Aquatic Mammals 2015, *41*(4), 400-411 DOI 10.1578/AM.41.4.2015.400

Behavioral Responses of a Harbor Porpoise (*Phocoena phocoena*) to 25.5- to 24.5-kHz Sonar Down-Sweeps With and Without Side Bands

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Abstract

Signals used in naval and long-range fish detection sonar often contain harmonics which may influence the behavior of harbor porpoises (*Phocoena phocoena*) more than the lower fundamental frequencies, so the behavioral effects of 25-kHz FM signals with and without high-frequency side bands (71 and 121 kHz) on a harbor porpoise were quantified in a pool. Sequences of sonar signals were transmitted at four average received sound pressure levels ($SPLs_{av.re.}$) to determine the dose-response relationship. Sequences, lasting 30 min, consisted of 50 ms, 25.5- to 24.5-kHz down-sweeps (2-s pulse interval), with and without side bands, with identical SPLs at the fundamental frequency. Behavioral effects were quantified as the harbor porpoise's distance from the transducer, respiration rate, number of jumps, and relative swimming speed. The distance to the transducer changed little in response to the sounds. Respiration rate increased with increasing SPL to maximum respiration rate increases of ~39%, accompanied by jumps, for sweeps with side bands at an $SPL_{av.re.}$ of 148 dB re 1 µPa. At similar broadband SPLs, signals with side bands had a greater effect on the harbor porpoise's behavior than signals without. Side bands may influence behavioral responses, both by making sounds more audible and by affecting the way sounds are perceived by harbor porpoises. Mitigation of active sonar impact could be achieved by reducing the level of side bands (or harmonics). This would benefit species, such as the harbor porpoise, that are likely to have lower hearing thresholds for the frequencies of the harmonics than for the fundamental frequency.

Key Words: fisheries sonar, naval sonar, noise impact, behavior, mitigation, odontocete

Introduction

Active sonars used in anti-submarine warfare produce intermittent underwater noises of various types, including frequency swept signals (sweeps). Some navies operate in the Baltic Sea, which is relatively shallow (increasing the occurrence of reverberations) and has low salinity (reducing sound absorption). Under these conditions, naval operatives use active sonar systems with specific sounds which are of higher frequencies than those used by most North Atlantic Treaty Organization (NATO) navies (Pihl & Ivansson, 2009). Such sounds are often ultrasonic. Worldwide and on a much larger scale, long-range fish detection sonars such as SIMRAD SU90 and SX90 make use of similar signals: high-power, 20- to 30-kHz narrow-band FM chirps (Simrad, 2015a, 2015b).

Marine mammals use sound as a means of orientation; communication; and for locating prey, conspecifics, and predators (Richardson et al., 1995). Therefore, marine mammals are likely to be disturbed by noise in their environment, which may cause negative behavioral, physiological, and auditory effects (e.g., masking or temporary and permanent hearing threshold shifts) (Nowacek et al., 2007; Wright et al., 2007).

The potential effects of high-frequency sonar signals on the hearing and behavior of the harbor porpoise (*Phocoena phocoena*) are of particular interest because this small odontocete occurs in the Baltic Sea as well as in the coastal waters of the North Atlantic, North Pacific, North Sea, and Black Sea, and has acute hearing (the 50%

hearing threshold between 100 and 140 kHz is ~33 dB re 1 μPa). This species also has functional hearing over a very wide frequency range (range of best hearing, defined here as within 10 dB of maximum sensitivity, is from 16 to 140 kHz; Kastelein et al., 2002, 2009, 2010). Harbor porpoises are relatively easily deterred by anthropogenic underwater noises (Amundin & Amundin, 1973; Polacheck & Thorpe, 1990; Kastelein et al., 1995, 1997, 2000, 2001, 2005b, 2006; Laake et al., 1998; Culik et al., 2001; Johnston, 2002; Olesiuk et al., 2002; Koschinski et al., 2003; Teilmann et al., 2006; Tougaard et al., 2009). Behavioral response threshold levels of harbor porpoises have been determined for noise bands and tonal signals around 12 kHz (Kastelein et al., 2005b), for a continuous 50 kHz tone (Kastelein et al., 2008a), and for continuous and pulsed 70 and 120 kHz tones (Kastelein et al., 2008b). The spectrum and the perceived level of an underwater noise, in combination with the duty cycle (i.e., signal duration and presentation rate), appear to determine the effect that sound has on the behavior of harbor porpoises.

The hearing sensitivity of harbor porpoises increases with increasing frequency up to about 125 kHz (Kastelein et al., 2010). As a result, the sensation level (i.e., the difference between the SPL of the sound and the 50% hearing threshold at a specific frequency), as experienced by the harbor porpoise, may be higher for the high-frequency content (e.g., the harmonics) of certain complex sounds than for the fundamental frequency. This means that the harbor porpoise perceives these harmonics to be louder than the fundamental frequency sounds. The broadband hearing thresholds of a harbor porpoise for 1- to 2-kHz sweeps (signals resembling those used in low-frequency active sonar) with harmonics of a certain level were lower than the thresholds for the same fundamental sweeps without harmonics (Kastelein et al., 2011a). In addition, an individual harbor porpoise responded more strongly to sweeps with harmonics than to sweeps without harmonics with the same broadband sound pressure level (SPL; Kastelein et al., 2012).

