Echolocation range of captive and free-ranging baiji (*Lipotes vexillifer*), finless porpoise (*Neophocaena phocaenoides*), and bottlenose dolphin (*Tursiops truncatus*)

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The interclick intervals of captive dolphins are known to be longer than the two-way transit time between the dolphin and a target. In the present study, the interclick intervals of free-ranging baiji, finless porpoises, and bottlenose dolphins in the wild and in captivity were compared. The click intervals in open waters ranged up to 100-200 ms, whereas the click intervals in captivity were in the order of 4-28 ms. Echolocation of free-ranging dolphins appears to adapt to various distance in navigation or ranging, sometimes up to 140 m. Additionally, the difference of waveform characteristics of clicks between species was recognized in the frequency of maximum energy and the click duration. © 1998 Acoustical Society of America. [S0001-4966(98)06609-0]

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INTRODUCTION

Acoustic characteristics of dolphin sonar signals provide various underwater behavioral information. The waveform characteristics of clicks are different in the harbor porpoise (*Phocoena phocoena*), the Dall's porpoise (*Phocoenoides* dalli), and the bottlenose dolphin (*Tursiops truncatus*) (Kamminga et al., 1996). The source level of clicks is affected by the target range (Au, 1980; Au et al., 1985; Thomas and Turl, 1990).

Click intervals of free-ranging dolphins and porpoises are possibly used as an indicator of their echolocation range in the wild. Click intervals of trained dolphins have been demonstrated to be longer than the two-way transit time between the dolphin and a target. This has been demonstrated in bottlenose dolphins (Au *et al.*, 1974; Penner, 1988) and in a false killer whale, *Pseudorca crassidens* (Thomas and Turl, 1990). Penner (1988) reported that the click intervals of bottlenose dolphins were much longer in a target-absent task than a target-present task. Thomas and Turl (1990) suggested that the false killer whale may have searched for a target at several locations along the range, since miss or false alarm trials had more variable interclick intervals in the target discrimination tasks. Dolphins seemed to change their echolocation range depending on the sensory demands.

The echolocation range of free-ranging dolphins and porpoises are not well known, mainly due to the difficulty of recording high-frequency underwater sounds in open waters. Continuous observations of clicks from the baiji (*Lipotes vexillifer*), the finless porpoises (*Neophocaena phocaenoides*), and the bottlenose dolphins in open waters and in tanks were conducted, using a high-frequency adapted digital data recorder and a hydrophone.

I. MATERIALS AND METHODS

A. Dolphins

Clicks of a single baiji in a Semi-Natural Reserve and another single specimen kept in a circular tank were observed. The Semi-Natural Reserve is a horse-hoof-shaped oxbow of the Yangtze River, 1-2 km wide and 21 km long, situated in Shishou, Hubei, China. The Reserve was established as a conservation area for the highly endangered baiji. Observations were conducted in January 1996, one month after the capture of the wild female baiji from the Yangtze River. The baiji lived alone without being fed by humans in the Reserve. It was 2.29 m in body length, 150 kg in weight, and was estimated to be 10-15 years old when captured. A 6-m small boat was operated for the recordings. A hydrophone was suspended at 3 m in depth. The baiji was frequently observed in the downstream area of the Reserve, so we waited for the dolphin to appear in this area. During the recording, an engine of the observation boat was stopped and the boat drifted without an anchor. The absolute distance and swimming direction of the baiji could not be observed.

Vocalizations of a male baiji named "QiQi," kept in a circular tank (13 m diameter) of the Institute of Hydrobiology, the Chinese Academy of Sciences (IHCAS), for 16 years in January 1996, were also recorded. QiQi was 2.15 m in body length, 125 kg in weight, and estimated to be 17–18 years old at that time.

Fourteen finless porpoises (nine male, four female, and

one calf) lived in the Semi-Natural Reserve in January 1996. The calf was born in the Reserve. Five or more finless porpoises were usually observed together. Vocalizations of these individuals were recorded in the manner similar to those of the baiji. Two male finless porpoises (1.90 and 1.59 m in body length, respectively) in a rectangular tank ($8 \times 5 \times 2 \text{ m}^3$) of Izu-Mito Sea Paradise, Shizuoka, Japan, were used for observations of captive finless porpoises.

