

# Echo features used by human listeners to discriminate among objects that vary in material or wall thickness: Implications for echolocating dolphins

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Echolocating dolphins extract object feature information from the acoustic parameters of echoes. To gain insight into which acoustic parameters are important for object discrimination, human listeners were presented with echoes from objects used in two discrimination tasks performed by dolphins: Hollow cylinders with varying wall thicknesses ( $\pm 0.2$ , 0.3, 0.4, and 0.8 mm), and spheres made of different materials (steel, aluminum, brass, nylon, and glass). The human listeners performed as well or better than the dolphins at the task of discriminating between the standard object and the comparison objects on both the cylinders (humans=97.1%; dolphin=82.3%) and the spheres (humans=86.6%; dolphin=88.7%). The human listeners reported using primarily pitch and duration to discriminate among the cylinders, and pitch and timbre to discriminate among the spheres. Dolphins may use some of the same echo features as the humans to discriminate among objects varying in material or structure. Human listening studies can be used to quickly identify salient combinations of echo features that permit object discrimination, which can then be used to generate hypotheses that can be tested using dolphins as subjects. © 2007 Acoustical Society of America. [DOI: 10.1121/1.2400848]

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## I. INTRODUCTION

Echolocating dolphins emit broadband sonar sounds and perceive objects from the echoes of these sounds. They can detect and discriminate among objects using echolocation (for a review see Au, 2000). However, it is still not clear which echo acoustic features convey object properties such as size, shape, and material to an echolocating dolphin, i.e., which features are important to dolphins during object discrimination. One approach to identifying the acoustic features in echoes that dolphins may use to discriminate among objects is to present a dolphin with an echoic discrimination task, then measure the object echoes and analyze acoustic differences among the objects in conjunction with the dolphin's error patterns (see DeLong *et al.*, 2006b).

Another approach is to ask human listeners to discriminate among echoes and determine the relevant echo acoustic features. Research to date indicates that the inner ear of dolphins appears to function similarly to the human inner ear (or any other mammalian ear) except for the dolphins' ability to hear much higher frequencies (Johnson, 1967). For example, both humans and dolphins can discriminate between sounds that differ in intensity by 1 dB (Evans, 1973; Green, 1993) and the frequency discrimination abilities of humans and dolphins for tonal stimuli are comparable in the range of best

hearing for each species (Herman and Arbeit, 1972; Thompson and Herman, 1975; Wier *et al.*, 1977). There are some differences between humans and dolphins that could result in differences in the perception of echo stimuli (e.g., sharp frequency tuning and short auditory integration time in dolphins; see Supin and Popov, 1995). Even so, some insight into dolphins' use of echo features may be achieved using human listeners.

The major advantage of using human listeners is that, unlike dolphins, they can report which acoustic features allowed them to discriminate among objects. Other advantages are that human listening studies are inexpensive, can be performed in a few weeks, and there are abundant research subjects. In contrast, dolphin experiments can take months to years due to extensive training time, and there are few animals at present who are available and can undertake this work. The expense of performing experiments with dolphins is very high, so the choice of experiments is scrutinized. Human listeners can quickly identify salient combinations of echo features that permit object discrimination, which can then be used to generate hypotheses that can be tested using dolphins as subjects.

Both blind and blind-folded human listeners with normal vision can judge the distance, shape, size, and surface texture of distal objects using echolocation (Kellogg, 1962; Rice, 1967). The humans in these studies investigated objects by projecting self-generated broadband signals such as tongue-

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clicks, snaps, or hisses and listening to the returning echoes. When using self-generated signals, dolphins are better able to discriminate smaller differences among objects than humans. When presented with echoes that were generated using broadband dolphin signals instead of using their own signals, humans are typically capable of discriminating among objects as well or better than dolphins (Au and Martin, 1989; DeLong *et al.*, 2006a; Fish *et al.*, 1976; Helweg *et al.*, 1995). For example, DeLong *et al.* (2006a) presented human listeners with echo trains from objects used in a three-alternative match-to-sample task performed by a dolphin. The six object sets varied in size, shape, material, and surface texture. In two experiments, the human listeners ( $M=84\%$ ) performed as well or better than the dolphin ( $M=55\%$ ) on five of the six sets (chance performance=33%). The human listeners reported using echo features such as overall loudness, pitch, and timbre, and the pattern of changes in loudness and pitch across the echo train.

To determine whether the echo features reported by the humans were likely to have been used by the dolphin, DeLong *et al.* (2006a) compared the error patterns of the humans and the dolphin. Matching error patterns implied use of similar features whereas mismatching patterns implied use of different features. The results suggested that the dolphin attended to the pattern of changes in acoustic features as an object is scanned across a range of orientations to discriminate among the objects that varied in shape, and that it did not rely on overall amplitude differences to discriminate among the objects that varied in size. It was unclear whether the dolphin used the same cues as the humans for the objects that varied in material and texture.

In the current study, human listeners were presented with echoes from aspect-independent objects that were used in two different dolphin experiments: Hollow cylinders that varied in wall thickness (Au and Pawloski, 1992), and spheres made of different materials (Aubauer *et al.*, 2000). The hollow cylinders were presented to the human listeners in an effort to clarify the echoic cues that were used by the dolphin. The dolphin could have used time domain cues (time differences between two echo highlights), frequency domain cues (changes in frequency of prominent spectral features such as notches), or a cue derived from time domain cues called time-separation pitch (TSP). In humans, TSP is a perceived pitch of  $1/T$  Hz that results from two highly correlated broadband pulses separated by time  $T$  (Thurlow and Small, 1955). The spheres were presented to the human listeners to better establish the kinds of cues that are available in objects that vary only in material. The objects used in the study by DeLong *et al.* (2006a) were intended to vary in material, but also had some variations in shape and size, so it was unclear whether the reported cues were associated with the material, size, or shape of the objects. The spheres used in the current study were machined to be exactly the same size and shape, thus ensuring that any differences in the echoes would be due to the material.

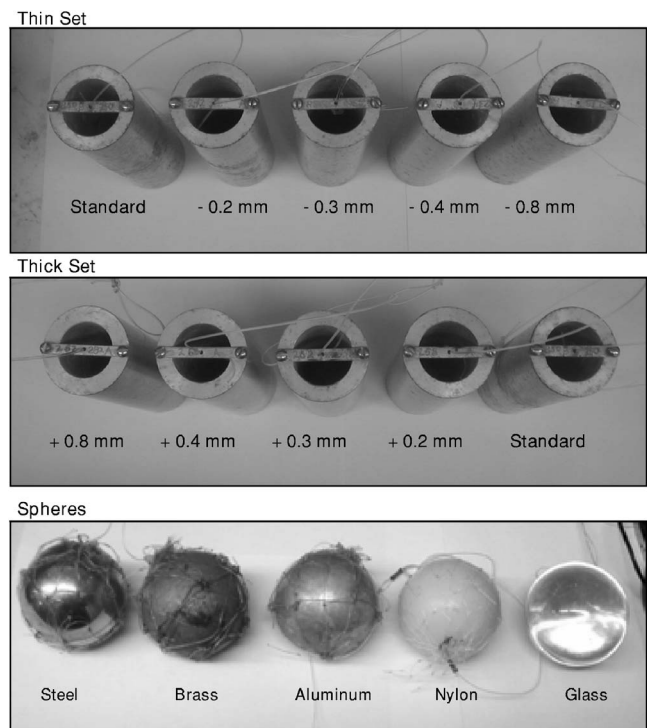


FIG. 1. Object sets. Top two panels show the thin and thick cylinder sets. The hollow aluminum cylinders were all 12.7 cm in length and 37.85 mm in outer diameter but differed in wall thickness. The standard cylinder is 6.35 mm and the comparison cylinders differ by  $\pm 0.2$ , 0.3, 0.4, and 0.8 mm. The bottom panel shows the sphere set (all are 7.62 cm in diameter).

## II. METHOD

### A. Participants

Sixteen participants (eight males and eight females) were recruited to participate in the study. Participants ranged in age from 18 to 33 years ( $M=23.9$ ). All participants were students at Brown University or residents of Providence, Rhode Island. Before their participation, all participants were screened for normal hearing using a standard hearing test (Digital Recordings, 2002) administered via headphones on a laptop computer. At the time of testing no participants reported any hearing difficulties and all were able to detect the echo stimuli during the experiment. Participants who completed the study were paid \$10.