The fundamental frequencies of the signals of naval sonar systems used in the Baltic Sea and around the world in fisheries (generally around 25 kHz) are higher than those of mid-frequency (6 to 7 kHz) and low-frequency (1 to 2 kHz) naval sonar systems. Many sonar signals also contain a great deal of energy in the higher frequencies (harmonics). If the effect of the sonar signals on harbor porpoise behavior is influenced by these harmonics, mitigation could be achieved by reducing their level. Therefore, the goal of the present study was to compare the behavioral response of a harbor porpoise to a series of frequency modulated (FM) sonar signals with the same fundamental frequency (25 kHz), but with and without high-frequency harmonic content.

Methods

Study Animal and Study Area

The male harbor porpoise (ID No. 02) was 7 y old at the time of the study (body mass: ~ 40 kg, body length: 146 cm). His hearing was assumed to be representative for harbor porpoises of his age and was similar to that of two other young harbor porpoises (Kastelein et al., 2002, 2009, 2010). The study animal received four meals of fish per day.

The study animal was kept at the SEAMARCO Research Institute, the Netherlands, in a pool complex specifically designed and built for acoustic research, consisting of an indoor pool (described in detail by Kastelein et al., 2010) connected to an outdoor pool (12 × 8 m, 2 m deep) in which this study was conducted. During the study, the animal could move freely in the large outdoor pool, and the gate to the indoor pool was closed. The walls of the outdoor pool were covered with 3-cm thick coconut mats with their fibers embedded in 4-mm thick rubber (reducing reflections mainly above 25 kHz). The bottom was covered with sand. The water circulation system and aeration system for the biofilter were made as quiet as possible and were switched off 30 min before research sessions and kept off during sessions so that there was no current in the pool during sessions. The equipment used to produce the sound stimuli was housed out of sight of the study animal in a research cabin next to the pool. For more details of the study area, see Kastelein et al. (2012).

Audio Equipment, Test Stimuli, and Video Recording

The digitized sequences (WAV files; sample frequency 96 kHz, 16-bit) were played back by laptop computer 1 (Acer Aspire – 5750) with a program written in *LabVIEW*, Version 2010, to an external data acquisition card (National Instruments – USB6259), the output of which was digitally controlled in 1 dB steps with the *LabVIEW* program. The sounds were projected under water via a toroidal beam transducer (EDO Western Corporation-TB 337; resonance frequency ≥ 37 kHz). The transducer was suspended 1 m below the water surface at one end of the pool.

The signals used in this study were not intended to mimic specific sonar signals as, during operation, the spectra of the signals can be varied by the sonar operator depending on the situation, and also because they depend on the transmission source level. Therefore, a generic sweep in the general fundamental frequency band of high-frequency naval and fisheries sonars was used. Two sound types were tested: (1) a hyperbolic (Ainslie, 2010) FM signal centered around 25 kHz (a down-sweep from 25.5 to 24.5 kHz) with high-frequency side bands centered around 71 and 121 kHz (for the spectrum, see Kastelein et al., 2015), without amplitude on and off ramps; and (2) the same hyperbolic FM signal centered around 25 kHz without side bands (Figure 1). The side bands were produced in the electronic sound generating system and were not onset artifacts or harmonics. Signals without side bands were produced with the same WAV files, but filtered with a 35-kHz low-pass filter (Krohn-Hite – 3362, Butterworth; 48 dB/octave). Even at the highest output SPL used in the study, the spectra of both signals remained undistorted.

The output of the sound system to the transducer was monitored by means of an oscilloscope (Tektronix – 2201), a voltmeter (Agilent – 34401A), and a spectrum analyzer (Velleman – PCSU1000). The attenuation system was linear over the entire SPL range used in the study.

During test sessions, the animal was filmed from above by a waterproof camera (Conrad – 750940) with a wide-angle lens and a polarized filter to prevent saturation of the video image by glare from the water surface. The camera was placed on a pole 9 m above the water surface on the northwestern side of the pool. The entire surface of the pool was captured on the video image. The output of the camera was fed through a video multiplexer (MX-8-CSX) which added the time and date to the images. Thereafter, the output was digitized by an analog-to-digital converter (König – grabber) and stored on laptop computer 2 (Medion – MD96780). The animal was also filmed by two black and white video cameras (Ocean Systems Inc. – Delta Vision) on the northwestern side of the pool, just above the water surface. The images from these cameras were visible to the operator on two monitors in the research cabin.

The background noise was monitored up to 16 kHz via a hydrophone (Labforce – 90.02.01; 0.1 to 60 kHz) and a custom-made conditioned charge pre-amplifier (SEAMARCO – CCAMS1000-3). The output of the pre-amplifier was digitized via the analog-to-digital converter and recorded on laptop computer 2 in synchrony with the video images. The output of the pre-amplifier was also fed to an amplified loudspeaker (Medion – MD5432) so that the operator in the research cabin could monitor the background noise during sessions.

The sequences of the test sound were recorded via a custom-built hydrophone and a custom-built ultrasound detector, and were stored on laptop computer 2. The output of the ultrasound detector was fed into the other audio channel of the analog-to-digital converter and, thus, also was recorded in synchrony with the video images. The operator could check the underwater transmission of the test sounds via the loudspeaker of the ultrasound detector. The recordings from the ultrasound detector were not used for sound measurements.

