Changes in consistency patterns of click frequency content over time of an echolocating Atlantic bottlenose dolphin

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Echolocation clicks were recorded from an Atlantic bottlenose dolphin *Tursiops truncatus* trained to discriminate frequency filtered phantom targets in 1998 and in 2004. These clicks showed consistency within their spectra intensity profiles but only in a certain band of frequencies. In 2004 almost all the clicks were consistent within the 0–42 kHz band regardless of the presented target or the click source level. This region corresponded with previous data showing that in 2004 the dolphin perceived frequencies only from within the 29–42 kHz band during echolocation. Above 42 kHz the consistency was lost. In 1998 the consistent region was found only in the 90–100 kHz band showing a shift had occurred with time. This suggests the dolphin's echolocation strategy for these discrimination tasks centered on the use of clicks with the same controlled standard frequency content in a certain frequency band to investigate different targets. This consistent region shifted over time to maintain maximum signal to noise ratio of the echoes given certain changing limitations to the echolocation system. The shift in consistency over time indicates these consistent regions were not simply artifacts of click production but rather an active control of frequency content. © *2010 Acoustical Society of America.* [DOI: 10.1121/1.3419905]

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I. INTRODUCTION

Dolphin echolocation is a sophisticated sonar system. In the wild, dolphins can use this sonar to locate food, discriminate between objects, and avoid obstacles in low visibility situations. Dolphins can determine the position, shape, size, movement, and material composition of objects using only echolocation (Au, 1993; Nachtigall, 1980). Experiments have shown that at a distance of 8 m dolphins can use their echolocation to distinguish between hollow cylinders that differ in wall thickness by just a fraction of a millimeter (Au and Pawloski, 1992). Although these abilities have been well documented, little is known about what specific acoustic cues are used by the dolphin to make these discriminations.

A starting point to identify and understand these cues is the functional bandwidth of a dolphin, the frequency band that the dolphin pays attention to while actively echolocating. Previous work has shown that the functional bandwidth can be determined using phantom echo techniques (Ibsen *et al.*, 2009). The functional bandwidth was determined by having the dolphin discriminate frequency filtered phantom targets from unfiltered ones. The functional bandwidth of the dolphin used in those experiments was 29–42 kHz. The dolphin did not perceive changes to the frequency content of the phantom echoes outside of this region, but could detect changes within this region. The upper limit corresponded to this dolphin's upper hearing limit of 45 kHz. The lower limit corresponded to an abrupt drop in click frequency content intensity below 30 kHz.

It is unknown how the frequency content of the clicks within this functional bandwidth might vary from click to click and from target to target. An analysis of these variations can shed light on the possible acoustic cues the dolphin is using and how the dolphin is optimizing both its click production and hearing attentiveness to accentuate those cues. It is also unknown how these functional bandwidths may change over time.

This paper is an analysis of the dolphin clicks collected during the functional bandwidth experiments mentioned above in 2004. The phantom system used for the functional bandwidth experiment provided a unique opportunity to correlate each dolphin click with the corresponding echo received allowing both to be analyzed together. To see how patterns may change over time, clicks were also analyzed from a previous phantom experiment conducted in 1998 (Aubauer *et al.*, 2000).

Both the 1998 and 2004 experiments used the same experimental subject, the same recording hydrophones, a go/no-go experimental paradigm, and a stainless steel phantom target as the standard. They both used similar experimental procedures. The phantom generator used in 2004 was an updated version of the one used in 1998 but the overall function was the same. The main difference between the two experiments was the type of comparison targets presented. In 1998 the comparison was a brass phantom target while in 2004 the comparisons were frequency filtered versions of the standard target.

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II. MATERIALS AND METHODS

A. Subject

The clicks used in this analysis were collected during experiments conducted at the Hawaii Institute for Marine Biology, Marine Mammal Research Program. The subject was an adult female Atlantic bottlenose dolphin *Tursiops truncatus* named BJ, who was 16 years of age in 1998. She was housed in a floating wire-net enclosure in Kaneohe Bay, HI. She was fed a total daily ration of approximately 6.3 kg of herring and silver smelt.

B. Materials

1. Experimental setup

The experimental setup was the same for the 1998 and 2004 experiments and is described fully in Ibsen *et al.*, 2009. Briefly, the experimental enclosure consisted of two parts. The first was a floating pen frame, $8 \times 10\ \mathrm{m}^2$, used to house BJ that had a wire-net bottom and sides. The wooden framework was supported from underneath by 55 gal barrel floats. The second was a target pen that did not have a wire bottom and was used to house the hydrophone and transducer of the phantom system. The wire-net bottom was omitted from the target pen to prevent the production of extraneous echoes during echolocation. During a trial, BJ would station in a hoop looking into the target pen so that her head location was fixed and so she would have unobstructed echolocation access to the target pen.

2. The phantom echo generator system

The phantom system used in 2004 was similar to that used in 1998 in terms of function and purpose. The systems are described briefly here. For a more complete description, see Aubauer *et al.*, 2000; Ibsen *et al.*, 2009.