### B. Materials

#### 1. Objects

Stimuli for this experiment consisted of pre-recorded echoes from two groups of objects: Cylinders and spheres (Fig. 1). The cylinders were previously used in a study with a bottlenose dolphin (Au and Pawloski, 1992). The hollow aluminum cylinders were all 12.7 cm in length and 37.85 mm in outer diameter but differed in wall-thickness. The cylinders had open ends, so they were filled with water when submerged. Two sets of cylinders (thin and thick), each consisting of a standard and four comparison cylinders, were used. The standard cylinder had a wall thickness of 6.35 mm. The comparison cylinders had wall thicknesses that differed from the standard by  $\pm 0.2$ ,  $\pm 0.3$ ,  $\pm 0.4$ , and  $\pm 0.8$  mm. All of the cylinders were machined to a tolerance of 0.025 mm. The

thin set contained the standard cylinder and comparison cylinders that were thinner than the standard. The thick set contained the standard cylinder and comparison cylinders that were thicker than the standard. The spheres were made of stainless steel, aluminum, brass, glass, and nylon (all solid and 7.62 cm in diameter) and previously used in a study with a bottlenose dolphin (Aubauer *et al.*, 2000). The standard object was the steel sphere, and the other four spheres were the comparison objects. Participants viewed 20 cm × 28 cm photographs of each of the two cylinder sets and the spheres during the study.

## 2. Echo measurements and formatting

The object echoes were recorded in a cylindrical tank (1.31 m in height by 2.41 m in diameter, and contained 8.3 m<sup>3</sup> of seawater). A custom-made transducer consisting of a 6.35 cm diameter circular, 6.35 mm thick, 1–3 composite piezoelectric element was used to transmit the signals and receive the echoes. The transducer and targets were placed 1 m below the water surface separated by approximately 2 m. Individual targets were hung with monofilament line. The transmitted signal was a broadband dolphin echolocation signal that was 70  $\mu$ s long with a peak frequency of about 120 kHz that has been used in numerous studies (see Au, 1993). This signal was recorded from a bottlenose dolphin and is considered to be a typical, average signal similar to the ones used by the dolphins in both Au and Pawloski's (1992) study and the Aubauer *et al.* (2000) study. The dolphin signal was generated by a Qua-Tec WK10 function generator housed in a "lunch-box" PC and amplified by a Hafler P3000 Transnova power amplifier. The received signal was gated, filtered and amplified with a custom made gated-amplifier, before being digitized at 1 MHz using a Rapid System R1200 data acquisition system. Two hundred echoes were collected for each object. The cylinder and sphere echoes were recorded on different days.

The frequency span of the stimuli was slowed down to shift the spectra of the echoes into the human hearing range using Audition version 1.0 (Adobe, 2003). The original echoes were digitalized at 1 MHz and had center frequencies around 120 kHz. The echoes were all time stretched by a factor of 167 by converting the echoes to a sampling rate of 6 kHz. The time-stretched echoes had center frequencies around 719 Hz. This stretch factor of 167 was chosen so that the echoes presented to the human listeners would fall near their range of best sensitivity (Green, 1976). The original amplitude relations among echoes was retained but each subject was allowed to adjust the overall amplitude level of the echoes once before beginning the experiment. In previous experiments, the echoes presented to human listeners were at low rates (e.g., 4/s.) compared to the much higher rates that dolphins emit sounds and receive echoes (e.g., 10–50/s; Au, 1993). To better mimic the trains of signals emitted by dolphins, echoes were grouped into clusters of six that lasted 100 ms (echo repetition rate of 60/s.).

The echoes used for training and testing the participants were randomly selected from the set of 200 recorded echoes per object and appeared in random order (each echo was used no more than once for either training or testing). There

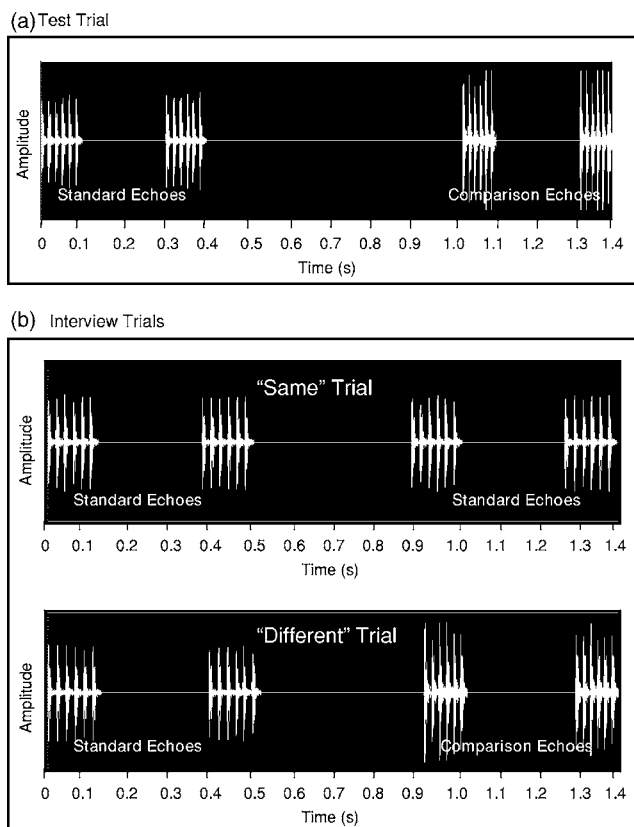


FIG. 2. (a) Example test trial. Two groups of six echoes from the standard object and two groups of six echoes from the comparison object were presented. The standard echoes were presented first on 50% of the trials. In this example, the comparison echoes are from the +0.8 mm sphere. (b) The two types of trials used in the interview phase. "Same" trials contained only echoes from the standard cylinder while "different" trials contained echoes from the standard and one comparison cylinder.

was one training trial created for each object. Each training trial consisted of six echoes followed by 0.6 s silence and then another six echoes (all 12 echoes came from the same object, but each individual echo was different). The echoes used in training trials were not used in the test trials to avoid pre-exposure effects.

Figure 2(a) shows an example of a test trial. Each test trial consisted of two sets of six echoes from the standard object and two sets of six echoes from one of the comparisons (there was no time separation between individual echoes within a set). In half of the test trials the standard echoes came first, and in the other half the comparison echoes came first. The duration of each test trial was approximately 1.35 s. Each set of echoes was approximately 0.1 s in duration and sounded like a single sound (i.e., the four groups of echoes sounded like four separate sounds, not 24 separate sounds).

Each cylinder test session consisted of two blocks, each containing eight trials, for a total of 16 trials per participant. In each of the two eight-trial blocks, each of the four comparison cylinders was presented twice. The sphere test session consisted of two blocks, each containing 16 trials, for a total of 32 trials per participant. In each of the two 16-trial blocks, each of the four comparison spheres was presented four times. For all test sessions the order of the test trials was



randomized separately for each participant. Participants completed the test sessions with no pause between the blocks.

### C. Procedure

The dolphins in the previous studies were required to discriminate between a standard target and a set of comparison objects in either a left/right two-alternative forced choice procedure by pressing a paddle on the same side as the standard (Au and Pawloski, 1992) or a go/no-go procedure by pressing a paddle for the standard and remaining still for the comparisons (Aubauer *et al.*, 2000). To simulate the dolphins' tasks, the human listeners in the current study were required to discriminate between the standard target and the comparison targets in a two-alternative forced choice procedure in which they were played sequences of recorded object echoes and had to verbally identify which set of echoes came from the standard. In addition, the human listeners were also asked to identify which of the comparison stimuli was presented on each trial (not a task done by the dolphins) so that they would be encouraged to listen carefully to each stimulus in order to be better able to report the echo features that allowed them to discriminate among the objects.

The human listening experimental set-up consisted of a single experimenter with a laptop computer that channeled the echo stimuli via two Koss UR29 headphones to both the participant and the experimenter (for the purpose of monitoring the echoes). To control for inadvertent cueing, the participant sat faced away from the experimenter during testing. The experimenter ran a randomized playlist for each participant using Panther OS X iTunes software (Apple, 2004) which controlled the sequence of trials and object sets.

Participants were tested individually in a quiet, sound-attenuating room. The participants heard a set of instructions and read a vocabulary sheet with terms to describe the echoes. On the vocabulary sheet were four terms and their operational definitions: "Loudness" (how loud or soft the sound is, i.e., sensation derived from sound intensity), "pitch" (how high or low the sound is, i.e., sensation derived from sound frequency), "duration" (the length of the sound), and "timbre" (the property in musical tones that makes it possible to distinguish one instrument from another or to distinguish voices from instruments, i.e., tone color/sound quality). This procedure ensured that all the participants had the same minimum set of descriptive tools with which they could describe echoic cues (although it was emphasized that they could also use terms not on the list). This vocabulary sheet was available for the participant to reference throughout the experiment. Participants were played pure tone sounds demonstrating each of the terms as they viewed the vocabulary sheet (these sounds were not the echoes used in the experiment). They were presented with a set of sounds that differed in loudness only (same pitch and timbre), a set of sounds that differed in pitch only (880 Hz tone vs 220 Hz tone; same volume and timbre), and a set of sounds that differed in timbre only (middle C played by a french horn, muted trumpet, and soprano sax at the same volume).