SPL of the Playback Sequences

The two sound types were each produced in 30-min sequences of 878 signals and were characterized in terms of their broadband SPL (in dB re 1 μPa, root mean square). The duration (t90) was determined as the time interval between the points when the cumulative sound exposure reached 5 and 95% of the total exposure—that is, the duration contained 90% of the total energy in the signal (Madsen, 2005). The mean t90 of the signal was 43 (SD: ± 10 ms). The SPL was determined from the power sum of 1/3-octave bands from 1 to 160 kHz (broadband), taking into account the frequency-dependent sensitivity of the hydrophones. The harbor porpoise was exposed to average received (based on all 154 measurement locations in the pool; Figure 2) broadband SPLs between 77 and 148 dB re 1 μPa (Table 1). The SPL range was established during a previous study with the FM signals with side bands (Kastelein et al., 2015). The range was limited at the low end by a level which elicited no response and at the high end by the maximum level that could be produced without distortion of the signals. The 1/3-octave SPL of the fundamental frequency (25 kHz) was equal for both signal types, but the broadband SPL of the FM signal with side bands was on average 6 dB higher than that of the signal without side bands.

The SPL in the pool was measured when sonar signal sequences were being produced and the animal was not present. The recording and analysis equipment consisted of two hydrophones (Brüel & Kjær [B&K] – 8106; 0.1 to 100 kHz) with a multichannel high-frequency analyzer (B&K PULSE – 3560 D), and laptop computer 3 with software (B&K PULSE, *Labshop*, Version 12.1). The system was calibrated with a pistonphone (B&K – 4223); the sample rate was 524.288 Hz.

Acoustic Measurements and Sound Distribution in the Pool

To determine the sound distribution in the pool, the SPL for the 25-kHz sweep with side bands was measured at 77 locations at two depths (0.75 and 1.5 m). The received SPLs of one signal per sequence per location at the 154 positions in the pool are shown in Figure 2. The received

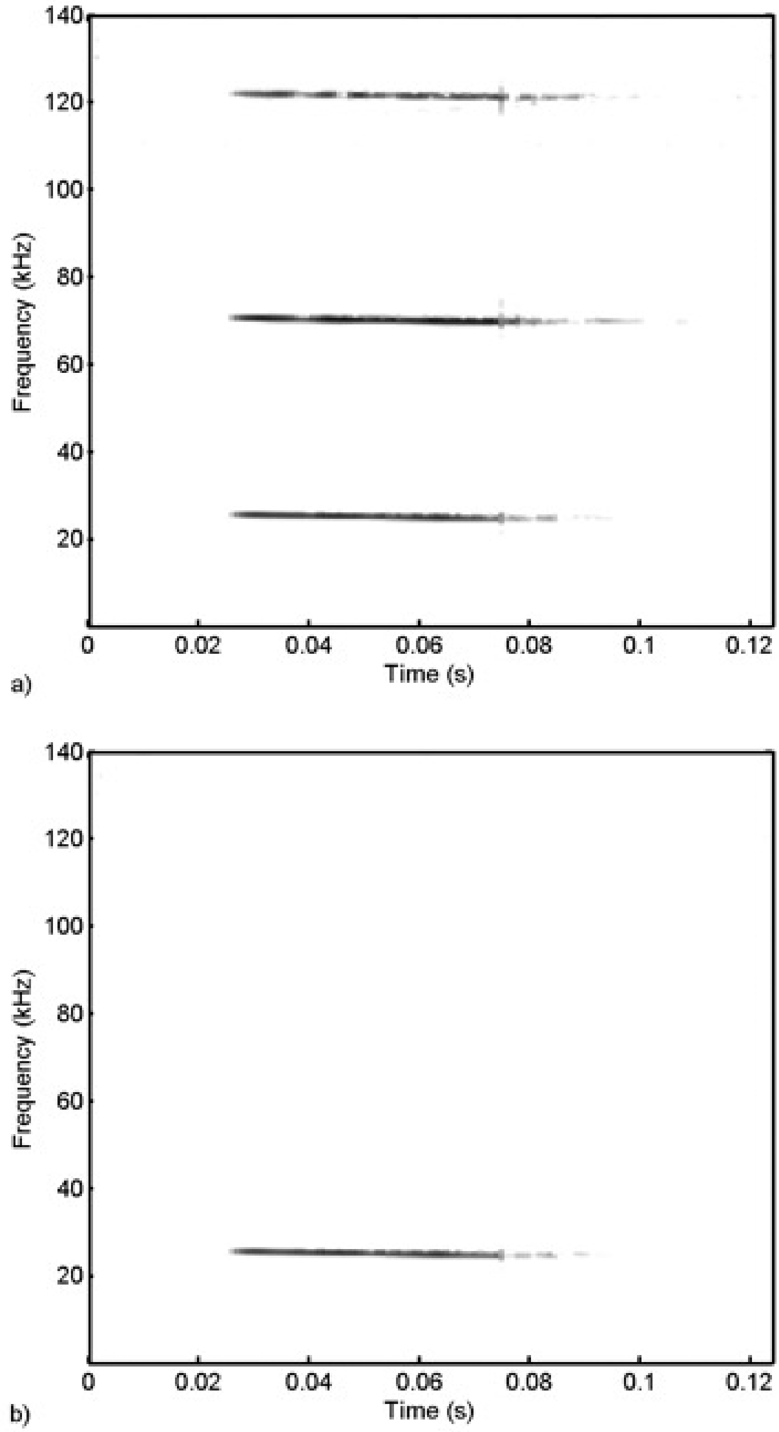


Figure 1. Sonograms of the 50-ms, 25.5- to 24.5-kHz down-sweep with side bands (a), and only the 25.5- to 24.5-kHz down-sweep (b), from recordings made in the outdoor pool 2 m from the source; the average received broadband SPL was 148 dB re 1 µPa for the signal with side bands (a) and 142 re 1 µPa for the signal with the 25-kHz fundamental frequency only (b).

