The perception of complex tones by a false killer whale (*Pseudorca crassidens*)

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(Received 7 July 2006; revised 18 December 2006; accepted 2 January 2007)

Complex tonal whistles are frequently produced by some odontocete species. However, no experimental evidence exists regarding the detection of complex tones or the discrimination of harmonic frequencies by a marine mammal. The objectives of this investigation were to examine the ability of a false killer whale to discriminate pure tones from complex tones and to determine the minimum intensity level of a harmonic tone required for the whale to make the discrimination. The study was conducted with a go/no-go modified staircase procedure. The different stimuli were complex tones with a fundamental frequency of 5 kHz with one to five harmonic frequencies. The results from this complex tone discrimination task demonstrated: (1) that the false killer whale was able to discriminate a 5 kHz pure tone from a complex tone with up to five harmonics, and (2) that discrimination thresholds or minimum intensity levels exist for each harmonic combination measured. These results indicate that both frequency level and harmonic content may have contributed to the false killer whale's discrimination of complex tones. © *2007 Acoustical Society of America.* [DOI: 10.1121/1.2436640]

PACS number(s): 43.80.Lb [WWA] Pages: 1768–1774

I. INTRODUCTION

Complex tones are prevalent throughout the environment, from musical instruments to bird songs to sea lion pup calls to the human language. The perception of harmonics and complex tones has been a contentious and well-documented phenomenon in human auditory research. However, very limited research has analyzed this ability in other vertebrate species (Ward Tomlinson and Schwartz, 1988).

The evidence that nonhuman vertebrates possess the capability to discriminate individual components of a complex tone has been accumulating (Ward Tomlinson and Schwartz, 1988). The research thus far has primarily focused on terrestrial species. While no experimental data were collected about the perception of complex tones by a marine mammal species, there is a significant amount of information describing the auditory sensitivities (Nachtigall *et al.*, 2000) and acoustic production systems of odontocetes (Au, 1993; Au *et al.*, 2000).

There are three categories of sounds that odontocetes make. The first includes echolocation sounds of high intensity, high frequency, high repetition rate, and very short duration (Au *et al.*, 2000). The second category of odontocete sounds is comprised of pulsed sounds. Burst pulses are generally very complex and fast, with frequency components sometimes above 100 kHz and average repetition rates of 300 per second.

The final category of odontocete sounds is the narrowband, low frequency, tonal whistles (Caldwell *et al.*, 1990; Au *et al.*, 2000). With most of their energy below 20 kHz, whistles have been observed with an extensive variety of frequency patterns, durations, and source levels, each of which can be repeated or combined into more complex phrases (Tyack and Clark, 2000). The categorization of odontocete whistles can be subjective and detailed, and several differences are observed between habitats, species, and phylogenetic relationships. The classification of signature whistles is based on the frequency contours of the fundamental component. Whistles have been characterized based on general contours, such as whistle slope, downsweeps, and upsweeps (Bazua-Duran and Au, 2001). There also seems to be a common correlation that animals with longer length produce whistles with lower maximum frequencies (Ketten, 2000). Resident killer whales produce whistles that are more complex than most delphinid species, with longer durations and greater frequency modulations (Thomsen *et al.*, 2001). This complexity was suggested to have a function for close-range interactions. Beluga whales were observed to increase the high frequency components, such as the amplitude of their whistles with increasing depth (Ridgway *et al.*, 2001). The change in depth may also have changed the air flow and density for the sound production of the whistles. The interesting result was that hearing thresholds did not change with depth despite the changes in whistle production.

Whistles recorded from odontocetes in both laboratory and wild environments have an important role in odontocete social communication as individual signature calls or calls to synchronize group behaviors (Caldwell and Caldwell, 1965; Caldwell *et al.*, 1990; Tyack and Sayigh, 1997). Signature whistles have been observed to facilitate group cohesion (Janik and Slater, 1998), especially when mothers were separated from their calves and possibly facilitating their reunion (Caldwell *et al.*, 1990; Sayigh *et al.*, 1990). Signature whistles were recorded from bottlenose dolphins exclusively in an isolation context, additional evidence for the functional importance of group cohesion (Janik and Slater, 1998). Sig-

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nature whistles were also documented to contain context-related information and not only identification during discrimination tasks (Janik *et al.*, 1994).

