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In an echolocation experiment, the target detection performance of a beluga and a bottlenose dolphin were similar, but each produced different patterns of echolocation click trains. The beluga emitted three different patterns of echolocation clicks. A pattern I click train started with low-amplitude clicks, followed by packets of clicks. A packet contained several clicks with interclick intervals less than the two-way travel time to the target; the interpacket intervals were greater than the two-way travel time. A pattern II click train consisted of a combination of individual clicks, some with intervals less than and some greater than the two-way travel time. This pattern did not contain packets. The third pattern of click trains consisted of individual clicks with interclick intervals less than the two-way travel time. However, the bottlenose dolphin always emitted clicks with interclick intervals greater than the two-way travel time. These differences in click patterns suggest that the beluga has a different echolocation strategy than the bottlenose dolphin.

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INTRODUCTION

In echo ranging, the distance to a target can be calculated by measuring the time interval between a transmitted signal and the detection of an echo. If c is the velocity of sound in water and t is the elapsed time between the signal and echo, the range r is

$$r = ct/2.$$

The relationship of a bottlenose dolphin's pulse repetition rate and target range has been the subject of discussion for nearly 30 years. Kellogg *et al.* (1953) suggested that the echolocation system of *Tursiops* operated in a manner similar to that of a pulse modulated sonar. They suggested that the clicks could be used for echo ranging if time were allowed after each pulse for the echo to be reflected back to the animal. Norris (1964), citing Norris *et al.* (1961), concluded that, since the repetition rate did not increase in a rigid, systematic manner as the animal approached a target, as in echo ranging, "the repetition rate seems to function solely in relation to the degree of discrimination desired by the animal at any moment, and not to the speed of sound in water in relation to distance from a target. Thus the term 'echo-ranging' seems inappropriate when speaking of sound mediated navigation and discrimination of porpoises."

Evans and Powell (1967) and Johnson (1967) reported that a bottlenose dolphin increased its pulse repetition rate as the distance between the animal and target decreased, but the variability in the pulse rate at any time and distance from the target prevented them from making any conclusions about the pulse repetition rate for target discrimination or distance.

Norris *et al.* (1967) used pulse repetition rate to distinguish "discrimination" and "orientation" click trains. In their experiment, a blindfolded bottlenose dolphin was re-

quired to discriminate between different sizes of small steel spheres, detect and report the standard target, and then locate a fish reward thrown into the test pool. The authors reported that, during the discrimination runs, there was no regular sequential change in the repetition rate as the animal closed upon the target; however, the bottlenose dolphin emitted orientation click trains after it turned away from the response levers. These were described as clicks emitted at a "very slow repetition rate perhaps indicating their use for detection of relative distant objects."

Other experimental evidence suggests that a bottlenose dolphin changes its pulse repetition rate as the distance between the animal and target varies. Norris (1969) reported that *Tursiops* adjusted the pulse repetition rate so that the echo falls in the interclick interval following the emitted signal. Morozov *et al.* (1972) reported that the average interclick interval of *Tursiops* was between 3 and 20 ms longer than the time necessary for a pulse to travel to a target and return to the animal. They suggested that a bottlenose dolphin emits each successive pulse only after receiving the echo from the preceding pulse and that time difference between the echo reception and the production of the next pulse represents the time required to process the echo. Au *et al.* (1974) measured a bottlenose dolphins' interclick intervals while the animal was detecting a target at 60 or 80 m. The average interclick intervals were 30–50 ms greater than the calculated two-way travel time. Penner and Kadane (1980) trained two bottlenose dolphins to detect targets at 40, 60, 80, 100, and 120 m. They reported that, at all target distances, the bottlenose dolphin's average interpulse intervals were about 20 ms greater than the calculated two-way travel time.

