Localization of brief sounds by a bottlenose dolphin

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Abstract. Spatial hearing in dolphins is believed to be similar to that in humans. However, we found that directionality of the bottlenose dolphin sonar transmission and reception could account for most results on underwater object localization and spatial discrimination. In this paper passive localization and spatial discrimination of brief signals by a bottlenose dolphin is examined. A bottlenose dolphin was able to discriminate a lead click from a lag click at azimuth separation between transducers as small as 0.25° compare to a 1.8° localization threshold for a single click. The lead-lag localization of uncorrelated noise pulses proved to be almost as accurate as that of correlated clicks. The results suggest that the precedence affect is not present in the auditory system of the bottlenose dolphin. The smallest lag delay at which the dolphin was capable of discriminating the lead and lag noise pulses was found to be as small as 18-20 µs. In order to discriminate brief signals at small azimuth separations between transducers, the bottlenose dolphin appeared to use the edges of the sonar receive beam.

1 Introduction

Spatial hearing in dolphins is believed to be similar to that in humans [1]. The same binaural phenomenon known for humans is used to explain sound localization in dolphins. On the other hand, dolphins have active sonar whereas humans have only passive hearing. Transmission and reception of dolphin's sonar clicks is directional with around 10° in both the horizontal and vertical planes, whereas binaural hearing in humans does not involve any substantial directionality. The ability of a bottlenose dolphin to localize a sound in the vertical plane as accurate as in the horizontal plane appears to undermine, to a certain degree, binaural phenomenon concept in dolphin sonar [2]. The spatial hearing in the bottlenose dolphin appears to lack so-called "precedence effect" [3-5], which is an important attribute of binaural hearing in humans.

We found that at target azimuth separations smaller than 2°-3° the dolphin would turn on the left side by almost 90°. The dolphin placed the targets into the sagittal plane where there are no interaural differences in time and intensity and, as a result, the binaural phenomenon does not work. When targets were presented at the same azimuth but at different elevations, the dolphin never turned on its side so that the targets were again kept in the saggital plane [4, 5].

Threshold azimuth separations between the different targets located at the same ranges was found to be 0.4°-0.5°. The threshold angular separation in vertical plane was also around 0.4° (at a 1-m depth) [4, 5].

When the dolphin task was to discriminate identical targets located at different distances (Fig. 1), the threshold azimuth separation was as small as around 0.2°. In humans when two similar sounds are presented from different locations with a small delay relative to each other, only one sound is heard in direction of a lead sound [6]. This auditory phenomenon is commonly known as the precedence effect (also known as the "law of the first wave" or "echo suppression"). At delays longer than around 5 ms, the perceptual fusion of the lead and lag breaks and most of listeners hear two sounds, although localization dominance of a lead sound remain for delays more than 10 ms. In humans, minimum audible angle (MAA) for a single sound is always smaller than MAA for a lead sound localization in which precedence effect is assumed to operate [7]. In the bottlenose dolphin, the lead-lag target localization threshold of 0.2° proved to be almost ten times better than a single target localization threshold of 1.8° [4]. Therefore, if the precedence effect were present in the dolphin, he would have certainly failed to localize the fused target echoes at the target azimuth separation of 0.2°. So, how could the dolphin discriminate the targets at extremely small azimuth separations?

When discriminating targets at small angular separations, the dolphin rotated the sonar transmit beam by more than ± 10° to the right or left from both targets (Fig. 1). Using steep edges of the transmit beam the dolphin apparently perceived two targets as a single one with the echo parameters correlated with relative position of the targets [4, 5]. For targets having a single highlight echoes, the transmit beam rotation generated for the dolphin time-reversed double-highlight echoes (large-small highlights and small-large highlights) with identical energy spectra (Fig. 1, waveform insertions).

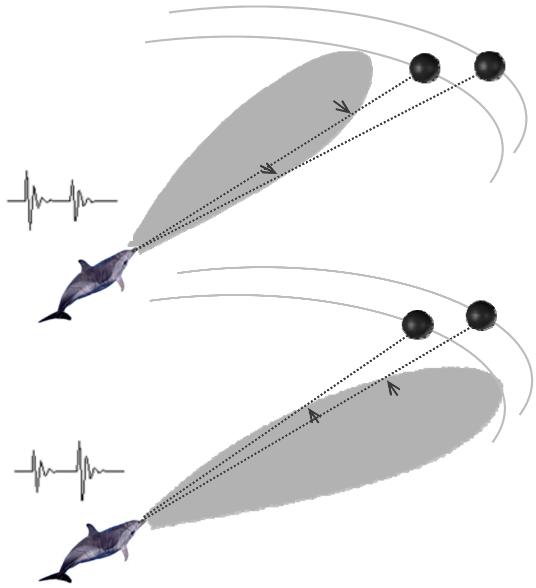

Fig. 1. Rotation of a dolphin's sonar transmit beam to the left and to the right of both targets. The insertions are the echoes returned to the dolphin from the both targets each consisted of a single highlight. Computer simulation.

