Changes in signal parameters over time for an echolocating Atlantic bottlenose dolphin performing the same target discrimination task

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This study documents the changes in peak frequency, source level, and spectrum shape of echolocation clicks made by the same dolphin performing the same discrimination task in 1998 and in 2003/2004 with spherical solid stainless steel and brass targets. The total average peak frequency used in 1998 was 138 kHz but in 2003/2004 it had shifted down nearly 3.5 octaves to 40 kHz. The total average source level also shifted down from 206 dB in 1998 to 187 kHz in 2003/2004. The standard deviation of these parameter values within time periods was small indicating a consistent difference between time periods. The average parameter values for clicks used when exposed to brass versus steel targets were very similar indicating that target type did not greatly influence the dolphin's average echolocation behavior. The spectrum shapes of the average clicks used in 1998 and in 2003/2004 were nearly mirror images of each other with the peak energy in 2003/2004 being concentrated where the 1998 clicks had the lowest energy content and vice versa. Despite the dramatic differences in click frequency content the dolphin was able to perform the same discrimination task at nearly the same level of success. © *2007 Acoustical Society of America.*
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I. INTRODUCTION

Much work has been done in the past to characterize the different clicks that are used by dolphins while performing echolocation tasks. There can be a large variation in the various parameters of the clicks, such as source level and peak frequency, between species, between individuals within the same species, and even between clicks of the same individual (Au, 1993). However, by averaging clicks together an idea of the general click behavior begins to emerge. It is this average click that has been used to understand the echolocation behavior of dolphins and allows for comparisons between individuals. The average click can also be used to study how an individual changes its echolocation behavior in different environments.

By looking at average click behavior it has been shown that cetaceans can make gross adjustments to the frequency content of their sonar signal when exposed to different levels of background noise. Such is the case with beluga whales which have been shown to shift the peak frequency of their clicks upwards due to background noise level changes (Au *et al.*, 1985). An individual whale produced clicks with peak frequencies between 40 and 60 kHz in San Diego Bay, but then produced clicks with peak frequencies between 100 and 120 kHz in Kaneohe Bay where the background noise was 12–17 dB greater. This upward shift in peak frequency also occurred along with an increase of up to 18 dB in click intensity.

It has been demonstrated that dolphins can be trained to make gross adjustments to their average click peak frequency while performing simple target detection tasks. A *Tursiops truncatus* was successfully trained to emit low frequency clicks with peak frequencies below 60 kHz when given a specific audio cue and to emit high frequency clicks above 105 kHz when given a different audio cue (Moore and Pawloski, 1990). The dolphin had the same level of success in determining the presence or absence of the target with the high frequency clicks as with the low frequency clicks. These observed changes in frequency content were not a natural behavior of the dolphin. The echolocation task was also a simple target present or absent determination which did not require any fine frequency content discrimination.

One aspect that has not yet been looked at is the natural stability of the average click used by an individual dolphin over a time period of years while performing the same fine target discrimination task in an environment with a nearly constant background noise level. Observing how the same dolphin might voluntarily change its average click over time in such a situation can provide insight into what cues might be used for these discrimination tasks. This study focuses on documenting the changes in the average clicks produced by a female bottlenose dolphin (*Tursiops truncatus*) during two similar target discrimination experiments conducted in 1998 and 2003/2004. These discrimination tasks were not simple target present or absent tasks, but rather more difficult dis-

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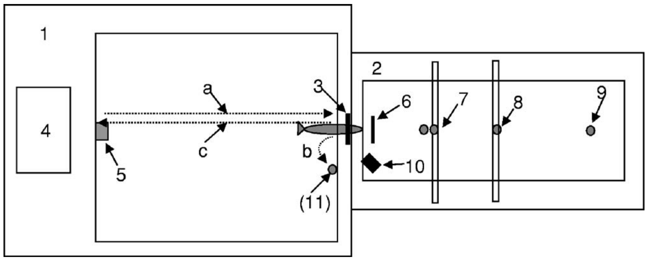

FIG. 1. The experimental setup for the phantom system. The different components are referred to in the text.

criminations between two targets with similar sound reflection characteristics. This information combined with information from additional experiments will set the stage to understand the implications of these findings as they pertain to possible discrimination cues and dolphin echolocation strategies.