However, some documented evidence disputed the signature call hypothesis, revealing a shared whistle type rather than distinct individual calls (McCowan, 1995; McCowan and Reiss, 1997; 2001). The limitations and discrepancies for categorization methods of whistles may be a significant factor contributing to contrasting measurements and perspectives (Janik, 1999).

Observations of wild populations of dolphins have included signature whistles that were correlated with coordinated group behaviors, such as foraging, feeding, courtship, and mating (Herzing, 2000). One proposed social role of whistles was that of matching interactions (Janik, 2000). Bottlenose dolphins were observed to use learned whistles to respond to conspecifics with the same whistle with both aggressive and affiliative interaction. A recent study suggested that the harmonic structure of whistles could provide an acoustic direction cue to aid the coordinated movement of a group of Hawaiian spinner dolphins (Lammers and Au, 2003). It is advantageous for species that are highly mobile to use cohesion calls or signals to maintain their association with the larger group, assuring recognition with specialized signals.

Despite the rich variety of tonal signals produced by whistling odontocetes, little is known not only about what behavioral and ecological information is perceived from whistle signals, but also about how the animals hear the complex sounds. Determining the relative contribution of each partial in the harmonic signals may clarify how these sounds are identified and resolved by odontocetes.

The echolocation and hearing systems of the false killer whale are adapted for efficient perception of the underwater environment (Madsen *et al.*, 2004; Thomas *et al.*, 1988; 1990; Thomas and Turl, 1990). The vocalizations produced by false killer whales include all three types mentioned earlier, some of which occur in distinct groups while other occurrences are on a gradual continuum transitioning from pulses that are widely spaced apart to whistles that are continuously sinusoidal (Murray *et al.*, 1998). However, no experimental evidence exists regarding odontocete detection of complex tones or their discrimination of harmonic frequencies. Therefore, the objectives of this research project were: (1) to examine the ability of a false killer whale to discriminate pure tones from complex tones, and (2) to determine the minimum intensity level of the harmonic tone required for the whale to discriminate a fundamental frequency and a fundamental frequency plus harmonics.

II. METHODS

A. Animal subject

This adult female, false killer whale named Kina was the subject of a variety of echolocation and audiometric experiments (Supin *et al.*, 2004; 2005; 2003; Thomas *et al.*, 1990; Yuen *et al.*, 2005), and since 1987, she resided at the Hawaii Institute of Marine Biology's Marine Mammal Research Program located in Kaneohe Bay, Oahu, HI. The whale had not previously been trained to perform a passive hearing discrimination task and had no prior deliberate exposure to anthropogenic, complex tone stimuli.

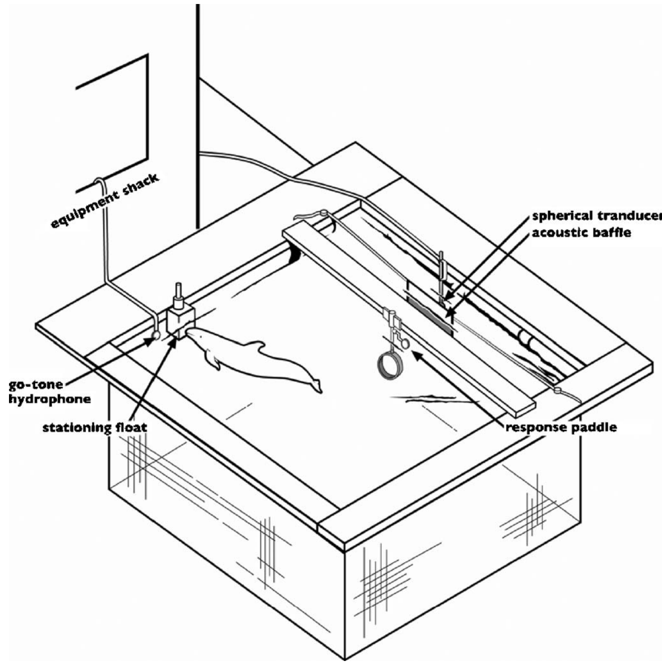

FIG. 1. Experimental configuration for the complex tone discrimination task by a false killer whale.