The bottlenose dolphins are capable of discriminating the time reversed double clicks (Fig. 2) with identical energy spectra [8-12].

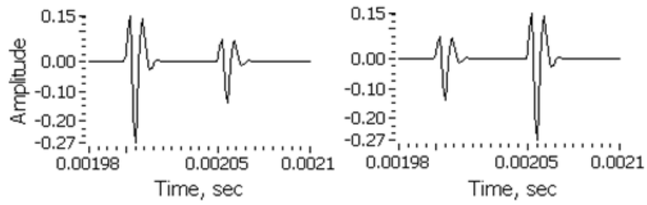

Fig. 2. Time reversed double clicks with identical energy spectra.

In our experiments three bottlenose dolphins were able to discriminate the time reversed double clicks with a small-to-large click ratio as small as around 1 dB (Fig. 3) and interclick intervals as short as 5-10 µs. The edges of the bottlenose dolphin transmit plus receive beams appear to be steep enough to provide 0.5-1 dB amplitude difference between the lead and lag echoes from targets separated by 0.2-0.25°.

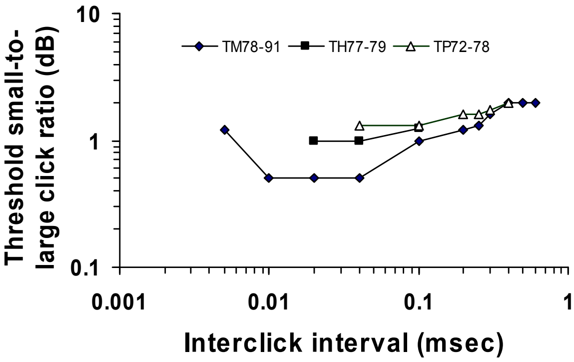

Fig. 3. Threshold amplitude difference between small and large clicks sufficient for bottlenose dolphins to discriminate the time-reversed double clicks as a function of interclick interval [10].

The reason the dolphin rolled to the side by almost 90° could be that the edges of the transmit beam in the sagittal plane is steeper than the beam edges in the horizontal plane [1]. The steeper the beam edges, the larger the difference in intensity of the incident sonar click between the left and right targets closely situated along the same edge. As a result, there should be larger differences in composite echo from the two targets between the left and right beam orientation.

The dolphin sonar directional transmission and reception both contribute to localization and spatial discrimination of targets. With a view to assessing the auditory system contribution to the spatial hearing, we examined a passive localization and spatial discrimination of brief signals by a bottlenose dolphin. In this paper the results are discussed in relationship with the bottlenose dolphin auditory time resolution and the "precedence effect" phenomenon well known for binaural system of humans.

2 Methods

Stimuli were correlated clicks as well as uncorrelated noise pulses. First, azimuth localization threshold for a single click was measured. Second, a threshold azimuth separation between the transducers at which the dolphin was able to discriminate simultaneously transmitted click and noise pulse (Fig. 4A) was determined. Third, the lead sound localization thresholds were measured. The dolphin discriminated between correlated lead and lag clicks (Fig. 5A) or between uncorrelated lead and lag noise pulses (Fig. 5B). Lead and lag noise pulses were produced using two uncorrelated analog generators. In humans, uncorrelated noise pulses do not produce the precedence effect. Listeners reported hearing two sounds regardless of delay [6]. Finally, a minimum lag delay at which the dolphin was able to discriminate between the lead and lag noise pulses was determined for a 0.8° azimuth separation between transducers.

