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NASAL PRESSURE AND SOUND PRODUCTION IN AN ECHOLOCATING  
WHITE WHALE, Delphinapterus leucas

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INTRODUCTION

At the Jersey conference on Animal Sonar Systems in 1979 we gave strong evidence that dolphins produce sound in the nasal system rather than in the larynx as most mammals do (Ridgway et al. 1980). With electromyography (EMG), we studied the activity of laryngeal muscles and nasal muscles, making comparisons between the two groups of muscles during sound production. Certain muscles of the nasal system were active during all dolphin whistles and click trains while muscles of the larynx were active during respiration but not during sound production. Perhaps more importantly, we measured pressure in the nasal cavities and in the trachea adjacent to the larynx. During sound production, intranasal pressure increased markedly but intratracheal pressure remained unchanged. Subsequently, Amundin and Andersen (1983) replicated the EMG and pressure monitoring aspects of our study in Tursiops and Phocoena.

Finally, we put a catheter or tube in the nasal cavity and sealed the opening of the tube with a thumb, the dolphin could produce sound with this sealed tube in place, but if the thumb was lifted, releasing pressure in the nasal cavity, the animal could not phonate.

In none of the previous studies was the dolphin making an echolocation discrimination during the tests, so we could not be certain that we were studying the actual echolocation generating system. Therefore, we decided to study the Arctic white whale Delphinapterus leucas in a more sophisticated experiment.

MATERIALS AND METHODS

The experimental animal was a male Delphinapterus about 10 years of age that was collected near Churchill, Manitoba, Canada, in the summer of 1977 and had been with our program since that time. At the time of these experiments the whale was 340 cm in length and weighed 450 kg. During training the whale was fed 18 to 20 kg per day of Columbia River smelt, Pacific mackerel, and herring.

The whale was conditioned to allow its trainer to place opaque suction cups over its eyes, to station on a plastic bite bar one meter underwater and behind an acoustically opaque screen made from a closed cell air-foam material, and when the screen was raised to make a discrimination of target present or target absent. The target was a cylinder of 10 X 3.81 cm aluminum pipe with a wall thickness of 0.32 cm suspended on monofilament line one meter in front of the bite bar at one meter depth. The animal was trained to whistle when the target was present and to remain silent for at least 15 seconds when no target was present.

Since this is the first instance we know of in which a cetacean has been trained to vocally report target-present in an echolocation task, perhaps the method used to train this behavior