All participants were tested on three object sets. Participants were randomly assigned to one of four object set or-

ders: A (spheres, thick cylinders, thin cylinders), B (spheres, thin, thick), C (thick, thin, spheres), and D (thin, thick, spheres). For each object set session there were three phases: training, testing, and interview. The participants completed all three phases for a single object set session before moving on to the next object set session.

#### 1. Training

At the beginning of the object set session participants were given the photograph of the object set (see Fig. 1). Training stimuli were played twice in the same order. For the thin cylinder object set the order was standard,  $-0.2$ ,  $-0.3$ ,  $-0.4$ , and  $-0.8$  mm; for the thick cylinder object set the order was standard,  $+0.2$ ,  $+0.3$ ,  $+0.4$ , and  $+0.8$  mm; and for the sphere object set the order was standard, aluminum, brass, nylon, and glass. Participants then listened to a sample of a single test trial and were given instructions regarding the testing procedure (see below). The sample test trial was the same for each participant and contained echoes that were not used in any of the actual test trials. After listening to the sample test trial, then presentation of the training stimuli was repeated again in the same order as before. Finally, participants were allowed to have the training stimuli repeated again as many times as they thought necessary, and in any order, before beginning testing. Participants were not allowed to review the training stimuli once they began the test phase.

#### 2. Testing

The test phase immediately followed the training phase. Each test trial began with a presentation of a test trial stimulus [see Fig. 2(a)]. Participants were allowed to listen to the test trial stimulus as many times as they liked before responding. They had to respond to two questions for each trial: (1) Was the standard object the first or second group of echoes? and (2) which comparison object did the nonstandard echoes come from? For each trial, following the participant's response, the experimenter told the participants whether they were correct or incorrect, and then indicated the correct choice if the participants were incorrect.

#### 3. Interview

Participants immediately began the interview phase when the test phase was completed. The interview phase had two parts: (1) The open-ended interview followed by (2) the close-ended interview trials. The close-ended interview trials presented an opportunity to test whether the participants would describe the same cues as they did in the open-ended interview (when they freely recalled the cues) compared to when they were blind to the identity of the object in the close-ended trials. In the open-ended interview which lasted approximately 5–10 min, participants' responses to the question "What cues did you use to discriminate among the objects?" were tape-recorded. Then participants listened to a series of close-ended interview trials. There were eight trials for each of the three object set sessions. Four of the interview trials contained echoes only from the standard object ("same" trials) and the other four trials contained echoes

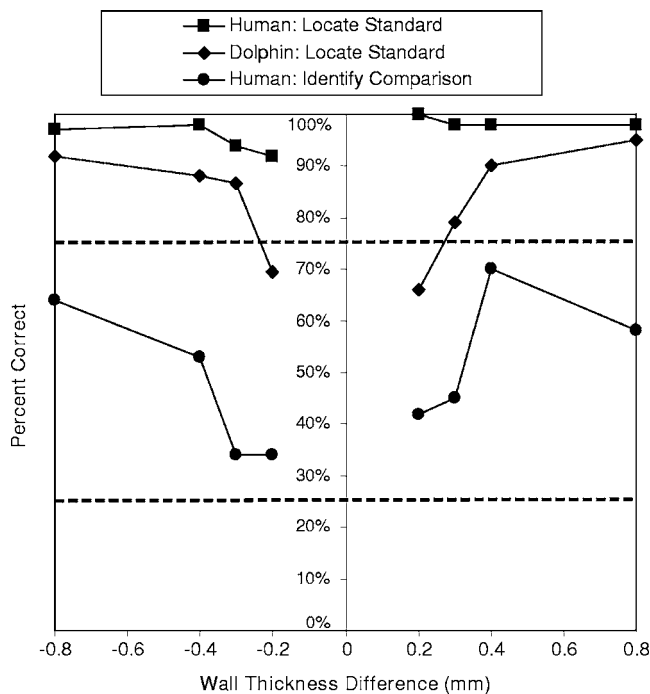


FIG. 3. Performance of the human listeners and the dolphin on the cylinder sets. The top two solid lines show the performance of the human listeners on the task of locating the standard cylinder. The middle two solid lines show the performance of dolphin on the same task (from Au and Pawloski, 1992). The first dotted line shows the 75% correct threshold for the “locate standard” task. The bottom two solid lines show the performance of the human listeners on identifying the comparison cylinder. The bottom dotted line shows chance choice performance (25% correct) on the “identify comparison” task.

from the standard and one comparison object [“different” trials; see Fig. 2(b)]. The participants were required to indicate (1) whether they perceived a difference between the first group of echoes and the second group of echoes and (2) if yes, they were asked to briefly explain which echo features sounded different. Participants were able to complete the training, testing and the interview phase for a single object set session in approximately 20 min. All participants completed the entire experiment in approximately 1 to 2 h ( $M=58$  min).

### III. RESULTS

#### A. Cylinders

##### 1. Performance accuracy

*a. Locate standard.* The human listeners were able to determine whether the standard echoes were in the first or second group of echoes with nearly perfect accuracy (overall  $M=97.1\%$ ). Figure 3 shows the human listeners’ choice accuracy for each of the cylinders (top two lines). The performance of the dolphin is also shown in Fig. 3 (middle two lines, taken from Au and Pawloski, 1992). Au and Pawloski (1992) used a response level of 75% correct to determine the wall thickness discrimination threshold. Interpolation of the dolphin performance data indicated a discrimination threshold of  $-0.23$  mm and  $+0.27$  mm (i.e., the dolphin could not discriminate the  $\pm 0.2$  mm cylinder from the standard but it could discriminate the  $\pm 0.3$  mm cylinder from the standard). The same 75% response level was used to determine the discrimination threshold for the human listeners.

To determine whether the human listeners’ performance was above 75% on each cylinder, a t-test was performed separately for each cylinder using one score for each participant (average performance on the cylinder) and comparing the participants’ scores to a value of 0.75. The participants’ performance was significantly above 75% for all eight cylinders ( $-0.2$  mm,  $t(15)=4.6$ ,  $p<0.001$ ;  $-0.3$  mm,  $t(15)=3.9$ ,  $p<0.01$ ;  $-0.4$  mm,  $t(15)=15.0$ ,  $p<0.001$ ;  $-0.8$  mm,  $t(15)=10.3$ ,  $p<0.001$ ;  $+0.3$  mm,  $t(15)=15.0$ ,  $p<0.001$ ;  $+0.4$  mm,  $t(15)=15.0$ ,  $p<0.001$ ;  $+0.8$  mm,  $t(15)=15.0$ ,  $p<0.001$ ; t-test could not be performed for the  $+0.2$  cylinder because all participants achieved 100% correct). A one-way analysis of variance (ANOVA) revealed that the performance of the human listeners did not vary significantly across all eight cylinders,  $F(7, 120)=1.12$ ,  $p>0.05$  [preliminary analyses indicated no effect of gender, object set order, block, or position of standard echoes (first or second) so these factors were not included in subsequent analyses].

*b. Identify comparison.* The human listeners were able to identify six of the eight comparison cylinders (see Fig. 3). Chance choice accuracy is 25%, because the participants could choose from among four alternatives (four cylinders in each set). To determine whether the participants’ performance was above chance for each cylinder, a t-test was performed separately for each cylinder using one score for each participant (average performance on the cylinder) and comparing the participants’ scores to a value of 0.25. The participants’ performance was above chance for all of the cylinders in the thick set ( $+0.2$  mm,  $t(15)=3.2$ ,  $p<0.01$ ;  $+0.3$  mm,  $t(15)=3.9$ ,  $p<0.01$ ;  $+0.4$  mm,  $t(15)=8.7$ ,  $p<0.001$ ;  $+0.8$  mm,  $t(15)=4.4$ ,  $p<0.01$ ) and for two cylinders in the thin set ( $-0.4$  mm,  $t(15)=5.6$ ,  $p<0.001$ ;  $-0.8$  mm,  $t(15)=6.5$ ,  $p<0.001$ ). The participants’ performance was not significantly different from chance on the  $-0.2$  mm cylinder [ $t(15)=1.7$ ,  $p>0.05$ ] or the  $-0.3$  mm cylinder [ $t(15)=1.5$ ,  $p>0.05$ ].

A one-way analysis of variance (ANOVA) revealed that the performance of the human listeners varied significantly among the eight cylinders,  $F(7, 120)=5.24$ ,  $p<0.001$ . Simple effects tests indicated that performance on the  $-0.8$  mm cylinder was significantly better than performance on the  $-0.2$  and  $-0.3$  mm cylinders, and performance on the  $+0.4$  cylinder was significantly better than performance on the  $\pm 0.2$  and  $\pm 0.3$  mm cylinders.

