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Behavioral Responses by Captive Bottlenose Dolphins (*Tursiops truncatus*) to 15- to 50-kHz Tonal Signals

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Abstract

Anthropogenic noise has received much attention as a potential factor affecting the behavior of marine mammals. For behavioral responses to occur, a sound stimulus would have to be a certain number of decibels (dB) above noise levels and the animal's audiogram. Bottlenose dolphins (*Tursiops truncatus*) have good hearing sensitivity in the mid- to high-frequency range (15 to 50 kHz). Thus, in this study, two captive bottlenose dolphins housed in a floating pen were subjected to three tonal signals of 15, 20, and 50 kHz with the same signal durations and duty cycles. The effect of each signal was judged by comparing the dolphins' surfacing locations, number of surfacings, and number of echolocation clicks during test periods with those during baseline periods. The location of the sound source did not change during the study. The results showed that the two dolphins swam away from the sound source and came up to the surface more often, but the dolphins exhibited a slight degree of habituation to the sounds. The two dolphins produced fewer echolocation clicks when the three signals were produced. The average avoidance threshold sound pressure level (SPL) of bottlenose dolphins for the three test signals were approximately 65, 70, and 83 dB above the hearing threshold SPL, respectively.

Key Words: acoustic exposure, behavioral response, bottlenose dolphin, *Tursiops truncatus*, hearing, anthropogenic noise

Introduction

Anthropogenic contributions to underwater noise have increased rapidly in recent years. The physiological and behavioral effects of anthropogenic noise may be detrimental to marine mammals worldwide (Jepson et al., 2003; Fernández et al., 2005; Nowacek et al., 2007; Southall et al., 2007; Rolland et al., 2012; Kastelein et al., 2018). The effects of underwater noise on the hearing abilities of marine mammals are of particular concern (Finneran, 2015; Ketten, 2017). Determining effects of noise depends on the characteristics of the sound (level, frequency content, duration, duty cycle, etc.), the sound propagation environment, and animals' behavioral contexts. It is very difficult to protect marine mammals from the potential impact of sound exposure because little is known about the consequences of sound exposure to marine mammals (Houser et al., 2013). Dose-response functions have been suggested as an effective approach to assess the impact of sound on the behavior of marine mammals (Southall et al., 2007; Pater et al., 2009; Tyack, 2009). Behavioral responses likely depend on prior experience, age, gender, health, context, current behavioral state, etc., but the details or mechanisms are still unknown (Erbe, 2013). Different species may respond differently to the same sound stimuli. Thus, it is necessary to acquire numerous types of possible sound exposures to repeatable and predictable changes of behaviors exhibited across individuals, species, and populations.

Over the past 20 years, there has been increased research effort on behavioral responses of many species to various types of sound. These studies focused on harbor porpoises (*Phocoena phocoena*), harbor seals (*Phoca vitulina*), and bottlenose dolphins (*Tursiops truncatus*) (Kraus et al., 1997; Culik et al., 2001; Johnston, 2002; Kastelein et al., 2006, 2008a, 2008b, 2009a, 2009b, 2013). For example, Cox et al. (2003) examined the responses of bottlenose dolphins to a commercial gillnet equipped with three acoustic alarms and concluded that alarms were unlikely to reduce bycatch of bottlenose dolphins in gillnet fisheries because of the limited behavioral responses observed in the experiment to the noise. Leeney et al. (2007) tested the effects of a continuous pinger and a responsive pinger (a newly developed pinger that is only activated when an internal hydrophone receives clicks from a dolphin between 10 and 150 m from the pinger) on the behavior of wild bottlenose dolphins in a controlled experiment. In the experiment, both active continuous and responsive pingers appeared to affect bottlenose dolphin behavior. Niu et al. (2012) showed experimentally that a continuous 50-kHz tonal signal can deter bottlenose dolphins from the general area (approximately 30 m) around the pinger. Houser et al. (2013) investigated the exposure amplitude and repetition effect on bottlenose dolphin behavioral responses to simulated mid-frequency sonar signals and found rapid habituation to repetitive exposures with received sound pressure levels (SPLs) ≤ 160 dB re 1 μPa. However, no habituation was observed at received SPLs ≥ 175 dB re 1 μPa, and all dolphins refused to participate in trials when the received SPL was 185 dB re 1 μPa. Pirotta et al. (2015) used passive acoustic techniques to quantify how boat disturbance affected bottlenose dolphin foraging activity and indicated the effect was escalated for increasing number and size of boats. Branstetter et al. (2018) examined the effects of vibratory pile driver noise on dolphin-sustained target detection capabilities through echolocation. The results showed that a decrease in vigilant behavior occurred due to the vibratory pile driver noise.