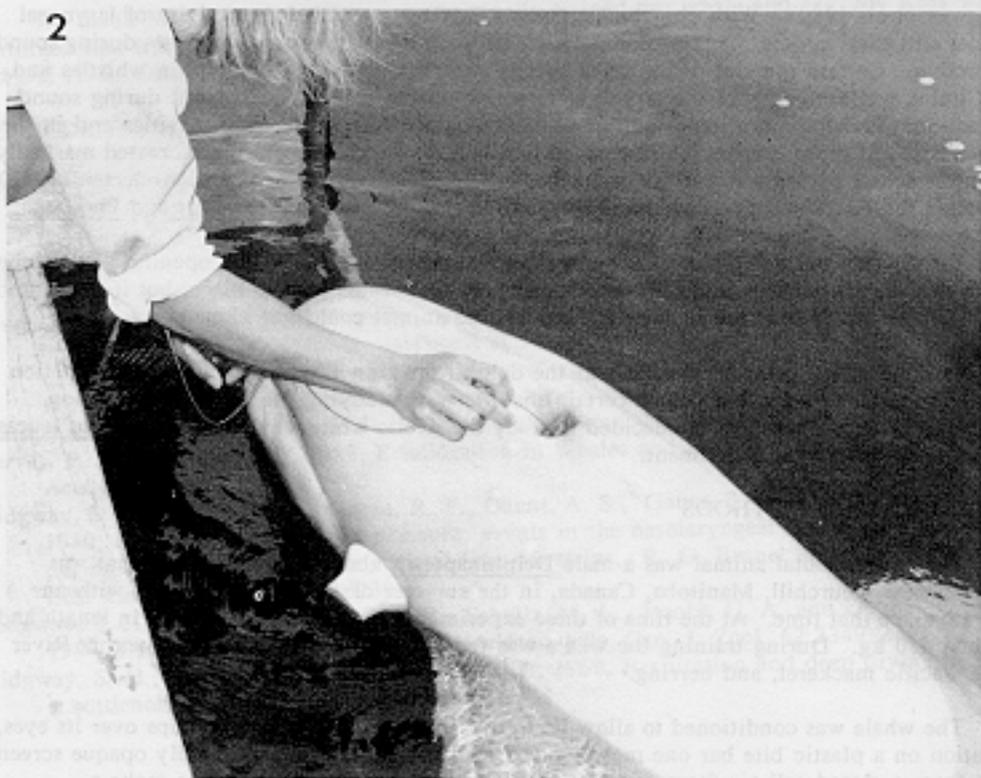
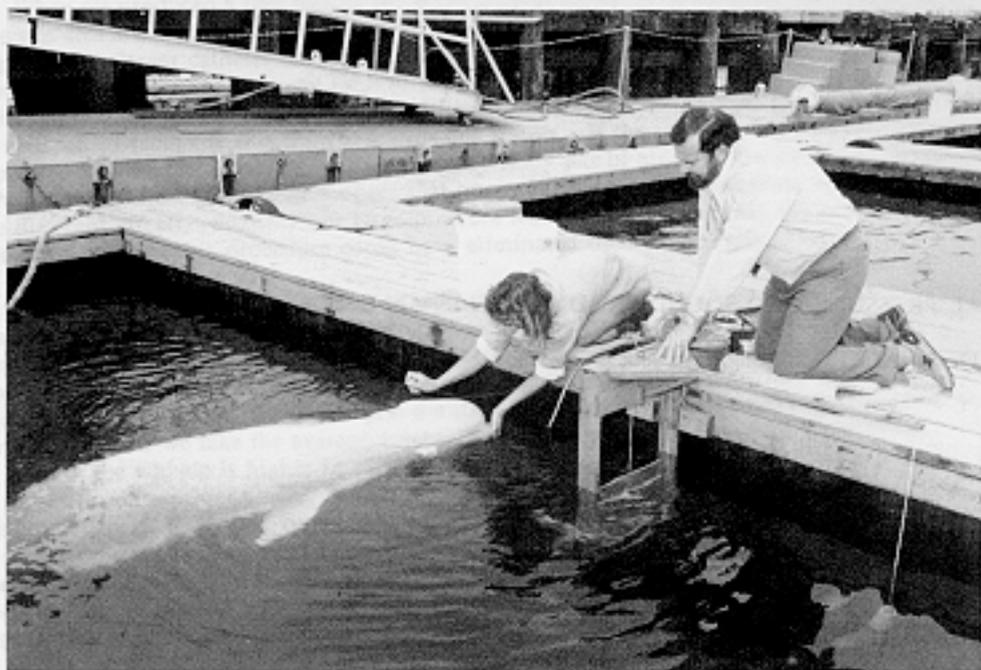


Figure 1. (1) The whale stations at the surface in front of the trainer who is shown inserting the catheter before sending the whale down to the bite bar to wait for the screen to raise for a detection trial. The target is suspended 1 m forward of the screen. (2) A closer view of the trainer inserting the catheter into the whales blowhole. The suction cup blindfolds are made of soft silicone rubber.

deserves special mention. We noticed that when the whale whistled, there was a characteristic movement along the left posterior margin of the blowhole often with the escape of some air. Our trainers quickly induced the whale to repeat vocalizations by tapping with a finger or manipulating the area of the blowhole where movement and air escape had been detected. After whistles were reliably elicited in this manner, the signal was transferred slowly to a simple stroke of the whale's melon. Now, with the blindfolded whale on the bite bar and the target in the water in front of the screen, the trainer raised the screen and then reached down to stroke the whale, eliciting the whistle for which the trainer sounded a bridge signal and gave the whale a fish reward.