Table I shows the choices made by the participants in response to the question “What is the identity of the comparison cylinder?” For the thin set, the participants often confused the  $-0.2$ ,  $-0.3$ , and  $-0.4$  mm cylinders (e.g., when the test stimulus was the  $-0.3$  mm cylinder, participants reported that it was the  $-0.4$  mm cylinder 44% of the time). For the thick set, the participants often confused the  $+0.2$  mm cylinder with the  $+0.3$  mm cylinder. These confusions suggest that the participants thought the  $-0.2$ ,  $-0.3$ , and  $-0.4$  mm cylinders sounded similar, as did the  $+0.2$  and  $+0.3$  mm cylinders.

##### 2. Reported use of acoustic cues

Table II shows the echoic cues reported by the human listeners during the open-ended interview and Table III shows the cues reported during the closed-ended interview

TABLE I. Participants' choices on "identify comparison" task for cylinders and spheres.

		Choice			
Cylinders: Thin Set		−0.2 mm	−0.3 mm	−0.4 mm	−0.8 mm
Sample	−0.2 mm	<b>34%</b>	31%	16%	19%
	−0.3 mm	8%	<b>34%</b>	44%	14%
	−0.4 mm	11%	30%	<b>53%</b>	6%
	−0.8 mm	14%	20%	2%	<b>64%</b>
		Choice			
Cylinders: Thick Set		+0.2 mm	+0.3 mm	+0.4 mm	+0.8 mm
Sample	+0.2 mm	<b>42%</b>	36%	13%	9%
	+0.3 mm	30%	<b>45%</b>	17%	8%
	+0.4 mm	9%	20%	<b>70%</b>	0%
	+0.8 mm	23%	14%	5%	<b>58%</b>
		Choice			
Spheres		Aluminum	Brass	Nylon	Glass
Sample	Aluminum	<b>55%</b>	17%	11%	16%
	Brass	13%	<b>60%</b>	4%	23%
	Nylon	14%	6%	<b>74%</b>	5%
	Glass	27%	16%	18%	<b>39%</b>

Note. Each cell represents the percentage of choices made by all 16 participants for each object. Correct answers are shown in bold print (e.g., when the −0.2 mm cylinder was the sample, the participants correctly chose the −0.2 mm cylinder 34% of the time).

trials. The results of the open-ended interview and the closed-ended interview trials were consistent, showing that the participants reported the same cues whether they were asked to recall the cues for each object from their memory (open-ended) or instantly analyze the difference between two sets of echoes without knowing the identity of the objects (close-ended). Thus, the results of both the open- and closed-ended interviews will be discussed together.

The primary cue reported by the participants to discriminate between the standard and the comparison cylinders was pitch and the secondary cue was duration. The participants tended to report using more than one cue (e.g., both pitch and duration). For both the thin and the thick set, participants reported that the pitch of the  $\pm 0.2$ , 0.3, and 0.4 mm increased

incrementally relative to the standard (e.g.,  $\pm 0.3$  mm was higher than  $\pm 0.2$  mm, and  $\pm 0.4$  mm was higher than  $\pm 0.3$  mm). They also reported that the  $\pm 0.8$  mm cylinders were an exception to this trend. Instead of being higher in pitch than the  $\pm 0.4$  mm cylinder, it was either higher than the standard but lower than the  $\pm 0.2$  mm cylinder, equal in pitch to the  $\pm 0.2$  mm cylinder, or slightly lower than the standard. Participants reported that the duration of the  $\pm 0.2$ ,  $\pm 0.3$ , and  $\pm 0.4$  mm cylinders was shorter than the standard. A minority of participants reported using timbre or loudness as cues (e.g., four thought that the  $\pm 0.8$  cylinder was louder and had a different timbre than the standard).

### 3. Cylinder echoes

Figures 4(a) and 4(b) show the cylinder echoes. Two features were measured for each of the 200 echoes per cylinder: (1) Overall duration and (2) the time separation  $T$  between the peaks of the first and second highlights of the echo. The time separation  $T$  was used to derive a third feature: Time-separation pitch TSP ( $1/T = \text{TSP}$ ). Duration was defined as the time between the start of the echo and the end of the last major highlight. Highlights are local maxima in echo amplitude and an example of how major highlights were counted is shown in Fig. 4(d). These features were measured from the original dolphin echoes, then scaled by a factor of 167 since the human listeners listened to slowed-down versions of the original echoes. These "slowed-down" echo features are shown in Table IV.

There were minor differences in the overall durations of the individual cylinder echoes, such that the  $\pm 0.2$ ,  $\pm 0.3$ , and  $\pm 0.4$  cylinders were about 0.001–0.002 s shorter than the

TABLE II. Echoic cues reported by human participants during the open-ended interviews.

Echoic Cues	Object Set		
	Cylinders		Spheres
	Thin set	Thick set	
Pitch	16	16	13
Loudness	2	3	6
Timbre	4	4	14
Duration	5	10	1
Average number of cues reported per person	1.7	2.1	2.1

Note. Each cell contains the number of participants ( $N=16$ ) who reported using each cue for each of the object sets. Participants could report multiple cues for each set.

TABLE III. Echoic cues reported by human participants for the cylinders during closed-ended interview trials.

Echoic Cues	Thin set				Thick set			
	-0.8	-0.4	-0.3	-0.2	+0.2	+0.3	+0.4	+0.8
Pitch	15	16	14	14	16	15	16	12
Loudness	1	1	1	0	1	0	1	4
Timbre	2	2	4	3	2	1	3	2
Duration	4	10	9	6	10	9	11	7
Average number of cues reported per person	1.5	1.8	1.8	1.4	1.8	1.6	2.0	1.6

Note. Each cell contains the number of participants ( $N=16$ ) who reported using each cue for each of the object sets. Participants could report multiple cues for each set.

standard. Since the human listeners listened to groups of 6 cylinders, it may be better to compare durations of echo groups (see Table IV), which shows that the echo groups for the  $\pm 0.2$ ,  $\pm 0.3$ , and  $\pm 0.4$  cylinders were about 0.006–0.012 s shorter than the standard. The human listeners reported that they thought the  $\pm 0.2$ , 0.3, and 0.4 mm cylinders sounded shorter than the standard, which accurately reflects the actual measured duration of the echoes.

The time separation between the first and second highlights of the echoes and time-separation pitch also varied between cylinders, but the TSP did not increase incrementally from the thinnest to the thickest cylinders. For the thin cylinders, the lowest TSP was generated by the  $-0.8$  mm (176.8 Hz) and then the cylinders increased in TSP from the standard to the  $-0.4$  mm (standard=179.8 Hz,  $-0.2$  mm =187.8 Hz,  $-0.3$ =192.7 Hz,  $-0.4$ =196.8 Hz). For the thick cylinders, the lowest TSP was generated by the standard (179.8 Hz) and the comparison cylinders were all higher than the standard. From lowest to highest they were as follows:  $+0.8$  mm (186.4 Hz),  $+0.3$  mm (191.4 Hz),  $+0.4$  mm (193.7 Hz), and  $+0.2$  mm (203.7 Hz). The participants' reports reflected these changes in TSP. They reported that the

pitch of the  $\pm 0.2$ , 0.3, and 0.4 mm cylinders was higher than the standard and that the  $\pm 0.8$  mm cylinders were an exception to this trend ( $\pm 0.8$  mm were not higher than  $\pm 0.4$  mm, but slightly higher or lower than the standard). [Note that humans can distinguish between two tone bursts under 200 Hz that differ by less than 1 Hz so all the cylinders should be discriminable using TSP (Wier *et al.*, 1977).]