Each click was handled individually by the phantom generator system. Each click was first recorded by a B&K 8103 hydrophone that was located 2.5 m from the hoop. The click was amplified and sent to a Measurement Computing Corporation PCI-DAS4020/12 analog to digital board which digitized the signal at a sample rate of 1 MHz. A custom written LABVIEW program convolved the click signal with the transfer function of the stainless steel sphere target or comparison target to produce the resulting echo waveform. The computer also saved each click to the hard drive. The convolution of each click allowed the system to produce phantom echoes that were as flexible as the real target echoes in terms of response to intensity and frequency content changes from click to click. The resulting phantom echo waveform was loaded onto the memory of a Strategic Test UF6011 arbitrary waveform generator board and then outputted to an International Transducer Corporation ITC-1042 transducer 5 m away from BJ with a sample rate of 1 MHz. The echo was delayed by the appropriate amount of time to simulate an echo from a target located 7.6 m in front of the hoop. The hoop, the two recording hydrophones, transducer, and phantom targets were all at a depth of 1 m. The system could handle up to 30 clicks/s using this algorithm without significantly skipping clicks. BJ usually clicked at a rate of 25 clicks/s.

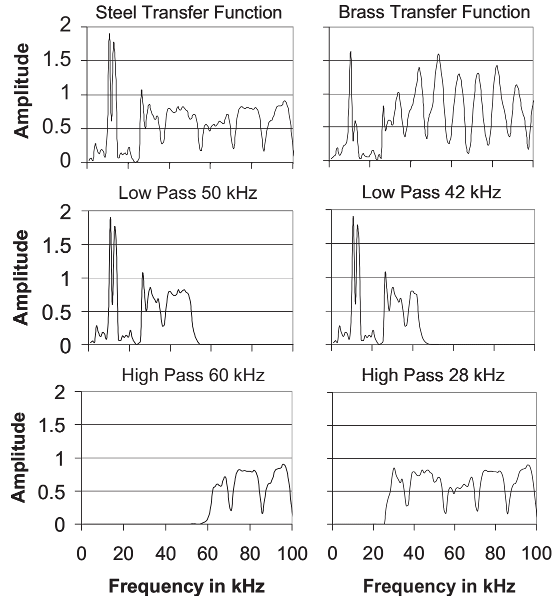

FIG. 1. The frequency spectra from selected phantom steel target transfer functions that have been modified with different filter types as labeled and from the phantom brass target. The complete list of filters used included high pass filters at 60, 40, 35, 30, 28, 27, 26, and 20 kHz and low pass filters at 50, 45, 42, 41, 40, 35, 30, 25, and 20 kHz and a band pass filter from 30 to 40 kHz. These comprised the transfer functions for all the phantom targets that BJ echolocated on for this experiment.

BJ interacted with the system in the same way she interacted with the real targets using on average the same number of clicks, the same click intensities, and the same click frequency content. This indicated that BJ was indeed performing a real echolocation task when presented the phantom targets (Ibsen *et al.*, 2009).

3. Phantom targets

a. Phantom targets used in 2004 The stimuli that were presented to BJ were simulated echoes from a 7.6 cm diameter solid stainless steel sphere. A sphere was chosen because BJ had demonstrated her ability to distinguish between a solid steel sphere and a solid brass sphere from a distance of 8 m in past experiments (Aubauer and Au, 1998). The sphere was also radially symmetrical in shape eliminating changes in the echo due to variations in orientation. The phantom system was designed to emulate the sphere echoes in both frequency content and intensity. The standard stimulus was an unfiltered version of the phantom steel target. The comparison stimuli were filtered versions of the phantom steel target. Figure 1 shows the amplitude spectra of selected phantom steel target transfer functions that were altered with the filters as labeled and from the phantom brass target. The filters were chosen based upon BJ's consistent use of clicks that had an average peak frequency of 40 kHz (Ibsen *et al.*, 2007). The filters used included high pass filters at 60, 40, 35, 30, 28, 27, 26, and 20 kHz and low pass filters at 50, 45, 42, 41, 40, 35, 30, 25, and 20 kHz, a band pass filter from 30 to 40 kHz, and no target. These transfer functions were convolved with the click signals to produce the filtered phantom steel target echoes. The transfer function in the upper left hand corner was the unfiltered stainless steel sphere transfer function and was used to create the standard unfiltered stimulus.

b. Phantom targets used in 1998 In the 1998 experiments (Aubauer *et al.*, 2000) only two phantom targets were presented to BJ: the standard steel and the comparison brass. The 1998 phantom steel was similar to the 2004 phantom steel and both were modeled after the same real target.

4. Analysis software

Custom-written programs were created to analyze the clicks from both the 1998 and 2004 experiments. Echoes were recalculated for the analysis using the same algorithms used in the phantom echo generator. The analysis programs worked with both the clicks and the echoes to correlate them with the conditions they were collected under as well as group them based on similar distinguishing characteristics of peak frequency, rms bandwidth, and intensity.

C. Experimental procedure

For both the 1998 and 2004 experiments each trial was started with a hand signal to cue BJ to swim to the hoop facing into the target pen. BJ would station in the hoop and would be cued to begin echolocation when the movable baffle was lowered out of the way giving her free echolocation access to the target pen. The clicks were recorded and saved by the phantom system and the stimulus phantom echoes sent back using the transducer.

