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The beluga whale produces two pulses to form its sonar signal

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Odontocete cetaceans use biosonar clicks to acoustically probe their aquatic environment with an aptitude unmatched by man-made sonar. A cornerstone of this ability is their use of short, broadband pulses produced in the region of the upper nasal passages. Here we provide empirical evidence that a beluga whale (*Delphinapterus leucas*) uses two signal generators simultaneously when echolocating. We show that the pulses of the two generators are combined as they are transmitted through the melon to produce a single echolocation click emitted from the front of the animal. Generating two pulses probably offers the beluga the ability to control the energy and frequency distribution of the emitted click and may allow it to acoustically steer its echolocation beam.

Keywords: echolocation; beluga; click; double pulse; sound production; phonic lips

1. INTRODUCTION

The echolocation faculty of odontocete cetaceans allows them to probe the aquatic environment with higher acuity than any existing man-made sonar systems (Au 1993). They accomplish this by emitting highly directional, short (<200 μ s), broadband clicks in rapid trains. Since the discovery that odontocetes use echolocation (Kellogg 1958), the production mechanism of their biosonar signal has been a topic of vigorous investigation. Early works hypothesized that sounds are produced by the larynx (Purves 1966; Purves & Pilleri 1983), but convincing evidence has since established that the source is in the upper nasal region within a structural ensemble termed the 'monkey lips/dorsal bursae' (MLDB) complex (Cranford *et al.* 1996; Cranford 2000). It has been previously shown that two separately controlled 'phonic lips' exist in the MLDB, and that both are capable of producing sonar clicks either independently or simultaneously (Cranford *et al.* 2000). It has been further suggested that both generators might work together to create the emitted sonar click (Lilly 1967; Norris *et al.* 1972; Cranford *et al.* 1996; Cranford & Amundin 2003), but the process has never been directly observed acoustically during echolocation.

In this study, we investigated the sonar click production of a captive beluga whale (*Delphinapterus leucas*)

by recording emitted clicks at a close range from the presumed sound source along a 180° horizontal arc around the animal's head while it echolocated on a target hydrophone. We simultaneously recorded the clicks on the axis of the emitted sonar beam and also to the animal's side, off-axis of the beam. This gave us the opportunity to observe and characterize sonar signal production between 90° and -90° to either side of the centre (0°) of the beam.

2. MATERIAL AND METHODS

The animal used for the experiment was a 9-year-old female beluga housed at L'Oceanografic aquarium in Valencia, Spain. The animal was trained to enter a stationary steel hoop 1 m below the surface and echolocate upon command on a target hydrophone (ITC 1094A) suspended 1.5 m below the surface and 5.0 m directly in front of the position of the blowhole. A second hydrophone (ITC 1094A) was placed at an offset angle relative to her longitudinal axis. This hydrophone was suspended 1.1 m below the surface at a horizontal distance from her blowhole of 1.25 m. While maintaining the depth and distance constant, the angle of the second hydrophone relative to the axis of her echolocation beam was changed on successive experimental sessions by 15° from -90 to 90° off axis (excluding 0°). For each session, the animal was made to enter the hoop 10–12 times and echolocate on the target hydrophone. The signals from the off and on axis hydrophones were amplified by 56 and 36 dB, respectively, before being low-pass filtered at 150 kHz and recorded simultaneously using a Measurement Computing PCI-DAS4020/12 analogue-to-digital converter sampling at 500 kHz. Recordings were obtained when it was established that the animal's head was stationary and directed towards the target hydrophone. The data were analysed using algorithms developed in MATLAB release 14.

3. RESULTS

All recordings made off axis at $\pm 90^\circ$, $\pm 75^\circ$, $\pm 60^\circ$ and $\pm 45^\circ$ exhibited the presence of two distinct pulses for the corresponding singular sonar click observed on axis (figure 1). The interval between these double pulses was greatest $\pm 90^\circ$ off axis and progressively decreased with each 15° closer to the centre of the beam (table 1). At $\pm 30^\circ$ off axis a single pulse was observed with multiple peaks, while at $\pm 15^\circ$ and 0° only one dominant peak was evident, which remained consistent throughout the experiment.