Raising the screen invariably resulted in a train of echolocation pulses from the whale. If the target was absent, the trainer did not stroke the whale to elicit the whistle. Gradually the trainer's stroke was omitted as the whale began to whistle when the target was present. When the target was absent, only echolocation clicks were emitted by the whale. The echolocation task was apparently simple for the whale and over 98% correct responses were achieved during several sessions.

Training the catheter insertion was the most difficult step. The trainer touched the whale just behind its blowhole until the animal opened the blowhole. First the whale was rewarded for leaving his blowhole partly open and allowing the trainer to insert the catheter only about 1 cm. Gradually the insertion depth was increased until the catheter could be placed 20 cm into either right or left nasal cavity. Once the whale would allow the catheter to be placed in the nasal system, he was rewarded for sealing his blowhole around it.

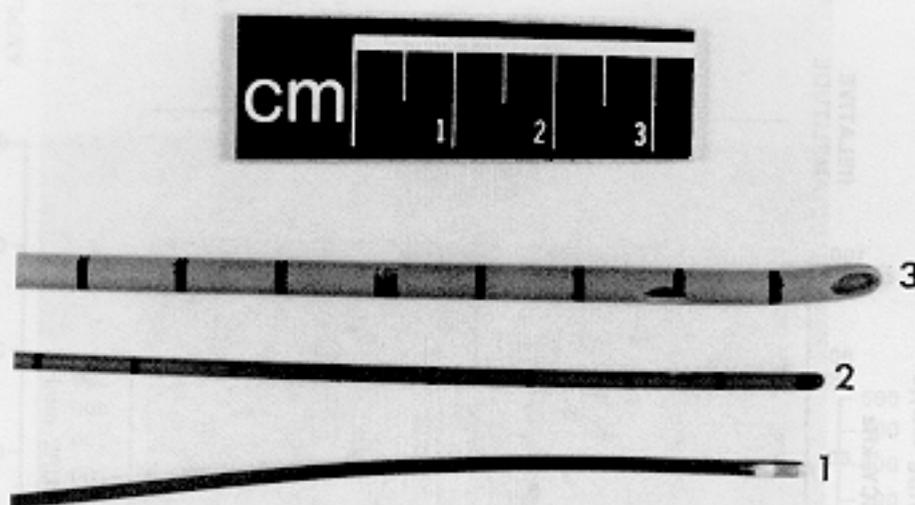


Figure 2. Three catheters were used in the experiment. The closed Millar catheter (1) contains a pressure transducer that rapidly measures pressure (frequency response to 35 kHz) with an electronic sensor under the white area near the tip. A voltage proportional to pressure was amplified from wire leads and recorded. The other two catheters (2) and (3) are intravascular catheters. The larger has an outside diameter of about 3 mm and an inside diameter of 2 mm. The smaller one has an outside diameter of 1 mm and an inside diameter of about 0.5 mm.

Finally, the sequence of trained behaviors was as follows: The whale stationed on the surface near the trainer, the trainer placed the eye cups on the whale, the trainer touched the whale behind the blowhole, the whale opened its blowhole, the trainer inserted the catheter (Figure 1), the whale closed the blowhole, the trainer touched the whale's melon signalling it to go on the bite bar one meter under water, the trainer raised the screen, and the whale pulsed and responded with a whistle when the target was present or no whistle when the target was absent. The screen was then lowered. With a correct response, the trainer sounded a bridge and the whale surfaced for a fish reward. Gradually, the series was extended so that the whale would make three to five responses during one submersion on the bite bar. If the whale's response was

was incorrect, the trainer splashed the water and required the whale to surface and station without reward before she sent the animal back to the bite bar for another series. The target presentation was randomized by referring to a Gellerman series.

Three types of catheters (Figure 2) were used: a 1-mm tube catheter with an opening of about 0.5 mm, a 3-mm tube catheter with an opening of about 2 mm, and a closed Millar pressure transducer catheter with a frequency response of about 35 kHz. All of these catheters were used alone or in combination.

