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Characterizing the graded structure of false killer whale (*Pseudorca crassidens*) vocalizations

Scott O. Murray^{a)}

Center for Neuroscience, University of California, Davis, Davis, California 95616

Eduardo Mercado and Herbert L. Roitblat

Department of Psychology, 2430 Campus Road, University of Hawaii, Honolulu, Hawaii 96822

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The vocalizations from two, captive false killer whales (*Pseudorca crassidens*) were analyzed. The structure of the vocalizations was best modeled as lying along a continuum with trains of discrete, exponentially damped sinusoidal pulses at one end and continuous sinusoidal signals at the other end. Pulse trains were graded as a function of the interval between pulses where the minimum interval between pulses could be zero milliseconds. The transition from a pulse train with no inter-pulse interval to a whistle could be modeled by gradations in the degree of damping. There were many examples of vocalizations that were gradually modulated from pulse trains to whistles. There were also vocalizations that showed rapid shifts in signal type—for example, switching immediately from a whistle to a pulse train. These data have implications when considering both the possible function(s) of the vocalizations and the potential sound production mechanism(s). A short-time duty cycle measure was developed to characterize the graded structure of the vocalizations. A random sample of 500 vocalizations was characterized by combining the duty cycle measure with peak frequency measurements. The analysis method proved to be an effective metric for describing the graded structure of false killer whale vocalizations. © 1998 Acoustical Society of America. [S0001-4966(98)03609-1]

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INTRODUCTION

One of the most remarkable characteristics of dolphin (*Delphinidae*) behavior is the diversity and apparent complexity of their vocalizations. Most descriptions of dolphin vocalizations have used aural analysis and/or visual analysis of spectrograms (e.g., Caldwell and Caldwell, 1968; Dahlheim and Awbrey, 1982; Evans and Prescott, 1962; Ford, 1989; Herzing, 1996; Kaznadzei *et al.*, 1976; Lilly and Miller, 1961; McCowan and Reiss, 1995; Sjare and Smith, 1986; Tyack, 1986). As a result of such studies, dolphin vocalizations have been classified traditionally into three distinct signal types: (1) click trains; (2) burst-pulse sounds; and (3) whistles. Click trains and burst-pulse sounds are collapsed sometimes into a single category: pulsed sounds/pulse trains (e.g., Herman and Tavolga, 1980).

Click trains are comprised of a sequence of brief acoustical pulses spaced over time. The pulses can be described as exponentially damped sine waves and range in duration from approximately 40 μ s in bottlenosed dolphins (Au, 1993) to over 10 ms in killer whales (Steiner *et al.*, 1979). Because their durations are short, pulses have a wide frequency bandwidth, making them sound clicklike. Their peak frequencies can vary tremendously, from 5 kHz (Steiner *et al.*, 1979) to over 150 kHz in some species (Au, 1993). The repetition rate of pulses within a click train range from a pulse every 1–2 s to hundreds of pulses per second (Ford and Fisher, 1978; Dawson, 1991); pulse rate can also change over the course of

a “train.” Click trains can contain a few to hundreds of clicks.

When the interval between pulses in a pulse train is sufficiently brief (around 5 ms or less), human perception can no longer separate the pulses in time and the vocalization is perceived as a continuous tonal sound. Although such pulse trains may be structurally identical to click trains, to the human ear they sound very different and are given a different name: burst-pulse sounds, which sound subjectively like screams, squeals, or moans (Caldwell and Caldwell, 1967; Dahlheim and Awbrey, 1982; Dawson and Thorpe, 1990; Schevill and Watkins, 1966). The peak frequencies of burst-pulse sounds vary between species. For example, killer whales produce burst-pulse sounds with peak frequencies below 20 kHz (Ford, 1989). Hector’s dolphins (Dawson and Thorpe, 1990) and Commerson’s dolphins (Evans *et al.*, 1988), however, produce burst-pulsed sounds with peak frequencies above 100 kHz. Burst-pulse sounds range in duration from tens of milliseconds to several seconds (Ford, 1989; Overstrom, 1983). Finally, whistles are narrow-band, tonal sounds that are usually frequency modulated. Most species of dolphins produce whistles between 5 and 20 kHz with ranges in duration similar to burst-pulse sounds (Caldwell *et al.*, 1990; Richardson *et al.*, 1996). While all dolphin species produce pulsed sounds, some species may not produce whistles (Herman and Tavolga, 1980).

A. Traditional analysis

Determining the *type* of vocalization (e.g., whistle, burst-pulse, click train) has often been the first step in past analyses of dolphin vocalizations. As previously mentioned,

^{a)}Electronic mail: smurray@braindev.uoregon.edu

most characterizations of dolphin vocalizations have been based on aural impressions and visual inspections of spectrograms. Through aural analysis, labels such as “whistles,” “squawks,” “screams,” “clicks,” etc. are derived. Signals may be reliably classified by individual researchers using such labels, but such classifications are highly subjective and generalize poorly across researchers. Additionally, these categories are highly dependent upon the perceptual capabilities of humans. We may be incapable of distinguishing or recognizing subtle differences in the underlying acoustic structure and, consequently may be forming categories that are irrelevant for dolphins.

Researchers have also analyzed spectrographic representations of dolphin vocalizations in attempts to describe their structure. These analyses have relied on the notion that different signal types yield visually discriminable spectrograms. For example, because clicks are short, broadband signals, click trains are represented on a spectrogram by a series of vertical lines with intervals between lines corresponding to the intervals between clicks. A whistle, on the other hand, appears as one or more horizontal lines with the bottom line usually representing the fundamental frequency of the signal and lines above it representing harmonics.

Forming categories based on visual inspection of spectrograms can be problematic. The determination of whether one whistle or burst-pulse sound looks different from another is highly subjective and thus may generalize poorly between investigators. Additionally, spectrograms are subject to a time versus frequency resolution tradeoff. A gain in time resolution results in a loss in frequency resolution, and vice versa. Therefore, the choice of the analysis bandwidth can dramatically affect the visual representation of the signal. It is possible to arrive at similar looking spectrograms through quite different underlying waveforms. For example, what may appear to look like a whistle (a line on a spectrogram with many harmonics) can be created by pulsing a signal faster than can be resolved by the analysis window of a spectrogram (Davis, 1964; Watkins, 1967). Simply decreasing the size of the analysis window will resolve the pulsed signal into what appears to be a click train. In other words, with one signal and two window sizes, you can arrive at two very different looking spectrograms.