II. MATERIALS AND METHODS

A. Subject and experimental conditions

The clicks used in this analysis were collected during experiments conducted at the Hawaii Institute for Marine Biology in Kaneohe Bay, Oahu, HI. The subject was an adult female Atlantic bottlenose dolphin (*Tursiops truncatus*), named BJ, who in 1998 was 13 years old. She was housed in a floating wire-net enclosure in Kaneohe Bay.

The experimental setup is shown in Fig. 1 and was the same for the 1998 and 2003/2004 experiments. The experimental enclosure consisted of two parts. The first was a floating pen frame, 8×10 m, that had a wire-net bottom (1) and was used to house BJ. The frame consisted of 55 gallon barrel floats underneath a wooden framework. The second was a target pen (2) that did not have a wire bottom and was used to support the recording hydrophone as well as the targets. The wire-net bottom was omitted from the target pen to prevent the production of extra confounding echoes during echolocation. BJ would station in a hoop (3) so that her head location was known and so she would have unobstructed echolocation access to the target pen (2). The computer system was set up in an electronics shack (4). The experimenters remained in the shack for the entire session. Each click that BJ produced was recorded by a hydrophone (7) that was located 2.5 m from the hoop. Clicks were recorded for all trials. An underwater camera (10) was set up to monitor BJ's stationing in the hoop to assure uniformity of her body orientation with respect to the hoop between trials. The hoop (3), recording hydrophone (7), transducer (8), and targets (9) were all at a depth of 1 m and all four parts were arranged to ensure all clicks recorded from BJ were on axis.

B. Experimental procedure

The procedure was the same for both the 1998 and 2003/2004 experiments. Each trial was started with a hand signal to cue BJ to swim from the stationing pad (5) to the hoop (3) along the dotted path (a) into the stationing hoop. The target would be lowered into the water with minimal splash, and BJ would begin echolocating when the movable baffle (6) was lowered out of the way to provide an acoustically unobstructed path to the target pen (2).

A go/no-go paradigm was used in which the go response was associated with the standard steel target and the no-go response was associated with the comparison brass target. For the go response BJ backed out of the hoop and followed path (b) to touch a paddle and then returned to the shack along path (c). For the no-go response BJ stayed in the hoop for the duration of the 6 s trial. If BJ made a correct response, the trainer bridged her with a whistle and she was given a fish reward after returning to the stationing pad (5). If BJ made an incorrect response, she was recalled to the stationing pad (5) without a fish reward.

C. Click recording hardware and software

The click recording equipment for the 2003/2004 experiments used two hydrophones aligned such that one was directly behind the other when facing the dolphin. The two hydrophones were 5 cm apart and the time delay between the signal arriving at the first hydrophone and the second was enough to trigger the system to record the entire click with the second hydrophone. The first hydrophone was used only as a trigger for the system and did not record any information. The signal from the triggering hydrophone was amplified 56 dB and sent to a Measurement Computing Corporation PCI-DAS4020/12 analog to digital data aquisition board, set to a dynamic range of ±5 V, which digitized the signal at a sample rate of 1 MHz and triggered the system to begin recording with the second hydrophone. The click was then recorded in its entirety by the second hydrophone, amplified 36 dB, and then sent to the second channel of the same board using the same sampling rate of 1 MHz. No low pass filters were used because the high sampling rate itself prevented aliasing. A custom written LABVIEW program was used to control the data acquisition board and record each click straight to the hard drive of the computer for future analysis. This click recording equipment was based on the device used to collect clicks during the 1998 experiments, which is discussed in Aubauer and Au (1998).

D. Targets

There were two main targets: a solid brass sphere and a solid stainless steel sphere (both 7.62 cm in diameter). The steel sphere was considered the standard target and the brass was the comparison. These two targets comprised 92% of the target presentations. The other 8% of the target presentations were phantom targets. The generation of the phantom targets is covered thoroughly in Aubauer and Au (1998), but is briefly described here. Essentially the phantom targets were computer-generated targets whose acoustic reflection properties simulated those of the two real targets described earlier. The computer system calculated the echo from either the brass or steel spheres based upon the dolphin click that was recorded and played it back to the dolphin through a transducer. The system was fast enough to generate an echo specific for each incoming click. These phantom targets were presented to the dolphin in both the 1998 and 2003/2004 time periods as four nonreinforced phantom probe trials per session, two phantom steel and two phantom brass (Aubauer *et al.*, 2000). The probe trials were designed to understand if BJ would classify the phantom targets, especially the phantom steel, as the actual real standard target or as comparisons. The clicks made during these probe trials were included in the analysis because the target reflection characteristics of the real and phantom targets were very similar and because BJ made the same response to the phantom targets that she made to the real targets (e.g., she made the go response for phantom steel and real steel targets and the no-go response for the phantom brass and real brass target) (Aubauer *et al.*, 2000).