Acoustic deterrent devices (ADDs) and acoustic harassment devices (AHDs) have been used to help reduce cetacean bycatch (Taylor et al., 1997; Johnston & Woodley, 1998). However, one undesirable side effect of these acoustic devices is noise pollution, which is likely to damage the marine environment and affect marine mammals. Sound used in ADDs and AHDs should have characteristics such that they reduce cetacean bycatch but also cause minimal noise pollution. For bottlenose dolphins, the ideal alarms would be audible to them but not to fish and other marine mammals. It is therefore important to study the influence of different types of signals on bottlenose dolphins. Although the range of best hearing of these dolphins is from 15 to 110 kHz (Johnson, 1967; Brill et al., 2001), we chose 15-, 20-, and 50-kHz tonal signals as sound stimuli due to limitations of the transducer at higher frequencies. The goal of the present study was to perform a controlled exposure study using pulsed signals of three frequencies played back to two bottlenose dolphins in a floating pen and to discover which signals have the most effect on dolphin behavior.

Methods

Study Animals

The study was carried out on two captive male bottlenose dolphins that had been rehabilitated in April 2008. During June 2017, six frequencies ranging from 15 to 80 kHz were measured by an auditory evoked potential (AEP) method (F. Niu, unpub. data). The results showed that the two dolphins had normal hearing. In the present study one bottlenose dolphin was around 17 years old, healthy, and weighed around 136 kg. The other bottlenose dolphin was around 13 years old, healthy, and weighed around 121 kg. The two dolphins in the present study were exposed to a continuous signal for 40 sessions (15-min test periods every hour, four sessions per day) in January 2009 (Niu et al., 2012). From February 2009 to June 2010, the dolphins were not exposed to experimental sound stimuli. The dolphins were fed mackerel (*Scomber scombrus*) three times a day: at 0830, 1330, and 1630 h. All procedures of the study were approved by the Aquaculture Technology Extension Station of Xiamen.

The bottlenose dolphins were housed in a square floating pen (29 m × 29 m; 6 m deep in much of the pen; Figure 1) at a dolphin rehabilitation center located in Xiamen Bay, China (24° 32' 3.1" N, 118° 10' 14" E). The center was built in 2006 for the purpose of rescuing dolphins, science education, and scientific research. The depth of water in the pen is approximately 6 m at low tide and 11 m at high tide. During the experimental period, the average monthly water temperatures were 25.6°C in June 2010 and 27.3°C in July 2010.

Acoustic Stimulus

The acoustic stimulus signals in the experiment were produced by a portable computer (Model T61; Lenovo, Quarry Bay, Hong Kong), a programmable arbitrary waveform generator (Agilent 33220A; Agilent, Santa Clara, CA, USA), a power amplifier (Model HFVA-42; Nanjing University of Aeronautics and Astronautics, Nanjing, China), an underwater transducer manufactured by the Chinese Academy of Sciences (5-cm diameter, 10-cm length; Beijing, China), and a digital storage oscilloscope (TDS 210; Tektronix, Beaverton, OR, USA). The sound projection pattern of the transducer was omnidirectional in all planes with a flat frequency response between 5 and 50 kHz. The transducer was placed at 1.5 m below the water surface at the edge of the east of the center line of the pen (Figure 1), using a piece of lead to keep it vertical. The transducer was in the same position and depth during all experiments. The transducer was calibrated by the China National Defense Underwater Acoustics Calibration Laboratory prior to test experiments.