B. Electronic equipment

Standard pure tones and complex tones were digitally synthesized with a customized LABVIEW 6I program from a desktop computer implemented with a National Instruments PCI-MIO-16E-1 DAQ card. Using an update rate of 500 kHz, each harmonic component of the complex tone was created and attenuated. Each harmonic component of the complex tone could be turned on or off depending on the stimulus combination presented. The signals were then projected through an ITC-1032 60 mm spherical piezoceramic transducer. A Techtronix TDS 1002 Oscilloscope monitored the signal as it was sent from the computer to the transducer. A second ITC 1032 transducer that had a flat frequency response (±3 dB) up to 40 kHz was used to calibrate the frequency levels of the signal as it was received in the center of the hoop where the animal was positioned during the stimulus presentation.

C. Experimental setup

The study was conducted within a 6×9 m floating pen in Kaneohe Bay, off the island of Oahu, HI (Fig. 1). This was the same test pen used for an earlier audiogram methodology comparison (Yuen *et al.*, 2005). This wire-fence enclosed pen was supported by floating buoys under the pen's wooden frame.

The transmitting hydrophone was suspended 1 m below the water surface and secured at the center of one side of the pen deck. An acoustic baffle was made of a 0.6×0.9 m aluminum sheet, covered with neoprene on the side facing the transducer, and was hung at the surface of the water at the half-distance (1 m) between the transducer and the animal. The acoustic baffle reduced the surface reflection of the sound reaching the animal underwater. The animal's hoop was placed 2 m from the sound source, and it was fixed firmly from a wooden beam that stretched across the pen deck. Above the surface of the water, a Styrofoam™ ball response paddle was attached to the wooden beam directly above the hoop. During the intertrial intervals, the animal waited next to a Styrofoam float at the water surface about 3 m away from the hoop, and about 5 m away from the transducer. A small transmitting hydrophone was placed in the water near this float, and projected only a 7 kHz tone. This tone was used to send the animal to the hoop at the beginning of each trial.

D. Discrimination task

There were two phases to this project: a training phase and an experimental phase. During the training phase, the whale was trained to respond to a standard 5 kHz pure tone with a constant amplitude level. The experimental phase included a comparison of the standard pure tone to a complex tone. The fundamental frequency was the same standard pure tone presented in the training phase, and the complex tone included up to five harmonic frequencies. The whale discriminated between the pure tone and the complex tone with different combinations of the components.

During the first part of the training phase, only the standard pure-tone (fundamental only) of 5 kHz was played for a duration of 5 s. The whale was rewarded for touching the response paddle when this tone was played. However, the challenge to this new paradigm was that the whale's only experience with hearing projects required the detection of any sound. She had to be retrained to wait for the entire duration of the tone in order to make a decision.

The next part of the training phase introduced the discrimination task of the standard pure-tone versus a variety of contrasting sounds in order to facilitate the training of the animal to "go" or respond only when the fundamental was heard and to "no-go" or not respond when any other comparison sound was heard. Three different comparison sounds were played: (1) computer-generated white noise, (2) sawtooth shaped tones (as opposed to sine waves), and (3) frequency-modulated tones. The whale was trained to reject these sounds and to remain in the hoop. Novel sounds were first introduced to the animal with very short durations of about 1 s. The duration of each trial was progressively increased as the animal improved her discrimination ability. The whale remained stationed on a target as the duration of the nonpure tone sound gradually increased to 3 s and then to 5 s. After the whale demonstrated that she was able to remain positioned in the hoop while these comparison sounds were played, the target was slowly faded out of each trial until no assistance was necessary for the animal to correctly reject all non-5 kHz comparison sounds.