Each session consisted of 50 trials. Half of the trials were the standard steel target presentations (23 real steel and 2 phantom steel) and the other half of the trails were comparison brass target presentations (23 real brass and 2 phantom brass). The order of stimulus presentation was determined using a standard Gellermann series (Gellermann, 1993).

E. Click analysis

Custom designed and written programs were created to analyze the clicks from both the 1998 and 2003/2004 experiments separately. The analysis programs calculated the amplitude spectra for each click and determined the peak frequency. The peak-to-peak source level for each click was also determined based upon the known distance of 2.5 m between the dolphin and the recording hydrophone. The peak-to-peak source levels were reported in units of dB re 1 μPa at a reference distance of 1 m.

A large amount of variation was found in the peak frequency and source level between individual clicks making direct comparison between groups of clicks difficult. To develop a concept of the general trend that the clicks were taking it was necessary to average the clicks together in groups allowing direct comparison of the general behavior of the clicks made during exposure to different targets and at different times. In order to determine the general click behavior, clicks from each session were separated into those made during exposure to the (real and phantom) steel target and those made during exposure to the (real and phantom) brass target. The peak frequency values and source levels of each click made during exposure to the steel target were averaged together to yield the average peak frequency and average source level for the steel for each individual session. The same was done for the clicks made during exposure to the brass targets for each individual session. This allowed for direct comparisons of clicks between sessions within the same time period.

The averaging process was taken one step further by averaging the peak frequency values and source level values from all clicks made in 1998 and again separately in 2003/2004. These total average values allowed for a general comparison between both time periods. Averaging was also performed on all the clicks made during exposure to steel targets in 1998 and separately in 2003/2004 yielding a steel average for each time period. The same was done for the clicks made during exposure to the brass targets yielding a brass average.

A total of 4 sessions (200 trials) were analyzed from 1998 and 4 sessions (200 trials) from 2003/2004. Even though each time period contained the same number of sessions and trials, BJ used twice as many clicks in 1998 as she did in 2003/2004. Since the focus of this study is to compare BJ's click behavior between the two time periods the number of clicks were not equalized between the two time periods because it was not possible to choose which clicks to include and which to exclude from the analysis without possibly skewing the results. To maintain the focus on general click behavior it was more important to maintain a constant number of trials between both time periods than to maintain a constant number of clicks. Therefore, the total average values reported for each time period contain different numbers of clicks but reflect the general click behavior over entire sessions.

III. RESULTS AND DISCUSSION

The results from the above-described analysis are summarized in Tables I and II. As can be seen, there was a high degree of consistency with the average click peak frequency and source level between sessions within their respective time periods. In 1998 the total average peak frequency was 138 kHz with a standard deviation of 7 kHz, just 5% of the average. In 2003/2004 the total average peak frequency was 40 kHz with a standard deviation of 2 kHz, also just 5% of the average. However, between the 1998 and 2003/2004 time periods the total average peak frequency dropped 98 kHz, nearly 3.5 octaves.

Not only did the peak frequencies change but so did the entire spectral shape. The average click amplitude spectra are shown in Fig. 2 for six normalized characteristic clicks from 1998 and six normalized clicks from 2003–2004. The clicks were first normalized before averaging so the spectral shapes could be compared directly without intensity differences causing additional distortions because the interest is to analyze just the spectral shapes. As can be seen, the 2003/2004 clicks peak in the region where the 1998 clicks have the least amount of energy. They are nearly mirror images of each other in terms of where BJ concentrated the energy. The error bars show the upper and lower limits of the variability between the individual clicks. Even with the large amount of variability from click to click the inverse nature of the shapes is still evident. The average 1998 amplitude spectra does not peak at a relative normalized amplitude of one because the individual peaks differed by a few kilohertz from one another and ended up decreasing the peak value of the average frequency content. The 2003/2004 clicks all consistently peaked at 40 kHz causing the average spectra to peak at a value of one. The time domain wave form representation of characteristic echolocation clicks from both time periods is shown in Fig. 3 and reflect the frequency content differences described earlier.