For both the 1998 and 2004 experiments a go/no-go paradigm was used where the go response was required with unaltered phantom steel targets. The no-go response was required with all other comparison phantom targets (brass, no target, and filtered steel). For the go response BJ backed out of the hoop and touched a paddle. For the no-go response BJ just stayed in the hoop for the duration of the 6 s trial. Each session consisted of 50 trials. Half of the stimuli were the standard stimuli and the other half consisted of the comparisons. Up to five different filtered comparison targets per session were presented to BJ in groups of five trials each. The order of stimuli presentation was determined using a standard Gellerman series (Gellerman, 1933). All correct responses were rewarded with fish.

BJ's baseline performance in both experiments was maintained during each session because half of the targets were the standard. If BJ's performance with the standard target was less than 95% correct within a session it was determined she was not operating as expected in the go/no-go paradigm, and the data from that session were removed from the final data set. There were 75 sessions analyzed from the 2004 experiment and 4 sessions from the 1998 experiments, totaling 120 000 clicks.

III. RESULTS

A. Results from the 2004 experiments

1. Lack of correlation between click parameters and target type

To determine if BJ preferentially used a certain click frequency content for a certain target, the peak frequency and rms bandwidth of each click was determined. There was a great deal of variation with each of these parameters between clicks regardless of target. To compare large numbers of clicks used for different targets the distribution of peak frequencies and distribution of rms bandwidths were considered for each target. It was found that the click distributions for the different targets significantly overlapped with each other. For example, the maxima of the peak frequency distribution, the most commonly used peak frequency, was always between 40 and 50 kHz regardless of target. A nonparametric Kruskal–Wallis test found that the widths of the peak frequency distributions were not significantly different ($p=0.06$). The same test found that the maxima of the click rms bandwidth distributions were not significantly different ($p=0.02$). This showed that the most commonly used click rms bandwidth was the same for each target.

The analysis showed that despite the variation between clicks there was no consistent pattern between the 24 different targets BJ was presented. She did not appear to preferentially use any click type for any particular target nor did she tailor her entire click to any particular target. This was consistent over the 75 sessions of the experiment that spanned a period of 11 months.

2. Consistent patterns of frequency content between clicks

To better see the large variation in source level and frequency content of the clicks as described above, the amplitude spectra from the first 250 clicks BJ made during session 59 are shown in Fig. 2(A). These are all low frequency clicks. Other dolphins with upper hearing limits around 50 kHz have been shown to favor the use of low frequency echolocation clicks as well (Houser *et al.*, 1999). As can be seen there is a great deal of variability in the source level of the clicks. Click source level did not appear to be a variable that BJ controlled very consistently.

To understand the variance in frequency content from click to click the source level differences can be eliminated by normalizing each spectra. This allows the spectra from clicks of different source levels to be directly compared for frequency content alone. Overlaying the normalized spectra from many different clicks reveals trends of consistency or inconsistency in the click frequency content over time, independent of source level. The result of normalizing the spectra of the 250 clicks is shown in Fig. 2(B). Despite the large differences in click source level, a consistent spectra profile pattern exists from click to click in the 0–42 kHz region. The vertical line shows the upper limit of BJ's functional bandwidth. Above this region the frequency content can be quite different from one click to another. The standard deviation of the normalized intensity values for all 250 clicks at a single frequency, 35 kHz, was 0.04 but rapidly increased to 0.27 at