The third part of training included a discrimination of different pure tones of varying frequencies, starting with higher frequencies that were most different from the standard 5 kHz. Three different frequencies were used: 20, 16, and 11 kHz. When the whale demonstrated that she could successfully discriminate the different pure tones, the final part of the training was to introduce a complex tone with five defined harmonics. Following the establishment of this discrimination, the experimental phase and data collection began.

During the experimental phase, the sequence of the trials was based on the Gellermann series, preventing more than three consecutive trials of the signal present or absent (Gellermann, 1933). A sequence with only half of the trials with a pure tone and the other half with a complex tone prevented response bias of the whale as well as any prediction of trial order.

The whale responded following a go/no-go modified staircase procedure. The whale was trained to remain in an underwater hoop with her pectoral fins touching the hoop at the signal of the trainer. When stationed correctly, the standard, 5 kHz pure tone was transmitted underwater. If the whale heard this tone, she exited the hoop and used her head to go and touch a response paddle suspended above the surface of the water. If a complex tone was transmitted, she was trained to remain stationed in the hoop and not to touch the response paddle, thereby making a correct rejection, or a no-go response. After 10 s, the trainer whistled to signal to the whale that she performed the correct response. For either correct response, the whale was rewarded with fish.

However, failure to respond to the 5 kHz pure tone was an incorrect rejection and termed a "miss." After the 10 s trial, she was called to the trainer and no reward was given. An incorrect detection, also called a "false alarm," occurred if the whale touched the response paddle when a complex tone was played instead of a 5 kHz pure tone, and no reward was given. Ten warm-up trials began each session and were used to gauge the whale's response behavior. During five of the trials a standard easy pure tone was transmitted according to the Gellermann series, and during the other five a complex tone was presented. The remainder of the session only proceeded if at least 90% of the warm-up trials were correct.

The whale discriminated the 5 kHz pure tone from a 5 kHz pure tone with added harmonics. The presence of the harmonics was the cue to the animal that this signal was different from a pure tone, and that she should not respond. The whale's ability to perceive the difference between pure tones and progressively decreasing components of the complex tones was then examined by selectively lowering the amplitude of the harmonic components. Therefore, after each correct rejection of a complex tone (no-go trial), the intensities of all of the harmonic components were jointly attenuated by 2 dB. After each miss, e.g., perceiving the complex tone as a pure tone, the intensities of the harmonic components were increased by 2 dB. In both instances, the trial was considered to be a "reversal," or a switch from increasing to decreasing intensity and vice versa.

At the beginning of each session, the standard pure tone was set at an intensity level 20 dB above sensation level (SL), and each of the harmonic components was also set at least 20 dB above the relative SL. SL is defined as the sound pressure level (SPL) of a sound above its auditory threshold for the individual (Yost, 1994). As in the *A*-weighted func-

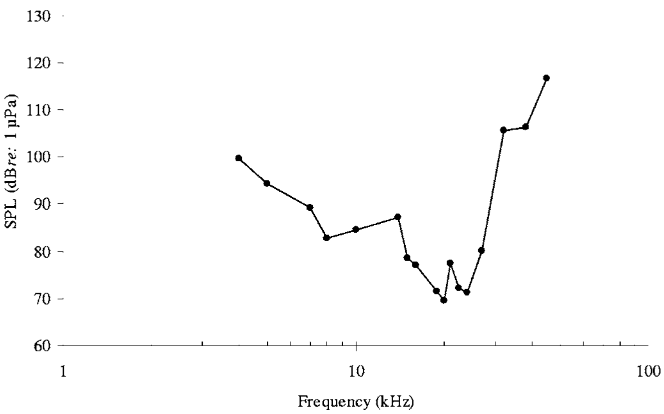

FIG. 2. Average hearing thresholds of three behavioral audiograms of a false killer whale. Thresholds were measured from 2001 to 2003 (from Yuen *et al.*, 2005).

