

## Behavioral Responses by Icelandic White-Beaked Dolphins (*Lagenorhynchus albirostris*) to Playback Sounds

Marianne H. Rasmussen,<sup>1,2</sup> Ana C. G. Atem,<sup>2,3</sup> and Lee A. Miller<sup>2</sup>

<sup>1</sup>Húsavík Research Center, University of Iceland, Hafnarstétt 3, 640 Húsavík, Iceland  
E-mail: mhr@hi.is

<sup>2</sup>Institute of Biology, University of Southern Denmark, Campusvej 55, DK-5230 Odense M, Denmark

<sup>3</sup>Rua Nevada, 85 Jardim, Quebec Londrina – PR, CEP 86060-238, Brazil

### Abstract

The aim of this study was to investigate how wild white-beaked dolphins (*Lagenorhynchus albirostris*) respond to the playback of novel, anthropogenic sounds. We used amplitude-modulated tones and synthetic pulse-bursts. (Some authors in the literature use the term “burst pulse” meaning a burst of pulses or clicks.) The tones were 2 s in duration at frequencies of 100, 200, or 250 kHz in three separate playback experiments. The pulse-bursts consisted of 10 different pre-recorded white-beaked dolphin clicks from which one was chosen randomly and repeated at a rate of 300 clicks/s for 2 s. The estimated received levels for tonal signals were from 110 to 160 dB and for pulse-bursts were 153 to 166 dB re 1  $\mu$ Pa (peak-to-peak). Playback of a file with no signal served as a *no sound* control in all experiments. The animals responded to all acoustic signals with nine different behavioral responses: (1) circling the array, (2) turning around and approaching the camera, (3) underwater tail slapping, (4) emitting bubbles, (5) turning their belly towards the set-up, (6) emitting pulse-bursts towards the loudspeaker, (7) an increase in swim speed, (8) a change in swim direction, and (9) jumping. A total of 157 playbacks were conducted, 123 of which contained sound; the rest were controls. The dolphins responded behaviorally to 90 playbacks with sound. They never responded when we projected the no sound control. The data do not allow assigning specific behavioral responses to specific acoustic stimuli. We also warn of using sounds to determine hearing thresholds of wild marine mammals since their auditory sensitivity is so acute they could possibly react to distortions of the test signal and not to the intended frequency. These results clearly show, like those of earlier studies, that sounds can induce a response and a change in the natural behavior of a marine mammal—in this case, wild white-beaked dolphins.

**Key Words:** behavioral responses, white-beaked dolphins, *Lagenorhynchus albirostris*, playback

### Introduction

Acoustic playback is a technique that consists of playing natural or synthetic signals to individuals of a chosen species to study specific behaviors. It has been used to study responses of amphibians, birds, primates, and marine mammals (Morgan, 1979; Falls, 1992). Acoustic playback has been used with marine mammals to study prey-predator interactions, kin recognition, the function of vocalizations, reactions to anthropogenic sounds, and its use in wildlife management (Deecke, 2006). Regarding the latter, it is important to know how marine mammals react to anthropogenic sounds since these could impact their overall fitness. There are numerous examples of how anthropogenic sounds disturb ongoing and normal behavior of cetaceans (see Tyack, 2009, for a review).

Dolphins produce mainly two kinds of signals: (1) whistles and (2) clicks. Whistles are thought to be used for communication, and clicks are used primarily for echolocation (Popper, 1980). Clicks emitted at high rates (pulse-bursts) are sometimes used during courtship, dominance, or aggressive behavior (Overstrom, 1983; Connor & Smolker, 1996). The clicks in a pulse-burst have similar spectral properties as those used for echolocation (Connor & Smolker, 1996; Blomquist & Amundin, 2004). Pulse-bursts recorded from captive bottlenose dolphins (*Tursiops truncatus*) could have rates as high as 940 pulses/s and last over 1 s (Blomquist & Amundin, 2004). Pulse-bursts from spotted (*Stenella frontalis*) and bottlenose dolphins have been recorded in contexts such as affiliate and aggressive behavior, play, courtship, discipline, distress, and foraging, which is probably the terminal buzz associated with prey capture (Herzing, 2000). Pulse-bursts recorded from white-beaked dolphins (*Lagenorhynchus*

*albirostris*) have inter-click intervals as short as 2.9 ms, corresponding to 345 pulses/s, and their clicks contain frequency components up to 250 kHz (Rasmussen & Miller, 2002). White-beaked dolphins also emit communication whistles with a fundamental frequency of up to 35 kHz (Rasmussen & Miller, 2002) and harmonics up to 65 kHz (Rasmussen et al., 2006).

Tonal signals have been used to determine behavioral auditory thresholds and frequency discrimination. Historically, Kellogg & Kohler (1952) determined the upper limit of hearing in odontocetes to be at least 80 kHz using tonal signals. Later, Johnson (1967) determined the upper limit of bottlenose dolphin hearing to be at least 150 kHz by using tones projected to trained animals.

The communicative properties of vocalizations have received much attention. Sayigh et al. (1999) showed that female bottlenose dolphins responded with heads turning to playbacks of their weaned offspring, who responded in kind with heads turning to playbacks of their mothers' whistles. These results show true individual recognition between mothers and calves. Janik et al. (2006) showed bottlenose dolphins turning their heads towards a loudspeaker broadcasting sounds from related dolphins in a test for individual recognition. They showed that individual identity is encoded in the shape and frequency contour of the whistle, denoted as a *signature whistle*.