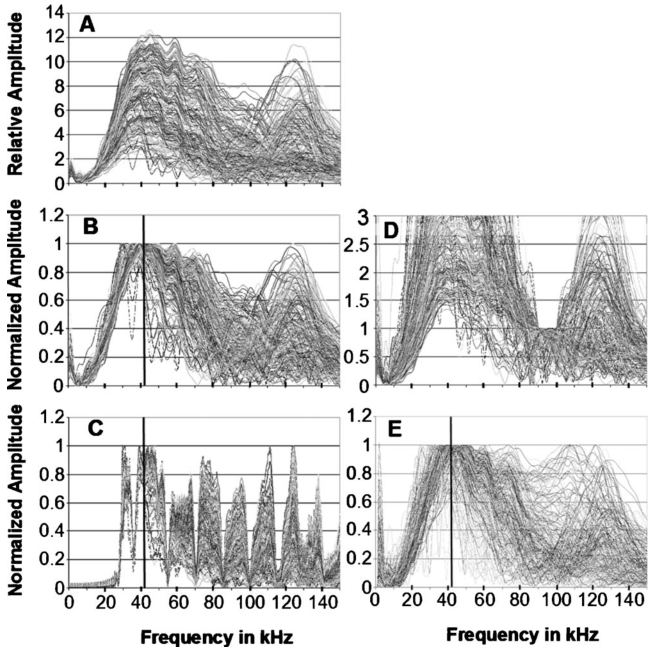

FIG. 2. Normalized click and echo frequency spectra graphs from 2004. (A) The amplitude spectra from the first 250 clicks that BJ made in a row on both unfiltered and filtered phantom steel targets. There is a general lack of consistency in intensity and apparently in frequency content. (B) These are the same spectra shown in (A) but they have been normalized so they all have the same maximum intensity of 1. This removes the intensity differences so the frequency content can be directly compared. There is striking consistency in frequency content between 0 and 42 kHz and a general lack of consistency above 42 kHz. The vertical black line shows the upper limit of BJ's functional bandwidth at 42 kHz. (C) The amplitude spectra of the echoes produced from the 250 clicks that BJ made in (B). These have also been normalized to have the same maximum intensity of 1. There is striking consistency in frequency content between 0 and 42 kHz and a general lack of consistency above 42 kHz. This is the same pattern found with the clicks. The vertical black line shows the upper limit of BJ's functional bandwidth at 42 kHz. (D) The partial normalization of the spectra from the clicks shown in (A) but in the region of 90–100 kHz. It does not result in a consistent pattern. This indicates that BJ was not controlling the frequency content in this region. This lack of consistency is the same for different normalized bands of frequencies above 42 kHz. (E) Randomly chosen click spectra. To demonstrate the consistency was a general trend, 3 clicks from each of the 75 sessions were chosen at random and plotted together. This shows the consistent pattern in BJ's clicks in the 0–42 kHz range held across time and the 24 targets presented to BJ. The vertical black line shows the upper limit of BJ's functional bandwidth at 42 kHz.

70 kHz. A nonparametric Wilcoxon rank sum test preformed at a 0.05 significance level showed that the standard deviation values for normalized frequency intensities in the 0–42 kHz region and the 43–159 kHz region were significantly different ($p<0.001$) confirming that the 0–42 kHz region was more consistent in frequency content than the 43–105 kHz.

To understand how these consistent and variable regions in the spectral profile might affect the echoes BJ received, the phantom echoes were recalculated. The resulting echo amplitude spectra for each of the 250 clicks shown in Fig. 2(B) are shown normalized and overlaid in Fig. 2(C). The consistency in the frequency content of the clicks was preserved in the echoes.

Normalizing an entire spectra by the maximum value of that spectra is useful if the consistent parts have the highest amplitude. However, if there are regions of the spectra that are consistent from click to click, but have lower intensity than other regions, their consistency would not line up due to drowning out by higher amplitudes in surrounding frequency bands. These localized regions of consistency could show up by normalizing just a selected band of frequencies and looking for consistencies in that selected band. If there was consistency in a narrow band of choice, and the whole spectra was partially normalized by the maximum intensity value in that narrow band then one could see the spectra from different clicks line up consistently in that band. These "partial normalizations" use the maximum intensity value from a chosen 10 kHz band as the normalization factor for all the frequencies of that individual spectra. An example of this is shown in Fig. 2(D) where the maximum intensity value from the 90–100 kHz band was used as the normalization factor. The maximum value of the frequencies in this 90–100 kHz band is 1, but since this band often had less intensity than other frequency bands from click to click, those surrounding regions end up having a higher amplitude once normalized. The spread of normalized click intensity values in this 90–100 kHz band was much larger than when the 0–42 kHz region was normalized. The region between 0 and 42 kHz was the only frequency band that showed consistency upon partial normalization. This emphasizes the lack of consistency above 42 kHz.

This consistency was not just isolated to clicks produced in session 59. Figure 2(E) shows a graph where 3 clicks were randomly collected from each of the 75 sessions. Again, the standard deviations between the normalized intensity values in the 0–42 and 43–105 kHz bands were significantly different ($p<0.001$). There are a few click spectra displayed which do not follow the consistent pattern. These clicks were termed aberrant clicks and a study was done to determine if there was a pattern to their appearance and will be discussed later. Despite these aberrant clicks, the consistency with which BJ produced clicks over the span of 75 sessions and when exposed to 24 different targets was significant.

B. Results from the 1998 experiments

The click spectra from 1998 were normalized just like the 2004 click spectra and are displayed in Fig. 3(A). It is evident that BJ did not use the same strategy in 1998 as she did in 2004. There is no correlation in the intensities of the frequency content. A partial normalization as described above was done on specific frequency bands. A partial normalization in the 90–100 kHz region is shown in Fig. 3(B) and a partial normalization in the 110–120 kHz region is shown in Fig. 3(C). These figures do not demonstrate correlations in the frequency content like there were in Fig. 2(B) for the 2004 clicks. Partial normalization of the frequency band regions 10–20, 29–42, 80–90, and 100–110 kHz yielded similar results to those shown in Fig. 3(C).

However, consistency patterns appeared when looking at the echoes that resulted from the 1998 clicks. The resulting normalized echo spectra from the 1998 clicks are shown in Fig. 3(D). A partial normalization of the 90–100 kHz band is shown in Fig. 3(E). The frequency band of 90–100 kHz in Fig. 3(E) had a pattern of consistency similar to what was