tions used in human audiometrics, the advantage of using SL will eliminate the differences caused by variability in the SPL in an audiogram. The presentation of the data is more comparable and easier to comprehend. SLs reflect how the animal is hearing the relative contribution of the complex tones based on her individual hearing thresholds. The relative intensity levels of each of the SLs for each frequency were calculated from the false killer whale's behavioral audiogram hearing thresholds (Fig. 2) measured from this whale from 2001 to 2003 (Yuen *et al.*, 2005).

The relative intensity levels of each of the harmonic components were reduced equally and simultaneously following each correct trial, until five reversals were completed. The average attenuation value of the five reversals was calculated as the attenuation threshold for that session, and the procedure was repeated until two consecutive sessions occurred with an attenuation reversal average within 5 dB. This final value was calculated to be the amount of attenuation necessary for the whale to discriminate the complex from the pure tone.

When the intensity of each harmonic was too low to hear, the whale most likely heard the fundamental frequency and responded to what she perceived as the standard pure tone. The difference between the fundamental tone and the complex tone represented a threshold for the perception of the combined harmonics within the complex tone.

III. RESULTS

Each of the 13 different combinations of harmonic components resulted in different attenuation threshold values (Table I). Given that all of the combinations were presented to the animal, some of the combinations had only a single harmonic frequency besides the fundamental 5 kHz tone. A comparison of the one-harmonic complex tones is presented in Fig. 3. The discrimination of the 5 kHz pure tone from the set of complex tones that included only one harmonic component (5+10, 5+15, 5+20, and 5+25 kHz), resulted with intensity thresholds that varied considerably, from 6.8 to 29 dB above the relative SL (Fig. 3). There was a substantial difference between the threshold values of these one-harmonic complex tones, with the three higher frequency combinations having thresholds that differed by exactly 3.4 dB. It appeared that these discrimination thresholds worsened, i.e., the intensity threshold above SL increased, as the frequency of the single harmonic increased. The highest frequency harmonic (5+25) was played at the loudest average intensity level above SL (29 dB) in order for the whale to discriminate it from the pure tone 5 kHz. Therefore, as the one-harmonic component increased in frequency, the intensity level or amplitude of the harmonics portion of the complex tone had to be played at louder intensities above sensation level in order for the whale to distinguish them from the 5 kHz pure tone.

This general order reversed however when additional tones were added. When the intensity thresholds for each of the complex tone combinations were arranged in an ascending order, the whale's discrimination of the different complex sounds from the 5 kHz pure tone appeared to follow a similar pattern. The harmonic combinations were sorted into different sets based on the frequency of the first harmonic

TABLE I. Stimulus set of complex tones with a 5 kHz fundamental frequency and up to five harmonics used in the discrimination task by a false killer whale. Also included are the corresponding discrimination thresholds for each complex tone, measured as relative intensity above sensation level (SL).

Complex tone	Frequencies (kHz)	Intensity above SL (dB)
F1+H2	5+10	6.8
F1+H2+H3	5+10+15	12.6
F1+H2+H3+H4	5+10+15+20	9.2
F1+H2+H3+H4+H5	5+10+15+20+25	7.6
F1+H2+H3+H4+H5+H6	5+10+15+20+25+30	6.8
F1+H3	5+15	22.2
F1+H3+H4	5+15+20	14.4
F1+H3+H4+H5+H6	5+15+20+25+30	2.4
F1+H4	5+20	25.6
F1+H4+H5	5+20+25	16.4
F1+H4+H5+H6	5+20+25+30	8.8
F1+H5	5+25	29
F1+H5+H6	5+25+30	18.2