Ivanov and Popov (1979) reported the results of experiments on the ability of a bottlenose dolphin to detect differ-

ent size targets located at different distances so that the target's scattering strengths were equivalent. They said there is a distance when a bottlenose dolphin's click train contains "pulse packets separated by time intervals more than twice as long as the time required by the sounding pulse to reach the target." Unfortunately, these authors did not provide information on the bottlenose dolphin's ability to correctly detect targets at these ranges.

In a masking noise experiment, Turl *et al.* (1987) reported that the threshold in masking noise of the beluga was 8–13 dB better than that of the bottlenose dolphin and that the interclick interval patterns of a beluga and a bottlenose dolphin were different at target distances of 16.5, 40, and 80 m. At 16.5 m, the beluga's click train consisted of interclick intervals that rarely exceeded the two-way travel time, but at 40 and 80 m, the beluga's click train consisted of interclick intervals that were less than the two-way travel time. The bottlenose dolphin always emitted clicks with interclick intervals greater than the two-way travel time for all three target distances. Au *et al.* (1987) described a beluga click train for a target at a distance of 80 m without masking noise. The click train started with interclick intervals of 44 ms, followed by interclick intervals of 193 ms. Occasionally, the beluga emitted a series of high-repetition clicks (1.7-ms intervals) at the end of a click train.

In this paper, we reexamine the interclick interval data discussed in Penner and Turl (1983). In that discussion, we described the difference between a beluga and a bottlenose dolphin echolocation click train for target distances between 40 and 120 m. For all target distances, the beluga's click train always started with interclick intervals at about 30 ms, which then increased to about 60 ms. For target distances greater than 80 m, the beluga had occasional intervals between 200 and 220 ms. The bottlenose dolphin's click trains always had interclick intervals greater than the two-way travel time. We concluded that, if we used bottlenose dolphin's click train patterns as a model to interpret the beluga's click train, then the beluga always scans from 30–160 m.

I. MATERIALS AND METHODS

The experiment was conducted in Kaneohe Bay, Oahu, Hawaii, using the same beluga and a bottlenose dolphins that were subjects in the masking noise experiment (Turl *et al.*, 1987). The test enclosure, the target range, and the target suspension system are shown in Fig. 1. The targets were raised and lowered separately with nylon monofilament line

extending back to the experimenter's station. An acoustic screen was in front of the underwater hoop station. When the screen was down, an animal in the hoop could ensonify the target. The center of the hoop station and the target depth were both at 1 m. The targets were aluminum cylinders. Acoustic measurements of the targets (see Au and Snyder, 1980) indicated that the average target strength of each cylinder was -12 ± 2 dB.

A trial began when the animal was in front of the experimenter, opposite the hoop station. Upon command the animal turned, swam across the pen, and inserted its head into the stationing hoop. The target was either gently lowered into the water or left out, and the acoustic screen was lowered, which cued the animal to begin echolocating. The animal echolocated for as long as it desired. Upon completion of its echolocation, the animal backed out of the hoop and responded by striking one of two response paddles to indicate whether it detected the target.

A data collection session consisted of 100 trials with an equal number of target present and absent trials. Five target distances were randomly presented during each session. Two different sets of target ranges were used. The first set consisted of target ranges between 40 and 120 m, separated in 20-m increments. The second set consisted of target ranges between 100 and 120 m, separated in 5-m increments.

The Apple II microprocessor system described by Au *et al.* (1982) measured the echolocation signals of both animals. An Edo-Western 6166 transducer 2 m from the hoop was used to detect each click during a trial. The signal data included the interclick interval, number of clicks per trial, and the peak-to-peak amplitude of each click.