B. Graded signals

The traditional model for classifying dolphin vocalizations assumes that their repertoires consist of acoustically discrete signal types (e.g., whistles, burst-pulse sounds, and click trains). However, click trains and whistles may be at opposite ends of a continuum (with burst-pulse sounds being intermediate). This continuum may have been previously unrecognized because subjective analyses and single window size spectral analyses have been the norm.

Determining whether the structure of dolphin vocalizations lie along a continuum or occupy discrete categories is important when considering the potential function(s) of the signals. For example, if the structure is graded, with no clear acoustic demarcations, some function(s) of the signals may not be discrete. One possible function of a graded structure may be to communicate arousal level or behavioral state. If,

however, the acoustic structure of the signals is comprised of discrete categories, it would suggest that the various signal types may serve unique functions.

The existence of a graded acoustic structure would also have implications for possible sound producing mechanisms. One of the questions regarding dolphin vocalizations¹ is the mechanism(s) responsible for producing sound. Many theories have been suggested; the two most commonly suggested sources being the larynx (e.g., Purves and Pilleri, 1983) and the nasal sac system (e.g., Cranford *et al.*, 1996). It is sometimes assumed that there is a generator for echolocation pulses and a separate site for whistles (e.g., Evans and Prescott, 1962). This assumption is partly due to the fact that whistles and clicks are regularly produced simultaneously, suggesting that there are two distinct mechanisms. If the vocal structure is shown to be graded, however, another possibility may be that the same mechanism produces both pulsed sounds and whistle-like vocalizations. The occurrence of simultaneous clicks and whistles could be the result of twin mechanisms each capable of producing whistles and clicks as well as all gradations in between.

C. Study goals

False killer whales (*Pseudorca crassidens*) are an extremely vocal delphinid species and have a diverse repertoire. They produce sounds that meet the “traditional” categories described above (clicks, burst-pulse, and whistles) as well as many other sounds that appear to be “intermediate” between categories (e.g., have both pulsed and continuous-wave characteristics). This diversity provides a unique opportunity to analyze the acoustic similarities between what have traditionally been considered distinct categories.

The determination of whether the structure of false killer whale vocalizations is graded or consists of discrete categories should be based on acoustic structure and not on human perception, which may introduce arbitrary groupings. Given the difficulties in describing signal type (e.g., pulsed versus continuous) through traditional methods such as aural analysis or visual inspection of spectrograms, this study developed an alternative measure of signal type based on a short-time duty cycle calculation. The advantage to this new technique was that it eliminated human judgment and subjected all vocalizations to the same measure. The signal type measure was combined with peak frequency measurements. Each vocalization, consequently, was characterized by simultaneous changes in signal type and peak frequency.

I. DATA COLLECTION

Recordings were made of two false killer whales, one male and one female, located at Sea Life Park, Oahu. They were approximately 3 years old when captured and approximately 9 years old when the recordings were made. At the time of recording, the male was 3.9 m and weighed approximately 600 kilograms and the female was 3.7 m and weighed about 450 kilograms. The two animals had been housed together since capture.

Recordings were made by moving each animal to a distant portion of its tank. The other animal remained behind a

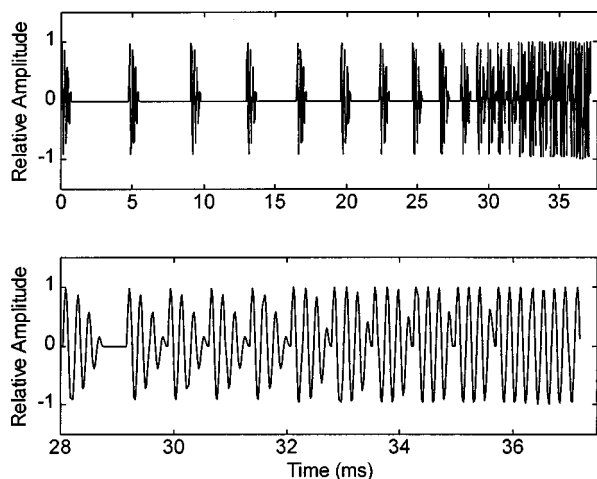


FIG. 1. A simulated signal representing the graded structure of the vocalizations. The bottom panel is a close-up view between 28 and 37 ms. From 0 to 29 ms, the signal is comprised of discrete, exponentially damped pulses and the inter-pulse interval is gradually reduced to 0.0 ms. From 29 ms to 36 ms the damping function is gradually reduced until a continuous sinusoid remains.

gate in another portion of the tank. The minimum distance between the animal being recorded and the other animal behind the gate was approximately 30 m. The trainer turned the animal on its back in order to get the melon (forehead region of the animal from which it is believed sound emanates) underwater and positioned the animal so that its head was about 1–2 m away from the hydrophone. Because the amplitude of the signals was higher in this upside down position, this procedure ensured very high signal-to-noise ratios as well as confidence concerning the identity of the animal making the sounds.

All sounds were recorded with a Sony Digital Audio Tape-recorder (DAT), TCD-D8, which uses a sampling rate of 44.1 kHz, for a frequency bandwidth to 22 kHz. A custom built hydrophone (W. Au) with a sensitivity of -185 dB and a bandwidth to 200 kHz was used for all recordings. Using a quasi-random procedure, 500 vocalizations were chosen for analysis and digitized onto a PC computer using a Sound-Blaster 32 sound card.

Pseudorca produce ultrasonic vocalizations (Au *et al.*, 1995; Kamminga and van Velden, 1987; Thomas *et al.*, 1988). To test whether higher-frequency signals were missed due to the relatively low bandwidth of the DAT recorder, broader band recordings were made using a RACAL reel-to-reel recorder at a tape speed of 30-in.-per-second, resulting in a bandwidth of 170 kHz. One additional recording session was made with this equipment.