The stimuli consisted of pure tone pulses of 15, 20, and 50 kHz (Table 1). The pulse duration and interval were the same as most AHDs (Johnston & Woodley, 1998). For each signal, the source level (SL) used in the experiment was selected through a pretest conducted on one afternoon before the experiment. The SL of each test signal was slowly increased until the sound clearly displaced the two bottlenose dolphins but did not drive them all the

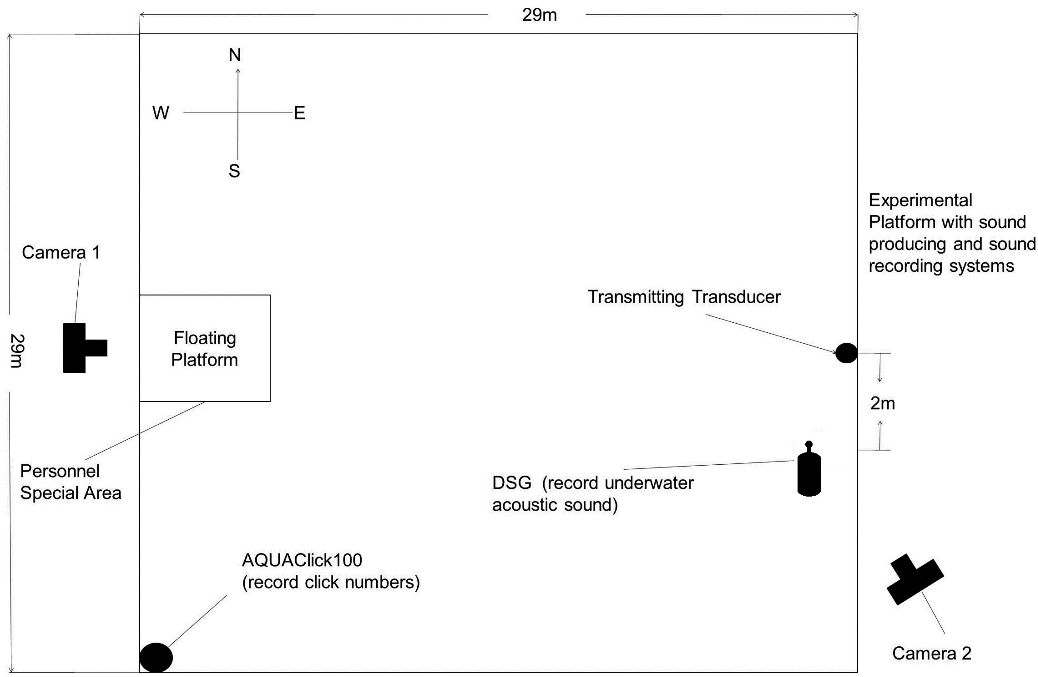

Figure 1. Top view of the study area, showing the locations of the underwater transducer, digital spectrogram long-term acoustic recorder (DSG), *AQUAClick100*, and two aerial cameras

way to the far end of the pool. For each test signal, the SL was measured in individual pulses.

Acoustic Recording and Analysis Equipment
The SPL of the signals in the pen was measured by a system composed of a broad-band hydrophone (Model 8104; Brüel & Kjær [B&K], Nærum, Denmark; frequency range from 0.1 Hz to 120 kHz with a receiving sensitivity of -205 dB re 1 V/µPa) and a 50-m extension cable connected to a conditioning amplifier (B&K Nexus Type 2692). The amplifier output was connected through a coaxial module (BNC-2110; National Instruments, Austin, TX, USA) to a computer (ThinkCentre, Lenovo) with a high-frequency data acquisition card (Model PCI-6122, National Instruments) on which signals were digitized with 16-bit resolution. During all experiments, sound signals were measured with a sampling frequency of 400 kHz. A hydrophone calibrator (B&K Model 4229) was used to calibrate the hydrophone, the conditioning amplifier, and the analogue to digital conversion. Reference data were logged separately and used in calculating the SPL. Signals were analyzed by *MATLAB*, Version 2013 (MathWorks, Natick, MA, USA). The single frequency Fast Fourier Transform (FFT) analysis with Hanning window covered a bandwidth from 20 Hz to 100 kHz.

All SPLs were corrected for the response curves of the measurement system. The SPLs of each

Table 1. Parameters of the three test signals: duration, interval, and source level (SL). SL_{pulse} = source level of per pulse cycle in dB re 1 µPa at 1 m distance from the transducer, and SL_{av} = averaged SL per pulse cycle (including duty cycle influence) over six pulse blocks in dB re 1 µPa at 1 m distance from the transducer.