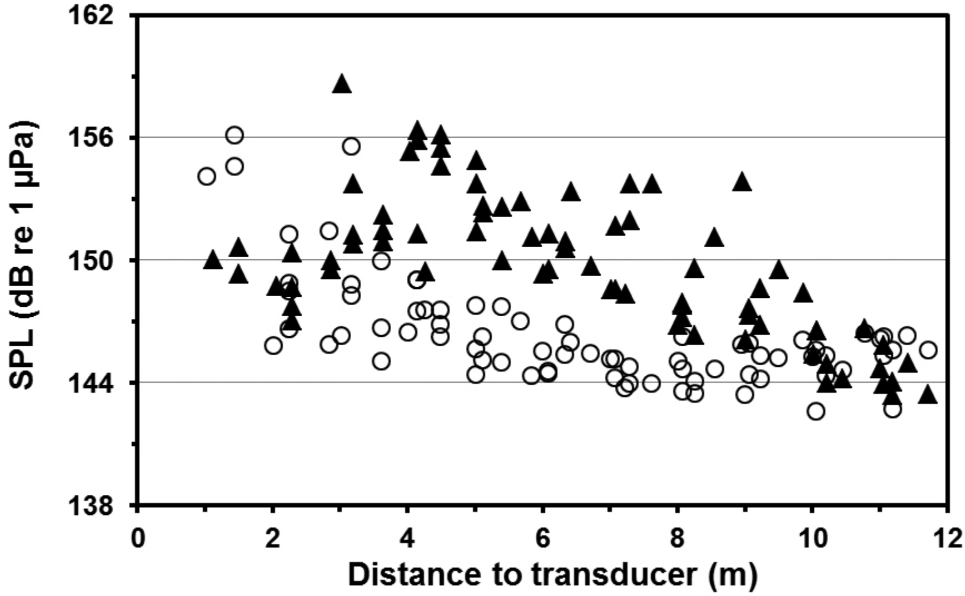


Figure 2. The 1/3-octave SPL distribution in the pool as a function of the distance to the transducer for two depths (0.75 m: ○ and 1.5 m: ▲) for the 25-kHz sweeps with side bands (77 measurement locations per depth) at a broadband $SPL_{av.re.}$ of 148 dB re 1 μPa

Table 1. The four average received broadband SPLs (up to 160 kHz; averages based on all 154 measurement locations in the pool; Figure 2) of the 25-kHz sonar sweep with side bands to which the harbor porpoise (*Phocoena phocoena*) was exposed in sequences. Levels were based on results from a previous behavioral response study (Kastelein et al., 2015) in which the same FM sweeps with side bands were used (respiration rate increases quantified for that study are also shown here). The FM sounds without side bands (created by using a 35-kHz low-pass filter) were also produced at four broadband SPLs (6 dB lower than those of the sound type with side bands, but with equal energy in the fundamental frequency).

Average received broadband SPL of the 25-kHz sweep with side bands (dB re 1 μPa)	Increase in respiration rate relative to baseline level (Kastelein et al., 2015)
77	<10% (just no effect)
125	20-35%
137	35-40%
148	50-55%

levels were generally higher at 1.5 m deep than at 0.75 m deep, and at each depth these levels decreased slightly with increasing distance from the transducer (the lack of a gradient was due to reverberations). The SPL varied due to depth almost as much as due to distance. The harbor porpoise swam freely throughout the pool during test periods, so the average received SPL ($SPL_{av.re.}$) was calculated as the mean of all 154 broadband SPL measurements in the pool at each of the four source levels at which the two signals were tested (Table 1).

Background Noise Level

The background noise in the pool between 1 and 160 kHz was measured twice during the study under test conditions (see "Experimental Procedure"). The background noise level was so low that above 3.5 kHz, the level was mainly determined by the self-noise of the recording equipment.

Experimental Procedure

The transducer producing the sequences was positioned in the water at the southwest end of the pool 10 min before the first session of each day. Sessions consisted of a 30-min baseline period (no sound emission), followed by a 30-min test period (sound emission). A post-exposure observation period was deemed unnecessary due to quick recovery times observed in previous acoustic behavioral response experiments with harbor porpoises (see "Discussion"). In each session, one sound type (FM sweeps with or without side bands) was tested at one of the four source levels. Both signals had durations of 50 ms (mean t90 was 43 ms), and sequences consisted of signals separated by intervals of 2 s, resulting in duty cycles of 2.4%. Each of the eight combinations (2 sound types × 4 SPLs) was tested in six sessions (48 sessions in all) in random order. To prevent disturbance and masking of the signals by background noise, tests were carried out only during test conditions (i.e., no rain, wind force below Beaufort sea state 5; only the operator in the research cabin within 10 m of the pool). Usually one or two sessions were conducted per day, 5 d/wk, beginning between 0900 and 1600 h in April and May 2012.

Response Parameters and Behavioral Data Recording

Three objective behavioral parameters were used to quantify the harbor porpoise's responses to the signal sequences: (1) his distance from the transducer (surfacing locations only), (2) his respiration rate (respirations were audible to the operator), and (3) the number of times he jumped out of the water. These parameters were quantified for baseline and test periods.