Researchers continue to use playback signals to study the reactions of whales—for example, how pilot whales (*Globicephala melas*) react to synthetic killer whale (*Orcinus orca*) sounds (Cure et al., 2012). Playbacks are an important and promising technique to study cetacean hearing, communication, and behavior. Naturally, it is assumed that the whale can hear the audio playback and will respond. However, an animal may not always respond even though it can hear the sound. Still, playback studies are important for understanding the biology and ecology of a species, which is important for its conservation.

The objectives of this study were to test if it was possible to use a playback experiment to roughly estimate high-frequency hearing capabilities of white-beaked dolphins when projecting tones and, if the tones can be heard, to investigate the behavioral responses to different received levels and frequencies of tonal stimuli. We also wished to test the hypotheses that pulse-bursts are used in aggressive encounters by dolphins by playing back artificial pulse-bursts to free-ranging white-beaked dolphins.

## Methods

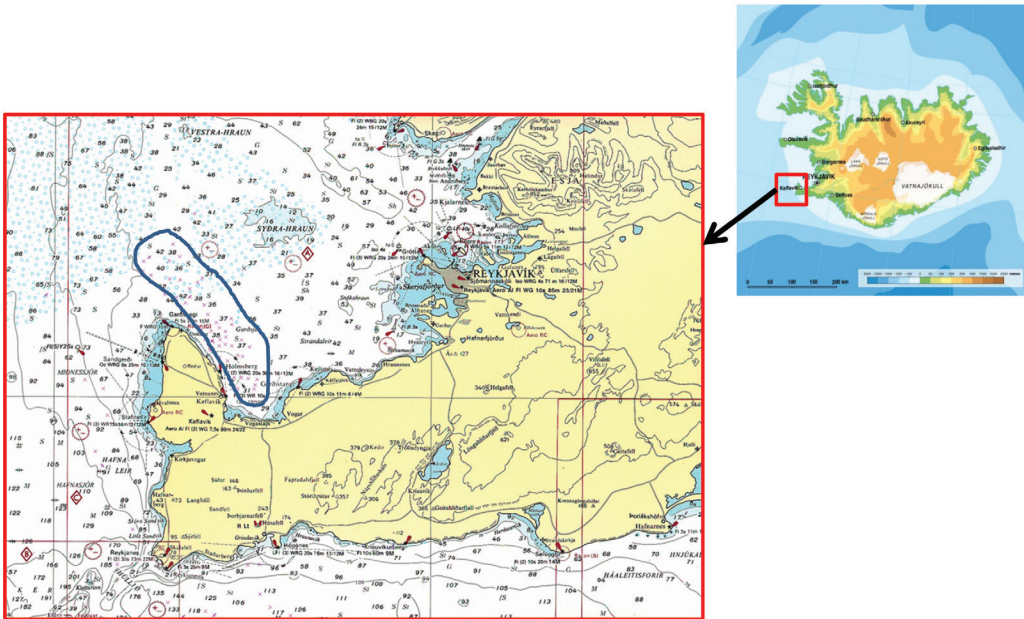
Playback experiments were conducted in Faxaflói Bay in the southwestern part of Iceland using a small fishing boat 6 m in length during the summers of 2003, 2004, and 2005 (see Figure 1). The experiments consisted of a playback portion and a recording portion. We projected amplitude-modulated tonal signals (2004) and pulse-bursts (2003 and 2005) to focal animals and recorded their acoustic and behavioral responses on digital files. A focal animal was a dolphin typically within a group of white-beaked dolphins (3 to 10 animals) that remained near the boat long enough to conduct a playback session. Only one animal, the focal dolphin, was in front of the video camera when sound was projected, and its responses, video and audio, were recorded. An observer on board commented on the dolphin's behavior, and these were also recorded. The different individuals could be recognized partly because photo-identifications of white-beaked dolphins have been conducted since 1998 (Rasmussen, 1999; Bertulli et al., 2015).

### *Sound and Video Recording Equipment*

The sound recording set up in 2003 and 2004 consisted of a 4-hydrophone "star" array (Reson TC4034 hydrophones; frequency range 1 Hz to 250 kHz  $\pm$  4 dB) connected to a five-channel amplifier (1 MHz bandwidth per channel; etec, <http://etec.dk>) and from there to a "lunch box" computer (the same used in Rasmussen et al., 2004) (see Figure 2).

The sample rate was 800 kS/s recorded directly to the computer hard disk. In addition, a video camera (Philips LTC0600/10) in a watertight housing was mounted 10 cm above the center hydrophone. A microphone was connected to one of the audio channels of a video recorder (JVC) to record comments on the behavior of the dolphins. A click detector (etec) was connected to the second audio channel of the video recorder, and the output led to a video card (Dazzle, Inc.) in the computer. Video and audio recordings were stored as files on the hard disk.

The sound recording system in 2005 consisted of a single hydrophone (HS150; frequency up to 150 kHz; Sonar Products, [www.sonar.co.uk](http://www.sonar.co.uk)) connected to one channel of a multi-channel amplifier (etec) and then to a click detector (etec). From here, the signal led to one of the audio channels of a video recorder (Sony DV – G1000E). A commentary microphone was connected to the second channel of the video recorder. The loudspeaker and the underwater video camera were mounted above the hydrophone.



**Figure 1.** Maps of the study area. The map on the right shows Iceland, with the square indicating the sea map on the left. The oval ring inscribes our study area.