Two hydrophones (B & K 8103) were used to record sounds from the whale. The one for recording echolocation was placed 2 m forward of the bite bar and 10 cm to the left of a line drawn from the blowhole through the target. The hydrophone for recording whistles was placed 50 cm to the left of the whale's melon. The hydrophone outputs, along with FM and analog pressure signals from the Millar catheter and a voice log, were recorded on a Racal instrumentation tape recorder at a speed of 60 inches (152.4 cm) per second. The recorded sound was analyzed on an SD-350 real-time spectrum analyzer with a filter bandwidth of 62.5 Hz or 125 Hz depending on the frequency range setting used.

## RESULTS

The whale maintained a high level of correct responses even when all three sealed catheters were placed into the blowhole. With one or more of the catheters in place, the whale responded correctly on more than 90% of the trials after an initial training period of approximately 500 trials was complete. We then recorded 238 trials (106 without a target) with

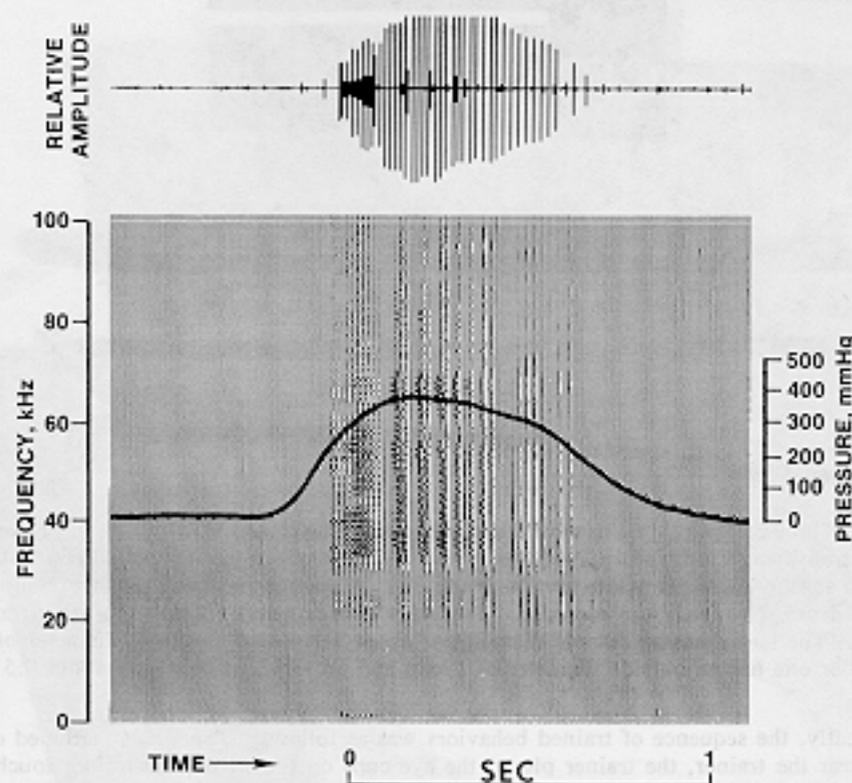


Figure 3. Spectrogram of a typical response by the white whale to a target absent trial. Only echolocation pulses are emitted by the whale. The upper tracing labeled relative amplitude records the peak acoustic amplitude in each 6.5 msec line of the spectrogram. The lower section is a 0 to 100 kHz spectrogram with a bandwidth of 62.5 Hz. The heavy black line indicates pressure. The output of the recorded pressure channel was fed into a voltage-controlled oscillator and calibrated to frequency-modulate a 40 kHz signal in proportion to pressure so that the pressure and acoustic events could appear on the same graph.

catheters in place in either the left or right nasal cavity. The whale responded correctly on 213 trials (89.5%). On 123 trials the whale correctly identified the target as present by whistling after the screen was raised. On 90 trials, the whale correctly responded to the absence of the target by refraining from whistling for 15 seconds after the screen was raised.

