Dolphin strategies for long-range object detection and change detection

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Dolphin strategies for detecting objects and changes in objects were investigated by having three trained bottlenose dolphins perform long-range echolocation tasks. The tasks featured the use of "phantom" echoes produced by capturing the dolphin's outgoing echolocation clicks, convolving the clicks with the impulse response of a physical target to create an echo waveform, then broadcasting the delayed, scaled echo waveform back to the dolphin. Dolphins were trained to report the presence of phantom echoes or a change in phantom echoes. Target simulated ranges varied from 25 to 800 m. At ranges below 75 m, all dolphins followed a single click-echo paradigm, where inter-click intervals exceeded the two-transit time (i.e., the dolphins waited to receive the echo from a click before emitting the next click). As the range increased beyond 75 m, two of the three dolphins increasingly produced bursts, or "packets," of several clicks, then waited for the packet of echoes to return before emitting another packet of clicks. The third dolphin instead utilized very high click repetition rates. The use of click packets may be a response to a limitation in the dolphin's ability to employ multi-echo processing with large inter-echo delays.

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INTRODUCTION

A number of studies with captive and wild animals have investigated the dolphin biosonar transmission and reception systems and the manner in which dolphins employ their biosonar to accomplish various tasks. These studies have revealed that dolphins utilize short duration (~50–80 µs), broadband sound pulses (called “clicks”), with peak frequencies up to 130 kHz (rev Au, 1993), and peak-peak sound pressure levels (SPLs) up to 220 dB re 1 µPa (Au, 1980; Au, 2004). Clicks are rarely emitted in isolation, but rather are normally produced as a sequence (a click train) whose temporal spacing may vary over time depending on the specific task and target range. Although the temporal pattern of a dolphin click train may be complex, when investigating a specific target, dolphins generally emit a single click, then wait to receive the echo before emitting the next click (rev Au, 1993; Au and Hastings, 2008). In this fashion, a dolphin could use the time interval between emission of a click and reception of the echo to determine the target range. In dolphins operating in this “single click-single echo” mode, the time interval between the emission of one click and the next (the inter-click interval, ICI) typically exceeds the two-way travel time (TWT, the time required for the emitted click to propagate to the target and return to the animal) by roughly 10 to 45 ms (Evans and Powell, 1966; Morozov et al., 1972; Au et al., 1974; Au, 1980; Au, 1993).

However, some previous studies have revealed click emission patterns dramatically different than the single click-single echo paradigm described above. In particular, dolphins and a beluga performing target detection experiments at ranges beyond 50 to 100 m have been shown to emit bursts or “packets” of clicks separated by time intervals that are larger than the corresponding TWT (Ivanov and Popov, 1978; Turl and Penner, 1989; Ivanov, 2004). In this operating mode, the ICI within each packet is well below the TWT, but the interval between packets is greater than the TWT; i.e., the animal emits a packet of clicks, then waits for the packet of echoes to return before emitting the next packet of clicks. Packet use in dolphins was first described by Ivanov and Popov (1978). Later, Turl and Penner (1989) reported a beluga using packets, but not a dolphin, while both performed the same target detection experiments with ranges from 80 to 120 m. Finally, Ivanov (2004) described packet use by a dolphin detecting physical targets at ranges up to 700 m.

In this study, dolphin strategies during long-range echolocation tasks were examined to better understand the conditions under which dolphins employ packets. Rather than use physical targets, as in previous work, phantom echoes were used. These were produced by recording a dolphin’s outgoing clicks and convolving them with a specific target impulse response, then scaling the amplitudes and delaying the signals before re-broadcasting back to the dolphin (Au et al., 1987a; Aubauer and Au, 1998). Two different tasks were conducted: echo detection and echo change detection. For each task, multiple target ranges were simulated, and multiple target strengths or echo levels were employed. The dolphins’ performance and click emissions were then analyzed to see how the animals adjusted their click emissions and how their performance varied with target range (echo delay) and echo amplitude.

METHODS

This study utilized a custom phantom echo generator (PEG) consisting of a TMS320C6713 digital signal processor (DSP) starter kit with an analog input/output daughter card. The dolphin click received by a hydrophone located in front of the subject was filtered and amplified, then digitized at a 1-MHz sampling rate and 12-bit resolution. The digitized hydrophone signal was then passed to a threshold-crossing click detector. If a click was detected, the click waveform was convolved with a target impulse response, scaled in amplitude, then stored in one of 16 discrete memory buffers. After time delays appropriate for the simulated target range, the contents of each echo memory buffer were converted to analog using a sampling rate of 1 MHz and resolution of 12 bits. The analog echo signal was filtered, amplified, and used to drive the echo transmitter.