To determine whether the study animal responded to the sounds by swimming away from the sound source, the locations where the harbor porpoise surfaced during the baseline and test periods were recorded on a grid superimposed on the computer screen. The grid corresponded to a pool grid of 1 × 1 m and was made by connecting lines between 1-m markers on the pool's sides. The grid square in which the harbor porpoise surfaced (or the grid square towards which he was heading if he surfaced exactly on a grid line) was determined, and the center point of the grid square was used to calculate the distance between the harbor porpoise's surfacing location and the transducer via triangulation. The water was always clear; and when light conditions (which depended on the weather and the time of day) were such that the bottom of the pool was visible, the harbor porpoise could be seen well below the water surface on the images from the camera. Such observations showed that the surfacing locations were a good indication of the harbor porpoise's general swimming area.

To determine whether the harbor porpoise responded to the sounds by increasing his respiration rate, the number of respirations in each baseline period was compared to the number during the test period.

In addition to the objective behavioral parameters (i.e., distance from the transducers, respiration rate, and number of jumps), a subjective behavioral parameter was recorded for each of the three 10-min sections of each test period: the harbor porpoise's swimming speed relative to the preceding baseline period (classed as 0: no difference in swimming speed; 1: increased swimming speed; or -1: decreased swimming speed). The average of the three 10-min sections (for each signal-sound level combination) was used to evaluate the change in swimming speed relative to the 30-min baseline period (which, by definition, had swimming speed class 0).

Analysis

Paired *t*-tests were used to compare in detail the distance from the transducer, the respiration rate, and the swimming speed in baselines and associated 30-min test periods. Bonferroni corrections were applied to the paired *t*-tests, resulting in a level of significance of 1.25%.

ANOVA was used to evaluate variation in the relative respiration rate (calculated as test minus baseline) due to the factors "sound type" (FM sweeps with or without side bands) and "level" ($SPL_{av.re.}$). Post-hoc Tukey tests were used to compare levels of SPL for which a significant effect was identified.

For all analyses, assumptions of the tests were conformed to Zar (1999), and analysis was carried out with *Minitab 13*. For the ANOVA, the general linear model procedure was used, and the level of significance was 5% (Zar, 1999).

Results

During the 48 baseline periods, the harbor porpoise usually swam large clockwise ovals in the pool, often surfacing multiple times in the same grid square. The mean distance between the animal's surfacing locations and the transducer (5.9 ± 1.1 m - mean ± standard deviation [SD]) and his respiration rate (104 ± 9 breaths in 30 min) were similar in all 48 baseline periods, and the harbor porpoise jumped only once.

Comparison of baseline and test sessions showed that, during test sessions with sequences of 25-kHz signals with side bands, the harbor porpoise's mean distance to the transducer increased slightly (as the SPL gradient in the pool was limited due to reverberations), but significantly, to a mean distance of 6.2 m, only at an $SPL_{av.re.}$

Table 2. *Baseline vs test*: Results of Bonferroni-corrected paired *t*-tests to compare the harbor porpoise's distance from the transducer, respiration rate in baseline and associated test periods, and swimming speed relative to zero (the baseline level) at four $SPLs_{av.re.}$ (dB re 1 µPa), for each sound type (sweeps centered at 25 kHz with and without side bands; see also Figures 3 & 4). The sample size for each test is six. Exact uncorrected *p* values are shown in bold where significant; NS = not significant ($\alpha = 0.0125$ following Bonferroni correction). In all cases for which the test was significant, the value for the test period was greater than that for the baseline period. The total number of jumps in test periods is also shown for each of the four $SPLs_{av.re.}$ for each sound type. Only one jump occurred in a baseline period before a test period of 25 kHz without side bands at 142 dB re 1 µPa.

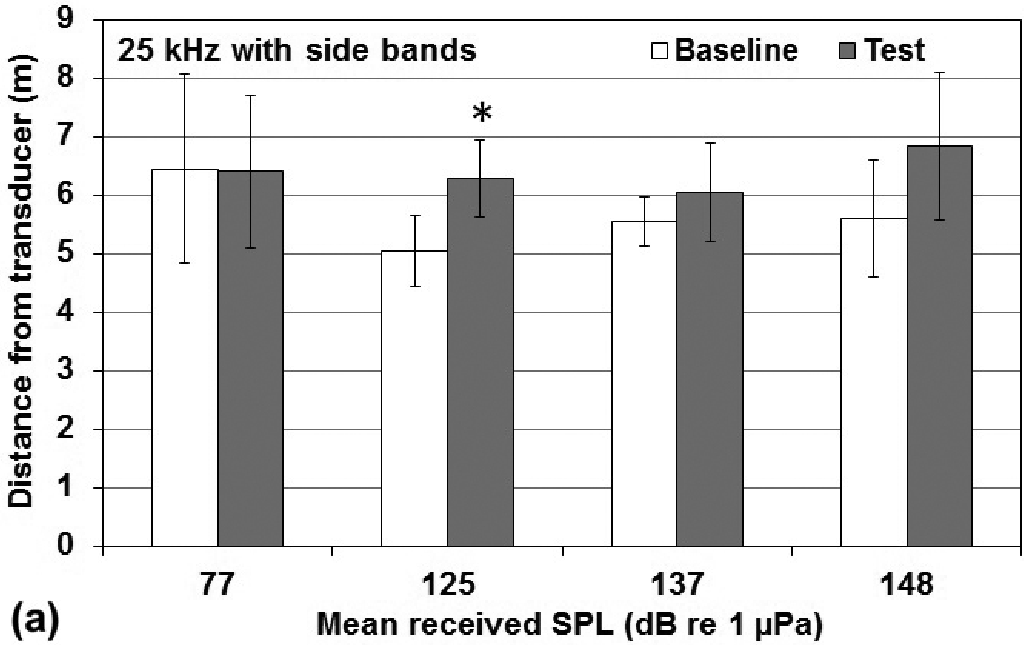
Mean received broadband SPL (dB re 1 µPa)	Distance to transducer	Respiration rate	Total jumps in 6 test periods	Swimming speed
		25 kHz with side bands		
77	0.915 (NS)	**0.006**	0	0.175 (NS)
125	**0.002**	**0.001**	3	0.025 (NS)
137	0.091 (NS)	**0.002**	5	**< 0.001**
148	0.026 (NS)	**0.001**	9	*
		25 kHz		
71	0.704 (NS)	0.020 (NS)	0	†
119	0.425 (NS)	0.024 (NS)	2	0.017 (NS)
131	0.327 (NS)	**0.001**	5	**0.003**
142	0.962 (NS)	**0.005**	6	**0.001**