Figure 5 shows histograms representing the number of echoes (out of 200 per cylinder) at each TSP for each cylinder in both the thin and thick sets. These graphs show that (1) each cylinder covered a range of TSP values, and (2) there was overlap between the cylinders such that there could be more than one cylinder with any given TSP. For example, an echo with a TSP of 193.16 Hz is almost equally as likely to have come from the  $-0.3$  or  $-0.4$  mm cylinder (there is also a small chance it could have come from the  $-0.2$  mm cylinder; see Fig. 5). The same is true for the thick cylinders: An echo with a TSP of 196.3 Hz could have come from the  $+0.2$  mm,  $+0.3$  mm, or  $+0.4$  mm cylinder. Since the echoes presented to the human listeners were chosen randomly from the 200 echoes recorded for each cylinder, it is likely they heard these variations in the pitch of the echoes from trial to

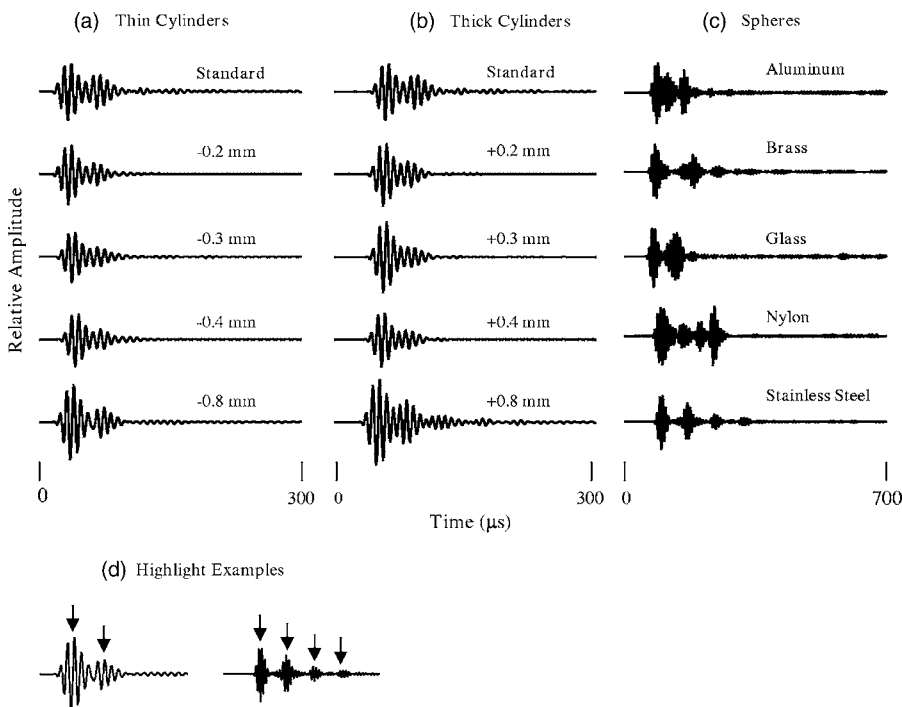


FIG. 4. Object echoes from the thin cylinder set (a), the thick cylinder set (b), and the spheres (c). Figure (d) shows the location of echo highlights in the  $-0.8$  mm cylinder (left) and the steel sphere (right).



TABLE IV. Cylinder and sphere echo measurements.

	Echo Feature					
	Time Separation $T$ (ms)		TSP (Hz)		Duration (s)	
	$M$	$SD$	$M$	$SD$	Indiv.	Group
<b>Cylinders</b>						
−0.8 mm	5.66	0.06	176.83	1.93	0.006	0.036
−0.4 mm	5.08	0.04	196.84	1.60	0.004	0.024
−0.3 mm	5.19	0.04	192.68	1.41	0.005	0.030
−0.2 mm	5.32	0.09	187.86	3.27	0.005	0.030
Standard	5.56	0.07	179.85	2.50	0.006	0.036
+0.2 mm	4.91	0.06	203.76	2.50	0.005	0.030
+0.3 mm	5.22	0.08	191.48	3.00	0.005	0.030
+0.4 mm	5.16	0.09	193.76	3.23	0.005	0.030
+0.8 mm	5.36	0.05	186.46	1.62	0.006	0.036
<b>Spheres</b>						
Steel	11.54	0.05	86.66	0.36	0.021	0.126
Aluminum	5.22	0.79	195.58	27.77	0.011	0.066
Brass	16.94	0.13	59.02	0.47	0.017	0.102
Nylon	11.27	1.12	89.70	9.91	0.017	0.102
Glass	8.36	0.57	120.07	7.39	0.011	0.066

Note. All measurements are given for the slowed down echoes that were presented to the human listeners, not the original echoes. Means ( $M$ ) and standard deviations ( $SD$ ) are calculated for 200 echoes per object.  $T$  = time separation between first and second highlight in the echo. Time separation pitch (TSP) is calculated from  $1/T$ . Duration is given for individual echoes and groups of six echoes.

trial. The participants' confusions between the comparison cylinders reflect that they may have heard these overlaps in TSPs (see Table I). For example, the participants' confusions suggest that they thought the −0.2, −0.3, and −0.4 mm cylinders sounded similar, and Fig. 5 shows that those three cylinders had overlapping values between 187 and 193 Hz.

## B. Spheres

### 1. Performance accuracy

*a. Locate standard.* The human listeners were able to determine whether the standard sphere was the first or second group of echoes (overall  $M=88.3\%$ ). Choice accuracy for each comparison sphere is as follows: Aluminum (89.1%), brass (80.5%), nylon (90.1%), and glass (93.0%). To determine whether the participants' performance was above chance (50%) for each cylinder, a t-test was performed separately for each cylinder using one score for each participant (average performance on the cylinder) and comparing the participants' scores to a value of 0.5. The participants' performance was significantly above chance for all four spheres (aluminum,  $t(15)=10.4$ ,  $p<0.001$ ; brass,  $t(15)=6.0$ ,  $p<0.001$ ; nylon,  $t(15)=9.7$ ,  $p<0.001$ ; glass,  $t(15)=13.3$ ,  $p<0.001$ ). A one-way analysis of variance (ANOVA) revealed that the performance of the human listeners did not vary significantly across the four spheres,  $F(3,60)=1.74$ ,  $p>0.05$ .

The dolphin was also able to discriminate between the standard sphere and the comparison spheres (Aubauer *et al.*, 2000). In the dolphin's go/no-go task, a single target (either a standard or comparison) was presented on each trial, unlike the humans' two-alternative forced choice task in which a set of standard and comparison echoes were presented on each trial. Thus, there is a score for the standard steel sphere

(93%), as well as each of the comparisons: Aluminum (77%), brass (89%), and nylon (100%; the glass sphere was not presented to the dolphin). Also, the dolphin received more brass trials ( $n=299$ ) than aluminum ( $n=13$ ) or nylon trials ( $n=13$ ). To determine whether the human listeners' performance was significantly different from the dolphin's, a t-test was performed separately for each sphere using one score for each participant (average performance on the sphere) and comparing the participants' scores to a value matching the dolphin's score (aluminum=0.77, brass=0.89, nylon=1.0). The human listeners' performance was not significantly different from the dolphin on the brass sphere [ $t(15)=-1.7$ ,  $p>0.05$ ]. The human listeners' performance on the aluminum sphere was significantly better than the dolphin's ( $M_s=89\%$  vs 77%;  $t(15)=3.2$ ,  $p<0.01$ ), but the dolphin's performance on the nylon sphere was significantly better than the humans' ( $M_s=100\%$  vs 90%;  $t(15)=-2.2$ ,  $p<0.05$ ).

*b. Identify comparisons.* The human listeners were able to identify three of the four comparison spheres. Choice accuracy for each comparison sphere is as follows: Aluminum (55.5%), brass (60.2%), nylon (74.2%), and glass (39.1%). Chance choice accuracy is 25%, because the participants could choose from among four alternatives. To determine whether the participants' performance was above chance for each sphere, a t-test was performed separately for each sphere using one score for each participant (average performance on the sphere) and comparing the participants' scores to a value of 0.25. The participants' performance was above chance for three of the spheres [aluminum,  $t(15)=5.3$ ,  $p<0.001$ ; brass,  $t(15)=5.2$ ,  $p<0.001$ ; nylon,  $t(15)=8.0$ ,  $p<0.001$ ] but not the glass sphere [ $t(15)=2.1$ ,  $p=0.05$ ]. A one-way analysis of variance (ANOVA) revealed