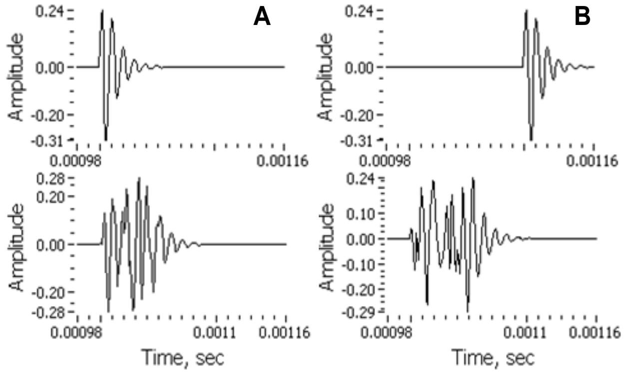

Fig. 4. Waveforms of a click and a 40-µs noise pulse transmitted simultaneously (A) and with some delay (B) relative to each other. Computer simulation at the acoustical side of the transducers

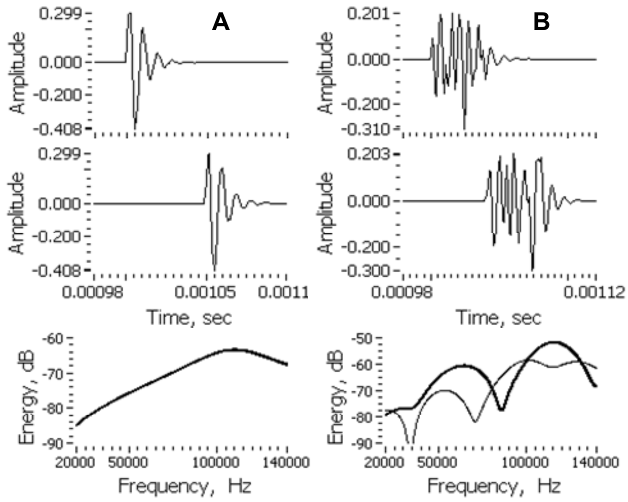

Fig. 5. Waveforms and energy spectra of lead and lag clicks (A) and 40-µs noise pulses (B).

The subject was adult Black Sea bottlenose dolphin (*Tursiops truncatus*). Experiments were conducted in a 28 x 13 x 4 m concrete pool. A two-response forced-choice procedure was used. The dolphin's start position was 5 m from two azimuthally separated transducers positioned at 1m depth (Fig. 6).

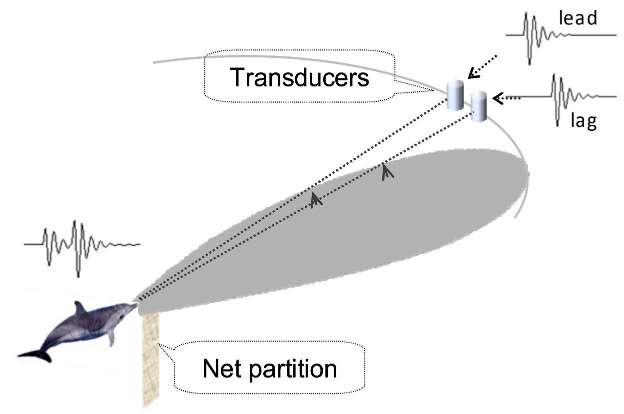

Fig. 6. Experimental setup.

The dolphin was required to indicate azimuth location of a standard signal by swimming to the left or right side of a net partition (Fig. 6). The standard signal was a single click, a noise pulse, when presented with a click (Fig. 4A), or a lead signal for lead-lag discrimination (Fig. 5). The choice of a transducer to transmit a standard signal for a given trial was randomized. Spherical transducers of 1.2 cm in diameter were used. The transducers transmitting response had maximum at 110-130 kHz and rolled off by 12 dB per octave toward lower frequencies (Fig. 5).

3 Results

Threshold azimuth separation between the transducers for a single click localization was found to be around 1.8° (Table 1, first row). This result is in an agreement with MAA of 0.9° (threshold shift from a midline) determined for a click in experiments with an Atlantic bottlenose dolphin [2]. The dolphin was able to discriminate between a click and a 40-μs noise pulse (Fig. 4A) at the transducer azimuth separation of around 1.2° (Table 1, second row). The same threshold azimuth separation was observed when the click followed (Fig. 4B) or preceded the noise pulse by 50 to 200 μs. The dolphin always approached the transducer of the noise pulse regardless temporal order of the click and noise pulse.

Similar to the target discrimination [4, 5], the passive lead-lag localization proved to be much more accurate than a single click localization. The lead-lag localization thresholds were as small as 0.2° and 0.36° for clicks and noise pulses, respectively.