### Sound Projecting Equipment

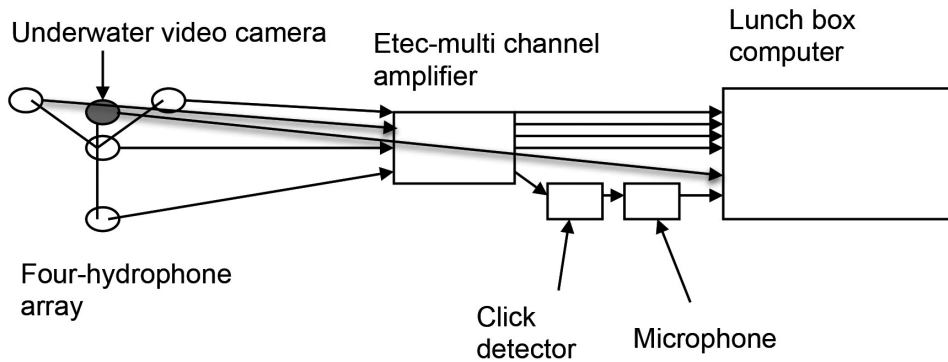
In 2003, pulse-bursts were generated using a Toshiba laptop computer (T3200) equipped with a digital signal processor working at a digital to analog rate of 444 kHz. The signal processor output led to a low-pass filter (180 kHz) and then to a battery-powered amplifier (etec PA1001) connected to a directional underwater loudspeaker (Reson TC2130; 100 to 250 kHz  $\pm$  7 dB).

Files of pulse-bursts were stored on the computer hard disk and played out following a manual trigger. A playback file (100  $\mu$ s in duration) consisted of one of ten previously recorded and randomly chosen white-beaked dolphin clicks (see “Experimental Design” below). These clicks were also digitally filtered between 150 and  $\sim$ 220 kHz, forming a second group of 10-click stimuli (high-pass [hp] filtered clicks) to test if white-beaked dolphins responded to the high-frequency part of their clicks (the energy above 150 kHz). A click was repeated at a rate of 300 clicks/s as a 2-s pulse-burst using either an unmodified, full bandwidth click or a hp-filtered click and projected to focal dolphins (see Figure 3B). Each click had a source level (at 1 m) of 179 dB re 1  $\mu$ Pa (peak-to-peak [p-p]). A no sound file with the same duration as a click (100  $\mu$ s) was repeated 300 times/s and projected as a 2-s control stimulus. The purpose of our no sound files was to make sure there were no

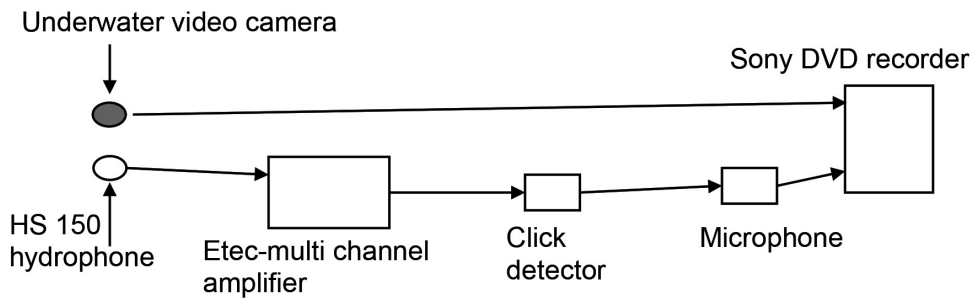
audible artifacts in our sound-generating equipment. In 2005, the same process described above was used to store and play back clicks, both full bandwidth and hp-filtered; however, an Agilent (33220A) 20-MHz function and arbitrary waveform generator was used in place of the laptop.

In 2004, amplitude-modulated tonal stimuli were generated with a 20-MHz function and arbitrary waveform generator (Agilent 33220 A) connected to a custom-built power amplifier linear up to 300 kHz (etec PA1001). An attenuator (865; Kay Elemetrics Corp.) was connected to the output of the amplifier and then to the underwater loudspeaker (Reson TC2130). We generated 2-s tonal stimuli with frequencies of 100, 200, and 250 kHz and a no sound file as a control (see Figure 3A). The 2-s electrical signals were shaped using a raised cosine function (Hann function) to reduce start-stop artifacts. Each modulated frequency had a different number of amplitude-modulation cycles to produce a 2-s stimulus. The modulation frequency was 24.41 Hz for the 100s kHz signal, 48.83 Hz for the 200 kHz signal, and 61.04 Hz for the 250 kHz signal.

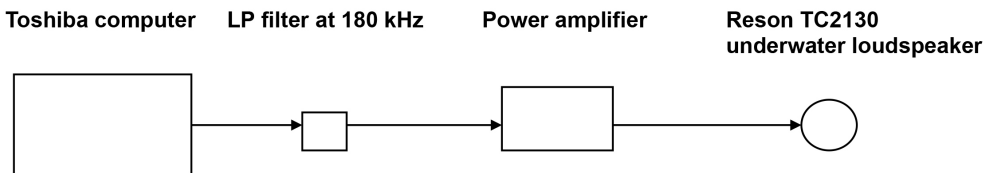
**A. Sound recording equipment in 2003 and 2004**



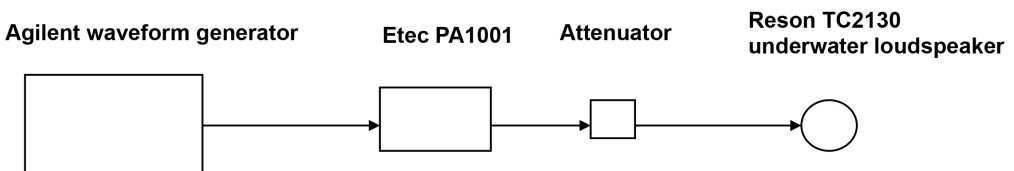
**B. Sound recording equipment in 2005**