II. RESULTS

The mean interclick interval for both animals is plotted in Fig. 2. The two-way travel time is shown as the diagonal line. Beyond 40 m, the mean interclick interval of the beluga click train was less than the calculated two-way travel time. The bottlenose dolphin's mean interclick interval increased with target distance and was always greater than the two-way travel time. Examples of typical beluga and bottlenose dolphin click trains for target distances from 40 to 120 m are shown in Fig. 3, with the calculated two-way travel time shown as a horizontal line. At 40 m [Fig. 3(a)], the beluga click train consisted of interclick intervals that were about equal to or less than the two-way travel time, and, at 60 m, [Fig. 3(b)] the interclick intervals were less than the two-

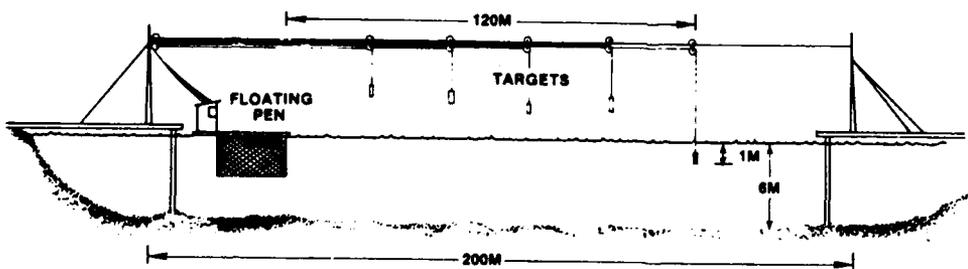


FIG. 1. Target range (Skyhook II) located in Kaneohe Bay, Oahu, Hawaii.

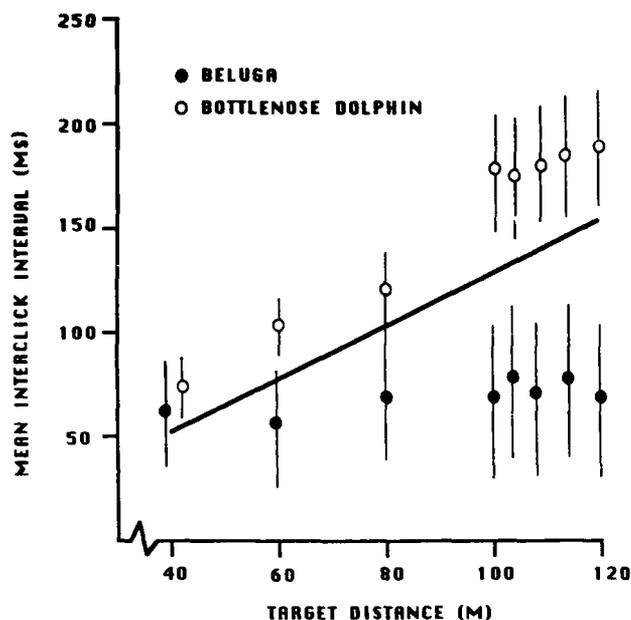


FIG. 2. Comparison of the mean interclick interval (± 1 s.d.) for the beluga and bottlenose dolphin for target ranges from 40 to 120 m. Diagonal line is the two-way travel time.

way travel time. Two different types of beluga click trains are shown in Fig. 3(c) (distance = 80 m): one with interclick intervals less than the two-way travel time and one with mixed interclick intervals. At all test distances, the interclick intervals of the bottlenose dolphin are greater than the two-way travel time.

We reviewed all the beluga click trains for correct detection and correct rejection target trials and identified three different patterns of interclick intervals. Pattern I [Fig. 4(a)] consists of three components and is plotted in Fig. 4(b) in the time domain. The abscissa [Fig. 4(b)] is the total time of the click train, and the ordinate is the relative amplitude of each click. Each pattern I click train [Fig. 4(b)] started with an initial series of clicks with average interclick intervals of 47 ± 19 ms. Following the initial series is a packet that contains 2–3 clicks, and the average interclick interval was 41 ± 19 ms. Each pattern I click train normally contains 3–4 packets. The interpacket interval is greater than the two-way travel time and the length of a packet is less than the interpacket interval. The relation of the length of the packets to interpacket interval is shown in Fig. 5(a) as a frequency of occurrence histogram. The length of packets varies between 80 and 120 ms, and the interpacket intervals are normally greater than 170 ms. A frequency of occurrence histogram [Fig. 5(b)] compares the peak-to-peak amplitude of the first click of a packet to the peak-to-peak amplitude of clicks that comprise packets for pattern I click trains. Approximately 55% of the first clicks in a packet had peak-to-peak amplitude greater than 218 dB re: $1 \mu\text{Pa}$, compared to about 25% of the other clicks within a packet.