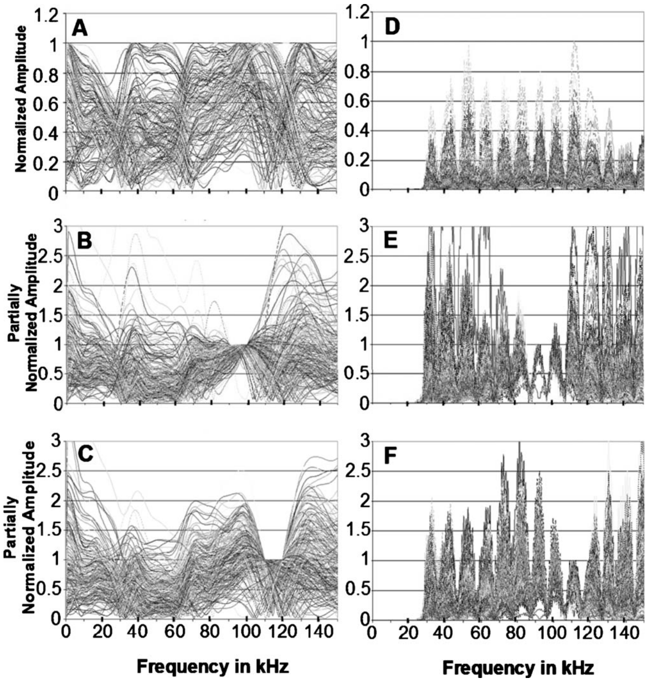

FIG. 3. Normalized click and echo frequency spectra graphs from 1998. (A) The normalization of the spectra from the 1998 clicks. Unlike the 2004 clicks this normalization did not result in a consistent pattern. This indicates that BJ used different clicks between those two time periods. (B) The normalization of the spectra from the 1998 clicks in the region of 90–100 kHz. It resulted in a more consistent pattern than found in the normalization of the 29–42 kHz region. This indicates that BJ was more actively controlling the frequency content in this region. (C) The normalization of the spectra from the 1998 clicks in the region of 110–120 kHz. It did not result in a consistent pattern. This indicates that BJ was not controlling the frequency content in this region. (D) The normalization of the echo spectra from the 1998 clicks. It does not result in a consistent pattern like that seen in the 2004 data especially in the 29–42 kHz region. This indicates that in 1998 BJ was not controlling the frequency content in this region as tightly as she did in 2004. (E) The partial normalization of the echo spectra from the 1998 clicks in the region of 90–100 kHz. It resulted in a consistent pattern very similar to that seen in the 0–42 kHz region from the 2004 clicks. This indicates that in 1998 BJ was carefully controlling the frequency content in this region. In 2004, BJ did not control the frequency content in this region [see Fig. 2(D)]. (F) The normalization of the echo spectra from the 1998 clicks in the region of 110–120 kHz. It did not result in a consistent pattern. This indicates that in 1998 BJ was not controlling the frequency content in this region.

seen in the echoes for the 2004 data shown in Fig. 2(C). The same analysis as described above showed that the standard deviation of the normalized intensities in the 0–42 kHz band from 2004 and the 90–100 kHz band from 1998 were not significantly different ($p=0.04$). A partial normalization of the 110–120 kHz band is shown in Fig. 3(F) and demonstrates a lack of correlation in this region.

IV. DISCUSSION

A. Consistency in frequency content

1. Consistency in frequency content for 2004 data

BJ's 2004 clicks showed a very high degree of consistency in the normalized frequency spectra profiles in the 0–42 kHz band and nowhere else. This consistency was not an artifact of BJ's click production system because the 1998 data did not show this consistency in the 0–42 kHz band. This suggests that in 2004 BJ was actively controlling the frequency content in the 0–42 kHz range to maintain the observed uniformity. BJ's functional bandwidth of 29–42 kHz matched well with the consistent region. All the frequencies between 29 and 42 kHz were being paid attention to by BJ while echolocating. The clicks rapidly lost frequency content below 29 kHz and so did not provide much echo content below 29 kHz. The frequencies above 45 kHz were not perceived by BJ.

It is likely that the observed lack of consistency above 42 kHz resulted from BJ's inability to perceive the higher frequencies eliminating any possible feedback necessary to control click frequency content in those regions. It is remarkable that BJ was able to control her click frequency content so tightly right up to her upper hearing limit and then have such a large loss of control above that.

One possible reason why BJ used this particular spectra profile for the 0–42 kHz frequency band is that it seemed to maximize the intensity of all the frequencies in the 0–42 kHz region. The upper limit of the envelope of the non-normalized clicks in Fig. 2(A) had the same profile as the normalized clicks in Fig. 2(B). The most intense clicks had the same profile as the least intense clicks showing that the frequency content in the 0–42 kHz region was independent of intensity at least for click source levels up to 187 dB. It appears that BJ was maximizing the intensity of the 0–42 kHz region to the extent that her click production system could manage.

BJ maintained this high level of consistency in click frequency content despite the very different reflection characteristics of the various phantom targets. Perhaps what BJ was doing was to use the click that provided the best echo signal to noise ratio for the 29–42 kHz range. She memorized some cue of the returned echo from the standard target. BJ's ability to remember target echo characteristics was demonstrated when she was able to correctly identify the standard target on the first try even after having not been exposed to it for 3 months. She then used the same consistent click to probe new targets. If the returned echo matched what she had memorized it was classified as the standard target. If the returned echo was perceived to be different then BJ knew it was a comparison target. This meant BJ needed to have very consistent clicks to be able to tell the difference between targets down to just 1 kHz of filtering. If her clicks all had different frequency contents from 29 to 42 kHz it would be much more difficult for her to memorize characteristics of the standard echo for each different intensity profile she used. It would also mean that probing new targets would be more difficult because a larger set of comparison data would have to be applied requiring more clicks, time, and effort.

2. Consistency in click frequency content for 1998 data

By comparing the frequency content of the 2004 echoes normalized from 29 to 42 kHz in Fig. 2(C) with the 1998 echoes normalized from 90 to 100 kHz in Fig. 3(E) it is apparent that in both cases BJ used a similar strategy of keeping the echo frequency content consistent between clicks independent of intensity. The 1998 and 2004 strategies differ in the frequency regions of consistency. In 2004 BJ was consistent in the 0–42 kHz range and let the higher frequencies have a random intensity distribution. In 1998 BJ was consistent in the 90–100 kHz region and allowed the other frequencies above and below this band have a random intensity distribution.