Test signal frequency (kHz)	Pulse duration (ms)	Pulse interval (s)	SL_{pulse} (dB)	SL_{av} (dB)
15	400	5	159	156
20	400	5	157	155
50	400	5	154	152

signal were measured at nine locations in the pen with the hydrophone at 1.5 m below the water surface, the same depth as the transducer (Figure 2). The mean exposure SPLs of the nine locations at 5 and 10 m depth were also estimated via propagation modeling. Transmission loss (TL) was estimated from spherical spreading and absorption loss (α) at the given range (R) following TL = 20log(R) + αR. The absorption coefficients, α, at 15, 20, and 50 kHz were 0.013, 0.015, and 0.018 dB m^{-1}, respectively. The SLs of each signal amplitude were calculated from the measured SPL at a distance of 2 m from the sound source and corrected to a reference distance of 1 m by adding 6 dB (Figure 2). In the open ocean environment, it is expected there would only be some low-level harmonic signals because of the free sound field. Considering the sound parameters influenced the bottlenose dolphins' behavior, an averaged source level (SL_{av}) was presented in calculation (Table 2). The SL_{av} was defined as time averaged over six pulse cycles (recording duration 30 s), thus including the influence of the duty cycle (Kastelein et al., 2006).

Experimental Procedures

The transducer was put into position (Figure 1) 2 h before the first session each day. Each session was composed of a 15-min baseline period (no sound produced), followed immediately by a 15-min test period (stimulus produced). Usually four sessions were conducted per day, with a 30-min interval between each session. The first session was started at 0900 h daily. The transducer was always kept in the water during all four sessions each day. Only one frequency per day was tested. The frequency was changed daily through rotation from 15 to 50 kHz (= 1 block) for a total of ten blocks (N = 40 sessions per frequency). During the experiment, visitors and vessels were not allowed to approach the pen. Between June and July 2010, 120 sessions

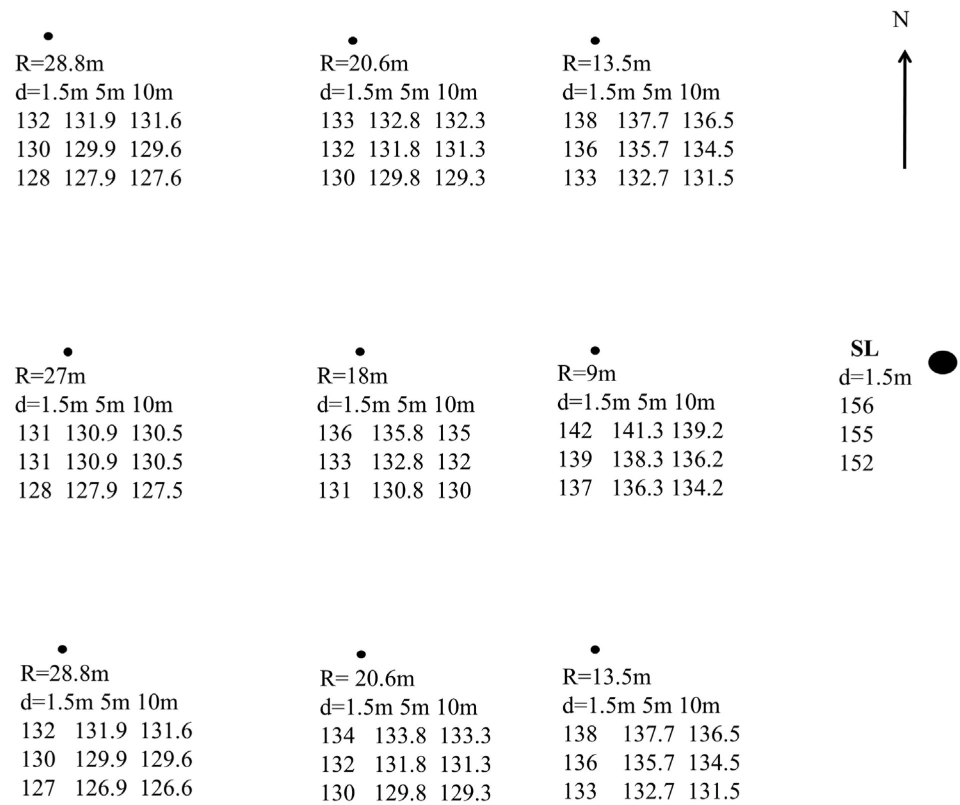

Figure 2. The average sound pressure level (SPL in dB re 1 μPa, root-mean square [rms]) distribution in the pen for the three test signals. Each column from top to bottom: distance from the sound source (R); depth (d); and signal 1 (15 kHz, top row), signal 2 (20 kHz, middle row), and signal 3 (50 kHz, bottom row).

were conducted. Tests were carried out under good weather conditions (no rainfall and wind speeds below Beaufort level 4) to ensure good visibility and low ambient noise. The trainers did not feed the bottlenose dolphins during the sessions to make sure that the dolphins' displacement was not influenced by their energy needs.