A pattern II click train [Fig. 6(a)] also consisted of an initial series of clicks, immediately followed by 4–7 clicks

with interclick intervals greater than the two-way travel time. A pattern II click train may have had 2–3 clicks with interclick intervals less than the two-way travel time at the end of the click train. A pattern III click train [Fig. 6(b)] consisted entirely of clicks with interclick intervals less than the two-way travel time.

The beluga emitted all three patterns for both correct detection and correct rejection trials. In Fig. 7, pattern I, II, and III histograms are shown for correct detection and correct rejection trials as a percentage of total trials. The beluga emitted more pattern I click trains for correct detection trials and pattern II click trains for correct rejection trials. Pattern III click trains were emitted only on a few occasions.

III. DISCUSSION

The *Tursiops* echolocation strategy is to emit a signal and wait until the echo returns before emitting the next signal. The bottlenose dolphin changes the pulse repetition rate as the target distance changes so that the signal echo is between the interclick interval. This strategy may not be applicable for all species of echolocating cetaceans. Ivanov and Popov's (1979) description of bottlenose dolphin click trains that contain packets may only occur at target distances beyond 140 m. We have not tested a bottlenose dolphin beyond 120 m in Kaneho Bay.

The difference in the beluga's interclick interval patterns suggests that this species may use a different echolocation strategy for targets at ranges less than 40 m. Since the initial series of clicks consists of interclick intervals less than the two-way travel time, the beluga is transmitting echolocation signals and receiving echoes simultaneously. This may provide the beluga with information about target presences or absences, but probably does not provide information about target range.

In pattern I click trains, the interpacket interval is longer than the total packet duration and greater than the two-way travel time. The beluga could be processing all echoes in a packet before the next echo packet returns to the animal. This suggests that the beluga may be processing multiple echoes within a packet. The first click of a packet is about 2–3 dB higher than the following clicks within a packet. In addition to the time between packets, the beluga may use the high amplitude of the first click to identify the beginning of a packet.

Click train patterns for correct detection and correct rejection trials were different. The beluga may emit pattern I click trains to determine target presence and pattern II click trains to determine target absence.

IV. SUMMARY

The beluga has a different echolocation strategy than does the bottlenose dolphin. At all target distances, the bottlenose dolphin's interclick intervals showed a systematic relationship between the interclick interval and the distance to the target. The bottlenose dolphin strategy insures there is no overlap between the transmitted signal and echo. The time interval at which the bottlenose dolphin may process echoes is the time difference between echo reception and signal transmission. This may not be true for other echolo-