II. GRADED MODEL

Through visual inspection of the waveforms, the following model was developed to describe how the structure of the vocalizations is graded. Clicks and burst-pulse vocalizations can be modeled as exponentially damped, brief sinusoidal pulses spaced over time. Figure 1 shows a computer generated signal that is comprised of exponentially damped, 5-kHz pulses. The figure begins arbitrarily with 5 ms between each pulse. The time interval between each pulse is reduced

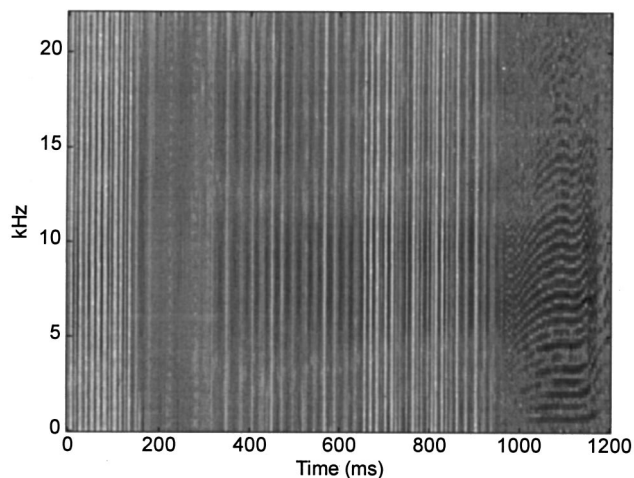


FIG. 2. The 256-point spectrogram of example 1 showing a vocalization grade from a click train to a burst-pulse sound. The horizontal banding between 1000 and 1200 ms is characteristic of rapidly pulsed signals.

gradually until there is no interval between the pulses (see Fig. 1, bottom panel). The signal is graded as a function of time between pulses, where the minimum interval between pulses is zero milliseconds. At an interval of zero milliseconds, the signal is pulsed in that it consists of damped sinusoids that regularly oscillate. It is continuous in that there is no interval in the vocalization without energy. From there, the signal grades into a “whistle” (i.e., continuous sinusoid) as a function of the degree of damping on the sinusoid, eventually reaching a continuous, nondamped sinusoid.

Visual examination of the waveforms of the false killer whale vocalizations revealed that there were vocalizations that represent each stage of the model. Moreover, some vocalizations gradually modulated through each stage of the model. Examples of such vocalizations are described below.

A. Example 1

The 256 point spectrogram of the first example is shown in Fig. 2. This example demonstrates the grading that occurs from pulses that are spaced apart to pulses that have no inter-pulse interval. This vocalization covers the traditional categories of click trains and burst-pulse sounds. The beginning of the vocalization is characterized by pulses with a maximum inter-pulse interval of 12 ms. The intervals gradually reduce in length. At 900 ms into the vocalization the pulses are approximately 5 ms apart. At 1000 ms they are about 2 ms apart and at 1100 ms there is no inter-pulse interval (see Fig. 3). The aural and spectrographic appearance of the vocalization changes dramatically from the beginning to the end. However, the only change in the waveform is the time between each pulse.

B. Example 2

This example of a pulse train (Fig. 4) demonstrates how the degree of damping changes on the pulses as they begin to approximate a sine wave. The waveform at 420 ms shows that the vocalization has approximately 2 ms between each pulse. At 1330 ms there is no interval between the pulses and at 1460 ms the damping function reduces and the waveform

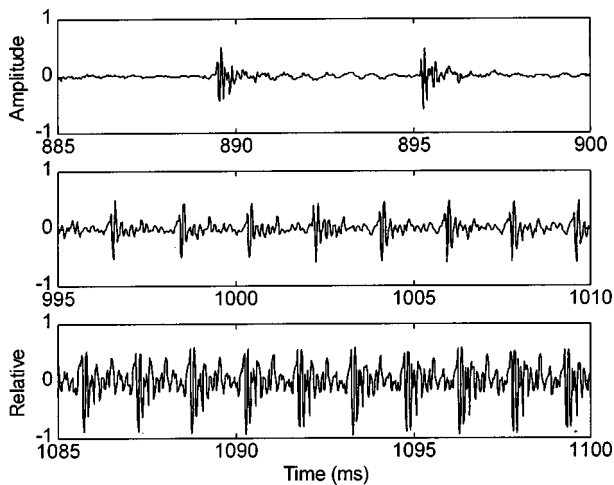


FIG. 3. Close-ups of the waveform of example 1 at three different locations in the vocalization. The three panels show the inter-pulse interval gradually reduce from approximately 5 ms in the top panel to 0.0 ms in the bottom panel.

begins to approximate a sinusoid. This vocalization resembles the model (Fig. 1) between 28 ms and 35 ms.

C. Example 3

The final example is a vocalization that appears aurally and spectrographically to be a whistle (see Fig. 5, top panel). In general, the spectrograms of false killer whale whistles look similar to whistles produced by other odontocete species (e.g., Herzing, 1996; Sjare and Smith, 1986; Sayigh *et al.*, 1990; Tyack, 1986). The peak frequency of the vocalization ascends from approximately 4 kHz to 7 kHz. The 128 point spectrogram shows a relatively narrow-band signal. A close examination of the waveform (Fig. 5, bottom panel) of the whistle, however, reveals that it has pulsed components. Between 8 and 16 ms the whistle is comprised of a series of

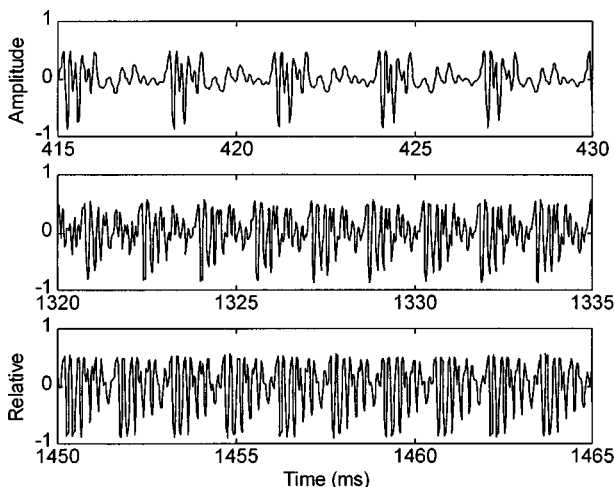


FIG. 4. The waveform of example 2 at three different locations. The top panel shows discrete pulses with an inter-pulse interval of approximately 3 ms. In the middle panel the inter-pulse interval is 0.0 ms. The damping reduces in the bottom panel and the signal is beginning to approximate a continuous sinusoid.