A digital spectrogram long-term acoustic recorder (Model DSG-ST; Loggerhead Instruments, Sarasota, FL, USA) was used to check whether the sound-generating equipment worked appropriately during testing sessions. DSG is a low-power acoustic recorder designed to sample at rates up to 80 kHz continuously. DSG was placed 2 m away from the transducer at the same depth as the transducer. Two video cameras (Model HDR-SR11E; Sony, Minato, Tokyo, Japan) mounted on 3-m-high poles were used to observe the water surface of the pen during testing sessions. Scan samples were taken every 10 s. In addition, one digital camera (D60; Nikon, Minato, Tokyo, Japan) was used to capture the moment when abnormal behavioral responses of dolphins appeared such as suddenly swimming faster, swimming close to the transducer and going back immediately, and so on.

Response Variables and Statistical Analysis

To quantify and compare the effects of the sound stimuli, we recorded the following behavioral parameters: the displacement of the bottlenose dolphins in the pen away from the transducer, the number of surfacings, and the number of echolocation clicks produced by the dolphins (Kastelein et al., 2006). The distances between the transducer and the locations where the dolphins surfaced were quantified to confirm whether the dolphins responded to the sounds by swimming away from the sound source. Details of the method were described in Niu et al. (2012). The echolocation clicks produced by the dolphins were recorded continuously during all sessions by using a click recorder (*AQUAclick100*; Aquatec Group, Basingstoke, UK). There were four sessions conducted every day to test potential habituation to the sounds during test periods.

Statistical analysis was performed by *MATLAB*, Version 2013, with a significance level of 0.05 (Kastelein et al., 2008b). Because of the large number of degrees of freedom (*df*) associated with the raw data, the average of the distances of each surfacing from the transducer for each of the baseline (four 15-min periods) and testing (four 15-min periods) sessions per day were used in the calculations to avoid pseudoreplication (Kastelein et al., 2006). Individual factors were carried out using one-way analysis of variance (ANOVA; Zar, 2009), and Tukey tests were performed to assess potential differences between the three frequencies.

The number of surfacings during the baseline periods was determined by calculating the average of all baseline periods. A one-way ANOVA was used to investigate if the number of surfacings during the test periods were higher than during the baseline periods and if the increased surfacings varied over the four 15-min test periods conducted each day. The same method was selected to analyze and determine whether the number of clicks produced by the bottlenose dolphins during the test periods were significantly different from the baseline periods. The length of an echolocation click produced by bottlenose dolphins is normally between 20 and 45 µs (Au, 1993); clicks within this length criterion were considered valid, and clicks which did not meet this length were deleted.

An *acoustic avoidance threshold SPL* is defined as the boundary between the areas that the bottlenose dolphins generally occupied during sound emission and the areas that they generally do not enter during sound emission (Kastelein et al., 2006). The avoidance threshold SPL is not a physical boundary but the SPL beyond which the dolphins move to when avoiding the test sounds.

Results

The two bottlenose dolphins moved away from the transducer when each of the three sounds was produced (Figure 3A). In all sessions, the two dolphins were on average significantly further from the sound source during test periods than during baseline periods. Furthermore, the average distances decreased slightly for each 15-min period across the four sessions per day (Figure 3A). A factorial ANOVA showed that there were significant interactions between the surfacing distances and the frequency of test sounds, order of testing sessions per day, and the block order of testing (10 blocks; Table 2). All one-way ANOVAs in the following were carried out using the average values of the surfacing distances per testing session of each day to reduce pseudoreplication. During all sessions per day, the average surfacing distances between the dolphins and the transducer increased significantly (13 m away from the transducer) at the first test sounds relative to the baseline period but decreased slightly (4 m away from the transducer) over the next testing sessions each day (Figure 3A; $df = 3$, $F = 182.1$, $p < 0.001$). The average surfacing distances varied between 13 and 15 m for the baseline periods each day and between 27 and 29 m for the first test period, between 22 and 26 m for the second test period, between 20 and 24 m for the third test period, and between 19 and 20 m for the fourth test period (Figure 3A). This pattern was repeated for all three frequencies ($df = 2$, $F = 1.5$, $p > 0.05$), and there was no change during