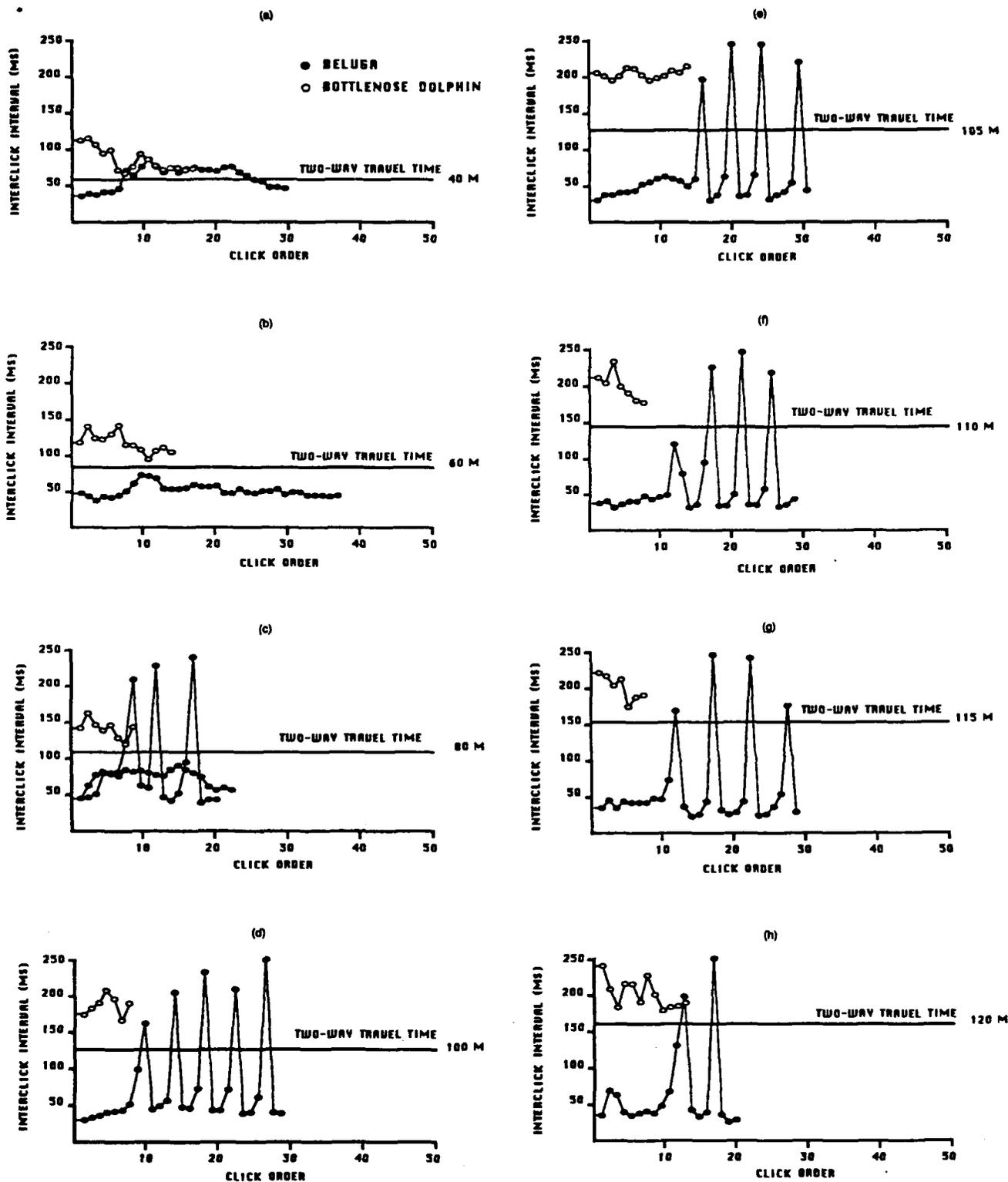


FIG. 3. Examples of typical correct detection click trains for the beluga and bottlenose dolphin for target ranges from 40 and 120 m.

cating delphinid species.

For the beluga, the pattern I click trains contain an initial series of clicks that have regular click intervals, and the packets have interpacket intervals large enough for all echoes in the packet to return to the animal before another pack-

et is transmitted. Within each packet, the signals have interclick intervals less than the two-way travel time. The length of a packet is generally shorter than the preceding interpacket interval, and the first click of a packet is about +2 dB higher than the following clicks in a packet. Packets are

