Click production during breathing in a sperm whale (*Physeter macrocephalus*) (L)

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A sperm whale (*Physeter macrocephalus*) was observed at the surface with above- and underwater video and synchronized underwater sound recordings. During seven instances the whale ventilated its lungs while clicking. From this observation it is inferred that click production is achieved by pressurizing air in the right nasal passage, pneumatically disconnected from the lungs and the left nasal passage, and that air flows anterior through the phonic lips into the distal air sac. The capability of breathing and clicking at the same time is unique among studied odontocetes and relates to the extreme asymmetry of the sperm whale sound-producing forehead. *© 2005 Acoustical Society of America.* [DOI: 10.1121/1.2126930]

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I. INTRODUCTION

The sperm whale (*Physeter macrocephalus*), the largest of the toothed whales, emits click sounds for echolocation (Møhl *et al.*, 2003a) and communication (Weilgart and Whitehead, 1993). During deep foraging dives, they emit so-called usual clicks with properties suited for long-range echolocation of mesopelagic fish and squid (Madsen *et al.*, 2002a; Møhl *et al.*, 2003a). When closing on prey they switch to creaks (Miller *et al.*, 2004) consisting of clicks repeated with much shorter intervals of about 20 ms (Madsen *et al.*, 2002a). For communication, sperm whales produce so-called codas, which are repetitive patterns of clicks (Watkins and Schevill, 1977) and other clicklike reverberant sounds known as "slow clicks," most commonly or exclusively heard from male sperm whales (Madsen *et al.*, 2002a).

Even though recent work has expanded the knowledge on the click properties and acoustic behavior of sperm whales, we still lack detailed knowledge on the sound-production mechanism and abilities of this species. The particular problem studied here is in which manner air is used to drive the sound-production system.

The nasal complex of the sperm whale is nature's largest sound generator. It consists of a set of wax-filled cavities, the largest being the spermaceti organ (Raven and Gregory, 1933). Below the spermaceti organ is the junk, consisting of wax-filled cavities interspaced by connective tissue. Two nasal passages extend through the nose from the separated bony nares to the blow hole on the left side of the tip of the nose (Fig. 1). Two air sacs divert from the right nasal passage, one at the front (the distal sac) and one at the posterior end of the spermaceti organ (the frontal sac). The anterior portion of the right nasal passage is surrounded by two lips of connective tissue called the monkey lips (Pouchet and Beauregard, 1885). This is the site of the initial sound production event (Madsen *et al.*, 2003). From anatomical observations (Norris and Harvey, 1972) it has been surmised that this initial event is created by pressurized air flowing through the monkey lips while opening slightly during a short instant of time (Cranford, 1999). This hypothesis is consistent with results from numerical modeling (Dubrovsky *et al.*, 2004) and acoustic recordings (Wahlberg, 2002). According to Møhl *et al.*'s (2003a) bent-horn model only a tiny fraction of the sound energy of a usual click is leaking out of the animal anteriorly (the p0 pulse in Fig. 1). The majority of the energy is channelled rearwards into the spermaceti organ, reflected at the frontal air sac and exits the whale through the junk. This is the p1 pulse (Fig. 1). Some stray energy is re-reflected at the distal air sac, makes another round through the spermaceti organ, and is detected in far-field recordings as p2 (Fig. 1). This process is repeated and gives rise to subsequent pulses of decreasing amplitude but fixed intervals, giving the sperm whale click its unique multi-pulsed structure (Backus and Schevill, 1966; Møhl, 2001; Møhl *et al.*, 2003b; Norris and Harvey, 1972). The p1 pulse is the

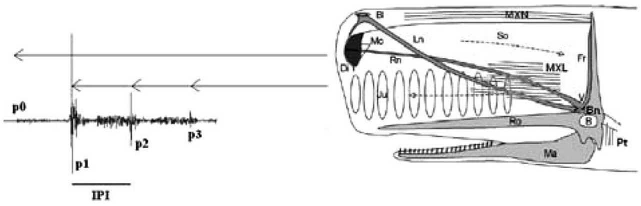

FIG. 1. Left: Sperm whale click, with the pulses labelled p0, p1, p2, p3. Right: The anatomy of the sperm whale head and suggested path of the p0 and p1 pulses. B=brain, Bn=bony naris, Bl=blowhole, Di=distal air sac, Fr=frontal air sac, Ju=junk, Ln=left naris, Ma=mandible, Mo=monkey muzzle, MXN=maxillo-nasalis muscle layer, MXL=maxillo-labialis muscle layer, Pt=pteropharynegel muscles, Rn=right naris, Ro=rostrum, So =spermaceti sac, and V=valve at the entrance of the bony naris. Modified after Madsen *et al.* (2002b) and Møhl *et al.* (2003a), with permission from the *Journal of Experimental Biology* and the *Journal of the Acoustical Society of America*.

most powerful transient sound produced in the animal kingdom and is at least as directional as dolphin clicks (Møhl *et al.*, 2003a; Zimmer *et al.*, 2005).