Clicks of wild bottlenose dolphins around Mikura Island in the Izu Archipelago, Japan, and three captive bottlenose dolphins (one male of 2.97-m body length and two females of 2.75- and 2.72-m body length each) in a circular tank (12 m diameter) in the Shinagawa Aquarium, Tokyo, were recorded. Mikura Island is known to be a dolphin sighting area in Japan. More than one hundred dolphins were identified by underwater video camera observations of field marks (T. Hishii and R. Soeda, 1997). A 6.7-m fishing boat was used for recordings. A hydrophone was suspend at 3 m in depth. To avoid disturbing the dolphins, the boat drifted during the recordings without an anchor. The absolute distance and swimming direction of the dolphins could not be observed. Sometimes, the engine of the boat was not stopped to avoid being close to the sea shore due to currents and waves around the Island.

B. Recording and analysis equipment

A hydrophone (B&K 8103, sensitivity -211 dB re: 1 V/μ Pa+2/-9 dB, up to 180 kHz, or OKI ST8004, sensitivity -220 dB re: 1 V/µPa, +3/-2 dB, up to 200 kHz), a 1-kHz high-pass filter to eliminate the various low-frequency noise, and a digital data recorder (SONY PCHB 244, sampling rate of 384 kHz) were used for recordings. The frequency response of the data recorder was flat from DC to 147 kHz within 3 dB. Most of the frequencies of maximum energy in dolphin clicks are limited to the range below 150 kHz, as reviewed by Au (1993) and Richardson et al. (1995). The hearing ranges of the baiji, the harbor porpoise (Phoc*oena phocoena*) which is the same family of the finless porpoise, and the bottlenose dolphin also stop at 150 kHz (Wang et al., 1992; Andersen, 1970; Johnson, 1967). Consequently, the total frequency response of the sound recording system was sufficient to receive and to store the clicks of the recorded animals.

The echolocation sounds are composed of highfrequency clicks. The duration of a typical click is between 40 and 600 μ s (Au, 1993) and the click intervals are highly variable, ranging from a few hundred μ s (Amundin, 1991) to 150 ms (Hatakeyama *et al.*, 1994). The data acquisition system must have the capacity to process such high repetition rate click series for real-time data analysis. The analog-todigital conversion, data comparison, and memory access had to be completed before the next detection of a click within the minimum click interval, such as less than 500 μ s.

A signal processing circuit (Click Detector; 14 cm in length, 10 cm in width, and 4.5 cm in height, operated up to 4 h using alkaline primary cells) converted each click to a 500- μ s rectangular signal with a voltage level corresponding to the peak level of the click (Fig. 1). A comparator in the Click Detector generated a trigger signal whenever the volt-

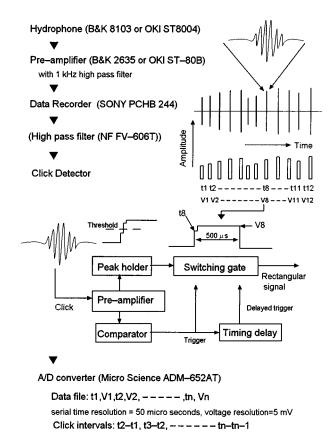


FIG. 1. Data acquisition systems and signal processing. The high-frequency recording system archived whole bandwidth sonar signals (clicks) of the dolphins. Peak sound pressure levels and the event time were recorded.

age level was larger than the threshold level in order to eliminate false activation of the Click Detector by background noises or reverberations of the pulse signals. The noise level lower than this threshold level did not activate the Click Detector. In the case of the analysis of bottlenose dolphins' vocalizations, a 20-kHz high-pass filter (NF FV-606T) was used to eliminate false-triggering by whistles.