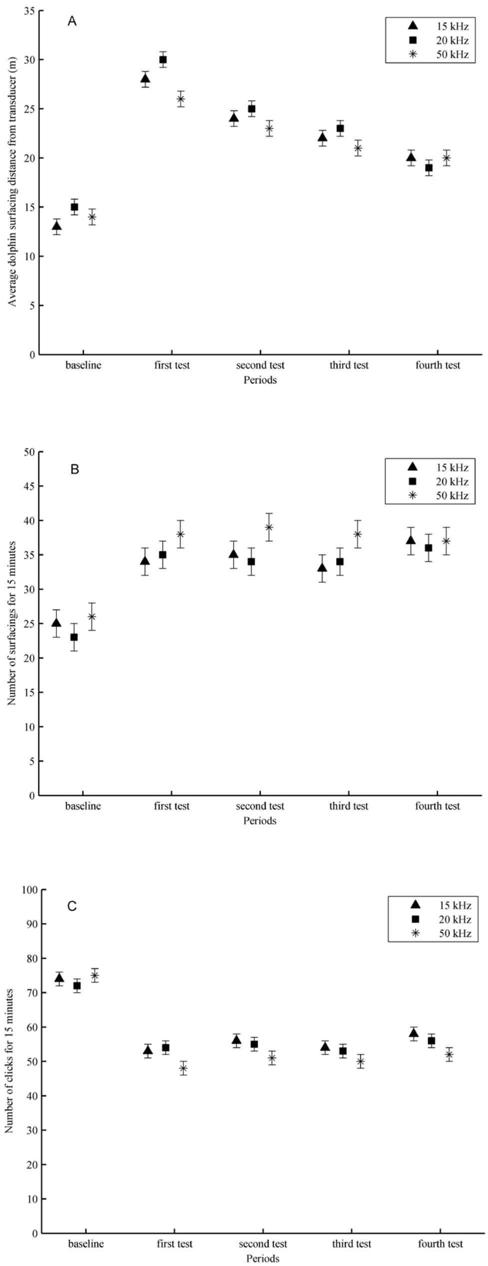

Figure 3. The average surfacing distances between the bottlenose dolphins (*Tursiops truncatus*) and the transducer (A), average number of surfacings of the dolphins (B), and number of clicks produced by the dolphins (C) during baseline periods and when exposed to pulses of 15, 20, and 50 kHz during four test periods per day ($N = 40$ sessions per frequency). The bars indicate standard errors. For all sound signals, there are significant differences in values between test periods and baseline periods.

the 30 experiment days ($df = 9$, $F = 4.7$, $p > 0.05$), thus there was little habituation observed during the entire experimental period. There were obvious differences between the surfacing distances relative to the transducer and frequencies ($df = 2$, $F = 7.2$, $p < 0.001$) and order of testing ($df = 3$, $F = 149.6$, $p < 0.001$). The average surfacing distances were 28 m for the 15-kHz test signal, 30 m for the 20-kHz test signal, and 26 m for the 50-kHz test signal.

The number of surfacings during the test periods were significantly higher than during the baseline periods (Figure 3B; $df = 9$, $F = 13.8$, $p < 0.05$). In the first three sessions, the number of surfacings when the dolphins were exposed to 50-kHz signals was slightly higher than when they were exposed to 15- and 20-kHz signals (Figure 3B; $df = 2$, $F = 11.6$, $p < 0.05$). For each signal, there were no significant differences in the increased numbers of surfacings between the four test periods per day ($df = 3$, $F = 1.7$, $p > 0.05$).

The number of valid clicks during the baseline periods and test periods were calculated and analyzed. During the test periods, the average number of clicks produced by the bottlenose dolphins was significantly lower than during the baseline periods (Figure 3C; $df = 9$, $F = 12.3$, $p < 0.05$). However, this pattern was not affected by frequencies ($df = 2$, $F = 2.3$, $p > 0.05$) and order of testing per day ($df = 3$, $F = 1.6$, $p > 0.05$).