Signals		The lag delay	Threshold azimuth separation
Click 30 μs			1.8°
Click 30 μs	Noise pulse 40 μs	0	1.2°
Click 30 μs	Click 30 μs	50-500 μs	0.25°
Noise pulse 40 μs	Noise pulse 40 μs	50-500 μs	0.36°
Noise pulse 300 μs	Noise pulse 300 μs	50-200 μs	0.4°

Table 1. Average threshold (75% correct response) azimuth separations between the left and right transducers.

The smallest delay between the lead and lag noise pulses, at which the dolphin still was capable of the lead-lag localization, was found to be 18-20 μs (Fig. 7, 40-μs noise pulses).

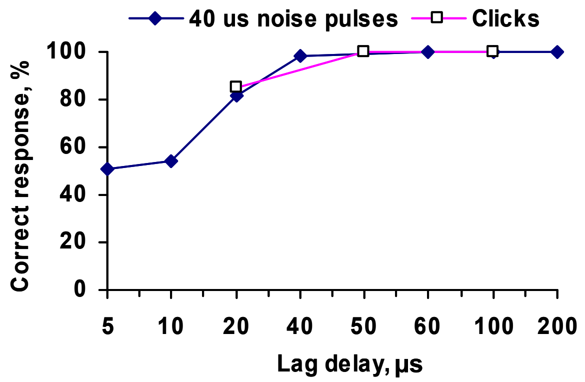

Fig. 7. Lead-lag discrimination as a function of the lag signal delay. Azimuth separation between the transducers was 0.8°.

We did not measure a threshold delay for the correlated clicks, but the lead-lag discrimination was still above 80% correct response for the lag delay of just 20 μs (Fig. 7, clicks).

It is almost obvious that the threshold azimuth separations are too small to represent angular resolution of the dolphin's auditory system. These results are clearly could not be easily fit in traditional binaural phenomenon known for humans. Even for the 1.2° threshold separation (for click-noise pulse discrimination) the interaural differences in time is just about 1 μs. For the 0.2° or 0.36° thresholds there is practically no time difference at all. It would be difficult to expect any interaural difference in intensities for such small angles as well. Besides, in humans, because of the "precedence effect" and "summing localization" phenomena, the sounds transmitted from two sources simultaneously or with a small delay relative each other would fuse into a single auditory image. In humans, the lead-lag localization thresholds are always larger than localization threshold for a single click or noise burst [7]. If the same binaural mechanisms were valid in bottlenose dolphins, the lead-lag localization threshold would have been no better that 1.8° threshold for a single click (Table 1).

Another important fact is that for uncorrelated noise pulses the lead-lag localization was almost as accurate as that for correlated clicks. In humans, the echo suppression does not work for uncorrelated signals [6]. Therefore, the results appear to confirm our previous findings that the precedence effect is absent in the bottlenose dolphin auditory system [3]. Interestingly, the precedence effect appears to be absent also in bats whatever the lag sound delay [13].

Because the comparison signals were identical clicks or uncorrelated noise pulses (Fig. 5), they could be discriminated only based on difference in position relative to each other. Even if the lead and lag signals do not fuse into a single image (in the absence of the precedence effect), the binaural auditory system still may be able to localize each of signals as two acoustic events separated in azimuth. Nevertheless, the only discrimination cue for the dolphin was a difference in the lead and the lag arrival times (the lag delay). In other words, the dolphin had to perceive the lead and the lag as two acoustic events coming with some delay relative to each other. Otherwise, if the lead and the lag are unresolved in time, the dolphin would perceive two identical signals in different directions but would not be able to discriminate them. The bottlenose dolphin appeared to perceive the lead and lag sounds as two separate acoustic events even at the lag delay as small as 18-20 μs (Fig. 7).

Even at very small azimuth separations the dolphin would pivot his head in horizontal plane by as much as ± 10°-15° similar to what was observed at target discrimination at small target separations [4]. This immediately suggests that the dolphin used the edges of the receive beam as shown in Fig. 6 to discriminate the sounds similar to another dolphin in our experiments that used edges of the sonar transmit and receive beams (Fig. 1). Using edges of the receive beam the dolphin apparently perceived the lead and lag signals as a pair of clicks (shown in Fig. 6 near the dolphin) with the lead-to-lag amplitude ratio correlated with position of the beam to the right or left from both transducers.