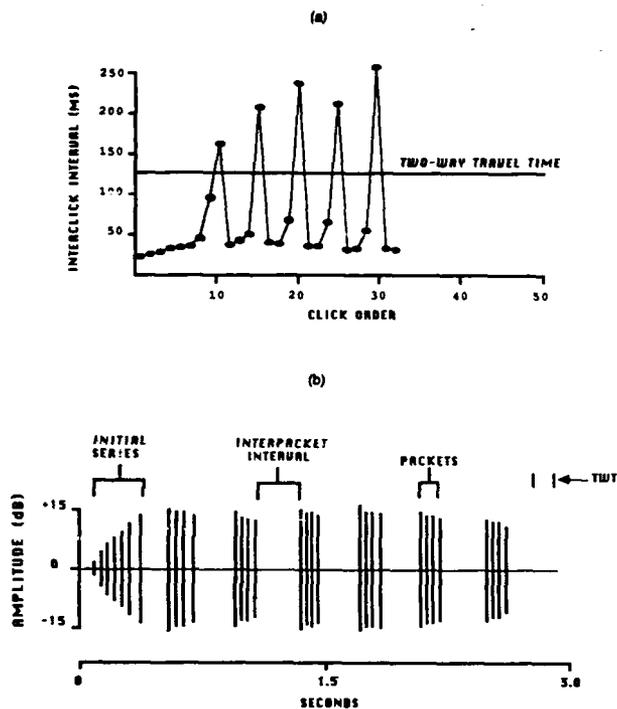


FIG. 4. (a) An example of a beluga pattern I click train for a target at 100 m. (b) A beluga pattern I click train [see (a)] plotted in the time domain showing the relationship of the initial series, interpacket interval, and packets.

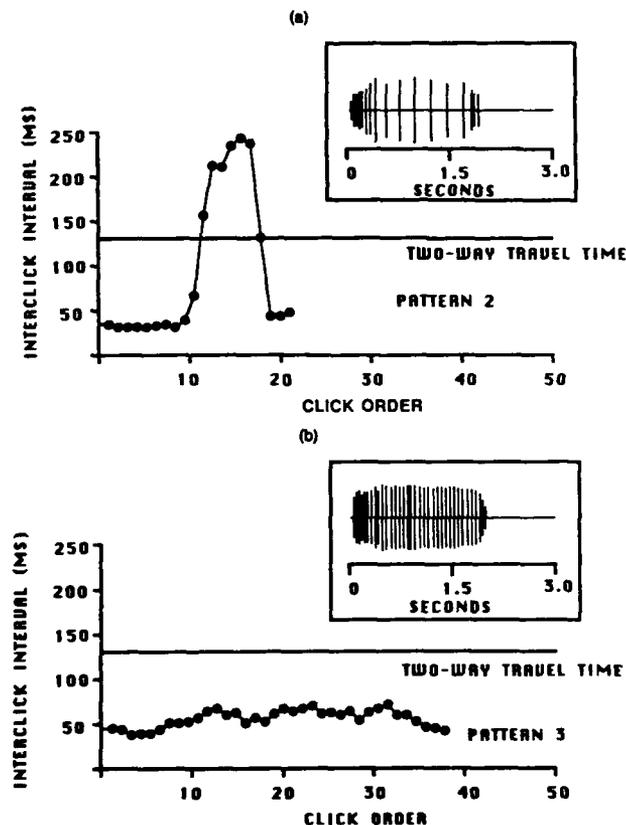


FIG. 5. (a) An example of a pattern II click train showing the absence of packets, and (b) an example of a pattern III click train with a regular repetition rate. Pattern II and III click trains are shown in the time domain as an insert above each figure.