High-speed tape recordings of these trials allowed us to directly compare air pressure within the nasal cavities with all sound produced by the whale during each trial. A spectrogram showing a typical response to a target-absent trial is shown in Figure 3. On the target-absent trials only echolocation pulses were emitted by the whale. In contrast, a target-present trial is shown in Figure 4. The intranasal pressure increased just as the screen was raised and just before the whale began to pulse. The pressure increased slightly as the pulse amplitude rose. A typical pulse from this train is shown in Figure 5. The first two high-amplitude peaks were very consistent, lasting 40 or 50 usec. The second component was smaller and much more variable, lasting 50 to 100 usec. Peak frequencies measured on our spectrum analyzer ranged from 50 to 80 kHz. With the end of the echolocation pulse train, intranasal pressure increased still more before the whistle began, and remained high during the whistle. During the whistle, pressure fell slightly as the tone swept down in frequency and rose as the tone swept up. Thus increasing frequency occurred with rising pressure and decreasing frequency with falling pressure.

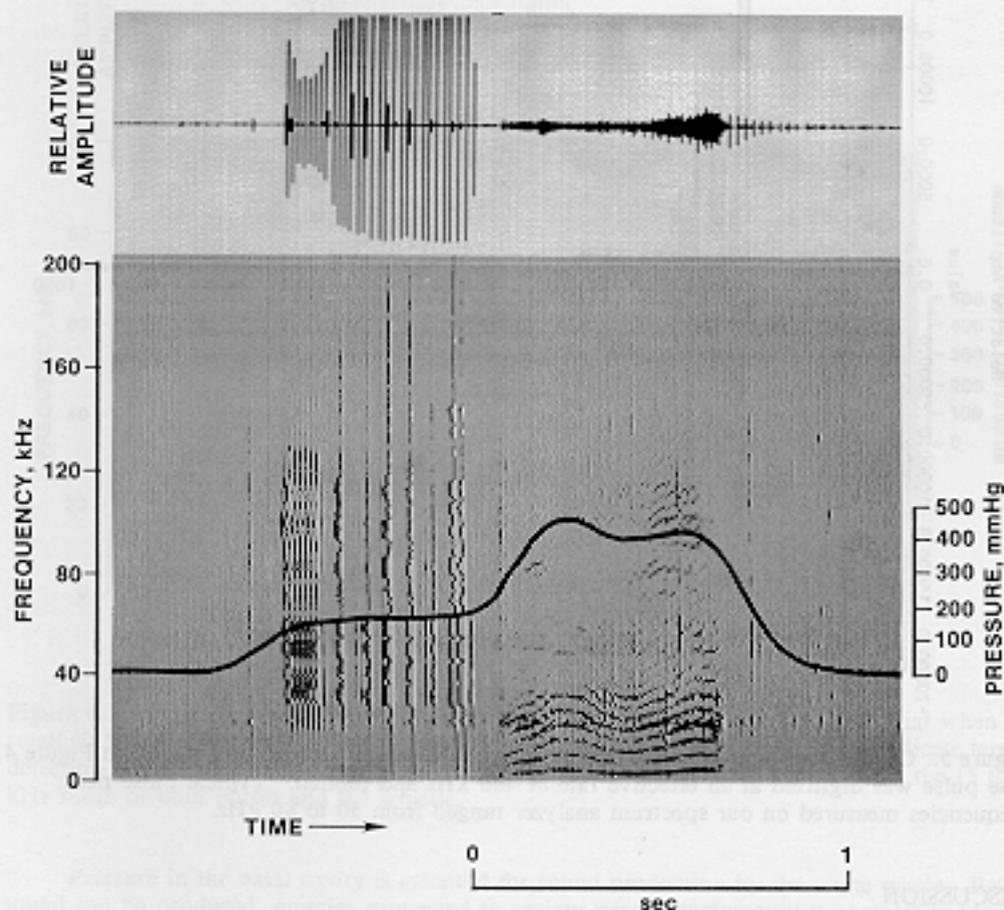


Figure 4. Spectrogram of a typical response by the white whale to a target present trial. Since the measured frequencies were 0 to 200 kHz the frequency bandwidth for this record was 125 Hz.

With the sealed pressure catheter in either the right or left nasal cavity, the whale was able to perform the task correctly. Whenever the whale pulsed or whistled, pressure was always increased. At times during whistles, intranasal pressure reached 800-mm Hg or more than an atmosphere of positive pressure.