The inter-pulse intervals (IPI) between the double pulses (table 1) were not consistent with any reflective paths present in the experimental environment. The nearest reflective area, the water's surface, was 1 m above the animal's head, resulting in an expected pulse interval of approximately 850 μ s. The nearest tank wall was 222 cm away, which would have produced a minimum pulse interval of approximately 1300 μ s when the off-axis hydrophone was at the -90° position. Additionally, the IPIs did not change when the stationing hoop was placed deeper, shallower or moved horizontally, supporting the conclusion that external reflections could not be the cause of the second pulse.

IPIs were also not consistent with delays expected from reflections within the head, such as those from air sacs or cranial features within a few centimetres of the MLDB complex. Tissue has an acoustic impedance similar to water (Ludwig 1950), so internal reflections would be expected tens of microseconds following the direct pulse, not hundreds as we observed (table 1). In addition, the second received pulse was frequently greater in amplitude than the first (discussed further below), requiring the presence of a better than perfect reflective surface to be viable as a potential origin.

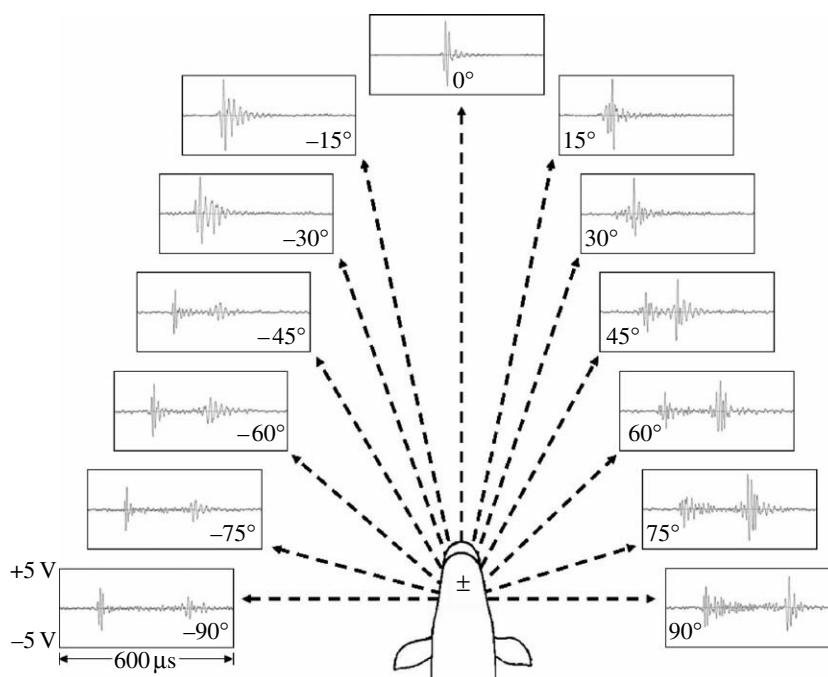


Figure 1. Sonar pulses produced by the beluga whale as recorded at 15° angular intervals in a 180° arc along the horizontal plane of the animal. The pulses shown are representative examples of the on-axis click and off-axis pulses measured separately for each angle.

The lack of possible external or internal reflective surfaces as the origin of the second pulse leaves two separate sound sources as the only viable explanation. However, this will also be problematic if the sound transmission path between the two sources and the off-axis hydrophone is assumed to be exclusively through tissue. At $\pm 90^\circ$ off axis, assuming a sound speed constant of approximately 1500 m s^{-1} , this places the two sources 38–46 cm apart, a distance too great to reconcile with the animal's head size (which measures 33 cm in diameter at the blowhole), unless a nonlinear transmission path is assumed.

On the other hand, if the two sources are presumed to be separated by air, with a constant of approximately 340 m s^{-1} , the calculated separation is 8.7–10.4 cm, which is approximately consistent with the expected horizontal separation between the phonic lips (extrapolated from evidence presented by Cranford *et al.* (2000) for a bottlenose dolphin, *Tursiops truncatus*). A transmission path through air is plausible because the MLDB complex is bounded dorsally by the vestibular sac, a large air-filled structure involved in air recycling during phonation (Dormer 1979). Both phonic lips terminate on the floor of this sac and can be observed vibrating when an endoscope is placed through the blowhole and into the vestibular sac (Cranford *et al.* 2000). Furthermore, the amplitudes of the pulses measured off axis are consistent with the loss expected from sound crossing the air–tissue boundary. The off-axis pulses we measured have estimated source levels (SLs) between 33 and 41 dB lower than the clicks measured on axis (table 1), which matches reasonably well with the 30 dB loss expected as a result of the air–water impedance difference (Caruthers 1977). It should also be noted, however, that air–water impedance

differences can be quite variable and difficult to predict in restricted spaces when the transmitted wavelength is equivalent or smaller to the space it is crossing due to reverberation effects (Weiss 1970).