For each signal, the average avoidance threshold SPLs (for the particular bottlenose dolphins in the present study), calculated from the distribution of sound fields in the pen, are shown in Table 3. Figure 4 shows the audiogram (hearing thresholds) and the average avoidance threshold SPLs of bottlenose dolphins for the three test signals (15, 20, and 50 kHz) in the present study. The average avoidance threshold SPLs are approximately 65, 70, and 83 dB above the hearing threshold SPL, respectively (Table 3). To compare deterring effects of a continuous signal at the same frequency, the avoidance threshold SPL for a continuous 50-kHz signal was given in Figure 4 (data from Niu et al., 2012). From this comparison, a pulsed 50-kHz signal appears to have a much stronger deterring effect than a continuous 50-kHz signal (Figure 4).

Hearing threshold SPL of the bottlenose dolphins in the present study was measured by the AEP method during June 2017 (F. Niu, unpub. data). The avoidance threshold SPL of the same dolphins for a continuous 50-kHz signal was taken from Niu et al. (2012).

Table 2. Factorial ANOVA on surfacing distances from the source; *df* = degrees of freedom, *MS* = mean square, *F* = test statistic, and *p* = significance level.

Source of variation	*df*	*MS*	*F*	*p*
Order of testing sessions per day	3	17,980	134.37	< 0.001
Frequency of sound	2	183	7.98	< 0.001
Block order of testing	9	135	6.11	< 0.001
Order × Frequency	6	68	1.23	> 0.05
Order × Block order	27	71	1.41	> 0.05
Frequency × Block order	18	83	3.2	< 0.05
Error	5,862	102		

Table 3. The avoidance threshold SPLs and hearing threshold SPLs for the three signals in the present study

Test signal frequency (kHz)	Avoidance threshold SPL (dB)	Hearing threshold SPL (dB)	Level above the hearing threshold SPL (dB)
15	141 ± 3	76	65 ± 3
20	138 ± 2	68	70 ± 2
50 (pulse)	135 ± 2	52	83 ± 2
50 (continuous)	144 ± 2	52	92 ± 2