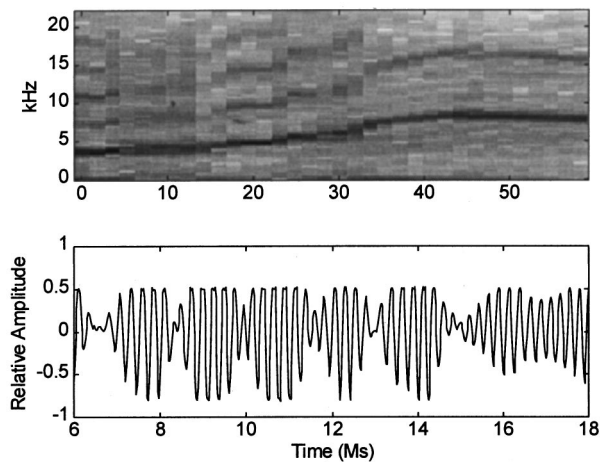


FIG. 5. The 128-point spectrogram (top panel) and a close-up of the waveform of example 3. There is a pulsed component to the signal between 6 and 16 ms shown in the bottom panel.

nondamped sinusoidal pulses (i.e., regular oscillations in amplitude) and looks very similar to the waveform of the model at 34 ms (see Fig. 1).

III. ANALYSIS PROCEDURE

A. Duty cycle

In order to describe the structure of the vocalizations with respect to the above model, a short-time duty cycle measure was developed in an attempt to characterize the shape of the waveforms and thus characterize changes in signal type. Duty cycle refers to the percentage of time that a signal is “on” versus the total length of the signal. At one end of the extreme are vocalizations comprised of widely spaced pulses (e.g., a click train) corresponding to a low duty cycle. That is, the pulses are very brief as compared to the interval between pulses. As the interval between pulses decreases, duty cycle increases until there is no interval between pulses: the vocalizations begin to approximate a constant sine wave and correspondingly have a high duty cycle. At this end of the extreme, the vocalizations sound whistle-like.

All signals were compared to a nonamplitude modulated sine wave. The duty cycle measure was calculated by taking the rectified digital waveform and converting each point to a percentage of the maximum value in 512-point “windows” (about 11 ms for a 44.1-kHz sampled signal). The average of these percentages was calculated and normalized to a sine wave value for the calculation. Therefore, if the signal was an unmodulated sine wave (“tonal”), it received a value very close to 1.0. A threshold was used such that windows that did not surpass the threshold received a value of 0.0. In this way it was possible to represent inter-pulse intervals that were longer than 512 points.

The duty cycle measurement took into account the degree to which the waveform of a signal deviated from an unmodulated sine wave. Signals received values between 1.0 (unmodulated sine wave—a “perfect” whistle) and 0.0 (no signal). Values between 1.0 and 0.0 reflected the degree of

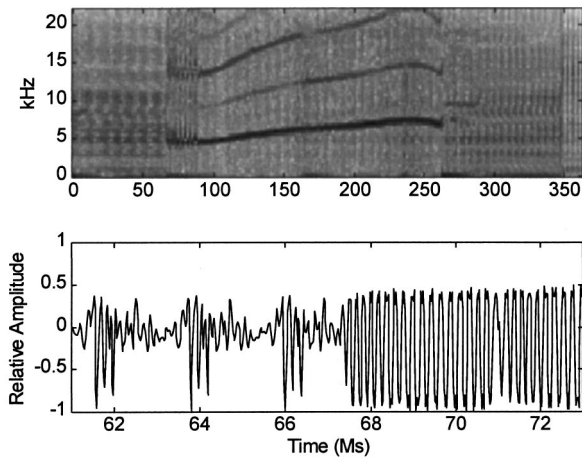


FIG. 6. The 128-point spectrogram of the first example (top) and a close-up view of the transition between the pulses and the whistle occurring at approximately 67 ms.

pulsing. For example, a typical click train might have a value of approximately 0.05, a typical burst-pulse signal between 0.3 and 0.6, and a typical whistle-like signal may have a value of 0.8 or greater.

There were additional circumstances in which values less than 1.00 could have arisen. For example, if the duty cycle measure was applied to a continuous sine wave that changed amplitude, values less than 1.00 would occur. Each point of the signal was expressed as a percentage of the maximum of the signal. The measure assumed that the overall amplitude of the signal was not changing. For this reason, choosing an appropriate window size was important. The 512-point window size was chosen after analyzing the waveforms of many vocalizations with changes in amplitude. In general, the overall amplitude of the vocalizations changed little in the 512-point window.

B. Peak frequency

Signals were also analyzed for peak frequency (i.e., the frequency with peak energy). A 512-point window was used (to correspond to the duty cycle window) and peak frequency was calculated. Thus each vocalization was characterized by changes in duty cycle and peak frequency.

IV. RESULTS

A. Analysis procedure

The following examples demonstrate how various vocalization types were represented by the analysis procedure. Vocalizations that changed waveform structure were common. The first vocalization has multiple sound types (whistle and burst-pulse) and is included to demonstrate how the duty cycle measure is able to represent changes in signal type over time. The second example is a click train. The examples are not meant to represent all of the observed signal types; the emphasis of the demonstration is on the performance of the analysis procedure.