On some trials we inserted an open catheter along with the pressure catheter. If we held a thumb over the open catheter, effectively sealing it, there was no change in the whale's behavior or sound production. However, if we lifted the thumb as the screen was raised, effectively producing an opening in the nasal cavity, the result was different. With our 1-mm catheter, which had an opening of about 0.5 mm, the whale was able to pressurize and produce a least one train of pulses. However there was often noise or distortion within the 15 to 40 kHz range and the whistle was always truncated and somewhat distorted (Figure 6). Even with the larger catheter in place the whale could pressurize its nasal system, echolocate, whistle, and perform the entire task correctly as long as the catheter was plugged. However, if we unplugged the larger 3-mm tube which had an opening of about 2 mm, we could feel the air rush out as the whale attempted to pressurize for echolocation when the screen was raised. With this larger catheter open in either nasal cavity the whale could not produce pulses or whistles.

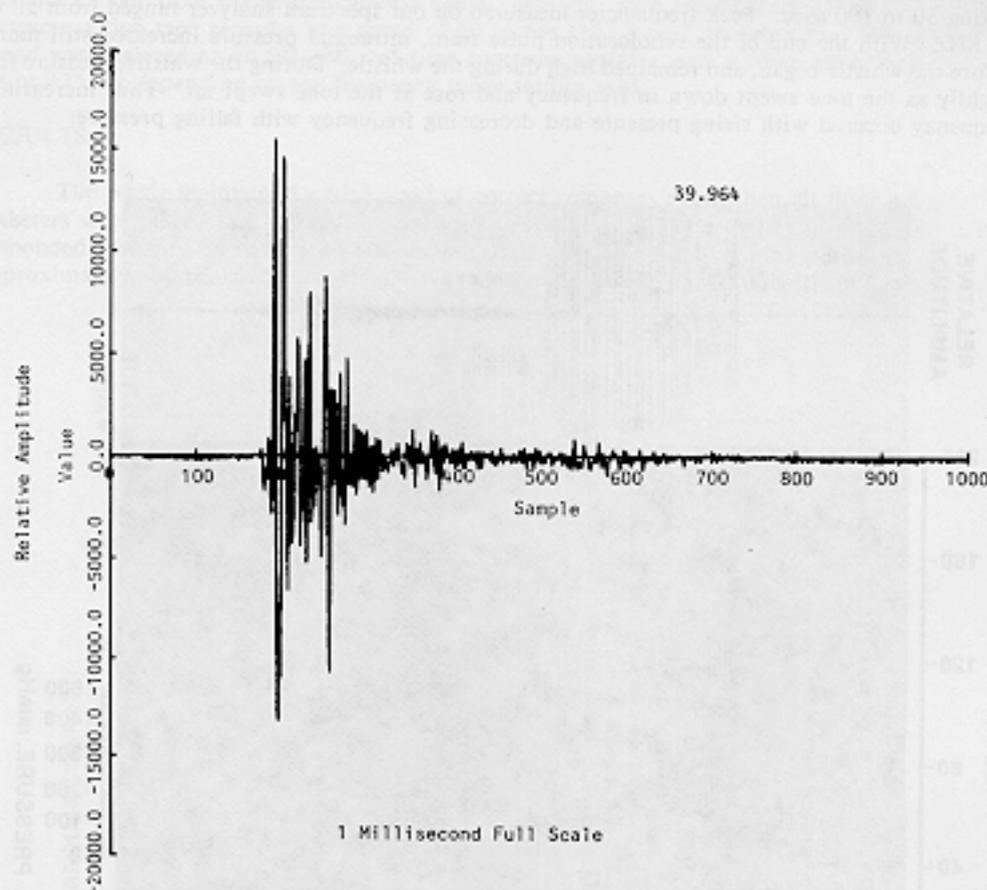


Figure 5. Oscillogram of an echolocation pulse from the target-present trial shown in Figure 4. The pulse was digitized at an effective rate of 480 kHz and plotted. Typical pulse peak frequencies measured on our spectrum analyzer ranged from 50 to 80 kHz.