Despite the dramatic differences in click frequency content, BJ was able to perform the same discrimination task at 92% correct in 1998 and at 98% correct in 2003/2004, nearly

TABLE I. A summary of the peak frequencies and source levels of clicks collected in 1998.

Date of data collection	Target type	Average peak frequency (kHz)	Average source level (dB)	Number of clicks analyzed
15 July 1998	Brass	145	205	996
	Steel	133	205	1202
15 July 1998	Brass	143	205	1187
	Steel	138	206	1334
24 July 1998	Brass	142	207	1675
	Steel	123	209	1431
13 August 1998	Brass	139	209	1576
	Steel	144	209	1285
Standard deviation:		7	2	Total: 10 686
Total average:		138	206	
Steel average:		135	207	
Brass average:		142	207	

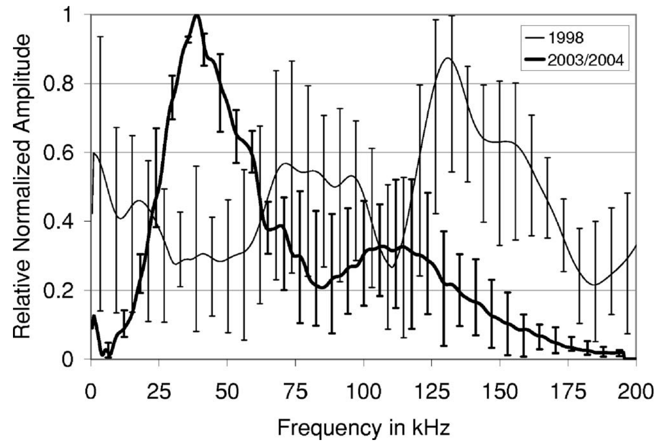

FIG. 2. Average echolocation click amplitude spectra from 1998 and 2003/2004. Six characteristic spectra from each time period have been normalized and averaged together to produce these spectra. The error bars show the upper and lower limits of the variation in spectral values for the respective time periods.

the same high level of success. Unless BJ used time separation pitch to perform the discrimination, it is probable that she used different reflection cues from the targets in both time periods because the clicks were so different. The ability to use such different click types indicates BJ might have been able to change the acoustic cues she used to discriminate the targets. The ability to adaptively change the cues used to discriminate targets would be of high adaptation value from a survival standpoint when faced with changing and sometimes unpredictable acoustic surroundings. Future publications will present additional research and results that when combined with these results will shed more light on the possible acoustic and echolocation strategies BJ might have been using to perform these discrimination tasks.

It is interesting to note that there were no large differences in the peak frequencies or source levels between the clicks made when exposed to steel or to brass. The average steel peak frequency in 1998 was 135 kHz while for brass it was 142 kHz, which is only a 5% difference. The average steel peak frequency in 2003/2004 was 40 kHz, while for brass is was 39 kHz. This indicates that the target type most likely did not influence BJ's echolocation behavior.

The source levels of the average clicks made by BJ were also very consistent within time periods but had large variation between time periods. The total average source level in 1998 was 206 dB re 1 μPa at a reference distance of 1 m with a standard deviation of only 2 dB. The total average source level in 2003/2004 was 187 dB with a standard deviation of only 2 dB, a drop of 19 dB. This indicates that the higher frequency clicks were produced by BJ mainly at the higher source levels. This increasing peak frequency with increasing source level is consistent with similar observations from other bottlenose dolphins and false killer whales (Au *et al.*, 1995; Houser *et al.*, 1999). This suggests physiological constraints that coarsely couple both source level and frequency content.

It is unknown what might have prompted BJ to change the average click she used to perform the discrimination task between both time periods. The same brass and steel targets were used in both experiments as well as the same experimental procedures and experimental setups. The high back-

TABLE II. A summary of the peak frequencies and source levels of clicks collected in 2003 and 2004.