1. Example 1

The first example (Fig. 6) is a whistle preceded and fol-

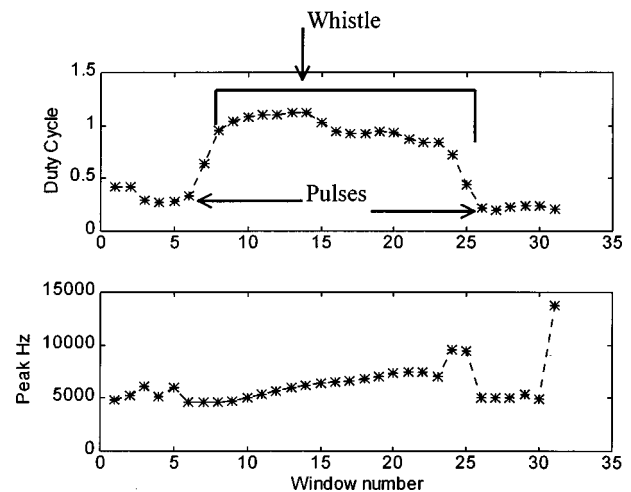


FIG. 7. Plots of the characterization vectors for the vocalization shown in Fig. 6. Duty cycle is shown in the top panel and peak frequency in the bottom panel. The initial and final duty cycle values are approximately 0.35, corresponding to the pulse trains. The values of close to 1.00 correspond to the whistle portion of the vocalization.

lowed by pulsed sounds. The inter-pulse intervals of the pulsed components vary but are approximately 2–3 ms. The pulsed portion of the vocalization (top panel) extends from approximately 0 to 65 ms and from 260 to 360 ms. The whistle shows as the series of dark lines beginning at approximately 65 ms. The bottom line represents the fundamental frequency of the whistle and the lines above it represent harmonics. Before and after the whistle are the pulse trains.

Although the vocalization is comprised of several sound types, it is treated as a single vocalization because there are no “breaks”—the transition between sound types is immediate. Figure 6, bottom panel, is a close-up view of the waveform showing the transition from a pulse train to a whistle that occurs at approximately 67 ms.

Figure 7 shows the measurement values for this vocalization. The top panel represents duty cycle values. The x -axis represents each analysis window and the y -axis represents duty cycle value. Visual examination of these values gives an easily interpretable representation of how signal type is changing over time. The whistle is clearly seen as values approaching 1.0. The pulse trains before and after the whistle are represented by the lower duty cycle values of approximately 0.35. The bottom panel of Fig. 7 represents peak frequency as it changed throughout the vocalization.

2. Example 2

The second example is a pulse train that is approximately 900 ms long. In the spectrogram display, each click is clearly visible as a vertical line (see Fig. 8). The duty cycle display, in Fig. 9, shows the relatively low values (less than 0.10). The zeros result from windows that did not exceed the threshold and represent inter-pulse intervals.

B. High-frequency recordings

Pseudorca also produce ultrasonic vocalizations (e.g., Au *et al.*, 1995). The ultrasonic vocalizations observed by Au *et al.* (1995) were produced in an echolocation task in

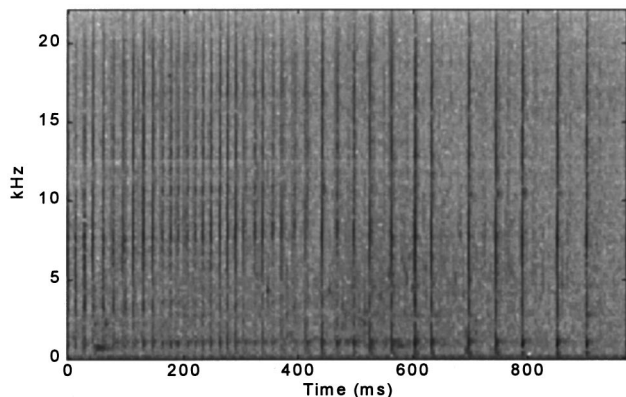


FIG. 8. The 256-point spectrogram of example 2 showing the inter-pulse interval gradually increasing.

which the animal had to detect small differences in the wall thickness of a target. The maximum peak frequency observed in that experiment was approximately 100 kHz. The DAT recorder used in this study has a bandwidth limited to 22.05 kHz. Therefore, it was necessary to evaluate whether higher-frequency vocalizations were being missed with the DAT recorder.

A total of 5 min of recordings made with the RACAL reel-to-reel recorder (bandwidth to 170 kHz) were analyzed for peak frequency. The analysis did not consider frequencies below 3.5 kHz in order to reduce tank noise. Each vocalization was analyzed in 512 point windows and the maximum value of the power spectrum was calculated. A total of 1% of peak frequencies were outside the 22-kHz range of the DAT recorder (see Fig. 10). The maximum peak frequency recorded with the RACAL was 50 kHz and was a pulse in a click train. Additionally, vocalizations with peak frequencies below 22 kHz often had ultrasonic harmonic components, and these components changed in parallel with the sonic peak frequencies. It appears that in this context ultrasonic vocalizations are rare. The observance of few vocalizations having peak frequencies above the limit of the DAT recorder suggests that the following discussion of peak frequency is valid.

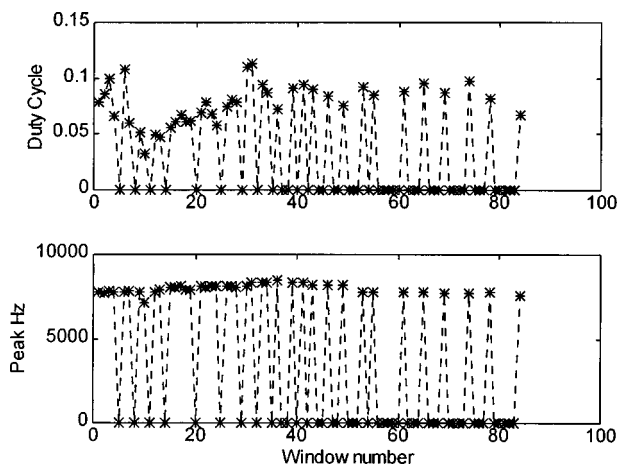


FIG. 9. The duty cycle (top panel) and peak frequency values for example 2. The zeros correspond to inter-pulse intervals.