## DISCUSSION

Since toothed whales routinely dive in search of food into waters where very little light penetrates, most species apparently rely on echolocation for finding food. Therefore, the animal must maintain a working sound production system as it dives in the sea and is continually subjected to pressure changes. Air in the thorax is compressed as the whale dives. If sound were produced in the larynx, as it is in most mammals, the resonant characteristics of the dolphin sounds would continuously change with the pressure change. However, the best evidence from the toothed whales that have been studied suggests that Tursiops, Delphinapterus,

*Delphinus*, *Phocoena*, and *Stenella*, at least, produce sound not in the larynx but in the nasal system (Dormer, 1979; Ridgway et al., 1980; Mackay and Liaw, 1981; Amundin and Andersen, 1983). Since the volume of the nasal system is relatively small, air moved from the lungs can maintain a sufficient volume for sound production as the lung is compressed. Because air pressure and water pressure are equilibrated at any depth, muscles will be able to operate the sacs and valves of the nasal system to produce pressure differentials.

White whales are capable of diving to depths of more than 600 m (Ridgway et al. 1984) where absolute water pressure is greater than 60 atmospheres. As the whale dives, air cavities within the whale are compressed; the whale's thorax is especially flexible to accommodate collapse as air in the lungs is compressed (Ridgway et al., 1969). Since the blood and tissues of the whale, like water, are nearly incompressible, only the air-containing portions of the animal are markedly affected by water pressure. The whale's heart does not have to pump blood against a large differential pressure as the animal dives. Water pressure is applied almost equally over the whale's body and is quite different from differential pressure within the whale's body like that we observed during sound production.

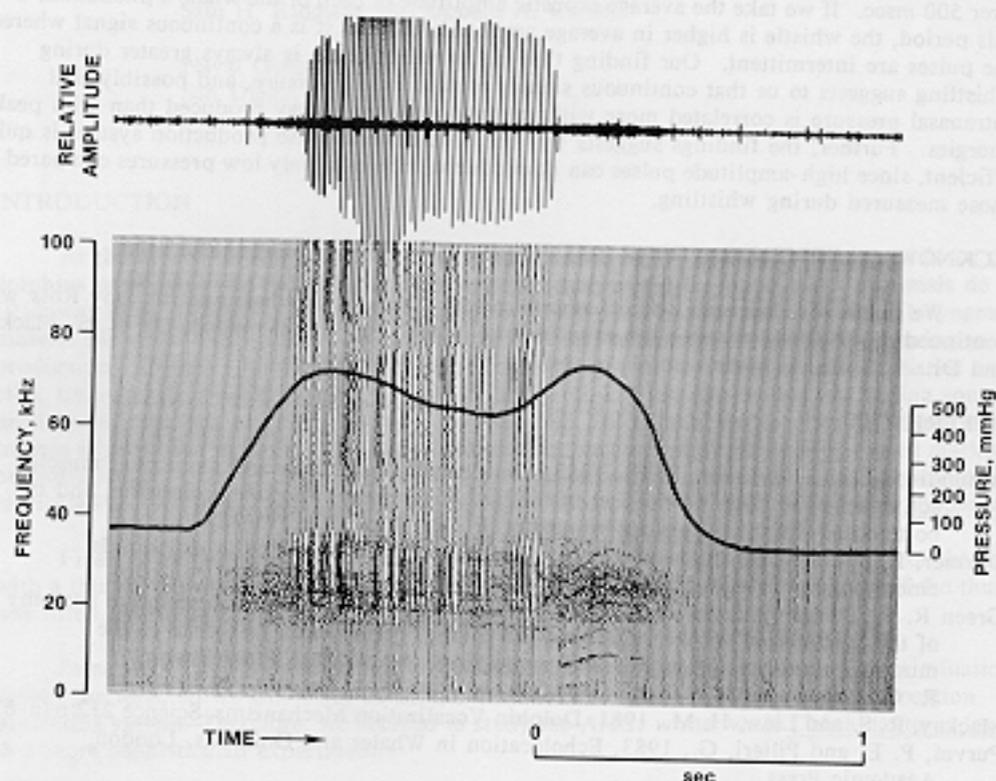


Figure 6. A spectrogram showing the whale's response during a target-present trial when a small (0.5 mm) open catheter was in the left nasal cavity. The whistle given to indicate target-detection is truncated and there is some distortion of the typical sound, especially in the 15 to 40 kHz range of both pulses and the whistle.