*No analysis conducted as all values for relative speed were identical (+1, indicating increased speed in all test periods).
†No analysis conducted as all values for relative speed were identical (0, indicating that the swimming speed in all test periods was the same as in associated baseline periods).

of 125 dB re 1 µPa (Figure 3a). The number of respirations increased significantly for $SPLs_{av.re.}$ of 77 dB re 1 µPa (to 110 breaths/30 min) and higher (Figure 4a). The greatest increase in respiration rate (on average 39%) occurred in response to the sounds with side bands with an $SPL_{av.re.}$ of 137 dB re 1 µPa (140 breaths/30 min). The animal started to jump at an $SPL_{av.re.}$ of 125 dB re 1 µPa. The number of jumps increased as the $SPL_{av.re.}$ increased (Table 2). The animal's swimming speed increased relative to the baseline for $SPLs_{av.re.}$ of 137 dB re 1 µPa and up (Table 2).

Comparison of baseline and test sessions (by means of paired *t*-tests) showed that, during test sessions with sequences of 25-kHz signals without side bands, the harbor porpoise's mean distance to the transducer remained around 6 m, which was similar to the distance in the associated baseline periods, even when the $SPL_{av.re.}$ was 142 dB re 1 µPa (Figure 3b). The number of respirations increased significantly for $SPLs_{av.re.}$ of 131 dB re 1 µPa (to 140 breaths/30 min) and higher (Figure 4b). The animal started to jump at an $SPL_{av.re.}$ of 119 dB re 1 µPa. The number of jumps increased as the average received SPL increased (Table 2). The animal's swimming speed relative to the baseline increased for $SPL_{av.re.}$ of 131 dB re 1 µPa and up (Table 2).

ANOVA was used to compare the effects of sounds with and without side bands at different levels; it showed that the presence of side bands had a significant effect on the porpoise's relative respiration rate (F[1,43] = 4.40, $p = 0.042$)—a greater increase in respiration rate was observed in response to slightly higher broadband SPL sounds with side bands than in response to slightly lower broadband SPL sounds without side bands. There was also a significant effect of level (F[1,43] = 1,604.8, $p < 0.001$). Post-hoc Tukey tests showed that the harbor porpoise's relative respiration rate was statistically similar at the lowest two of the four $SPLs_{av.re.}$ (71 without side bands/77 with side bands, and 119/125 dB re 1 µPa), at 119/125 and 142/148 dB re 1 µPa, and also at 142/148 and 131/137 dB re 1 µPa. This suggests that, broadly speaking and for both sound types combined, the effect of the sounds on the animal's respiration rate increased with the gradient in SPL.