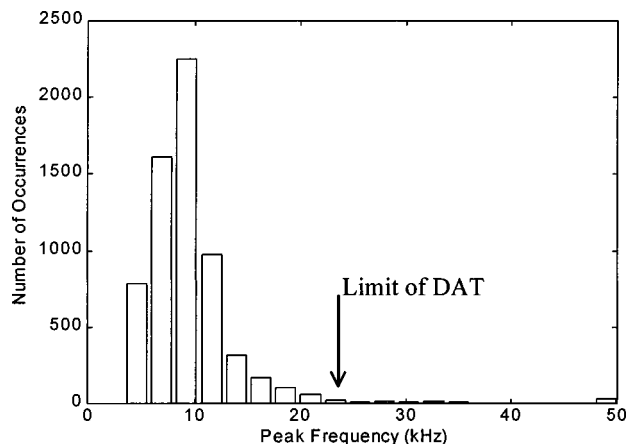


FIG. 10. The distribution of peak frequencies recorded with the RACAL reel-to-reel recorder (bandwidth to 170 kHz). Very few (1%) of the values are above the limit of the DAT recorder.

C. Peak frequency

Peak frequencies ranged from a low of 3 kHz (the minimum frequency considered in the analysis) to a maximum of 22 kHz (the frequency limit of the DAT). The average starting peak frequency for all 500 vocalizations was 6212 Hz (s.d.=2651 Hz). The average ending frequency was 7834 Hz (s.d.=2843 Hz). A two-sample *t*-test comparing the average starting and ending frequency revealed a significant difference, $t(499) = -10.59$, $p < 0.0001$. The trend for the vocalizations to begin at a low frequency and end at a higher frequency may have resulted from the frequent occurrence of short duration, ascending whistle vocalizations. Although whistles showed a variety of frequency modulations, the most common was an ascending whistle.

D. Duty cycle

Values on the duty cycle measure ranged from a minimum of 0.0 (inter-pulse intervals) to a maximum value of 1.31. Values above a score of 1.00, the theoretical limit of the scale, were not expected. A total of 3% of the values were above 1.00. Upon closer inspection, values greater than 1.00 seemed to result from distorted signals (possibly due to one of the recording instruments being overdriven).

A significant negative correlation (-0.49 , $p < 0.0001$, see Fig. 11) was found between the average peak frequency for each vocalization and the average value on the duty cycle measure (removing duty cycle values greater than 1.00 resulted in a correlation of -0.48). Low duty cycle vocalizations such as click trains tended to be higher in peak frequency than higher duty cycle vocalizations such as whistles. Whistles tend to be lower in frequency than pulses (e.g., Au, 1993; Popper, 1980). Employing the duty cycle measure revealed a direct linear relationship between waveform structure and peak frequency; peak frequencies drop as the vocalizations shift from pulse trains to whistles. Models of odontocete sound production must take this finding into account.

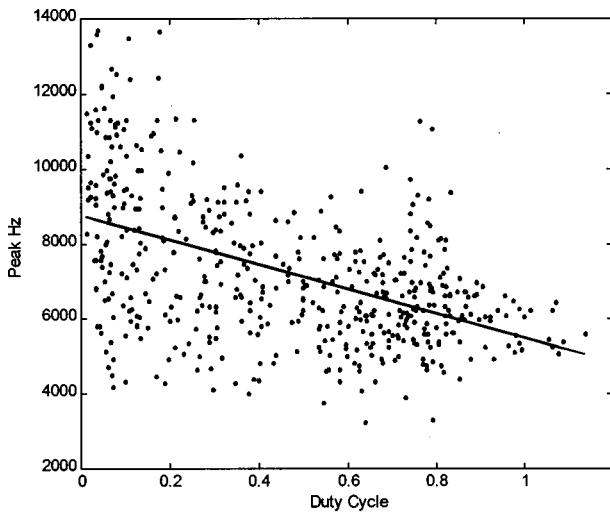


FIG. 11. The distribution and regression line ($r = -0.49$) of the relationship between average duty cycle and average peak frequency showing that as duty cycle increases peak frequency tends to decrease.

E. Duration

The duration of each vocalization was measured to the nearest millisecond. The average duration was 506 ms (s.d.=761 ms). Longer duration vocalizations tended to be pulse trains, evident in a significant negative correlation between the average duty cycle for each vocalization and duration (-0.37 $p < 0.0001$, see Fig. 12). This means that as duty cycle was lower, the average duration was longer, implying that there may be a limited air supply for each vocalization. This supply can be released to drive the production mechanism gradually, over a longer time in the form of pulse trains or more quickly in the form of whistles.

F. Graded signals

1. Distribution of duty cycle values

One way to examine whether the vocalizations are graded is to observe the frequency distribution of duty cycle

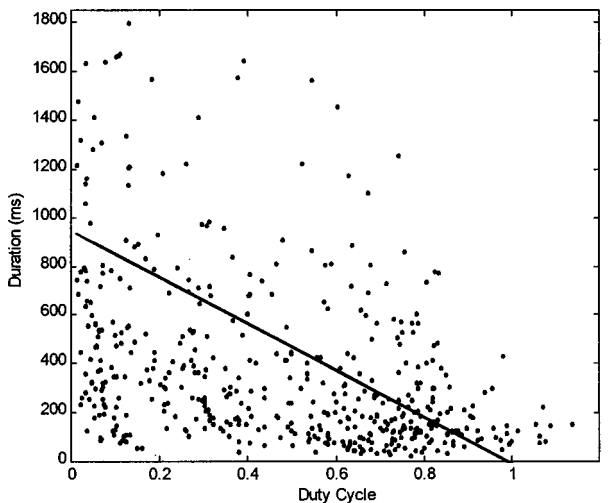


FIG. 12. The distribution and regression line ($r = -0.37$) of the relationship between duration and average duty cycle showing that the duration of the vocalizations tends to decrease with increasing duty cycle values.