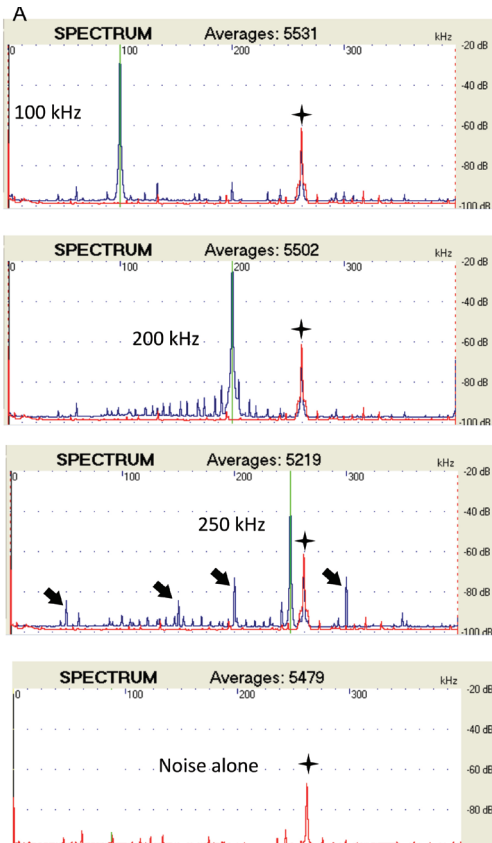
**C. Sound projecting equipment in 2003**



**D. Sound projecting equipment in 2004 and 2005**



**Figure 2.** Schematic drawings of the sound recording equipment used in 2003 and 2004 (A) and in 2005 (B), and the sound playback equipment used in 2003 (C) and in 2004 and 2005 (D). LP = low pass.



**Figure 3A.** The average amplitude spectra of three tonal frequencies (100, 200, and 250 kHz) used as playback signals and the background noise during calibration. The spectra in red show the no sound signal and background noise. The arrows in the 250 kHz spectrum show distortions of the acoustic signal, which are 35 dB or more below the fundamental frequency. The stars show electromagnetic interference at 262 kHz from a radio station near the calibrating site in Kerteminde, Denmark.

### Calibration

The sound system was calibrated each year at the Marine Biological Research Center in Kerteminde, Denmark, using a cedar wood test tank (3 m in diameter and 3 m deep) and checked using a small tank at Sandgerði Marine Center in Iceland. The sound system was recalibrated after returning from Iceland, and there was no change from the initial calibrations. The hydrophones were calibrated using a 250-Hz calibration tone from a 4223 Brüel & Kjær calibrator with a custom adapter fitted to the Reson hydrophones.

### Tonal Playback Signals (2004)

One goal of the study was to investigate the hearing range of white-beaked dolphins in the field. We used the 100, 200, and 250 kHz signals as well as the no sound control for this purpose. We used two different intensities for each frequency. This experiment was divided into three time periods in 2004, and each trip was conducted within 1 d. (See Table 1A for time periods and source levels of tonal playback signals.)

### Click-Burst Playback Signals (2003/2005)

The goal of conducting pulse-burst playbacks was to investigate how wild white-beaked dolphins reacted to synthetic click bursts using both full bandwidth white-beaked dolphin clicks (60 to 200 kHz) and just the high-frequency portion of the click (over 150 kHz). One of the predictions was that the dolphins would respond to the artificial pulse-bursts as if it had been from a conspecific (see Table 1B).