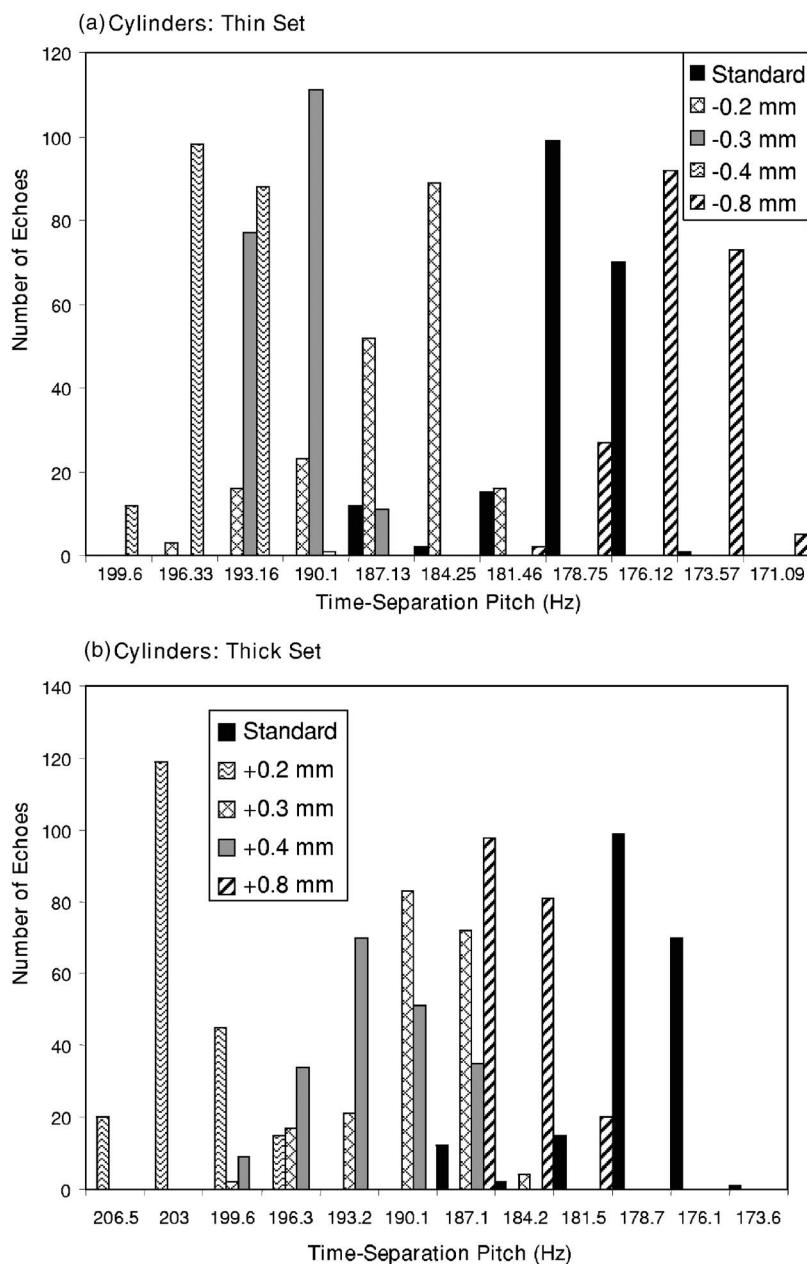


FIG. 5. Histograms representing the number of echoes (out of 200 per cylinder) at each time-separation pitch (TSP) for each cylinder in the thin set (a) and the thick set (b).

that the performance of the human listeners varied significantly among the spheres,  $F(3,60)=5.18$ ,  $p<0.01$ . Simple effects tests indicated that performance was best on the nylon sphere and worst on the glass sphere.

Table I shows the choices made by the participants in response to the question "What is the identity of the comparison sphere?" When aluminum was the sample, the participants confused it with brass or glass on 33% of the trials. When brass was the sample, the participants confused it with aluminum or glass on 36% of the trials. When glass was the sample, they confused it with aluminum on 27% of the trials. These confusions suggest that they thought the aluminum, brass, and glass spheres sounded similar. When nylon was the sample, they usually correctly answered "nylon" (74% of trials) and did not confuse it with the other spheres, which suggests that the nylon sphere sounded distinctive compared to the other spheres.

## 2. Reported use of acoustic cues

As with the cylinders, the results of the open-ended interview and the closed-ended interview trials were consistent for the spheres, so the results of both will be discussed together.

The two main cues reported by the participants to discriminate between the standard and the comparison spheres were pitch and timbre (see Tables II and V). The participants tended to report using more than one cue (e.g., both pitch and timbre). The majority of the participants reported that the timbre of the spheres varied, but their descriptions were diverse (e.g., the aluminum sphere was "percussive," or "flat;" the brass sphere was "hollow and distant" or "ringy;" the nylon sphere was "fuzzy" or "damp;" and the glass sphere was "sharp" or "crisp"). The majority of the participants reported that pitch was a cue, but opinions varied as to whether each comparison was higher, lower, or the same pitch as the

TABLE V. Echoic cues reported by human participants for the spheres during closed-ended interview trials.

Echoic Cues	Object			
	Aluminum	Brass	Nylon	Glass
Pitch	15	11	12	12
Loudness	0	4	5	3
Timbre	7	11	9	9
Duration	0	1	0	0
Average number of cues reported per person	1.5	1.8	1.8	1.5

Note. Each cell contains the number of participants ( $N=16$ ) who reported using each cue for each of the objects. Participants could report multiple cues for each set.

standard (e.g., in the open-ended interview, seven reported that aluminum was higher than the standard, four reported that it was lower). The majority opinion was that the nylon, brass, and glass spheres had a lower pitch than the standard, and the aluminum sphere had a higher pitch than the standard. A minority of participants reported using loudness and duration as cues, but there was no consensus as to how these features varied (e.g., two reported that glass was softer and one reported that glass was louder than the standard).

### 3. Sphere echoes

Figure 4 shows the sphere echoes and Table IV shows the echo measurements. The aluminum and glass echoes were the shortest in duration (0.011 s), followed by brass and nylon (0.017 s), and the steel echoes were longest (0.021 s). Only one participant reported using differences in echo duration to discriminate among the echoes, which suggests either the participants did not pick up on the duration differences in the echoes, or that duration was simply not as salient as the other two cues they reported (pitch and timbre) so they ignored duration differences.

For the spheres, even though there were more than two highlights in all the echoes, the time separation  $T$  was still defined as the time interval between the first and second highlight and TSP was calculated using that value. The TSP of the spheres from lowest to highest was as follows: Brass (59.0 Hz), steel (86.7 Hz), nylon (89.7 Hz), glass (120.1 Hz), and aluminum (195.6 Hz). Three of the spheres had large standard deviations, indicating that the values obtained for the 200 echoes were spread over a wide range (aluminum:  $M=195.6$ ,  $SD=27.8$ ; nylon:  $M=89.7$ ,  $SD=9.9$ ; glass:  $M=120.1$ ,  $SD=7.4$ ).

The participants reported differences in pitch among the sphere echoes, but the differences they reported between the standard steel echo and the comparison echoes accurately matched differences in the calculated TSP values for the aluminum, brass, and nylon spheres but not the glass sphere (see Table IV). The majority of participants reported that aluminum was higher in pitch than steel, and that brass was lower in pitch than steel, and both opinions match the actual TSP values. The majority of the participants reported that the nylon sphere was lower in pitch than the steel sphere, which in fact was the case for 55% (110/200) of the echoes since

TSPs for nylon ranged from 78.8 to 115.1 Hz. The majority of participants reported that the glass sphere was lower in pitch than the steel sphere, but the calculated TSP of all the glass echoes was higher than steel.

## IV. DISCUSSION

### A. Cylinders

Both the human listeners and the dolphin were able to discriminate between the standard cylinder and the  $\pm 0.8$  mm,  $\pm 0.4$  mm, and  $\pm 0.3$  mm comparison cylinders. However, the human listeners were able to discriminate between the standard and the  $\pm 0.2$  mm comparisons at the 75% correct response level whereas the dolphin could not. The human listeners' performance appeared to be significantly better than the dolphin's primarily on the  $\pm 0.2$  mm cylinders and the  $\pm 0.3$  mm cylinder (see Fig. 3).

The human listeners' performance could have been higher than the dolphin's for several reasons. First, the echoes for the human listeners were collected in a test tank and presented in a controlled laboratory situation. The echoes had a high signal to noise ratio and they did not contain any extraneous echoes (e.g., echoes from passing fish) whereas the dolphin's echoes may have contained background noise (e.g., from snapping shrimp) and extraneous echoes. A second reason the human listeners performed differently than the dolphin could be the way in which the echoes were presented to the human listeners in two groups of six echoes, whereas the dolphin made its choice based on variable numbers of echoes (e.g., it could emit 10 clicks on one trial and 50 clicks on the next). In the future, it would be useful to collect the dolphin's actual echoes during the task, and present those echoes to the human participants so that both the dolphins and the humans are basing their decisions on the same amount and quality of echo information.

The human listeners' performance could have been different from the dolphin's due to the rate at which the echoes were slowed down to bring them into the human hearing range. In this study the echoes were time-stretched by a factor of 167 so that their center frequencies were around 719 Hz. Other studies have utilized a time-stretch factor of 50, corresponding to an echo center frequency around 2.4 kHz (Au and Martin, 1989; Helweg *et al.*, 1995), or a time-stretch factor of 125 corresponding to an echo center frequency around 1 kHz (DeLong *et al.*, 2006a). It is possible that playing back the echoes at different frequencies (via different slow-down rates) could change the results.