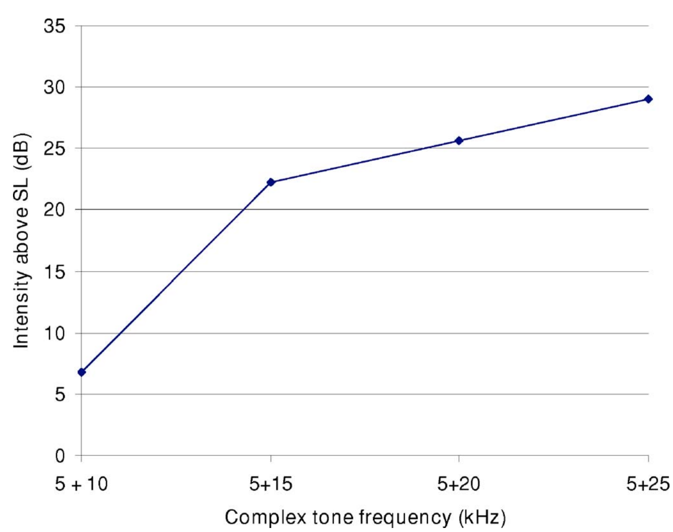

FIG. 3. Graph of the false killer whale discrimination thresholds for complex tones with one harmonic component of various frequencies.

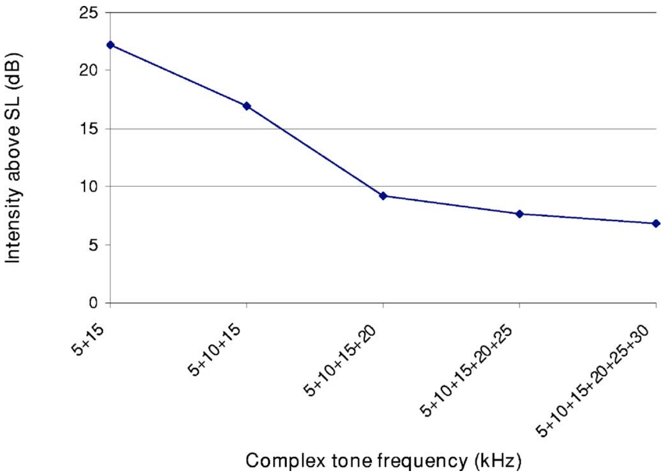

FIG. 4. Graph of the false killer whale discrimination thresholds for complex tones with harmonic components that contained 15 kHz.

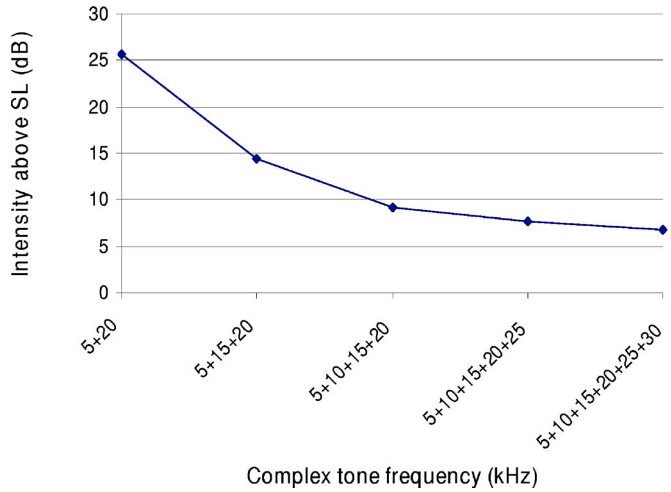

FIG. 6. Graph of the false killer whale discrimination thresholds for complex tones with harmonic components that contained 20 kHz.

added. For example, one set was organized by the harmonic combination of 5+15 kHz (Fig. 4). Each time a harmonic frequency was added to this complex tone, the discrimination ability of the whale improved. When 10 kHz was added, the intensity threshold decreased to 12.6 dB above SL, and then decreased again to 9.2 dB above SL when 20 kHz was added. Finally, as 25 and 30 kHz were added to the complex tone, the threshold again decreased to 7.6 and 6.8 dB above SL, respectively. It appeared that when a second harmonic was added, the discrimination became easier for the false killer whale. With the additional energy from the second harmonic, the complex tone was more discernible from 5 kHz, and the intensity levels were much closer to sensation level. This same pattern was observed as three, four, and five harmonics were added to the complex tone, where the harmonic components of the complex tone were played at lower intensities as more components were added.