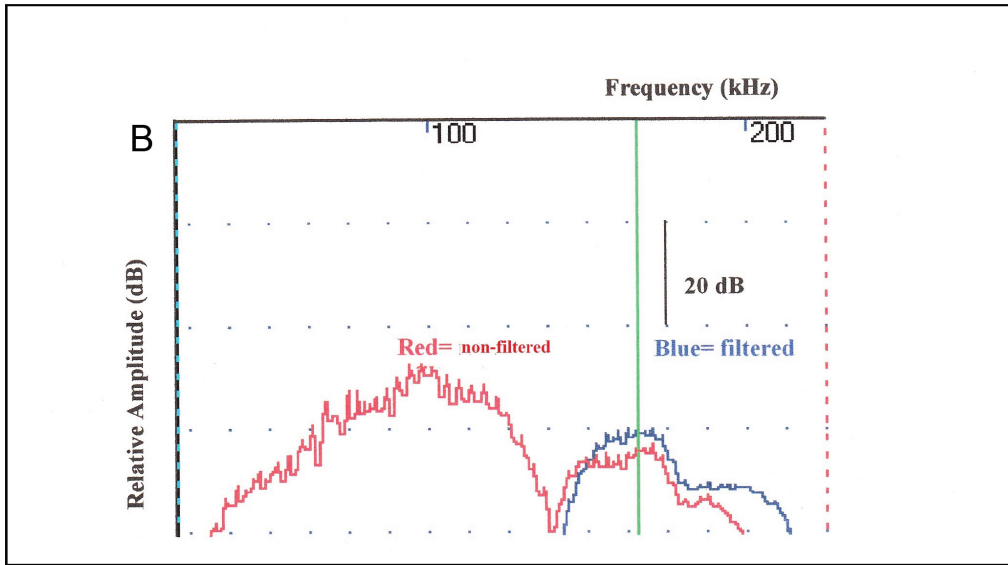
### Experimental Design

The design of our playback experiments followed the method of constant stimuli, using a double blind control (McGregor, 2000) and behavioral observations according to Mann (1999) and Martin & Bateson (2007). Neither the person responsible for projecting the sound nor the person recording the dolphin's responses knew what type of signal was projected. The signals and no sound controls were played back using a pseudo-random sequence (custom-written program; Hans Rasmussen, Århus, Denmark) that prevented the user from knowing which signal was being generated. Each signal was played back a maximum of three times in a row. The sounds were emitted when a dolphin was observed in the image from the underwater video camera, which was about 20° wide. One person triggered the sound generator, and another person made the video and audio recordings. The person responsible for the stimuli wrote down the precise time when the sound was projected, and the time was synchronized with the time on the computer used for saving the recordings. Everything was recorded on the video as *ad libitum* sampling in the field, and the analyses were conducted afterwards.

### Estimating Received Sound Levels

We used a 1-m stick filmed at several distances from the video camera to estimate the distance to a dolphin seen broadside in the video monitor. The average length of adult Icelandic white-beaked dolphins is from 2.5 to 3 m (Vikingsson & Olafsdottir, 2004). Using the ratios of images on the monitor, we could estimate the distance ( $r$ ) to a dolphin. Since we know the source level (SL @ 1 m) of the emitted sound, we can use the





**Figure 3B.** An example of two types of clicks used in burst stimuli: a full bandwidth click (in red) and a high-pass (hp) filtered version of the full bandwidth click (in blue). The green line shows the peak frequency (about 155 kHz) of the hp-filtered version of the broadband click.

**Table 1.** Parameters of playback signals; source levels are dB re 1  $\mu$ Pa (p-p) at 1 m.

**Table 1A.** Amplitude-modulated tonal signals used for each time period in 2004. Time period 1 (24 July to 11 August), time period 2 (12 to 23 August), and time period 3 (25 August to 4 September). The parentheses indicate the number of playbacks.

Sound type 2004	Frequency modulation in Hz	Source level in dB re 1 $\mu$ Pa in time period 1 ( <i>N</i> )	Source level in dB re 1 $\mu$ Pa in time period 2 ( <i>N</i> )	Source level in dB re 1 $\mu$ Pa a in time period 3 ( <i>N</i> )	Total <i>N</i> (128)
100 kHz	24.41	163 (12)	127 (10)	163 (18)	40
200 kHz	48.83	169 (13)	149 (8)	169 (16)	37
250 kHz	61.04	163 (8)	153 (8)	163 (9)	25
No sound	--	(11)	(9)	(6)	26

**Table 1B.** Pulse-bursts for 2003 and 2005. The data were pooled for the 2 y. The high-frequency (HF) pulse-burst contains frequencies high-pass (hp) filtered above 150 kHz. The number of playbacks is given in parentheses; the total number is 29.

Sound type (2003, 2005)	Source level in dB ( <i>N</i> )	Bandwidth
Pulse-burst	170 (15)	1-250 kHz
Pulse-burst (HF)	170 (6)	150-250 kHz
No sound	(8)	--

following relationship to estimate the received sound level (RL) at the dolphin:  $RL = SL - 20 \log(r/1)$ .

### Behavioral Descriptions

The first two authors analyzed the video files visually. Only videos where one or more dolphins were clearly visible when the sound stimulus was projected were used. Video recordings in which the dolphins reacted were classified into ten categories, and these included both states and events. To check our classifications, we asked five inexperienced observers to watch the videos from 2004, and three inexperienced observers to watch videos from 2003 and 2005. The naïve observers in 2004 were instructed to classify the dolphins' behavior to acoustic stimuli into ten different behavioral categories as found and defined by the first author. For 2003 and 2005, the naïve observers were instructed to classify the behavioral responses as a "response" or "no response."

### Statistics

Statistical tests, including chi-square tests, were conducted using *Excel* and *SigmaStat*.

## Results

We spent 131 h total at sea on 42 day-trips in 2003 to 2005, and conditions allowed for presenting acoustic stimuli 217 times during 11 h. In total, 157 playbacks were chosen for analysis. In these cases, the focal dolphin was in front of the video camera when the sound stimulus was projected. A session was defined as beginning with lowering the hydrophone array and loudspeaker into the water, projecting signals to a focal animal and sometimes other individual focal animals, and pulling the equipment out of the water. There could be from three to ten dolphins in a group, but we had no way of telling if the same dolphin was ensonified more than once during sessions in which more than one dolphin was stimulated.

In 2004, the experiment was divided into three time periods in which amplitude-modulated tones comprised the playback signals: time period 1 (seven trips in the time period 24 July to 11 August), time period 2 (seven trips in the time period 12 to 23 August), and time period 3 (four trips in the time period 25 August to 4 September). During time period 1, the highest intensity tonal signals were used, and these were 163 dB re 1  $\mu$ Pa (p-p) for 100 and 250 kHz, and 169 dB re 1  $\mu$ Pa (p-p) for 200 kHz. During time period 2, the intensity of the 100 kHz signal was lowered by 36 dB (to 127 dB), the 200 kHz signal was lowered by 20 dB (to 149 dB), and the 250 kHz was lowered by 10 dB (to 157 dB). The levels of the playback

signals during time period 3 were like those of time period 1. There were 26 playbacks with no sound as a control for our acoustic playback system in 2004 (Table 1A gives the source levels and the total number of playbacks [ $N = 128$ ] that could be used for each tonal frequency in the three time periods in 2004).