Date of data collection	Target type	Average peak frequency (kHz)	Average source level (dB)	Number of clicks analyzed
8 October 2003	Brass	41	187	498
	Steel	43	189	628
13 November 2003	Brass	36	183	439
	Steel	41	185	450
25 November 2003	Brass	38	189	627
	Steel	38	190	891
20 February 2004	Brass	40	188	667
	Steel	39	188	721
Standard deviation:		2	2	Total: 4921
Total average:		40	187	
Steel average:		40	188	
Brass average:		39	187	

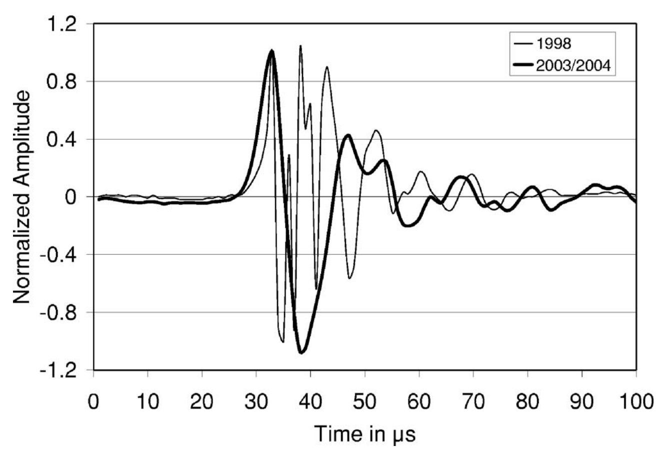

FIG. 3. Characteristic echolocation click time domain wave forms from 1998 and 2003/2004. Both wave form intensities have been normalized for easier comparison.

ground noise levels of Kaneohe Bay are largely caused by snapping shrimp whose activity did not have large changes between the two time periods as determined by occasional monitoring of the background noise levels in the bay. There is a tendency for an increase in snapping shrimp activity during the night, but the experiments were conducted during the day at about the same time.

One factor which might be involved is that BJ had a documented high frequency hearing loss when compared to other *Tursiops*. BJ's audiogram was measured using auditory evoked potential methods in 2001 and again in 2005 showing that she had an upper hearing limit of 45 kHz at both times with her most sensitive hearing being around 40 kHz. Audiograms from other *Tursiops* indicate that they can hear up to 150 kHz (Johnson, 1967; Au, 1993). With an upper hearing limit of 45 kHz, BJ would be able to hear less than 25% of the energy from the 138 kHz peak frequency clicks she made back in 1998. The most sensitive portion of her hearing range would not have been utilized with these clicks and in many cases there was a complete lack of energy in the click around this region. It seems there would have been little advantage for BJ to use the click amplitude spectra shapes from 1998 with an upper hearing limit of only 45 kHz. The clicks used in 2003/2004 were much better tailored for an upper hearing limit of 45 kHz because the average peak frequency in 2003/2004 was located right where her hearing was most sensitive at 40 kHz. She was able to perceive up to 42% of the energy in the 2003/2004 clicks making these clicks much more efficient.

Unfortunately, there are no audiograms for BJ before 2001 so her actual upper hearing limit in 1998 is unknown. However, the 1998 clicks appear to be much better suited for use with an upper hearing limit higher than 45 kHz. Perhaps the observed shift of the energy content of the clicks to lower frequencies between both time periods was an attempt by BJ to compensate for a possible high frequency hearing loss suffered between 1998 and 2003. Although the data presented here do not conclusively show that a hearing loss actually occurred and the possible cause of such a hearing loss in this specific case is not known, it has been shown that dolphins can lose their high frequency hearing. Possible factors that have been associated with reducing dolphin hearing ranges are age (Brill *et al.*, 2001; Ridgway and Carder, 1997) and long term residence in a noisy environment (Houser and Finneran, 2006).

Despite the large voluntary changes BJ made to her echolocation clicks, her ability to perform, the same task did not change. To better understand how BJ was able to do this, it is necessary to first understand the cues BJ used. The transfer function of the steel and brass targets show many subtle spectral differences in the way both targets reflect sound and any of these differences could have been potential cues. It is unknown which specific cues BJ might have been using to discriminate between the two targets and how those cues might have been affected by her voluntary change of echolocation clicks. One way for future experiments to really explore this issue is to experimentally change the reflection characteristics of the targets used in the discrimination task and behaviorally determine if BJ can perceive those changes. This can be accomplished by systematically filtering the frequency content of the returned echoes using the phantom echo technology described in Aubauer and Au (1998). The results of these experiments can show what frequency bands BJ pays attention to while performing discrimination tasks and that information can potentially reduce the set of possible auditory cues.

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