A 486 MPU (66 MHz) based personal computer with an analog-to-digital converter (Micro Science ADM-652AT) and a data acquisition program on Windows 95^{°°} were developed for real time analysis. Signal processing of the recording and the data acquisition system are illustrated in Fig. 1. The analog-to-digital converter was operated at a 20-kHz sampling rate by a data acquisition program. Serial time data and output voltage level of the rectangular signal were obtained every 50 μ s. The maximum voltage level and the initial sampled time in the rectangular signal were saved in the RAM of the personal computer. This algorithm avoided a lower voltage level at an onset of the click. The detection threshold of the system was set to be 127 dB re: 1 μ Pa (rms) which was changed +6 dB to +17 dB depending on the recording conditions. The data processing was fast enough to capture all of the event time and the sound pressure level of dolphins' clicks.

The digital oscilloscope LeCroy model 9304AM was used to digitize the waveform of each click. The frequency of maximum energy and the duration of a click, half pulse width of maximum amplitude, were analyzed by using the digitized waveform.

II. RESULTS

A. Acoustic characteristics of clicks

High-frequency and short-duration click series were frequently observed in all species. The waveform characteristics were different between species as shown in Fig. 2, interspecies differences of frequency of maximum energy and duration of a click are recognizable. The finless porpoises produced narrower band and longer duration clicks than the other two species. The click duration of baiji and bottlenose dolphins was similar, but the frequency of maximum energy of the baiji was lower than that of the bottlenose dolphin. In the Semi-Natural Reserve, the baiji and the finless porpoises sometimes were observed at the same time around the observation area. However, it was easy to distinguish the species by their waveform characteristics, and sighting observations supported their identifications. The swimming direction of free-ranging dolphins could not be observed, so the data contained off-axis signals. On-axis data obtained from the captive baiji whose swimming direction were recorded by a video camera depicted in the lower part of Fig. 2 has similar frequency range as the off-axis data of the free-ranging baiji.

B. Reverberation and simultaneous vocalization

An example of click intervals and received sound pressure levels (rms), 9 dB smaller than the peak-to-peak pressure value, at the hydrophone obtained from the captive baiji are illustrated in Fig. 3. The end of a click train was defined as 1-s or more interval.

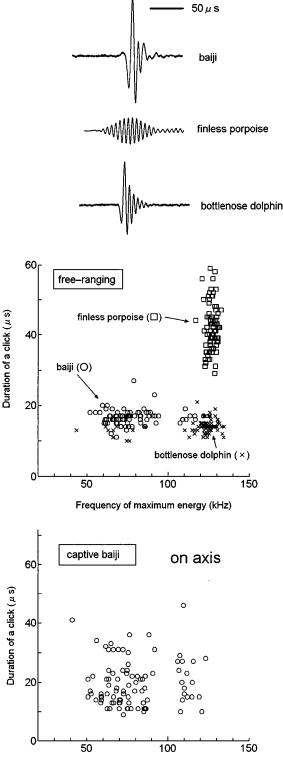
Train 3 had a 715-ms duration with 33 clicks. The mean click interval was 21.7 ms and the standard deviation was 0.81 ms. The regression coefficient between the click intervals and time elapsed was 0.00 013.

Pulse sounds reflected from the water surface, bottom, or tank wall showed alternating changes of click intervals and sound pressure levels. The reverberated pulses were mostly recorded within 1 or 2 ms after the direct path signals in a tank. Changes of sound pressure level of the reverberated signals were closely associated with the direct path signals in the time domain. Thus, 2 ms or fewer intervals were neglected for the analysis.

Simultaneous vocalization by two or more individuals also exhibit two independent changes of the sound pressure levels and the click intervals, which were clearly distinctive from the regular click. The irregular (two times or more and half or less) changes of successive click intervals were not counted as data.