Finally, the human listeners' performance could have been different than the dolphin's because of the exclusion strategy adopted by the dolphin. In the dolphin's task, one target was presented to the left and one target to the right of the dolphin (the standard and one comparison) and it was required to press a paddle on the same side as the standard. The human listeners had an analogous task of listening to echoes from the standard and one comparison and indicating whether the standard echoes came first or second. Thus, both the humans and the dolphins were presented with both the standard and comparison within each trial. However, measurement of the dolphin's echolocation signals indicated that

it emitted 96% of its signals toward the target located on the right, meaning that it did not typically listen to echoes from both the standard and the comparison within a single trial (Au and Pawloski, 1992). The dolphin had adopted an exclusion strategy in which it examined a single target and determined whether that target was the standard or not, i.e., the dolphin memorized the echo characteristics of the standard target and compared the received echoes from the right target to that template of the standard. In contrast, the human listeners always had access to echoes from both targets and had to listen to both stimuli before reporting a choice. Although the human listeners undoubtedly memorized some characteristics of the standard target, they may have performed better than the dolphin because they could have used a different strategy than the dolphin (listen to both targets, not just one).

There are some discrepancies between this study and Au and Pawloski (1992) in the echo measurements of the same cylinders. For example, Au and Pawloski (1992) measured echoes in 1992 and estimated that the TSP of the standard,  $-0.2$  mm, and  $-0.3$  mm cylinder were 28.3, 27.9, and 27.8 kHz, respectively. The current study, using a different set of echoes measured in 2005 estimated the average TSP of the same three cylinders as 30.0, 31.4, and 32.2 kHz.

There are at least two factors that may explain why the echo measurements of the same cylinders taken in 1992 and 2005 were not the same. First, the speed of sound of water is a factor since the wave travels through the water that is contained in the inner diameter of the target. The speed of sound varies in saltwater (1,513 m/s) vs fresh water (1,493 m/s), and the measurement tank may have had different quantities of salt water in the two years due to evaporation and rainfall. Second, the echoes from these cylinders are very sensitive to vertical orientation and just a minor shift in tilt cause by wind induced waves can cause large changes. Au and Pawloski (1992) suspended the target with a rig that probably provided good stability and vertical alignment (20 echoes per target were measured). In the current study, the cylinders were measured by suspending a line through the holding bar across the cylinders without perfectly stabilizing the cylinders (200 echoes per target were measured). The present measurements probably represent more closely what the dolphin encountered since a special rig was not used to present the targets to the dolphin. The current echoes presented to the human listeners probably represented the dolphin's situation more closely (i.e., having to make decisions based on echoes from the same target that vary slightly from trial to trial).

Au and Pawloski (1992) proposed three cues that could be used to discriminate among the cylinders: Time domain cues (time differences between two echo highlights), frequency domain cues (changes in frequency of prominent spectral features such as notches), and time-separation pitch (TSP). The first is linked to the envelope of the time waveform and the second is linked to the spectral envelope, and both are implicated in the perception of timbre (ANSI, 1960). A minority of the participants (up to 25%) reported using timbre, so it is possible that these first two cues played a role in discrimination. However, the primary echo feature reported by nearly all of the human listeners as a discrimi-

natory cue was pitch, and the pitch they heard could be the TSP created by the two main highlights in the cylinder echoes, since this type of signal would produce TSP in the human auditory system (Thurlow, 1957). The dolphin may also have used TSP cues.

Other researchers have proposed that dolphins could make use of TSP cues. Au and Martin (1988) suggested that a dolphin used TSP to discriminate among metallic plates that varied in material composition and thickness. Hammer and Au (1980) suggested that TSP cues were used by a dolphin to discriminate certain hollow aluminum standard cylinders from comparison cylinders of different material composition, or of the same material composition but with different wall thickness and internal structure (hollow or solid). Au and Pawloski (1989) have shown that dolphins can discriminate noise having a rippled power spectrum from noise having a nonrippled spectrum. Noise having a rippled spectrum produces TSP in humans, which suggests that a dolphin may also have the capability to perceive TSP. However, there is no direct evidence that a dolphin can perceive TSP. This study suggests that further research is warranted to determine whether dolphins perceive TSP cues.

## B. Spheres

Both the human listeners and the dolphin in the Au *et al.* (2000) study were able to discriminate between the standard steel sphere and the comparisons (brass, aluminum, nylon) with high accuracy (overall  $M_s=86\%$  vs  $89\%$ , respectively). Both the humans and the dolphin performed best on the nylon sphere ( $M_s=100\%$  vs  $90\%$ ) in the "locate standard" task. In addition, in the "identify comparison" task the humans performed relatively well with the nylon sphere ( $74\%$ ) compared with the other spheres (aluminum= $56\%$ , brass= $60\%$ ). They often confused the aluminum and brass spheres but did not often confuse the nylon spheres with the others. These results indicate that the nylon echoes may have been distinctive to both the dolphin and the humans compared with the other spheres' echoes. The human listeners' performance was also similar to the dolphin's on the brass sphere ( $M_s=80\%$  vs  $89\%$ ), although their performance on the aluminum sphere was significantly better than the dolphin's ( $M_s=89\%$  vs  $77\%$ ). Thus, the dolphin's and humans' performance was comparable on two (nylon, brass) of the three spheres. It is possible that the dolphin and the humans may have been using at least some of the same echo features to discriminate among the spheres.

The human listeners in the current study reported using primarily pitch and timbre to discriminate among the spheres of varying materials. The participants' reports of differences in pitch between the spheres sometimes but did not always match the TSP values that were calculated for the echoes. This could mean that the participants' perception of pitch was not always accurate (i.e., not reflecting the actual TSP of the echoes). One reason for this could be the large standard deviation in TSP values for three of the spheres that made TSP values inconsistent. Since they heard a random selection of echoes from the 200 recorded echoes per object, the TSP values for any given sphere were not always the same. Al-

ternately, the “pitch” reported by the participants could have been something other than time-separation pitch, like the “click pitch” reported by human listeners in Au and Martin (1989) and defined by the authors as the pitch associated with the peak frequency of the echo.

The results of this study compare favorably with the results of other human listening studies in overall accuracy rates and use of pitch and possibly also timbre as material discrimination cues (Au and Martin, 1989; DeLong *et al.*, 2006a). Au and Martin (1989) presented human listeners with echoes from cylinders varying in size and material that had been used in dolphin experiments (Hammer and Au, 1980; Schusterman *et al.*, 1980). The participants in Au and Martin’s (1989) study reported using pitch to discriminate between the aluminum, bronze, and steel cylinders (e.g., bronze had a lower pitch than aluminum). The authors suggest the participants were using time-separation pitch (bronze TSP=385 Hz, aluminum TSP=444 Hz). For the aluminum vs glass discrimination, the time between the first and second highlights was virtually the same, which eliminates TSP as a cue. The participants reported using echo duration to discriminate between the aluminum and glass echoes, but when Au and Martin (1989) eliminated duration as a cue, they reported a secondary cue they called “click pitch,” defined by the authors as the pitch associated with the peak frequency of the echo. This click pitch could be similar to what the participants in the current experiment called either the “pitch” or the “timbre” of the echo. DeLong *et al.* (2006a) presented human listeners with objects that varied primarily in material but also had some slight variations in shape and size and they reported using pitch and timbre. Taken together, all three studies (current study; Au and Martin, 1989; DeLong *et al.*, 2006a) show that human listeners report pitch and timbre and to a lesser extent duration and amplitude as material discrimination cues.

Echo features that contribute to the perception of pitch and timbre should be explored as material discrimination cues for dolphins. Yet it is difficult to determine exactly which features of echoes would give rise to the perception of timbre. Timbre is a complex sound quality that is a combination of acoustic parameters. According to the American National Standards Institute (1960), timbre is defined as “that attribute of sensation in terms of which a listener can judge two sounds similarly presented and having the same loudness and pitch as dissimilar” and that “timbre depends primarily upon the spectrum of the stimulus, but it also depends upon the waveform, the sound pressure, the frequency location of the spectrum, and the temporal characteristics of the stimulus.” Timbre is not independent from other acoustic parameters, but appears to arise from an interaction of pitch, amplitude, and time features. This may make it difficult to investigate whether dolphins perceive or use timbre.

### C. Conclusions

The human listeners in this study typically performed as well or better than the dolphin and they were able to report the echo features that allowed them to discriminate among the objects: Pitch and duration for wall thickness discrimina-

tion, and pitch and timbre for material discrimination. The echo features used by the humans could also have been used by the dolphins. However, the overall similar discrimination abilities in humans and dolphins found in this study are not conclusive evidence that they are using the same echo features. A more in-depth analysis of performance, such as the analysis of errors (object confusions), provides one way to determine whether humans and dolphins share the use of certain features. Two objects are confused to the degree that they share similar features. If the error patterns of the humans and the dolphin match (i.e., they confuse the same objects), it would imply that they may have used the same features. Conversely, if the error patterns do not match, it would imply they may have used different features. This error analysis was used successfully in a different study (DeLong *et al.*, 2006a). It was not possible in the current study because a two-alternative forced choice or go/no-go method was used with the dolphin instead of a method that yields object confusions (e.g., match-to-sample).