It can be hypothesized that the shift in echo consistency regions between 1998 and 2004 occurred do to a possible change in BJ's upper hearing limit between the two times periods. It has been shown that dolphins can acquire hearing deficits by the age of 23 (Brill, *et al.*, 2001; Ridgway and Carder, 1997). There are no audiograms from BJ before 2001 so it is not known exactly what her upper hearing limit was before 2001 but for the purpose of this hypothesis it could be assumed that BJ's upper hearing limit in 1998 was 100 kHz. This is not an unreasonable assumption because typical young bottlenose dolphins can hear up to 150 kHz (Johnson, 1967; Au, 1993; Nachtigall *et al.*, 2000). Evidence for a drop in BJ's hearing also comes from looking at the frequencies in the clicks where the most energy was contained. There would be little advantage for BJ to use the click intensity profiles from 1998 with an upper hearing limit of 45 kHz because only about 25% of the energy would be perceptible with the average peak frequency at 138 kHz. The clicks made in 2004 were much better tailored to a lower hearing limit because about 42% of the energy was detectable with the average peak frequency at 40 kHz where her most sensitive hearing was (Ibsen *et al.*, 2007).

Also, the 2004 data indicate that BJ did not seem to control the frequency content of her clicks in the region she could not hear including the 90–100 kHz region [see Fig. 2(D)]. It seems unlikely that there could be such good correlation in the 1998 echo frequency content without BJ perceiving those frequencies and controlling them.

One reason it would have been advantageous for BJ to use higher frequencies in 1998 is that her average click source levels were 207 dB. There is a loose correlation between click source level and frequency content with the higher source levels being associated with higher frequency content (Au *et al.*, 1995; Houser *et al.*, 1999). Since BJ might have been able to perceive those higher frequencies in 1998 she could get the largest signal to noise ratio for the echoes by using the louder clicks that contained more significant high frequency content. In 2004 BJ could not perceive those higher frequencies and so used clicks with an average source level of 187 dB that had more significant low frequency content than the louder high frequency clicks. BJ was maximizing the echo signal to noise ratio for a reduced hearing range.

To see what discrimination cues might have been produced from BJ's click frequency consistency in 1998, 130 clicks were used to calculate echoes normalized between 90 and 100 kHz for the steel and brass targets. The resulting echo spectra from both targets were overlaid and shown in Fig. 4. One can see a distinct and consistent difference between the two targets from click to click. If BJ was paying attention to this frequency range she could have used these differences as the discrimination cues. No other normalized band resulted in such a distinct and consistent difference between the targets.

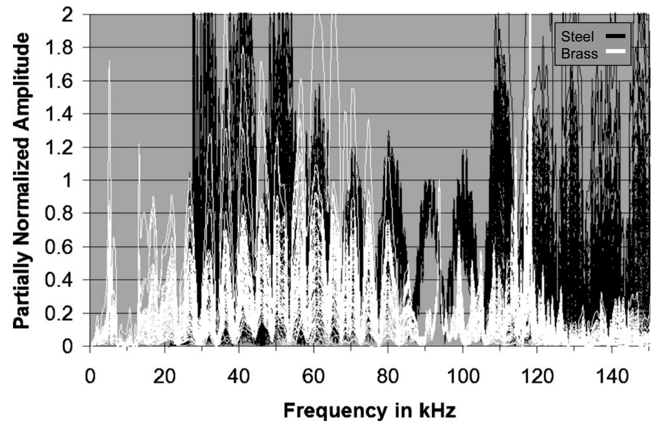

FIG. 4. Echo spectra, normalized between 90 and 100 kHz, for both phantom steel and phantom brass targets calculated from 130 clicks BJ made in 1998. There is a distinct and consistent difference in the spectra of the two targets in the 90–100 kHz range. This difference could have been used as the discrimination cue. No other normalized band had such a distinct difference between the two targets.

B. Echoes as feedback control for click production

Another interesting feature is the relative lack of frequency content consistency in the 1998 clicks normalized in the 90–100 kHz region as seen in Fig. 3(B) when compared to the consistency seen in Fig. 2(B) from the 2004 clicks. One of the implications of this is that BJ may not have been using her outgoing clicks as the input to the click control system. She needed some sort of feedback to tell whether her clicks had the desired frequency content. The tight consistency in the 1998 echoes that resulted from clicks that were less consistent indicates that BJ might have used the echoes as input. The phantom target showed the ability to absorb some variance in click spectra in the 90–100 kHz region while still showing spectral consistency in the echoes. As can be seen in Fig. 5 the 90–100 kHz region was bounded on both sides by null points in the target transfer function. This helped absorb inconsistencies in the frequency content of the clicks at the boundaries and produced consistent repeatable echoes. Looking at Fig. 6 for the 2004 data the functional bandwidth of 29–42 kHz was not bounded by null points. BJ had to maintain a higher level of consistency with her clicks in 2004 because the inconsistencies would not have been absorbed by the target and would have resulted in inconsistent echoes.