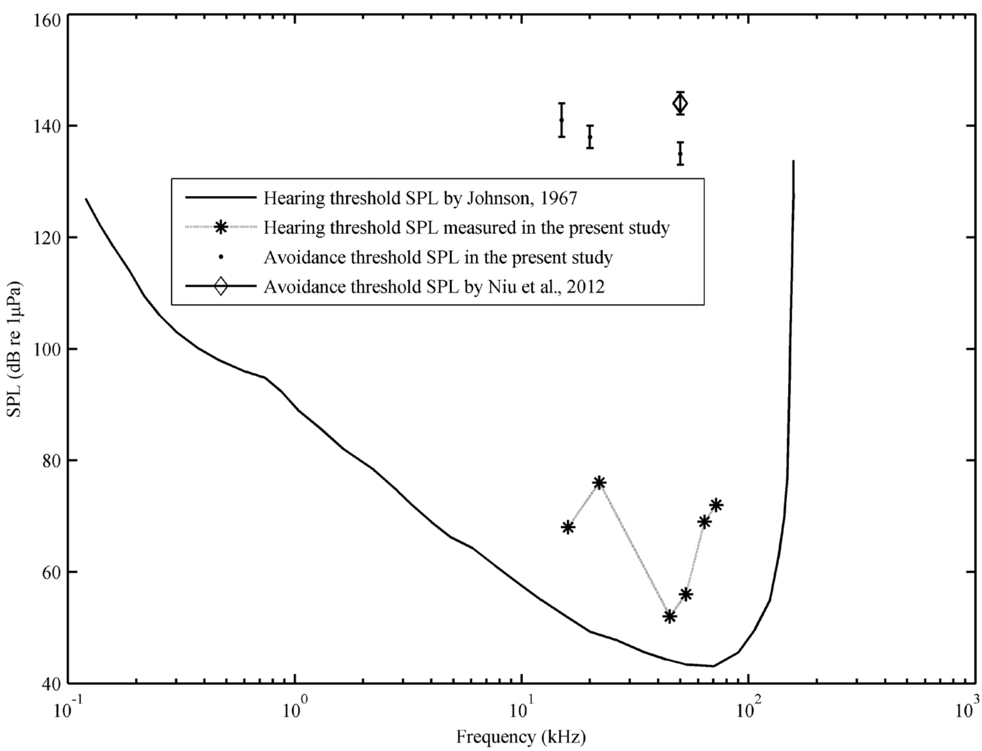

Figure 4. The avoidance threshold SPLs for the three test pulsed signals (15, 20, and 50 kHz) and hearing threshold sound pressure level (SPL) of bottlenose dolphins in the present study measured by auditory evoked potentials (AEPs). The avoidance threshold SPL of bottlenose dolphins for a continuous signal (50 kHz) (data from Niu et al., 2012) and hearing threshold SPL of bottlenose dolphins (data from Johnson, 1967) are also shown.

Discussion

This study provides a detailed account of the behavioral responses of bottlenose dolphins to pulsed signals of different frequencies. During all test periods, the three signals (15, 20, and 50 kHz) deterred the dolphins from the area of the pen where the sound source was located. During the four test periods per day, the dolphins exhibited a light habituation to the test signals and were displaced farther during the first test period than the following three periods, but the daily trend did not transfer between days. Although the cognitive abilities of the dolphins suggest that habituation may occur readily (Whitehead et al., 2004), the short duration of the testing sessions (15 min followed by at least 45 min without a test sound) appeared to prevent habituation in the present study.

The number of surfacings for the three test signals during the test periods was higher than during the baseline periods. This indicated that the way the bottlenose dolphins responded to the test sounds was not only by swimming further away from the sound source but also by raising their heads above the surface more often due to their increased breathing rate or to reduce the exposure amplitude. Although the dolphins increased distances to the underwater sounds, they appeared to be still disturbed by the sounds. Harbor seals can reduce the amplitude of underwater sounds they experience by putting their heads out of the water (Møhl, 1968; Terhune, 1991). Dolphins may also reduce the impact of underwater sound by surfacing more often as seals do.

Behavioral responses of cetaceans to underwater sounds can also be indicated by changes in vocalizations. Typical changes in vocalizations are a reduction or cessation in calling as shown in beluga whales (*Delphinapterus leucas*; Lesage et al., 1999), right whales (*Lissodelphis peronii*; Watkins, 1986), sperm whales (*Physeter macrocephalus*; Watkins & Schevill, 1975), and pilot whales (*Globicephala melas*; Bowles et al., 1994). However, not all cetaceans respond with a decrease or cessation of calls. Sperm whales continue calling when exposed to sound levels of 180 dB re 1 µPa from the discharge of a detonator (Madsen & Møhl, 2000). In the present study, the number of echolocation clicks produced by the two bottlenose dolphins during the test periods was less than during the baseline periods. The number of clicks was not significantly different between the three test signals ($p > 0.05$), however.

In many countries, ADDs have been used in the mitigation of interactions between marine mammals and fishing. Gazo et al. (2008) developed a field experiment to verify effects of acoustic alarms that emit wide-band frequency signals with the range between 20 and 160 kHz and average SLs of 145 dB re 1 µPa @ 1 m at 70 kHz. However, the results showed that the ADD did not completely stop bottlenose dolphins from approaching the fishing nets. It is possible that the dolphins rapidly habituated to sound exposures below a certain level, particularly if there is food motivation. To reduce habituation, variation in other signal parameters, such as using sweeps, irregular intervals, or harmonics, are also important in improving deterrent effects besides just increasing the exposure amplitude. The present study indicated that the three test signals may be suitable for ADDs and can deter the dolphins to a certain distance.

The bottlenose dolphins' movements in the present study were restricted by the size of the pen. If in the open sea, the dolphins may have swum further away when they were exposed to the sounds. Furthermore, sex, experience, and context may also influence the behaviors of individuals. Habituation was observed during the four test periods (15 min every period) per day, but there was no habituation between the 10 days of each test frequency. If the dolphins had been tested for a longer period of time, more habituation might be observed. However, the dolphins were not exposed to sounds for longer periods in the present study as an animal welfare consideration.

The present study shows that the three pulsed test signals (15, 20, and 50 kHz) can change the behavior of bottlenose dolphins. Behavioral responses of marine mammals to noise are highly variable, however, and depend on many factors (Kastelein et al., 2006).

Acknowledgments

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