Responses to pulse-bursts were studied during July of 2003 and August of 2005 in 24 trips totaling 91 h of fieldwork (Table 1B;  $N = 29$ ). Each of the ten clicks comprising a pulse-burst was chosen randomly in the 21 pulse-burst playbacks; thus, some clicks could have been used twice and others not at all. The playback signals were projected to single dolphins seen in the onboard video monitor.

The normal protocol was to get close to a group of dolphins before stopping the engine and lowering the hydrophone/loudspeaker array from the side of the boat. The underwater visibility was measured using a custom-made secchi plate lowered from the side of the boat, and the visibility was limited to about 10 m, though the dolphins were usually closer during sound stimulation. Typically, they stayed with the boat during the first playback. Sometimes it was possible to do an additional two or three playbacks to focal individuals before we pulled up the array (ending a session) and moved to either the same group of dolphins again or to a new group. The dolphins lost interest quite quickly, and sometimes the dolphins were not at all interested and would swim away as soon as the engine was stopped. The number of playbacks varied from 1 to 25 on any single trip. Voice comments were recorded onboard of the focal dolphin's general behavior such as circling the boat or array. The video recordings of focal dolphins were analyzed "offline" in the laboratory to determine the type of response or if there was no response. No judgments were made in the field. A sudden change in the dolphin's ongoing behavior was tallied as a "response" (Lehner, 1996). A "no response" was tallied when there was no change in the ongoing behavior to a playback sound or to a control playback.

Five untrained people (naïve observers) viewed video clips from the 128 tonal playbacks. Scores by the five observers were compared to the scores of the first author. The five untrained observers judged whether or not the dolphin was reacting to the projected stimulus, and they agreed with the first author 73% of the time for the tonal stimuli. When the first author did not observe a reaction to a tonal playback, the untrained observers agreed 67% of the time. For the videos where pulse-bursts were the playback signals, there were three naïve observers, and they agreed with the second author's categorization 55% of the time.





**Table 2B.** Number of different behavioral responses to pulse-burst playbacks. The stimulus was 2 s long with 300 clicks/s, and the source level of each click was 170 dB re 1  $\mu$ Pa (p-p).

Behavioral categories	Pulse-bursts		No sound
	Broadband	High frequency	
1. Tail slap	0	0	0
2. Showing belly towards camera	0	0	0
3. Emitting bubbles	0	0	0
4. Acoustic (buzzing towards the video camera/loudspeaker)	0	0	0
5. Jumping out of the water	0	1	0
6. Changing swimming direction	6	1	0
7. Speeding up	0	0	0
8. Turn around/approach the camera	3	2	0
9. Circling around the hydrophone array	5	2	0
10. No response	1	0	8
Total responses	14	6	8
Total playbacks	15	6	8

**Table 3.** The different types of playback signals with minimum and maximum received levels in dB re 1  $\mu$ Pa (p-p)**Table 3A.** Estimated received levels of tonal signals for white-beaked dolphins in the different time periods of 2004; the values are based on 27 measurements. The minimum values were determined at the maximum distance the dolphins were visible, about 7 m.

Tonal type	Min. received level in time periods 1 & 3	Max. received level in time periods 1 & 3	Min. received level in time period 2	Max. received level in time period 2
100 kHz	146	154	110	118
200 kHz	152	160	132	140
250 kHz	146	154	136	144

**Table 3B.** Estimated received levels for dolphins during playback experiments in 2003/2005 using pulse-bursts (broadband and high frequency)

Sound type	Min. received level	Max. received level
BB BP	153	161
HF BP	153	161

For comparison, Sayigh et al. (1999) found 49% of exact matches when comparing her behavioral observations to those of a research assistant; but for the sake of consistency, she chose to use only her scores. We chose the same strategy.

Our playback signals provoked behaviors that we could place into nine categories of responses. The tenth category was a "no response." A focal dolphin could respond with multiple behaviors to one and the same playback sound. We found that amplitude-modulated tones evoked aggression (responses 1 to 4 in Table 2A), avoidance (responses 5 to 7 in Table 2A), and responses of

interest (responses 8 and 9 in Table 2A). Pulse-bursts evoked mostly responses of interest and avoidance (responses 5 to 9 in Table 2B).

#### *Playback of Tonal Signals (2004)*

A significant difference was found between responses and no responses for playing back a sound compared to no sound for all three time periods (time period 1:  $\chi^2 = 69.25$ ,  $df = 1$ ,  $p < 0.005$ ; time period 2:  $\chi^2 = 57.92$ ,  $df = 1$ ,  $p < 0.005$ ; time period 3:  $\chi^2 = 56.4$ ,  $df = 1$ ,  $p < 0.005$  (Zar, 1996). Table 2A shows the distribution of responses for different behavioral categories across frequency,

intensity, and time periods. There were a total of 70 responses in 102 out of 128 playbacks and 26 playbacks with no response (Table 1A). One dolphin could exhibit more than one behavioral response to the same sound stimulus. For example, a dolphin could turn around or approach the camera (response 8 in Table 2) as well as buzzing (acoustic response) towards the camera (response 4 in Table 2). In general, more responses to all sound stimuli were found during time period 1 with higher intensity sound stimuli than during time period 2 with lower intensity sound. Fewer responses were found in time period 3 than in time period 1, even though the sound intensities were the same in both time periods. There was a significant difference in the responses between all three tonal frequencies when comparing time periods 1 and 3 (chi-square test in all comparisons,  $df = 9$ ,  $p < 0.001$ ; Table 2A). For all three frequencies, most responses were in time period 1, less in time period 2, and more in time period 3 (but less than in time period 1; Table 2A).