C. Click intervals

Click intervals in the baiji, finless porpoise, and bottlenose dolphin are presented in Fig. 4. In the large environments such as the open ocean and the Semi-Natural Reserve, a wide variety of click intervals was observed, up to 286 ms (90% of 14 294 intervals) from a baiji, 276 ms (90% of 2506 intervals) from finless porpoises, and 200 ms (90% of 37 025 intervals) from bottlenose dolphins, respectively. On the other hand, the baiji in the 13-m circular tank frequently produced 26–28-ms click intervals, and 90% of 329 940 in-



Frequency of maximum energy (kHz)

FIG. 2. Waveform characteristics of clicks and their differences between species. Waveform, frequency of maximum energy, and duration (half width of maximum amplitude) of clicks from baiji, finless porpoises, and bottle-nose dolphins were depicted. Acoustic characteristic differences between these species are clearly recognizable. On-axis data obtained from the captive baiji is depicted in the lower part of this figure.

tervals were less than 90 ms. Finless porpoises in the rectangular tank ($8 \times 5 \times 2$ m³) frequently produced 8–10-ms click intervals, and 90% of 36 647 intervals were less than 18 ms. The bottlenose dolphins in the 12-m circular tank frequently produced 4–6-ms click intervals.

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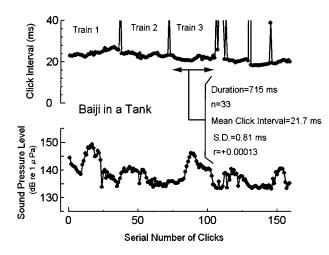


FIG. 3. Click intervals and rms sound pressure levels (dB *re:* 1μ Pa) of captive baiji. Duration, number of clicks, mean click interval, and its standard deviation of click train 3 are shown. A regression coefficient between the click intervals and time elapsed in train 3 was also calculated.

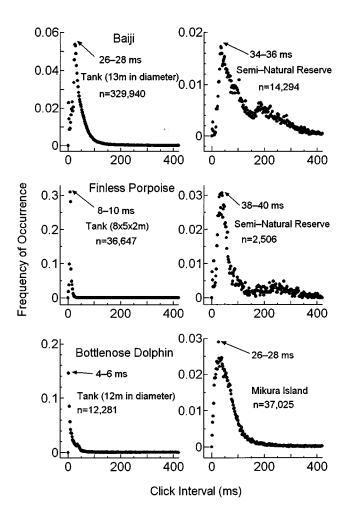


FIG. 4. Frequency of occurrence in click intervals of baiji, finless porpoise, and bottlenose dolphin. Clicks observed in open waters had a wide variety of intervals up to 400 ms. Click intervals in a tank were much smaller than in open waters. Differences of the click interval distributions between the different environments were much larger than those between species.

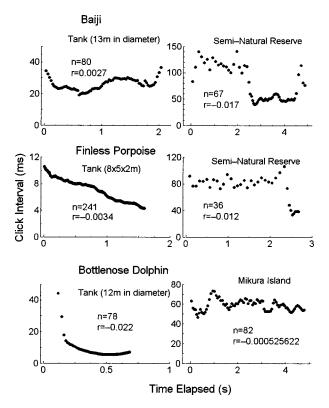


FIG. 5. Change of click intervals in a click train. The monotonous decrement of click intervals was observed in a tank. In open waters, the click intervals fluctuated in a train.

Besides a wide variety of click intervals in open waters, the difference of successive click intervals from animals in open waters were mostly less than 20 ms. In captive animals, successive click interval differences were much smaller than those in open waters.

Decreasing click intervals possibly correlated with target range were clearly observed in captive finless porpoises and bottlenose dolphins (Fig. 5). On the other hand, the change of click intervals observed in open waters did not show monotonous increment or decrement. The click intervals were fluctuated in a train and the successive click interval differences in the open waters were larger than that observed in a tank.

III. DISCUSSION

A. Differences of the waveform characteristics of clicks between species

The frequency of maximum energy and the duration of a click reflect the differences of species. Kamminga *et al.* (1996) also reported the differences of the frequency of maximum energy and the duration of a click between the *Phocoenidae* family and bottlenose dolphin. The lower frequency part in Fig. 2 might have caused by the off-axis signal due to the undetermined swimming direction of freeranging dolphins. However, on-axis clicks of captive baiji also have a lower frequency part. This suggests that the baiji produced the clicks of double-peak spectrum.