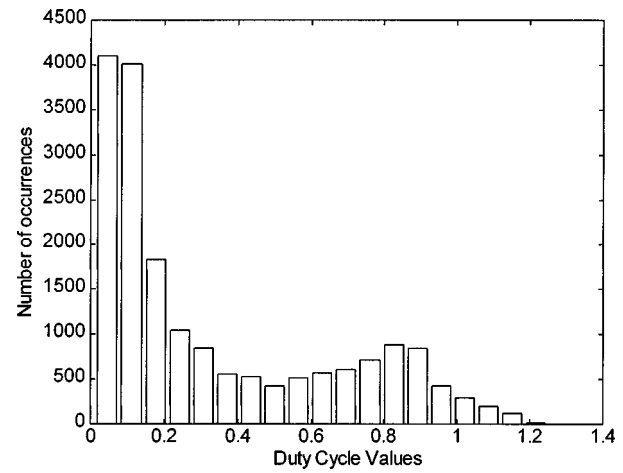


FIG. 13. The distribution of nonzero duty cycle values. There are many low values corresponding to pulse trains. The values above 1.0 appeared to result from distorted signals.

values. The values on this measure reflect signal *type* (e.g., click train, burst-pulse, whistle) by comparing each vocalization to a sine wave. If discrete signal types exist, they should be reflected as discontinuities in the values obtained on this measure.

The total of 18 515 nonzero duty cycle values were distributed throughout the entire range of possible values, indicating a graded structure with whistles and clicks being at opposite ends of a continuum (see Fig. 13). The distribution of duty cycle scores shows many (53%) low values (< 0.20) and many (14%) high values (> 0.80). These values roughly correspond to pulse trains and whistles, respectively.

G. Maintaining peak frequency

Many vocalizations contained more than one signal type. For example, a vocalization could begin as a whistle and switch to a pulse train. Approximately 10% of the vocalizations were whistles that switched suddenly to a pulse train. The peak frequency of many of these vocalizations was maintained across this switch in signal type (see Fig. 14). The spectrogram clearly shows the whistle ending and the pulse train beginning at approximately 100 ms. Figure 14 (bottom panel) also shows a plot of peak frequency where the line represents the peak frequency of the whistle and the asterisks represent peak frequency of the pulses. The peak frequency of the end of the whistle is 6.1 kHz and peak frequency of the first pulse is 6.0 kHz. A two sample t -test comparing the mean frequency of the whistle ($M = 5.32$ kHz, s.d.=0.18) and the mean frequency for the pulses ($M = 5.52$ kHz, s.d.=0.09) revealed no significant difference, $t(9) = -0.46$, $p < 0.33$. In other words, there was no change in peak frequency when switching from the whistle to the pulses.

Figure 15 shows the waveform of a transition between a whistle and a pulse train. The first pulse starts at the end of and is “attached” to the whistle waveform. The maintenance of peak frequency across changes in signal type, when considered along with the evidence of a graded vocal structure, strongly suggests that a single mechanism is the source of both pulsed and continuous signals.

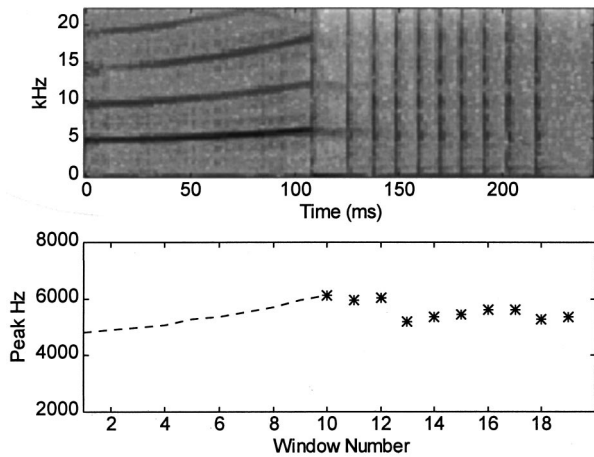


FIG. 14. The 128-point spectrogram (top) and a graph of peak frequency (bottom) of a vocalization switching from a whistle to a click train. The line represents peak frequency of the whistle and the asterisks represent peak frequency of the pulses in the click train. Peak frequency is maintained across the change in signal type.

H. Independent/simultaneous signals

The available evidence suggests that a single mechanism is able to produce both pulsed and continuous waveforms. However, there appear to be vocalizations comprised of “independent” and simultaneous signal types. There are numerous reports of other dolphin species producing simultaneous whistles and clicks (e.g., Lilly and Miller, 1961) and it appears that pseudorca do the same. Figure 16 shows an example of a concurrently produced whistle and pulse train. On the spectrogram (top panel), the whistle and pulses begin at different times. The bottom panel shows a disparity in amplitude between the two signal types with the lower amplitude portion of the waveform corresponding to the whistle; a higher amplitude pulse occurs at approximately 301 ms. It is difficult to explain the co-occurrences in signal type without the attribution of two production mechanisms, given that many of these co-produced vocalizations begin and end at different times and often have different amplitudes. We discuss this apparent contradiction later.

V. GENERAL DISCUSSION

The two false killer whales recorded in this study vocalized often and produced a wide variety of sounds. Most of

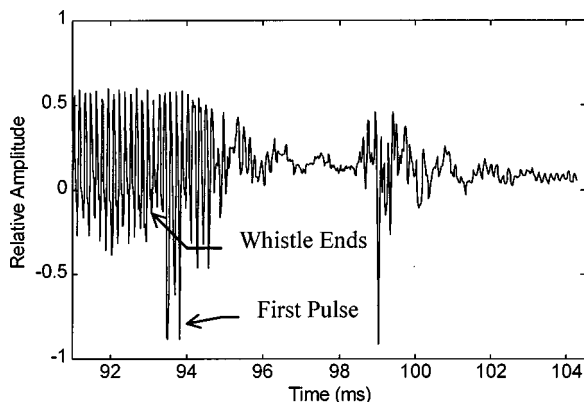


FIG. 15. An example of a whistle to click transition. The first pulse occurs at the very end of the whistle (approx. 93 ms).