Another combination of complex tones measured this effect of adding only the higher harmonics to 15 kHz without the first, lower harmonic of 10 kHz. Once again, the discrimination ability of the whale improved as higher frequencies were added (Fig. 5). The whale discriminated the 5 kHz pure tone from a 5+15 kHz complex tone at a threshold of 22.2 dB above SL. When the next higher harmonic of 20 kHz was added, the intensity threshold fell to 14.4 dB above threshold with a difference of 7.8 dB. Finally, when 25 and 30 kHz were included, the threshold decreased again to 2.4 dB above SL with a difference of 12 dB.

This relationship between the improved discrimination ability of the false killer whale and the increased number of harmonic components of a complex tone was evident in other data sets collected. When additional components were added to the complex tone of 5+20 kHz, the same trend of improved detection resulted (Fig. 6). And in yet another data set with the complex tone of 5+25 kHz, the addition of more harmonic components also resulted in more sensitive discrimination results by the animal (Fig. 7).

IV. DISCUSSION

The results from this complex tone discrimination task demonstrated: (1) that the false killer whale was able to discriminate a 5 kHz pure tone from complex tones with up to five harmonics, and (2) that discrimination thresholds or minimum intensity levels were measured for each harmonic combination. When the various complex tones were played to the false killer whale, she was able to discriminate each of them from a 5 kHz pure tone. Each harmonic combination was projected at different intensity levels above SL, each

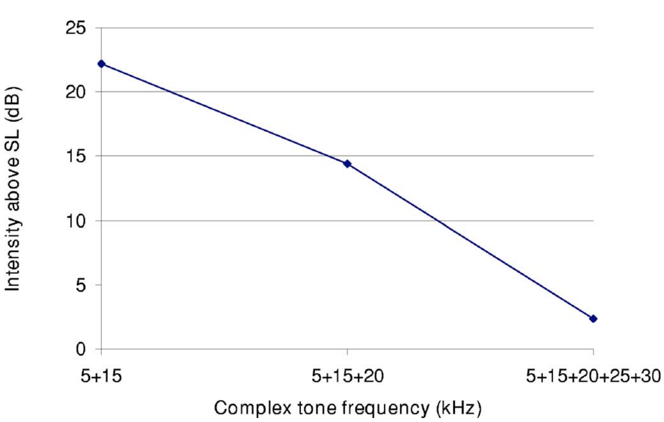

FIG. 5. Graph of the false killer whale discrimination thresholds for complex tones with harmonic frequencies of 15 kHz and higher.

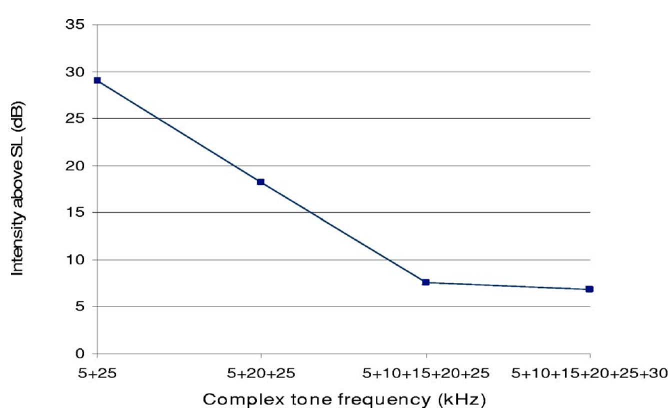

FIG. 7. Graph of the false killer whale discrimination thresholds for complex tones with harmonic components that contained 25 kHz.

with its own threshold level results at which the harmonics were barely audible and distinguishable from the pure tone. The results from this current investigation with a false killer whale were the first to demonstrate that a marine mammal has the ability to clearly identify a complex tone with up to five harmonics from a pure tone with the same frequency as the fundamental component.