Based on these observations, we conclude that the most viable explanation for the presence of the off-axis double pulses is that the beluga used both phonic lips to produce simultaneous or near-simultaneous signals. The interval between pulses, we believe, represents the delay in transmission through the air space of the vestibular sac, although we presently cannot entirely exclude a nonlinear refractive path through tissue.

The two-source explanation is further supported by the observations made during several instances when the animal momentarily turned away from the target hydrophone to face the off-axis hydrophone. Figure 2 shows the click train from such a case as it was recorded by the hydrophone positioned 45° off-axis. A click-by-click analysis reveals that when the animal was directed towards the target hydrophone, the off-axis hydrophone received paired pulses. When the animal briefly turned to face the off-axis hydrophone, the two pulses converged into one and then separated again into two as the animal's attention was re-directed towards the target hydrophone. This pattern could only arise if both pulses originated within the animal's head.

Measurements of the on- and off-axis recorded signals reveal trends in how double pulses are produced. Examining the SLs and centre frequencies of the two pulses shows a right–left bias (table 1). The relative difference in amplitude between pulses originating from the left and right phonic lips indicates that, on average, the left side produced higher amplitude pulses than the right (*T*-test: $t = -8.60$,

Table 1. Variability between double pulses recorded off axis. This table reports the temporal separation between double pulses, the average calculated off axis peak-to-peak source level (SL) of the first pulse, the difference between the SLs of the first and second pulses and the difference between the centre frequencies of the first and second pulses.

	degrees off axis										
	-90°	-75°	-60°	-45°	0°	45°	60°	75°	90°		
avg. interval (stdv) between pulses in μ s	306 (24)	246 (17)	196 (18)	151 (19)	n.a.	127 (23)	187 (11)	225 (20)	256 (25)		
avg. SL (stdv) of first pulse in dB re 1 μ Pa	140.9 (2.5)	147.9 (4.3)	144.6 (2.6)	140.9 (3.5)	182.1 (3.1)	147.3 (3.9)	145.6 (4.6)	142.4 (3.3)	141.5 (2.3)		
SL first pulse-SL second pulse in dB re 1 μ Pa	4.1	5.1	5.8	2.5	n.a.	-1.4	0.1	-2.3	-2.9		
ctr. freq. first-ctr. freq. second in KHz	28.0	37.9	28.9	26.2	n.a.	11.3	12.2	10.6	30.4		

$p < 0.001$, d.f. = 103). A similar comparison of the centre frequencies of the two pulses shows that, although the first pulse on both sides consistently has a higher centre frequency than the second, the difference between them is significantly greater on the left side (T -test: $t = -7.30$, $p < 0.001$, d.f. = 93). This implies that the pulse produced by the left phonic lip has, on average, a higher centre frequency than the right one.

4. DISCUSSION

Using both sound generators to produce the echolocation signal probably provides several advantages over using only one. One advantage may be that the summed energy of the two pulses is greater than the output each generator is capable of producing individually. A higher amplitude signal will transmit further and therefore provide a greater target detection range. In our experiment, the target hydrophone was only 5 m away, suggesting that the use of both generators may be inherent in the production of beluga sonar clicks rather than a distinct mode used to detect distant targets. Another advantage may relate to the bandwidth and spectral content of the emitted click. Since the pulse from each generator contributes energy at different frequencies, the summed click probably results in a broader spectrum than that of the individual pulses. A broad spectrum provides advantages for target detection and classification (Au 1993). Furthermore, modulating the amplitude of each pulse could provide greater control over the distribution of energy at different frequencies. In fact, clicks with multimodal spectra and variable frequency peaks are well documented in beluga and other odontocete species (Au *et al.* 1985; Moore & Pawloski 1990). Finally, an intriguing possibility is that the beluga may use slight time delays in the production of each pulse to actively control the width and orientation of its echolocation beam (Cranford & Amundin 2003; Cranford *et al.* 2008). Recent experiments with bottlenose dolphins (*T. truncatus*) have found that they in fact have such a control (Moore *et al.* 2008).