C. Sound beam focusing as the source of consistency and variation

It is interesting how BJ was able to have such tight control over the frequency content in just a band of frequencies. In 1998 it is not unreasonable to assume she could hear frequencies lower than 90 kHz. However, they were not apparently used as input to her click control system. So only the frequencies that she paid attention to were the ones that she controlled, although she had the ability and the potential to control other frequencies.

The source of click production has been traced to airflow pushing past pairs of internal phonic lip membranes creating a simple slapping mechanism (Cranford, 2000). The nature

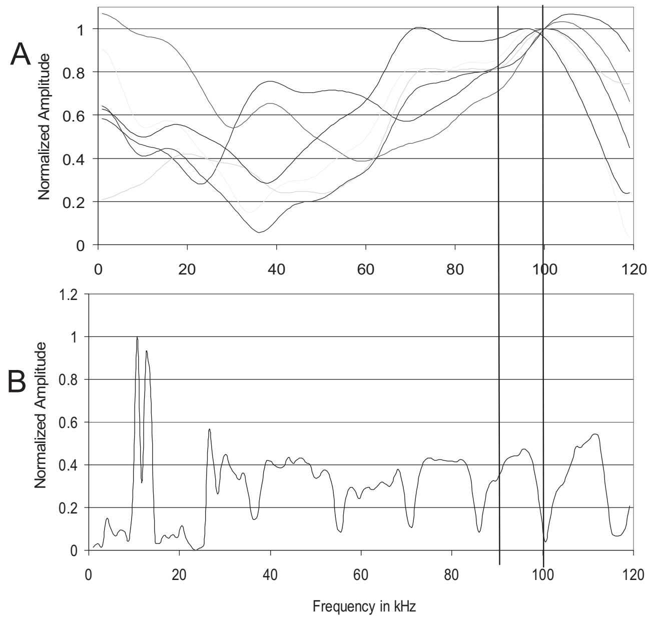

FIG. 5. Spectral analysis of (a) six characteristic click spectra made in 1998, (b) the steel transfer function. The region between the two black lines was the frequency region where BJ kept the echoes consistent. This might have been her functional bandwidth in 1998. The null points in the transfer function at 85 and 100 kHz allowed the variance in the click frequency content to be absorbed producing very consistent echoes between 90 and 100 kHz.

of slapping membranes could allow for frequency content manipulation of the entire click but it is unlikely that it could be manipulated for consistency in just a small band of frequencies while frequencies outside this band are allowed to change. The fact that there is consistency in a single band of frequencies suggests that the phonic lips are producing a fairly consistent click each time they slap, a consistency which is independent of overall intensity as long as there is a

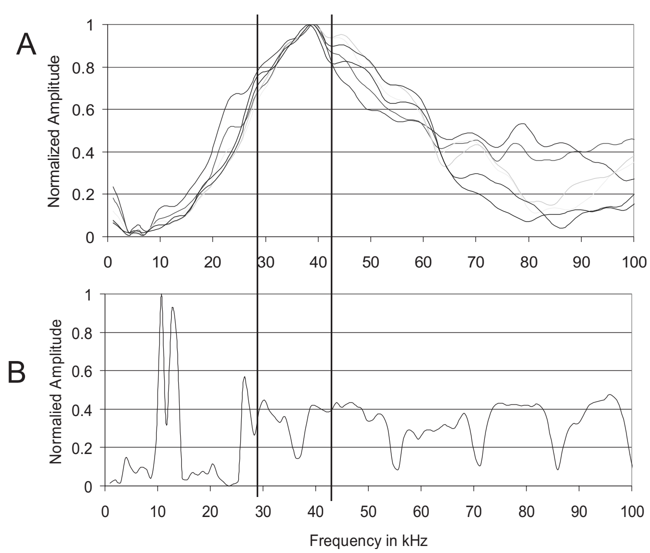

FIG. 6. Spectral analysis of (a) six characteristic click spectra made in 2004, (b) the steel transfer function. The region between the two black lines was BJ's functional bandwidth. BJ had to be more consistent with the frequency content of her clicks because the transfer function in this region did not have any null points that could absorb inconsistencies in the click frequency content. Inconsistent clicks in this region would produce inconsistent echoes.

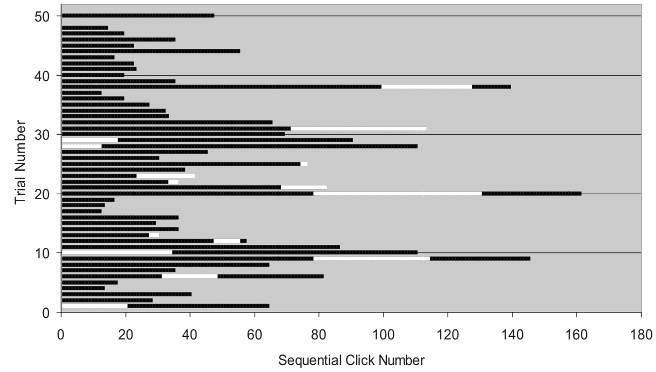

FIG. 7. The sequential appearance of aberrant clicks within different echolocation click trains. The black data points represent clicks that fit the general consistent pattern. The white points were aberrant clicks that did not fit that pattern. The aberrant click production was not random but occurred only at the beginning, middle, or end of a trial. This indicates that their production might have been tied to the limitations of the click production system during generation of the maximum number of high intensity clicks in a row.

certain threshold of airflow. Higher intensities result from higher airflow rates but the physical properties of the slapping membranes remain the same.