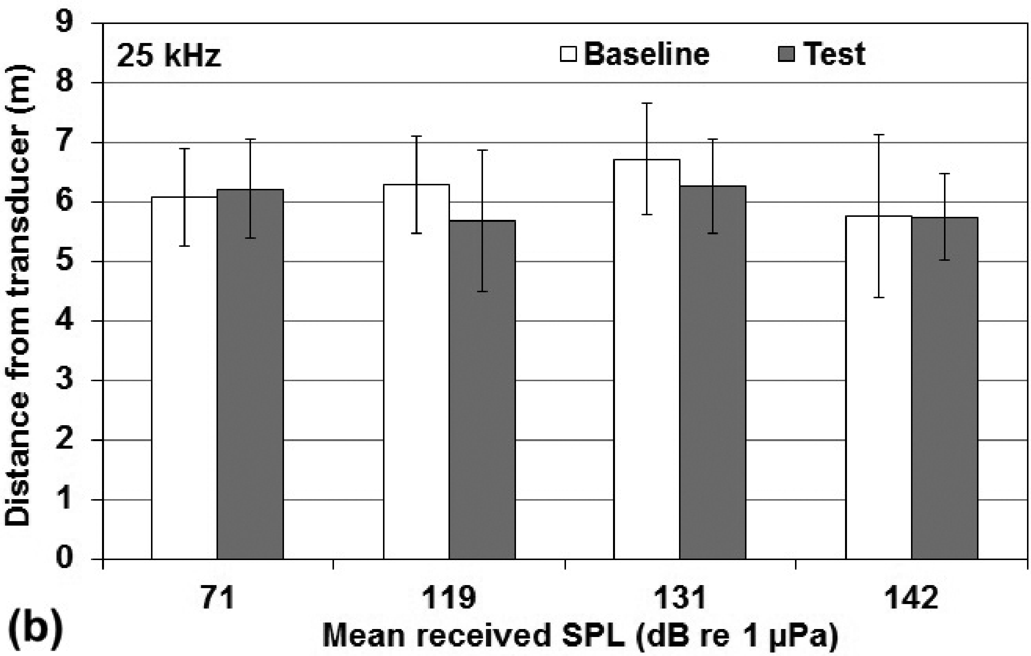


Figure 3. The mean distance of the harbor porpoise (*Phocoena phocoena*) from the transducer during 30-min-baseline periods and 30-min test periods in response to four average received broadband SPLs of the FM sweep with side bands (a) and without side bands (b). Bars indicate ± SD (n = 6), and * indicates a significant difference ($p < 0.0125$, following Bonferroni correction) between baseline and test periods (paired t-tests; see Table 2).

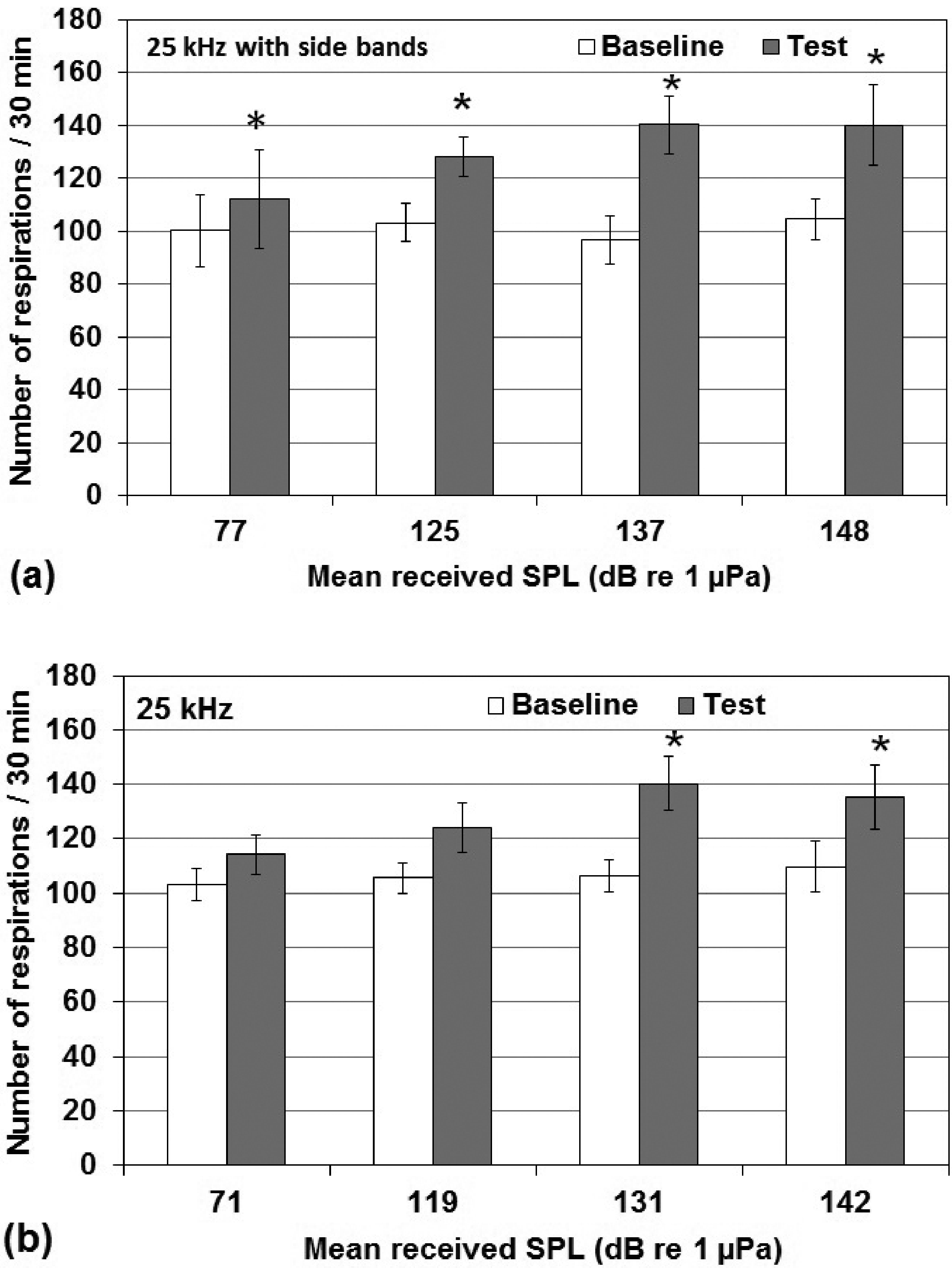


Figure 4. The mean respiration rate of the harbor porpoise during 30-min baseline periods and 30-min test periods in response to four average received broadband SPLs of the FM sweep with side bands (a) and without side bands (b). Bars indicate SD (n = 6), and * indicates a significant difference ($p < 0.0125$, following Bonferroni correction) between baseline and test periods (paired t-tests; see Table 2).

