et al. (2018) appear to be consistent with the exposure-level range at which the harbor porpoises responded to airgun sounds in the present study. The observed SnL of 45 to 60 dB at which Porpoise F05 did not respond was in the range of onset thresholds as reported by Tougaard et al. (2015) and Wensveen (2016).

Other sound parameters may determine the onset and severity of behavioral responses (e.g., Götz & Janik, 2011; Kastelein et al., 2014). These parameters include the sound's duration, duty cycle (continuous vs intermittent sounds, and in intermittent sounds, the combination of pulse duration and inter-pulse interval), type (tonal, sweeps, warble, noise, impulsive, non-impulsive, etc.), type of sweep (upsweep vs downsweep), and signal rise-time or kurtosis. The dataset presented in this study cannot be used to tease out the relative importance of these parameters.

Further dedicated experiments are required to quantify more precisely the effect of the frequency content of impulsive sounds on the responses of marine mammals. Such experiments should include more quantitative observations of behavior (e.g., Kastelein et al., 2011, 2013), systematic exposure conditions, and detailed characterization of the sound field in the entire pool (instead of at a single measurement location as was done in the present study). A dose-escalation experimental set-up, with different ratios of low-frequency (< 250 Hz) to high-frequency (> 250 Hz) energy (e.g., achieved by the use of a bubble screen), could be used to establish whether SELss or frequency-weighted SELss (as a proxy of SnL or loudness) correlates better to onset and severity of behavioral disturbance.

The hypothesis that the SnL or loudness level of the spectrum of a sound is an important driver for behavioral responses of harbor porpoises to sounds has implications for mitigation strategies, as many methods are more effective at shielding high-frequency sounds than low-frequency (< 250 Hz) sounds. Measures such as bubble screens are typically effective at reducing the energy above 100 Hz of broadband impulsive sounds—for example, sounds generated by airguns, detonations, and percussion pile driving (Bellmann, 2014; Lee et al., 2016; Dähne et al., 2017; Tougaard & Dähne, 2017; Brandt et al., 2018). In addition, new airguns are being designed that have reduced high-frequency components (outside the frequency band required to detect gas and oil; Coste et al., 2014). These new designs may both reduce the risk of hearing loss in harbor porpoises (Kastelein et al., 2017b) and reduce behavioral disturbance by the sounds.

The dependence of behavioral disturbance of harbor porpoises on the frequency content of sounds suggests that there may be a decrease in response with distance that is stronger than that suggested by the attenuation of the broadband SELss with distance. High-frequency sound is attenuated more strongly in water than low-frequency sound, and it is also more likely to be masked by ambient sound, which could reduce the potential for disturbance even further (e.g., Kastelein et al., 2011).

The present study shows that bubble screens can be useful to protect the welfare of harbor porpoises in captivity. Experimental set-ups with small bubble screens, as used in the present study, could be utilized to improve the living conditions of captive porpoises by reducing background noise levels, especially in the presence of loud broadband noise sources such as those sometimes used during construction activities.

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