Pressure in the nasal cavity is essential for sound production by the white whale. Before sound can be produced, muscles connected to various nasal structures must contract producing pressure inside the nasal cavity. Our studies have shown that this pressure is typically much higher, often four or more times higher, than blood pressure. With such high pressures it is important to isolate the pressure chamber driving sound production from the thoracic cavity. Such pressures must compress adjacent blood vessels and drive blood from adjacent tissue. This would be detrimental to critical circulation in the thorax. The bony nasal cavities, nasal sacs and the fibromuscular nasal plugs have a tough structure that can tolerate such differential pressures during sound production.

When we produced a tiny leak in the whale's nasal cavity by opening the small catheter the whale was still able to produce sound but with some distortion. When we produced a sizable leak by opening the larger catheter the whale could not produce sound. If the sounds were produced below the nasal cavity (i.e. in the larynx) this should not happen. Purves and Pilleri (1983) considered that "all pressure changes during phonation are initiated in the larynx". We think that it is difficult to reconcile this assertion with our results. If the echolocation pulses were "relaxation oscillations" produced in the nasal cavity by jets of air from the larynx as suggested by Purves and Pilleri (1983), we suspect that our experimental manipulations would have had quite different effects. Possibly our large pressure leak would have altered the pulses, but it is difficult to see how this procedure could have eliminated them completely.

Whistles that the whale produced to indicate that the target had been detected were always attended by higher pressures than the echolocation pulse train that preceded. This at first seemed paradoxical since the peak acoustic energy in each echolocation pulse is considerably higher than that of the whistle. However, the pulses are periodic signals lasting at most a few hundred msec. In Figure 4 the pulse train duration is just under 500 msec and the whistle is just over 500 msec. If we take the average acoustic amplitude of each of the whale's phonations over this period, the whistle is higher in average amplitude because it is a continuous signal whereas the pulses are intermittent. Our finding that intranasal pressure is always greater during whistling suggests to us that continuous signals require more pressure, and possibly that intranasal pressure is correlated more with the total acoustic energy produced than with peak energies. Further, the findings suggests that the echolocation pulse production system is quite efficient, since high-amplitude pulses can be produced with relatively low pressures compared to those measured during whistling.

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#### REFERENCES

- Amundin, M. and Andersen, S. H., 1983, Bony nares air pressure and nasal plug muscle activity during click production in the harbor porpoise, *Phocoena phocoena*, and the bottlenosed dolphin, *Tursiops truncatus*, *J. Exp. Biol.* 105:275-282.
- Dorner, K., 1979, Mechanism of sound production and air recycling in delphinids: cineradiographic evidence, *J. Acoust. Soc. Am.* 65:229-239.
- Green R. F., Ridgway, S. H. and Evans, W. E., 1980, Functional and descriptive anatomy of the bottlenosed dolphin nasolaryngeal system with special reference to the musculature associated with sound production. In: *Animal Sonar Systems*, R. G. Busnel and J. F. Fish, Eds. Plenum, New York, pp199-238.
- Mackay, R. S. and Liaw, H. M., 1981, Dolphin Vocalization Mechanisms, *Science* 212:676-678.
- Purves, P. E. and Pilleri, G., 1983, *Echolocation in Whales and Dolphins*, London, Academic Press.
- Ridgway, S. H., Carder, D. A., Green, R. F., Gaunt, A. S., Gaunt, S. L. L. and Evans, W. E. 1980, Electromyographic and pressure events in the nasolaryngeal system of dolphins during sound production. In: *Animal Sonar Systems*, R. G. Busnel and J. F. Fish Eds. Plenum, New York, pp239-249.
- Ridgway, S. H., Bowers, C. A., Miller, D., Schultz, M. L., Jacobs, C. A. and Dooley, C. A., 1984, Diving and blood oxygen in the white whale, *Can. J. Zool.* 62:2349-2351.
- Ridgway, S. H., Scronce, B. L. and Kanwisher, J., 1969, Respiration and deep diving in a bottlenose porpoise, *Science*, 166:1651-1654.