Discussion

The study animal's hearing was similar to that of two other young male harbor porpoises of similar age (Kastelein et al., 2002, 2009, 2010) and is considered representative of the hearing of harbor porpoises of his age. However, it is not clear what the range of behavioral response of this species is for the sonar signals. Behavioral response studies should be conducted with as many animals as possible as responses to acoustic stimuli vary between individuals, depending on parameters such as demeanor, history, age, and sex (Kastelein et al., 2000, 2001, 2008b). In addition, the context (e.g., social setting, season, water depth, geographic location, level of satiety, etc.) determines whether, and how, an animal reacts to sound.

The responses observed in the present study at the highest received levels, if observed in free-ranging animals, would be classed as 4 to 5 on the severity scale for ranking observed behavioral responses (range 1 to 9) presented by Southall et al. (2007). However, the effects observed in the present study occurred under very low background noise conditions. Under higher background noise conditions, the effect may be less severe as was observed in the same harbor porpoise for 6 to 7 kHz up-sweeps transmitted under ambient noise conditions resembling those during several different sea states (Kastelein et al., 2011b).

The behavioral response study was conducted in a pool, which had the advantages that the background noise could be controlled (which was very low), and that the animal's behavior could be filmed. The disadvantage was that only a small SPL gradient could be achieved in the length axis of the pool due to reverberations (Figure 2). Therefore, instead of offering one source level to the animal, we presented the sounds at four source levels, thus allowing a gradient in the behavior to be demonstrated. Statistical analysis showed little displacement of the harbor porpoise from the transducer. Due to the relatively small SPL gradient in the pool, the animal was not expected to move away from the sound source as a result of the sound exposures. However, the animal did increase his respiration rate significantly, especially at the highest sound levels. The high respiration rate is likely to be related to increased oxygen demand due to faster swimming and may have been a stress response (due to increased anxiousness). However, the SPLs were lower near the surface (Figure 2), so the higher respiration rate also may have been a behavioral avoidance response—an attempt by the harbor porpoise to reduce its received level.

The perceived level of a sound by harbor porpoises depends on the direction from which it comes, and the directionality of the hearing depends on the frequency content of the signal. An increase in frequency results in an increase in the directivity index (Kastelein et al., 2005a). For the sweeps centered around 25 kHz used in the present study, the perceived level could vary by up to about 12 dB from the received level, depending on the animal's orientation relative to the sound source (assuming no reflection occurred in the pool). This means that in the wild, harbor porpoises can locate high-frequency sonar sound sources fairly well and can reduce the potentially annoying perceived levels by orienting themselves away from sound sources and/or by swimming away.

The hearing threshold of this particular harbor porpoise for 50-ms, 25-kHz FM signals is ~53 dB re 1 µPa; for 71 kHz, it is ~52 dB re 1 µPa; and for 121 kHz, it is ~50 dB re 1 µPa (Kastelein et al., 2010). Due to the tonotopic organization of the basilar membrane, the fundamental frequency and the different side bands fall within different critical bands. Therefore, the sensation level cannot be calculated by simply adding the two levels at the side bands. At the broadband $SPL_{av.re.}$ of 148 dB re 1 µPa, for the signal with side bands, the sensation level of the harbor porpoise for the 25-kHz fundamental sound was ~89 dB; for the 71 kHz side band, it was ~85 dB; and for the 121 kHz side band, it was ~72 dB. This means that the differences in the harbor porpoise's response to the FM sounds with and without side bands could not have been caused by the difference in sensation level. In both signal types, the maximum sensation level was at 25 kHz (~89 dB). However, side bands, such as harmonics, can sometimes influence behavioral responses both by making sounds more audible (if the sensation level of a side band is higher than that of the fundamental frequency) and by affecting the way sounds are perceived by harbor porpoises (for instance, up-sweeps give the impression of something approaching).

Conclusion

The presence of side bands resulted in the increased effects of the 25-kHz FM sonar sounds—in particular, on the respiration rate of the harbor porpoise in the present study. An increase in respiration rate indicates a greater need for oxygen due to increased physical exercise (in this case, faster swimming), and probably indicates an increase in the level of anxiousness in an animal. In the wild, harbor porpoises probably swim away from sounds that they perceive as annoying or threatening. Side bands and high-frequency content may influence behavioral responses, both by making sounds more audible and/or by affecting the way sounds are perceived by harbor porpoises. The impact of active sonar could be mitigated by reducing the level of side bands (or harmonics). This would benefit marine species, such as the harbor porpoise, that are likely to have lower hearing thresholds for the frequencies of the harmonics than for the fundamental frequency (depending on the SPLs of the harmonics relative to the SPL of the fundamental frequency).

Acknowledgments

We thank Lean Helder-Hoek and Dorianne van Heerden for helping with data collection, Rob Triesscheijn for making some of the figures, and Bert Meijering (Topsy Baits) for providing space for the SEAMARCO Research Institute. Erwin Jansen (TNO) did the acoustic measurements. We thank Arie Smink for the construction and maintenance of the electronic equipment. We also thank Nancy Jennings (Dotmoth.co.uk) for the statistical analysis and for her comments on the paper, and Wim Verboom (JunoBioacoustics) and two anonymous reviewers for their valuable constructive comments on this manuscript. Funding for this project was obtained from the Swedish Defence Research Agency (FOI; Purchase Order No. 630100). The harbor porpoise was tested under authorization of the Netherlands Ministry of Economic Affairs, Department of Nature Management, with Endangered Species Permit FF/75A/2009/039. We thank Jan van Spaandonk (Netherlands Ministry of Economic Affairs) for his assistance in making the harbor porpoise available for this project.

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