Subjects consisted of three bottlenose dolphins: SAY (female, 33-y, ~245 kg), TRO (male, 20-y, ~175 kg), and IND (male, 10-y, ~175 kg). The dolphins SAY and TRO participated in the echo change detection task. During this task, eighty-percent of the trials were “change” trials, where the PEG impulse response changed from target A to target B after a random time interval of 5 to 10 s. If SAY or TRO produced a whistle response within 2 s of the target change (a hit), a buzzer was sounded indicating a correct response, the dolphin returned to the surface, and fish reward was delivered. Failure to whistle within the 2-s response interval (a miss) resulted in the dolphin being recalled to the surface, with no fish reward. The remaining 20% of the trials were “no-change” trials, where the impulse response remained at target A for the trial duration, which was randomized between 7 and 12 s. If the dolphin withheld the whistle response for the entire no-change trial period (a correct rejection), the buzzer was sounded and it was rewarded with fish (one capelin); if the dolphin whistled before the no-change trial end (a false
alarm), it was recalled and no reward was provided. If, during a change trial, SAY or TRO whistled before the actual target change, the trial was considered a no-change trial for analysis and the response was classified as a false alarm.

For the echo detection task, the dolphin IND was trained to echolocate while in the hoop and report the presence of phantom echoes by leaving the hoop and pressing a response paddle. Eighty-percent of the trials were “echo present” trials, where the PEG impulse response was changed from target 0 to target A after a random time interval of 0 to 5 s. If IND pressed the response paddle within 7 s of the appearance of the echoes (a hit), a buzzer was sounded indicating that he was correct and he returned to the surface for a fish reward (one capelin). Failure to press the paddle within the 7-s response interval (a miss) resulted in IND being recalled to the trainer, with no fish reward. Twenty-percent of the trials were echo-absent, where the PEG impulse response remained on target 0 (i.e., no echoes) for 5 to 10 s. If IND remained in the hoop for the entire echo-absent trial (a correct rejection), the buzzer was sounded and he was rewarded with fish (one capelin); if he left the hoop before the trial ended (a false alarm), he was recalled and no reward was provided. If IND left the hoop before the echoes appeared during an echo-present trial, it was also classified as a false alarm, and this trial was considered an echo-absent trial for analysis.

RESULTS AND DISCUSSION

As in previous studies, the dolphins exhibited a great deal of flexibility in their click amplitudes and click temporal patterns, and were capable of tight control over the click levels and ICIs. Click source levels for all three subjects were generally large, with the highest (mean) p-p source levels were near 217 dB re 1 µPa at 1 m for both SAY and TRO, and around 212 dB re 1 µPa at 1 m for IND.

At ranges below 75 m, all three dolphins followed a single click-echo paradigm, where ICIs exceeded the two-way transit time (i.e., the dolphins waited to receive the echo from a click before emitting the next click). As the range increased beyond 75 m, the dolphins SAY and IND increasingly produced bursts, or “packets,” of several clicks, then waited for the packet of echoes to return before emitting another packet of clicks (Fig. 1). The use of packets in both subjects occurred spontaneous, and appeared to be a natural response to target ranges of 75 m and beyond. In contrast to SAY and IND, TRO used packets on only a few trials, but was able to maintain performance similar to that of SAY. Rather than employ packets, TRO often utilized ICIs lower (often much lower) than the TWT (Fig. 2). The use of ICIs < TWT was also previously reported for belugas performing detection tasks with physical targets (Au et al., 1987b; Turl and Penner, 1989). This behavior was also seen in SAY and IND, and tended to occur at ranges from 25–100 m; above 100 m SAY and IND tended to employ packets rather than low ICIs. The use of low ICIs, rather than packets, was also more common when the echo levels were relatively high.

Taken together, the behaviors of SAY, TRO, and IND feature a common theme: as the range increased to 50 m and beyond, the animals did not wait for the echo to return before emitting the next click. All three responded to the increased range first by reducing the ICI below the TWT. As range continued to increase, SAY and IND increasingly moved to using packets, while TRO continued to emit single clicks with ICIs < TWT. There were few clicks with ICIs > 100 to 200 ms, indicating a strong preference by three dolphins to limit the ICI.

The strong preference for shorter ICIs may reflect a fundamental limitation in a dolphin’s ability to combine information across multiple echoes. Data suggest that dolphins can utilize multi-echo processing (Au et al., 1988; Altes et al., 2003); however, as the range increases, the time delay between successive echoes progressively increases the time required for multiple echoes to be received and subsequently processed. Depending on the range, dolphin speed, and target speed, it may be impossible to effectively track objects at long range if the ICI is too large. The dolphins may have increased the click repetition rate to receive more echoes in a shorter time frame, allowing the animal to take advantage of multi-echo processing; however, employing an ICI < TWT introduces range ambiguity, since the animal can no longer use the time delay between click emission and echo reception to determine target range. The use of packets may overcome this limitation and combine the best of both operating modes: the fast click repetition rates within the packets allow multi-echo processing over short time spans, while the temporal gap between packets allows echo-ranging to occur.
FIGURE 1. (a) Click instantaneous sound pressure and (b) inter-click interval recorded from the dolphin SAY during a trial with 200-m simulated range. TWT – two-way travel time (the time required for the emitted click to propagate to the target and return to the animal). The packets are identifiable by the closely spaced clicks with a bimodal ICI distribution. The very short ICIs indicate the clicks within a packet, while the ICIs near the TWT line indicate interval between packets.

FIGURE 2. (a) Click instantaneous sound pressure and (b) inter-click interval recorded from the dolphin TRO during a trial with 200-m simulated range. TWT – two-way travel time (the time required for the emitted click to propagate to the target and return to the animal). Unlike SAY, TRO rarely utilized packets and often used inter-click intervals well below the TWT.
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