#### *Playback of Pulse-Burst Signals (2003/2005)*

A total of 145 playbacks were conducted in 72 sessions. Despite the 145 playbacks, the dolphins were only in front of the underwater video camera 29 times and, therefore, these times were chosen for detailed analyses. Table 1B gives the number of playbacks for each pulse-burst along with the source levels. Table 2B gives the distribution of behavioral responses to the pulse-burst playbacks. There was a significant difference between the number of responses to the full bandwidth pulse-burst playbacks and the number of hp-filtered (150 kHz) pulse-burst playbacks (chi-square test,  $df = 5$ ,  $p = 0.004$ ). There were no responses to our no-sound stimulus for tonal playbacks nor for pulse-burst playbacks indicating that there were no acoustic artifacts in our playback system (Table 2).

#### *Minimum and Maximum Received Levels*

The distance between the dolphin and the equipment was estimated for 27 playbacks. This distance varied between 2.8 to 6.9 m. These 27 playbacks were chosen as subsamples to be representative of all playbacks since a dolphin could not be seen at a distance of more than about 7 m due to lack of water clarity. The source levels were the same in time periods 1 and 3 and, therefore, estimated received levels were the same as well. For tonal playback signals of 100, 200, and 250 kHz, the received level varied between 110 and 160 dB re 1  $\mu\text{Pa}$  (p-p) depending on the time period and frequency of sound stimulus (Table 3A). The estimated received levels for pulse-bursts ranged between 153 to 166 dB re 1  $\mu\text{Pa}$  (p-p) depending on the time period and the type of signal (Table 3B).

## Discussion

Many studies have documented that odontocetes respond to anthropogenic sounds, to sounds from their own species, and to sounds from other species (e.g., Morgan, 1979; Mobley et al., 1988; Parks et al., 2003; Tyack, 2009). Therefore, it is not surprising that the free-ranging white-beaked dolphins tested in our experiments responded in numerous ways to our playback sounds. The amplitude-modulated, 2-s tones and the 2-s, 300-Hz repetition rate pulse-bursts resemble the natural vocalizations of these dolphins, but are sufficiently modified to be considered novel sounds. We found that amplitude-modulated tones evoked responses of interest, avoidance, and aggression, while pulse-bursts evoked mostly avoidance responses.

#### *Tonal Playback Signals*

We observed nine different behavioral responses from white-beaked dolphins to amplitude-modulated tonal signals. Some of the behavioral responses, such as a tail slap, showing the belly towards the video camera, emitting bubbles, or "buzzing" the equipment, have been observed during courtship or aggression by spotted (*S. attenuata*) and bottlenose dolphins (Herzing, 2000; Blomquist & Amundin, 2004). We assume this is the same for white-beaked dolphins. We observed animals jumping out of the water three times; but in this context, it could not be determined if this was an aggressive or escape response.

Swimming away from the loud speaker when sounds were played can be interpreted as a short-term avoidance reaction. Schools of spotted dolphins, spinner dolphins (*S. longirostris*), and striped dolphins (*S. coeruleoalba*) swam away from an approaching ship (Au & Perryman, 1982), and bottlenose dolphins changed their swim direction in response to boat traffic (Nowacek et al., 2001; Lemon et al., 2006). A change in swim direction was mentioned by Southall et al. (2007) as a possible response of marine mammals to playback signals. This behavioral response was also observed for belugas (*Delphinapterus leucas*) and grey whales (*Eschrichtius robustus*) when subjected to playback of killer whale sounds. The belugas swam out of the Kvichak River against the tide in response to the playbacks (Fish & Vania, 1971), and migrating grey whales swam away from the sound source when exposed to the killer whale sounds (Cummings & Thompson, 1971).

Our white-beaked dolphins also reacted by increasing their swim speed, which can also be interpreted as an escape response. However, the dolphins sometimes approached the array after playing back tonal signals.

Circling the equipment and the boat was another frequent response. Circling behaviors could be explained by the “novelty” hypothesis pointed out by Mobley et al. (1988) and Parks (2003).

The white-beaked dolphins heard and responded to our tonal playback signals at 100 and 200 kHz since the received levels (110 and 152 dB re 1  $\mu$ Pa [p-p]) were higher than the auditory thresholds at these frequencies (~65 and ~140 dB re 1  $\mu$ Pa [p-p], respectively) (Nachtigall et al., 2008).

The maximum estimated received level at 250 kHz was 154 dB re 1  $\mu$ Pa (p-p), but the auditory threshold of a white-beaked dolphin could not be measured at 250 kHz (Nachtigall et al., 2008). However, the auditory threshold at the highest frequency (181 kHz) was about 136 dB re 1  $\mu$ Pa (p-p) (Nachtigall et al., 2008). The auditory threshold of the white-beaked dolphin at 250 kHz was probably higher than the received level at this frequency. So why did playback sounds at 250 kHz elicit responses? The dolphins were likely hearing and responding to distortions of the 250 kHz signal, the greatest of which was at about 135 kHz and about -45 dB relative to the peak intensity at 250 kHz (see Figure 3A). Thus, the 135 kHz distortion component would be 109 dB re 1  $\mu$ Pa (p-p). The auditory threshold of a white-beaked dolphin at 128 kHz was about 67 dB re 1  $\mu$ Pa (p-p) and somewhat higher but was not measured, at 135 kHz (Nachtigall et al., 2008). Consequently, the dolphin could easily hear the 135 kHz distortion component of the 250 kHz tonal stimulus. Thus, the white-beaked dolphins in our studies could hear and respond to all tonal frequencies, or their distortions, during all time periods.