Similarities and differences between human and dolphin auditory perception should be considered when deciding whether echo features reported by humans could be used by dolphins. Since both dolphins and humans can discriminate sounds that vary in intensity by about 1 dB (Evans, 1973; Green, 1993) and the frequency discrimination abilities of dolphins and humans for tonal stimuli are comparable in the range of best hearing for each species (Herman and Arbeit, 1972; Thompson and Herman, 1975; Weir *et al.*, 1976), differences in echo intensity and frequency should be available as cues to both humans and dolphins. This means that if humans report amplitude and pitch cues in the echoes it is reasonable to assume that dolphins also have access to these cues. However, dolphins have sharper frequency tuning curves than humans (Supin and Popov, 1995) so they may be better able to interpret frequency information in echo stimuli than the human listeners.

Temporal resolution is the ability to rapidly resolve stimuli that are close together in time (e.g., to identify two stimuli as separate events rather than a single stimulus). Popov and Supin (1997) recorded the dolphin auditory brainstem response evoked by a short gap in noise and found that the dolphin’s hearing is sensitive to extremely short gap durations as compared to other animals and humans. The dolphin gap detection threshold was 0.1 ms (100  $\mu$ s) whereas gap detection thresholds in humans were an order of magnitude longer than dolphins (about 2.2 ms; Snell *et al.*, 1994). At first this would appear to give dolphins an advantage over humans and it might be assumed that dolphins could access finer temporal cues. However, it is important to note that when the echoes are slowed down to bring them into the human hearing range, the duration of the echoes is lengthened relative to the echoes the dolphin hears. For the dolphins, the echoes in this study were approximately 24–125  $\mu$ s in duration. When the echoes were slowed down for the human listeners, they were each approximately 4–21 ms in duration. Because dolphins must be able to resolve temporal differences in signals that last for  $\mu$ s, whereas humans must be able to resolve temporal differences in signals that last for ms, the process of slowing the echoes down



may in effect allow the temporal processing abilities of humans to “catch up” to the dolphins’ abilities to some extent.

Human listening studies are just one way of elucidating how dolphins use information in echoes to discriminate among objects. Although caution must be used in interpreting the results, since there are some ways in which dolphin and human auditory detection and perception are different, it is still a worthwhile endeavor because of the relative challenge of performing experiments with dolphins (extensive training time, few research animals, expensive animal care and maintenance). In human listening studies, many experiments can be performed in a short time and subjects can verbally report salient acoustic cues. Human listeners can quickly identify salient echo features that permit object discrimination, which can be used to generate hypotheses that can be tested using dolphins as subjects. For example, this study suggests that time-separation pitch (TSP) is a cue potentially used for both material and wall thickness discrimination so it is worthwhile to conduct an experiment with dolphins to test their ability to perceive TSP, and then explore whether TSP is a salient echo feature for dolphins.

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- ANSI (1960). *American Standard Acoustical Terminology*, American National Standards Institute, New York.
- Au, W. W. L. (1993). *The sonar of dolphins* (Springer, New York).
- Au, W. W. L. (2000). “Echolocation in dolphins,” in *Hearing by whales and dolphins*, edited by W. W. L. Au, A. N. Popper, and R. R. Fay (Springer, New York), pp. 364–408.
- Au, W. W. L., and Martin, D. W. (1988). “Sonar discrimination of metallic plates,” in *Animal sonar: Processes and performance*, edited by P. E. Nachtigall and P. W. B. Moore (Plenum, New York), pp. 809–813.
- Au, W. W. L., and Martin, D. W. (1989). “Insights into dolphin sonar discrimination capabilities from human listening experiments,” *J. Acoust. Soc. Am.* **86**, 1662–1670.
- Au, W. W. L., and Pawloski, J. L. (1989). “Detection of ripple noise by an Atlantic bottlenose dolphin,” *J. Acoust. Soc. Am.* **86**, 591–596.
- Au, W. W. L., and Pawloski, D. A. (1992). “Cylinder wall thickness difference discrimination by an echolocating Atlantic bottlenose dolphin,” *J. Comp. Physiol., A* **170**, 41–47.
- Aubauer, R., Au, W. W. L., Nachtigall, P. E., Pawloski, D. A., and DeLong, C. M. (2000). “Classification of electronically generated phantom targets by an Atlantic bottlenose dolphin (*Tursiops truncatus*),” *J. Acoust. Soc. Am.* **107**(5), 2750–2754.
- DeLong, C. M., Au, W. W. L., Harley, H. E., Roitblat, H. L., and Pytko, L. (2006a). “Human listeners provide insights into echo features used by dolphins to discriminate among objects,” (in preparation).
- DeLong, C. M., Au, W. W. L., Lemonds, D. W., Harley, H. E., and Roitblat, H. L. (2006b). “Acoustic features of objects matched by a bottlenose dolphin,” *J. Acoust. Soc. Am.* **119**(3), 1867–1879.
- Evans, W. E. (1973). “Echolocation by marine delphinids and one species of fresh-water dolphin,” *J. Acoust. Soc. Am.* **54**, 191–199.
- Fish, J. F., Johnson, C. S., and Ljungblad, D. K. (1976). “Sonar target discrimination by instrumented human divers,” *J. Acoust. Soc. Am.* **59**, 602–606.
- Hammer, C. E., Jr., and Au, W. W. L. (1980). “Porpoise echo-recognition: An analysis of controlling target characteristics,” *J. Acoust. Soc. Am.* **68**, 1285–1293.
- Green, D. M. (1976). *An introduction to hearing* (Lawrence Erlbaum Associates, Hillsdale, NJ).
- Green, D. M. (1993). “Auditory intensity discrimination,” in *Human psychophysics*, edited by W. A. Yost, A. N. Popper, and R. R. Fay (Springer, New York), pp. 13–55.
- Helweg, D. A., Roitblat, H. L., Nachtigall, P. E., Au, W. W. L., and Irwin, R. J. (1995). “Discrimination of echoes from aspect-dependent targets by a bottlenose dolphin and human listeners,” in *Sensory systems of aquatic mammals*, edited by R. A. Kastelein, J. A. Thomas, and P. E. Nachtigall (De Spil Publishers, Woerden, The Netherlands), pp. 129–136.
- Herman, L. M., and Arbeit, W. R. (1972). “Frequency discrimination limens in the bottlenose dolphin: 1–70 Ks/c,” *J. Aud. Res.* **2**, 109–120.
- Johnson, C. S. (1967). “Sound detection thresholds in marine mammals,” in *Marine bio-acoustics*, edited by W. N. Tavolga (Pergamon, New York), pp. 247–260.
- Kellogg, W. N. (1962). “Sonar system of the blind,” *Science* **137**, 399–404.
- Popov, V. V., and Supin, A. Ya. (1997). “Detection of temporal gaps in noise in dolphins: Evoked potential study,” *J. Acoust. Soc. Am.* **102**(2), 1169–1176.
- Rice, C. E. (1967). “Human echo perception,” *Science* **155**, 656–664.
- Schusterman, R. J., Kersting, D. A., and Au, W. W. L. (1980). “Response bias and attention in discriminative echolocation by *Tursiops truncatus*,” in *Animal sonar systems*, edited by R. G. Busnel and J. F. Fish (Plenum, New York), pp. 983–986.
- Snell, K. B., Ison, J. R., and Frisina, D. R. (1994). “The effects of signal frequency and absolute bandwidth on gap detection in noise,” *J. Acoust. Soc. Am.* **96**, 1458–1464.
- Supin, A. Ya., and Popov, V. V. (1995). “Frequency tuning and temporal resolution in dolphins,” in *Sensory systems of aquatic mammals*, edited by R. A. Kastelein, J. A. Thomas, and P. E. Nachtigall (De Spil Publishers, Woerden, The Netherlands), pp. 95–110.
- Thompson, R. K. R., and Herman, L. M. (1975). “Underwater frequency discrimination in the bottlenose dolphin (1–140 kHz) and the human (1–8 kHz),” *J. Acoust. Soc. Am.* **57**, 943–948.
- Thurlow, W. R. (1957). “Further observations on pitch associated with a time difference between two pulse trains,” *J. Acoust. Soc. Am.* **29**, 1310–1311.
- Thurlow, W. R., and Small, A. M., Jr. (1955). “Pitch perception for certain periodic auditory stimuli,” *J. Acoust. Soc. Am.* **27**, 132–137.
- Wier, C., Jesteadt, W., and Green, D. (1977). “Frequency discrimination as a function of frequency and sensation level,” *J. Acoust. Soc. Am.* **61**, 178–184.