Acoustical monitoring seems to be an effective method to detect and discriminate baiji from other species. Endangered baiji are planned to be kept in the Semi-Natural Reserve or in a tank without any disturbance by water traffic and fishing activities. The Yangtze River has a wide basin and quite muddy water, so the acoustic survey seems to be an effective method to detect and discriminate baiji from finless porpoise that are observed more frequently in the Yangtze River.

B. Target range of dolphin echolocation

The free-ranging dolphins and porpoises changed their echolocation range in relation to the size of their environment. The two-way transit times of 286, 276, and 200 ms, as found in the baiji, finless porpoise, and bottlenose dolphin, respectively, correspond to two-way sound transmission distances of 207, 200, and 154 m calculated by the sound velocity of fresh or sea water (Medwin, 1975). It is only natural to increase the echolocation range in the large environment. Actually, the click interval does not precisely correspond to the two-way transit time between a dolphin and a target, since there is a lag time after receiving an echo before the next click is produced (see the review of Au, 1993, p. 116). The estimated target range of a bottlenose dolphin at the 200-ms interval is about 140 m, which is the same order as the 113-m maximum detection range for a 7.62-cm metal sphere by a bottlenose dolphin reported by Au et al. (1974).

On the other hand, the two-way transit time of underwater sound between the center of the tank and the hydrophone of the present study was about 9.0 ms for the baiji, 5.3 ms for the finless porpoise, and 7.9 ms for the bottlenose dolphin, respectively. The click intervals observed in these captive animals were mostly around 24-26 ms, 6-8 ms, and 4-6ms. The dolphins in captivity adapted their echolocation to short-range detection or navigation.

Previously reported click intervals seemed to be correlated to environmental size. Amundin (1991) reported 1– 3-ms click intervals of harbor porpoise in a 41-cubic-meter $(7 \times 5 \times 1.2 \text{ m}^3)$ tank. The click intervals of a harbor porpoise in another tank $(8.6 \times 6.3 \times 1.3 \text{ m}^3)$ were less than 2 ms close to an object (Kastelein *et al.*, 1995). Verboom and Kastelein (1995) also reported 0.5–5-ms click intervals of harbor porpoise in this tank. The click intervals of a Dall's porpoise in captivity were mostly 9.5 ms in a pool (7×5 ×3 m³) and ranged from 20–48 ms in a larger pool (12 ×8×3 m³) (Hatakegama and Shimizu, 1985).

A few broadband acoustical observations in the wild have been conducted. A stable interclick interval around 27 ms was observed in wild bottlenose dolphins (Goodson and Mayo, 1995). Herzing (1996) showed a wide variety of the click intervals that ranged from 0.5-125 ms in wild Atlantic spotted dolphin (*Stenella frontalis*) in the Bahamas. The Atlantic spotted dolphins produced 2–2.5-ms click intervals during echolocation with the rostrum in the sand. Hatakeyama *et al.* (1994) conducted broadband recording of Dall's porpoise in the North Pacific Ocean and the click intervals ranged from 8–150 ms. Goold and Jones (1995) reported decreasing click intervals from 2 to 0.5 s at the beginnings of a sperm whale (*Physeter macrocephalus*) dive. The intervals were comparable to the water depth in which sperm whales were feeding.

C. Change of click intervals in a train

Changes of sonar signal intervals correlated with distance from an approaching target were observed in foraging bat's echolocation of insect (Tian and Schnitzler, 1996). Dawson (1991) also reported the decreasing change of click intervals of the wild Hector's dolphin (*Cephalorhynchus hectori*). In the present study, decreasing click intervals of dolphins, similar to the terminal phase of a target interception by bats, were only observed in short click intervals. However, few terminal phases was observed in open waters, possibly due to the large fluctuation of click intervals.

If the click intervals reflect the target distance precisely as Lucke and Goodson (1997) suggested, the -0.0034 regression coefficient observed in the finless porpoise in the tank corresponds to a 2.6-m/s approaching speed to the target which is the usually observed swim speed of free-ranging dolphins.

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