The same argument applies to the high-frequency pulse-bursts ( $\geq 150$  kHz). The maximum received level was about 160 dB re 1  $\mu$ Pa (p-p), which is considerably higher than the auditory threshold of a white-beaked dolphin at 150 kHz (115 dB re 1  $\mu$ Pa [p-p]; Nachtigall et al., 2008).

We have no explanation for the differences in responses between time periods 1 and 3 (Table 2A). Perhaps the difference could be due to a seasonal change in the white-beaked dolphin population in Faxaflói Bay (Rasmussen et al., 2013) or to a seasonal change in behavior. For example, white-beaked dolphins might respond differently in the mating season compared to outside the mating season. The study in 2004 was conducted from the end of July until the beginning of September. This is also the mating season for white-beaked dolphins in Faxaflói Bay, and we observed mating and mating-related behaviour during our experiments. In fact, the frequency of mating behaviour increased over the period of our studies for each year.

The population of white-beaked dolphins in Faxaflói Bay has been studied using photo-identification (Rasmussen, 1999; Bertulli et al., 2015). The results from the photo-identification studies indicated a high mobility of white-beaked dolphins both within a summer season and between years. There is not a resident population in the bay; therefore, it was unlikely that sounds were played back to the same dolphin on different recording days or at different times in 1 d. In addition, data from one satellite tagged white-beaked dolphin indicated that this individual swam in and out of Faxaflói Bay four times over a period of 201 d (Rasmussen et al., 2013). Furthermore, the sex and age of the animals were unknown, which are attributes known to possibly influence the behavioral state and, thus, the responses of the individual to playback signals. The dolphins were generally difficult to approach when they were resting or travelling, but more curious when they were feeding or socializing. The behavior of white-beaked dolphins was different depending on the time of the day, and it also varied with group size (Rasmussen, 1999).

#### *Pulse-Bursts*

Pulse-bursts can be used for communication as well as during aggressive behaviors by dolphins and porpoises (Caldwell & Caldwell, 1967; Overstrom, 1983; Herzing, 1996, 2000; Blomquist & Amundin, 2004; Clausen et al., 2010). We consider the first four behavioral categories in Table 2B (tail slap, showing the belly, emitting bubbles, and buzzing our equipment) as aggressive responses (Herzing, 1996, 2000; Blomquist & Amundin, 2004). Consequently, we were surprised that our pulse-bursts, 21 in all, did not elicit aggressive responses but only responses in the last five categories and one “no response.” However, a pulse-burst signal could cause the receiving animal to flee as shown in harbor porpoises (*Phocoena phocoena*) (Clausen et al., 2010) and bottlenose dolphins (Blomquist & Amundin, 2004) in human care. Our white-beaked dolphins showed fleeing behaviors, staying at a distance, or approaching, but no behaviors that we considered to be aggressive when we presented a pulse-burst signal.

#### **Conclusions**

In conclusion, white-beaked dolphins reacted to amplitude-modulated tonal playback stimuli by exhibiting aggressive responses and responses of interest or fleeing. Dolphins ensounded with pulse-burst playbacks showed mostly responses of interest or fleeing and no aggressive responses. We saw no responses from the dolphins when we projected a no sound file through our equipment as

a control. There were more behavioral responses to tonal signals in time period 1 than in time period 2, with lower estimated received levels. Time period 3, which was later in the season, had fewer responses despite the same estimated received levels as in time period 1. The reason is unclear but might be a result of seasonal changes in dolphin behavior. The received levels were well above the hearing threshold for tonal playback signals at 100 and 200 kHz, but not for the 250 kHz playbacks. At this frequency, there was a prominent distortion at about 135 kHz—strong enough to be heard by the dolphins. This last fact illustrates one difficulty in using playback signals to determine an audiogram from wild animals.

Even though it is difficult to interpret the behaviors of free-ranging white-beaked dolphins to playback sounds, these results shed light on the types of reactions that can be expected from those sounds. Studies like ours can provide information on the tolerance and behavioral responses from odontocetes to anthropogenic and conspecific signals or noise, especially when the amount of noise in the world's oceans is increasing.

### Acknowledgments

This study was done in accordance with Icelandic laws and regulations. The study was supported by the Oticon Foundation, the Danish National Research Foundation, Julie von Mullens Fond, and the European Commission, Research Directorate-General, Human Potential Program, Access to Research Infrastructures (ARI). Thanks to Dr. Peter McGregor for valuable discussions when designing the playback experiment. Thanks to Drs. Paul Nachtigall, Peter Madsen, and Magnus Wahlberg for valuable comments on earlier versions of the manuscript. Also, thanks to the editor and two referees for their helpful comments. Thanks to Gudmundur Vidir Helgason and Jörundur Svarvarsson, Institute of Biology, University of Iceland. Thanks to Helga Ingimundardóttir, David Þór Olafsson, and the staff at the Sandgerði Marine Center, Iceland, for their helpfulness. Thanks to Hans C. Petersen for his statistical help. Special thanks to Jeppe Dalgaard Balle, Meike Linnenschmidt, René Swift, and Kimie Salo for assisting in the field in 2004.

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