This ability to produce consistency within the functional bandwidth, as well as simultaneous variability in frequencies outside the functional bandwidth, suggests that the frequency content of the echolocation beam might be mostly formed and controlled by manipulations of the melon and nasal air sacs. The shape of the melon and air sacs could be manipulated within a certain range for optimum focusing of the 90–100 kHz frequency band. The variation in shape within this optimal 90–100 kHz range might have affected the other frequencies differently. As long as the frequencies BJ paid attention to were not affected, BJ might not have perceived changes to the on axis focusing of other frequencies. BJ seemed not to attend to these frequencies, since they were not part of the echolocation process, and so did not try to control the melon to focus these frequencies consistently on axis. Sometimes the focus of these frequencies would line up with the recording hydrophone and sometimes not, thereby changing the recorded intensity of those frequencies from click to click even though the frequency content of the source generated click was the same. Future experiments using arrays of recording hydrophones will shed light on how the different frequencies might be focused relative to one another from click to click.

D. Aberrant clicks

The aberrant clicks that show up in Fig. 2(E) probably were not used by BJ for echolocation purposes. The aberrant clicks had a relatively low amplitude compared to those clicks that fit the consistent pattern. They appear to have the same amplitudes in Fig. 2(E) only because everything was normalized to remove intensity differences. In reality they had less than half the intensity of the loudest consistent clicks and usually much lower than that.

The appearance of the aberrant clicks within a click train was far from a random occurrence as seen in Fig. 7. The *x*-axis of the graph is sequential click number of the click train and the *y*-axis is the trial number in which these click trains were made. These data come from session 1 where BJ was first exposed to the phantom probes. She happened to use more clicks than normal on several trials. The black data points represent clicks that fit the consistent pattern and the white data points represent the aberrant clicks. The aberrant clicks mostly show up at the beginning or end of a click train. If they show up in the middle of a click train they usually occur in a block of 30–50 clicks after 70–90 sequential clicks of the consistent pattern.

Perhaps these aberrant clicks were produced when BJ had to recharge the air supply that supported her click production system. Dolphins have a finite charged air supply they can use to produce clicks in a single click train before they run out and must recycle the air to produce more clicks (Dormer, 1979). As BJ began to push air over the phonic lip membranes she might have had to ramp up pressure to get the airflow fast enough to produce sufficiently loud clicks. The flowing air produced force on the phonic lips giving them sufficient tension for optimal operation. The airflow probably decreased as she ran out of air and prepared to pull it back into the lower nasal passages to recharge the system to get more clicks. This reduction in airflow might have reduced the tension in the phonic lips, reducing click intensity, to the point that their acoustic properties became uncontrollable. But as soon as the airflow became sufficient, the click intensity might have returned to normal and the frequency content returned to the consistent pattern.

It may also have taken BJ a certain number of clicks to modify the shape of her melon and nasal air sacs to optimize the frequency content. This might explain the aberrant clicks at the beginning of some trials. If BJ began to echolocate and did not have the proper frequency content she would have to modify her click production system to compensate. She probably did not have to go through this process if she got the shape right to begin with.

V. CONCLUSION

It was found that BJ used echolocation clicks that had a high degree of similarity in their frequency content regardless of the target type she was exposed to. This consistency only occurred in certain frequency bands and was independent of click intensity. The region of consistency in 2004 was 0–42 kHz. Above 43 kHz the consistency was lost. This same level of consistency was found in the echoes resulting from these clicks. BJ's upper hearing limit was 45 kHz so it appears that she was not able to control the frequency content of clicks in regions she could not perceive. BJ's apparent target discrimination strategy was to investigate every target with clicks that had standardized frequency content within her functional bandwidth. She probably memorized the standard phantom target's echo that resulted from the standard click and compared that echo to those from new targets. These differences in the echo frequency content, as small as 1 kHz of filtration, were the cues she used to make the discriminations.

This echolocation strategy of creating standard clicks with consistent frequency content in certain regions was also used by BJ in 1998; however, the region of consistency was 90–100 kHz. In this case, the resulting echoes were more consistent than the clicks themselves. The target was able to absorb more variation in the click frequency content while still producing consistent echoes due to the location of null points in its transfer function. This indicates the echo itself might have been used as the feedback input for the echolocation click control system which regulated and maintained the consistency of the clicks. When comparing the spectra of the echoes from the steel and brass phantom targets there were consistent differences only in the 90–100 kHz range which could have been used as the discrimination cues. The 90–100 kHz region back in 1998 had an advantage over the 29–42 kHz region of 2004 because BJ was able to click with greater intensity at the higher frequencies resulting in better echo signal to noise ratios. The high frequency clicks had an average source level of 207 dB while the lower frequency clicks could only be produced at an average of 187 dB. The observed shift in consistency regions indicates that BJ's upper hearing limit may have shifted down between the two experiments forcing her to adapt her clicks to continue to provide the best echo signal to noise ratio. It would be adaptive for BJ to create the best signal to noise ratio because she could perceive more detail in the echo allowing the discrimination tasks to be preformed in less time and with fewer clicks.

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