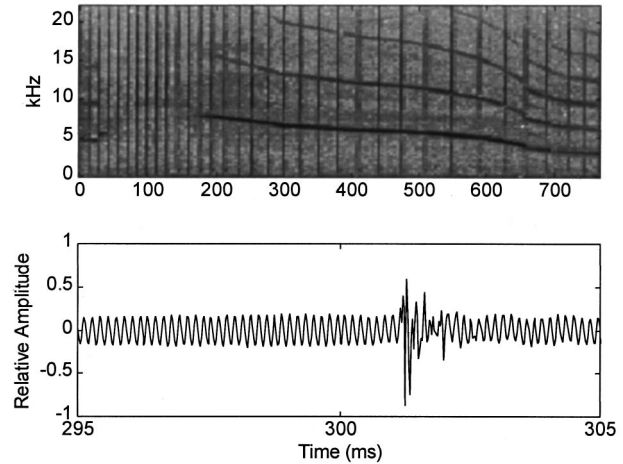


FIG. 16. The 256-point spectrogram (top) and a close-up of the waveform around 300 ms of a click produced simultaneously with a whistle. The click train and whistle begin at different times and have different amplitudes.

the vocalizations fit into the traditional categories of whistles, burst-pulse sounds, and click trains. However, based on detailed visual analyses of the waveforms, a better model does not recognize discrete categorical differences in signal (i.e., waveform) type. The vocalizations are graded; that is, they lie along a continuum with trains of discrete, exponentially damped sinusoidal pulses at one end, and continuous sinusoidal signals at the opposite end. Therefore, the traditional categories (e.g., pulse trains, burst-pulse sounds, whistles) should not be viewed as distinct, but instead, should be viewed as occupying locations along a continuum from widely spaced pulses to a continuous sinusoid.

Pulse trains are graded as a function of the interval between pulses where the minimum interval between pulses is 0.0 ms. The transition from pulse trains with no inter-pulse interval to a whistle can be modeled by gradations in the degree of damping. There were many examples of vocalizations that were gradually modulated from pulse trains to whistles, encompassing the entire continuum. There were also vocalizations that showed sudden shifts in signal type—for example, switching immediately from a whistle to a pulse train.

Because of the changes in signal type, it was important to have a measure that could objectively represent the location of a vocalization along the continuum. The short-time duty cycle measure seemed to be effective in this capacity. Values on the duty cycle measure occupied the entire range from zero to one, which seems to reflect the graded structure of the vocalizations. It was possible, however, to identify modal duty cycle values. The majority of values (53%) were below 0.20. These vocalizations subjectively sounded like click trains. There were also many duty cycle values (14%) above 0.70, which subjectively sounded like whistles.

Correlations between behavioral state and vocalizations have often been noted in both wild and captive animals and in a variety of dolphin species (e.g., Ford, 1989; Herzing, 1996; Morton *et al.*, 1986; Norris *et al.*, 1994). Describing the behavior of Hawaiian spinner dolphins, Norris *et al.* (1994) remarked, “One hears a quiet ‘muttering of clicks’ during (rest)...” (p. 179). They observed that as activity level

increased, the number of whistles and burst-pulse signals increased. There may be a strong correlation between the duty cycle values of the vocalizations and the activity level of the Hawaiian spinner dolphin. Anecdotally, a similar trend was observed with the false killer whales used in this study. At the beginning of each recording session, they were generally much more active and produced many whistles and rapidly pulsed vocalizations. Toward the end of each recording session, after resting on their back for 20–30 mins, the animals were much quieter and generally emitted only widely spaced clicks.

All of the recordings for this study were made in a single behavioral context: the animals were resting on their backs. It may be that modal duty cycle values shift as a function of behavioral state. For example, if the animal were highly active/aroused, the proportion of high duty cycle values might increase. If the animals were at rest, possibly at night, there would likely be many more low value signals.

Although the acoustic structure of the vocalizations is best modeled as lying along a continuum, this does not mean that the animals are perceiving them as such. In human speech perception, for example, continuous changes in voice-onset time are perceived discontinuously (e.g., Cutting and Rosner, 1974). Dolphins, in general, have a hearing system that is adapted for higher frequencies and greater time resolution than humans (Ketten, 1992). While false killer whales probably do not perceive their own vocalizations as humans do, categorical perceptual processes may be occurring.

The observation of the entire continuum (click train to whistle) in single vocalizations suggests that a single production mechanism can potentially produce all of the observed signal types. Additionally, the maintenance of peak frequency in single vocalizations across abrupt changes in signal type (e.g., whistle → click train) is further evidence for a single mechanism. However, seemingly independent signal types such as whistles and clicks commonly occur simultaneously. The two signal types would often begin and end at different times and exhibit differential changes in amplitude. Such occurrences are difficult to explain without invoking at least two production mechanisms.

The conflict between the likelihood that a single production mechanism can produce everything from click trains to whistles and the apparent need to posit two mechanisms may be resolvable. The sound production system in dolphins may be analogous to that found in birds in that there may be two production sites. The syrinx, the sound-producing organ in birds, is located at the junction of the two bronchi. This means that there are two potential sound sources, one in each bronchus (Catchpole and Slater, 1995). In some species (e.g., canaries) there is considerable lateralization where one side of the syrinx produces the majority of sounds (Nottebohm, 1971). In other species (e.g., catbirds), both sides contribute equally, each producing its own unique repertoire of sounds (Suthers, 1990).

Odontocetes have two separate nasal passages. Possibly there is a sound producing mechanism in each of them. Cranford *et al.* (1996) proposed that the likely mechanism for click generation is an oscillator driven by an air stream mov-

ing through the nasal passage. The air stream apparently passes between the so-called monkey lip/dorsal bursa (MLDB) region and causes the monkey lips to open and slap together. Cranford *et al.* suggest that pulse repetition rate could be regulated by such factors as air pressure and/or muscle tension on vibratory elements. Once muscle tension reaches a critical value, the monkey lips might operate harmonically and produce whistle-like sounds. There is a pair of monkey lips in each nasal passage, meaning that there are two potential sound producing mechanisms (Cranford *et al.*, 1996). Additionally, delphinids have moderately asymmetric MLDBs, suggesting that one side may be favored for high-frequency vocalizations and the other for low-frequency vocalizations: "...if the duration of the vibratory event and the event location (along the length of the monkey lips) are under voluntary control of the dolphin, then a rich variety of possible combinations could help explain the varied repertoire of signals recorded from delphinids" (Cranford *et al.*, 1996, p. 275).

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¹The use of the term "vocalization" in this paper is not meant to imply that vocal folds are necessarily the mechanism producing the sounds. It is used as a general term for dolphin sounds that are internally generated via air flow in the head region.

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