It seemed likely that the false killer whale's ability to discriminate pure tones from complex tones improved possibly due to the detection of increased intensity and spectrum width from the additional harmonics (Figs. 4–7). As harmonics were added, the overall intensity required to discriminate the complex from the pure tone decreased. In other words, as the spectrum width of the complex tone increased, the required intensity to discriminate decreased. The complex tones may have been stimulating the inner ear differently as more harmonic components were added and as the intensity and spectrum width increased, explaining the observed trend in this experiment.

This may have an ecologically significant role for maintaining pod associations by providing cues and signals that may be perceived in these higher harmonics. The high frequency components of killer whale calls were measured to be more directional than the lower frequency components, thereby changing the received spectral content that corresponded to the movement of the signaler (Miller, 2002). If so, the higher frequency harmonics may have a significant role for facilitating group cohesion by containing important information for synchronized behaviors between signalers and receivers.

The adaptive values for odontocetes to discriminate harmonic vocalizations are found in additional theories of group cohesion and identification, including theories of harmonics as an acoustic by-product necessary for louder, higher intensity sounds that travel great distances. In a recent study by Lammers and Au (2003), the harmonic content of Hawaiian spinner dolphin whistles were observed to contain valuable information for a direction of movement cue. The broadband whistles are directional with frequency, and depending on the location of the receiving dolphin, information of the animals' positions in the pod are proposed by the authors to be inferred in the harmonic energy of the whistles. This may contribute to the well-coordinated movements observed over great distances of the Hawaiian spinner dolphin as well as other whistling, delphinid species. Although this particular model has not been applied for other odontocetes, it has been demonstrated from the present results that the discrimination capability for these complex tones exists for the false killer whale.

In addition to these observations, there appeared contradictory evidence demonstrating that the whale may have altered her strategy for sound perception, and that frequency or spectral analysis was performed when the fundamental frequency was presented with only one harmonic (Fig. 3). It was probable that the whale was not able to resolve the individual harmonic component as the harmonic to fundamental ratio increased, for example when 5+25 kHz was compared to the standard 5 kHz pure tone. This difference may have resulted from the higher frequency of the widely separated, harmonic component perceived distinctly from the fundamental. If each area within the basilar membrane of the cochlea responded to a specific frequency, then it was possible that the combination of 5+10 kHz resulted with a greater stimulation of hair cells when discriminating the sound as the complex tone. However, the distance between 5 and 25 kHz may have been so large that each frequency was heard individually in the 5+25 kHz complex tone, thereby reducing the whale's ability to recognize this as a complex tone. This combination may not have been heard by the whale as a complex tone.

Although complex tones have been identified and characterized from odontocete vocalizations for decades, this was the first attempt to experimentally determine the ability of a marine mammal to perceive and distinguish harmonic combinations of sound. The results confirmed that a false killer whale, a species documented for producing complex sounds, can discriminate such complex sounds from simple, pure tones. Complex tones with as little as one harmonic to as many as five harmonics, and including various combinations in between, were all discerniable from the fundamental frequency alone.

ACKNOWLEDGMENTS

The authors are grateful for the support of Whitlow Au, Dera Look, Vincent De Paolo, T. Aran Mooney, Kristen A. Taylor, Jeff Pawloski, Christopher Kam, and Maurice Radke for the illustrations, and the Marine Mammal Research Program of the Hawaii Institute of Marine Biology at the University of Hawaii. The study was supported by Office of Naval Research Grant No. N00014-98-1-0687, for which the authors thank Robert Gisiner. This work was conducted under Marine Mammal Permit 978-1567 issued to Paul E. Nachtigall by the NMFS NOAA Office of Protected Resources. This is contribution 1260 from the Hawaii Institute of Marine Biology.

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