How widespread the use of double pulses is among odontocetes will need to be determined experimentally. However, the use of new fractional Fourier analysis methods to decompose *Tursiops* clicks has revealed a spectral structure with energy distributed between two main frequency bands delayed by 5–20 μ s, also hinting at the presence of two formative pulses in this species (Capus *et al.* 2007). Additionally, Miller *et al.* (2007) have shown that killer whales (*Orcinus orca*) produce biphonation tonal calls and demonstrated interaction effects consistent with two sources functioning simultaneously. Perhaps most telling, however, is the conserved nature of the MLDB complex across non-physeteroid odontocetes (Cranford *et al.* 1996), which suggest that double pulse production could be a common if not universal form of sonar signal generation in the entire sub-order.

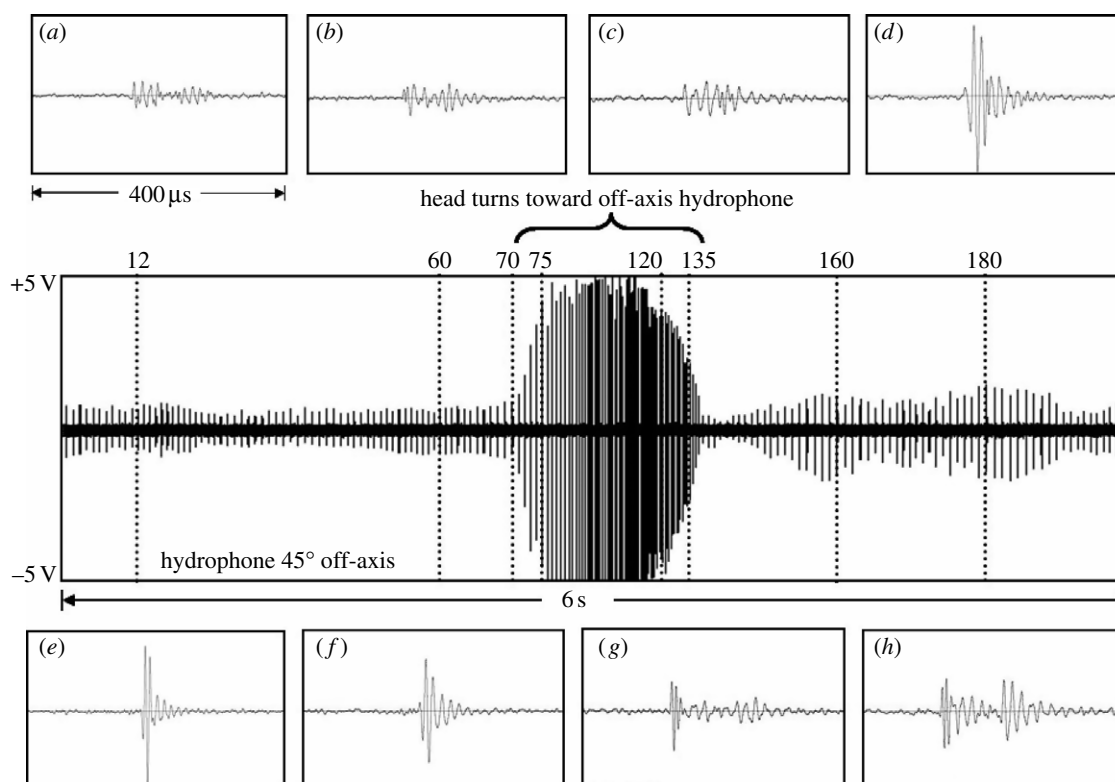


Figure 2. An example of the changes in pulse structure observed on the off-axis hydrophone as the beluga momentarily turns to ensonify it. The double pulse structure is present while the animal is facing the target hydrophone, then gradually changes to a single observed click as the off-axis hydrophone is ensonified directly, and then returns to the double pulse structure as the animal's focus is returned to the target hydrophone. (a) Click # 12, (b) click # 60, (c) click # 70, (d) click # 75, (e) click # 120, (f) click # 135, (g) click # 160 and (h) click # 180.

The experiment complied with the Principles of Animal Care, publication no. 86-23, revised 1985, of the National Institute of Health and also with current Spanish laws.

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