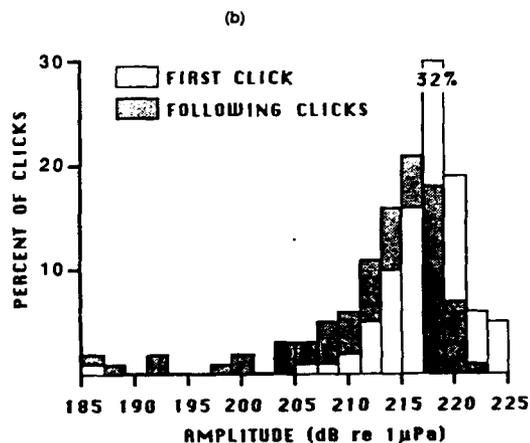
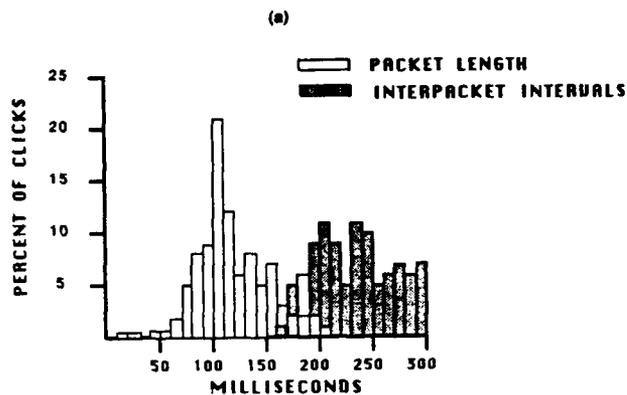


FIG. 6. (a) The relationship of interpacket intervals to packet length for targets at ranges from 100 to 120 m. (b) A frequency histogram comparing peak-to-peak amplitudes of the first click of a packet to the following clicks in a packet.

separated within a click train by time and, perhaps, by amplitude. The beluga favored pattern I click trains for correct detection trials and pattern II click trains for correct rejection trials. This difference may be related to a detection strategy.

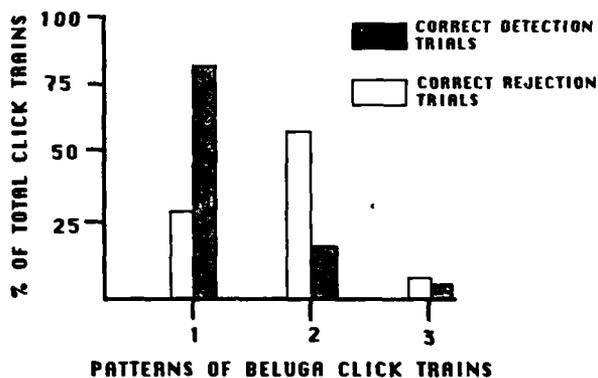


FIG. 7. A comparison of the three beluga click patterns for correct detection (target present) and correct rejection (target absent) trials for target distances between 100 and 120 m.

Between 40 and 60 m maintained a constant repetition rate of 40–57 ms. This suggests that the beluga may be processing echoes between the transmission of echolocation signals. Beyond 80 m, the beluga modulates the interclick interval so that all signals contained in a packet are received by the animal before emitting another packet. Using the time difference between the interpacket interval and packet length, the beluga may require about 50 ms to process a packet. This is similar to the times reported for the bottlenose dolphin to process single echoes.

The beluga lives in a high-noise and reverberant environment. It might be expected that the beluga's sonar system has developed optimal adaptations to minimize the effects of interference found in the arctic. In a masking noise experiment, the beluga's detection threshold was 8–13 dB better than the bottlenose dolphin and each animal had a different click emission strategy. We suggested that the beluga's better performance might be related to the possibility that the beluga simply had more information available to process than did the bottlenose dolphin. In this experiment, the click emission strategy of the beluga and bottlenose dolphin are different when performing the identical echolocation task. These differences suggest that the beluga may have different signal processing capabilities than does the bottlenose dolphin. Possibly the integration time of the beluga is sufficiently long so that the signals contained in pattern I packets are summed and present a coherent image. Also, the animal may have a greater receive directivity index than a bottlenose dolphin. Further investigations concerning the temporal resolving capability of the beluga could help isolate mechanisms used by the beluga that are relevant in this type of click emission strategy.

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