The receive beam pivoting in the horizontal plane would generate for the dolphin lead-lag double clicks with reversed order of a small and large clicks, similar to shown in Fig. 8 A and B. Because the lead and lag clicks were identical (Fig. 5A), the double clicks have the same energy spectra. There are, of course, some differences in the short-time frequency spectra (Fig. 8, bottom row) but in order to detect them, the analysis (integration) window should be comparable with the lag delay. Bottlenose dolphins appear capable of the time domain discrimination of brief signals with identical energy spectra with temporal acuity even higher than can be described by the auditory time resolution of 20-30 μs [14-17].

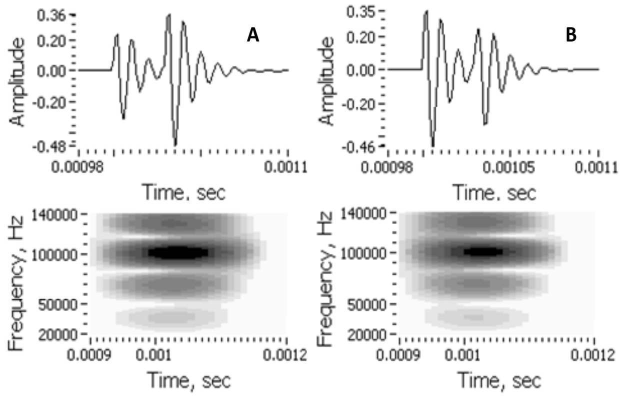

Fig. 8. A small click followed by a large click (A) and their time-reversed (large-small) counterpart (B). STFT-spectrograms were generated using 300-μs Hanning window and a time increment of 5 μs. The delay between the first and second clicks was 30 μs. A small-to-large click ratio was 3 dB. Computer simulation.

For the lead and lag noise pulses (Fig. 5B), the receive beam rotation in the horizontal plane (Fig. 6) would generate for the dolphin differences in envelopes similar to shown in Fig. 9.

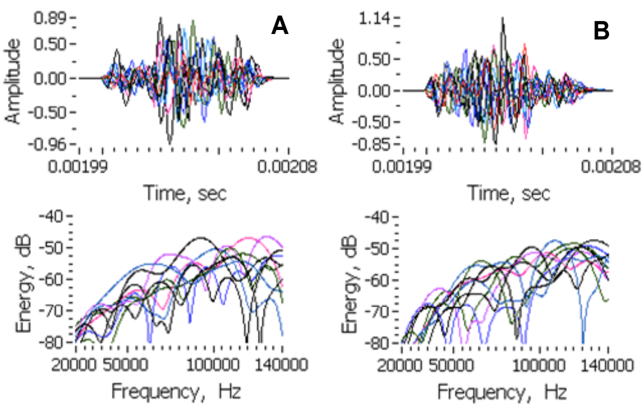

Fig. 9. Ten consecutive superimposed direct (small-large) pairs of 40-μs noise pulses (A) and time-reversed (large-small) pairs (B) and their energy spectra. The lag delay was 20 μs. A small-to-large noise pulse amplitude ratio was 3 dB. Computer simulation.

When the receive beam is directed to the side of the lag transducer as shown in Fig. 6, the envelope of the overlapped 40-μs lead and lag noise pulses begins with a well defined 20-μs step corresponding to the 20-μs lag delay (Fig. 9A). The step is much less apparent if the receive beam directed to the side of the lead transducer (Fig. 9B). The threshold lag delay of 18-20 μs appears to be one more estimate of the bottlenose dolphin auditory time resolution.

The edges of the receive beam should be steep enough to generate for the dolphin difference in the lead and lag click amplitudes of 0.5-1 dB (Fig. 3) for the threshold transducer azimuth separation of 0.25° (Table 1). At 120 kHz the bottlenose dolphin receive beam edges in vertical plane appear to be steep enough to generate around 1 dB difference per 1° [1]. When discriminating the lead and lag signals at a small azimuth transducer separation, the dolphin would turn on the left side by about 45° perhaps trying to place the transducers in the receive beam section with the steepest edges.

4 Conclusion

The lead-lag localization accuracy of 0.25°-0.4° proved to be much higher than a single click localization threshold of around 1.8°. The dolphin was capable of discriminating between lead and lag uncorrelated noise pulses at the lag delay as small as 20 μs which agrees well with the bottlenose dolphin auditory time resolution of 20-30 μs found in other behavioural experiments. The results suggest that the precedence effect is absent in the auditory system of the bottlenose dolphin. To discriminate between brief signals at small azimuth separations between transducers, the bottlenose dolphin appeared to use steep edges of the sonar receive beam.

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