Even though the sound production system of the sperm whale is homologus to that of smaller toothed whales (Cranford *et al.*, 1996) there are some important differences in the anatomy and thereby possibly in the pneumatic operation of the two systems. In dolphins both pairs of monkey lips open dorsally into a set of of vestibular sacs connected to the blow hole for which reason the air for lung ventilation must pass through the sound generating structures (Dormer, 1979). This is different from the sperm whale, where only one set of monkey lips is found in conjunction with the right nasal passage. The left nasal passage bypasses the sound generator mechanism connecting the blow hole and the lungs (Fig. 1).

Previously, sperm whale sound production has been studied using anatomy (Norris and Harvey, 1972; Cranford *et al.*, 1996; Cranford and Amundin, 2004), hydrophones attached to a captive specimen (Madsen *et al.*, 2003), recordings of sound projected into recently dead specimens (Møhl, 2001; Møhl *et al.*, 2003b), hydrophones deployed from boats (Gordon, 1991; Goold, 1999; Møhl *et al.*, 2003a; Thode *et al.*, 2002; Zimmer *et al.*, 2003), and acoustic tags attached to the whale (Madsen *et al.*, 2002b; Zimmer *et al.*, 2005).

The data presented here complement the above-mentioned techniques through combined visual and acoustic observations of a clicking sperm whale close to the surface. The whale emitted series of rapid clicks similar to the creak-type vocalization described above. Usually such sounds are heard when the whale is at great depths (Miller *et al.*, 2004). However, we have also recorded rapid clicks when sperm whales explore nearby vessels. Here we combine visual and acoustical observations to study concomitant clicking and ventilation in a sperm whale and discuss the implications for air-driven sound production.

II. MATERIAL AND METHODS

Field work was made from a 16-m-long motor vessel as a part of the long-term "Greek Sperm Whale Program" of Pelagos Cetacean Research Institute (Frantzis *et al.*, 2003). Data were gathered on July 25 and August 3, 2000 off South-West Crete (Mediterranean Sea) during two encounters with a previously photo-identified sperm whale. The whale was a 9.7 m long male, length estimated from coda click interpulse intervals (Gordon, 1991) and sex determined through genetic analysis of sloughed skin. On July 25 the sperm whale was observed by a free-swimming diver using an underwater handheld mini-DV video camera (Sony DCR-TRV900E) with a digital stereo sound track, sampled with 12 bits at 32 kHz. The stereo microphone of the video camera was inside an Ikelite water-proof housing. Although the automatic gain control (AGC) is of unknown nature, analysis of the recorded noise indicated that its effect was negligible on the analysis presented here (assuming that any self-induced noise from the recording system would have been affected by the AGC). During the recordings the range between the diver and the whale was estimated to be 1–15 m and recordings were made in aspects to the whale ranging from approximately head-on to rearwards.

Simultaneous in-air filming was made from a distance of 10–30 m to the whale with a Sony Hi-8 hand-held video camera on the research vessel. The in-air video recordings were synchronized to underwater sound and video recordings to the closest video frame (1/25 of a second), i.e., with a resolution around 40 ms. This was possible through identifying the starting point of human vocalizations (diver) audible in both the in-air and underwater video. The acoustic travel time from the diver to the in-air video camera may have caused an additional delay in the in-air video recording of up to 100 ms relative to the underwater video recording. On August 3 the same individual sperm whale was recorded at a distance of 5–20 m from the vessel with the mini-DV video camera held above water. During this encounter sounds were recorded with a towed two-hydrohone array (Benthos AQ-4 elements, each with separate, 30 dB gain preamplifiers; frequency response: flat within 2 dB between 0.1 and 15 kHz) connected to a DAT recorder (Sony TCD-D8, 16 bits, 48 kHz sampling frequency). The array was left to sink into a nearly vertical orientation 100 m below the stern of the drifting vessel. The array recordings were synchronized to the in-air video recordings through connecting the signal from the array to the video camera a few minutes after the observations analyzed here were recorded. During this recording, the synchronization error was less than 110 ms, resulting from the video frame interval (40 ms) and the delay between the video and acoustic recordings (up to 70 ms) due to the travel time of sound from the whale to the array.

Twelve video sequences where the whale was close to the observer were selected for analysis. Sound and video recordings were digitally transferred to a computer. Clicks were extracted and their amplitude and interclick intervals were measured using Cool Edit Pro ver. 2 (Syntrillium, Inc.) and routines written with Matlab 6.2 (MathWorks, Inc.).

No other whales were observed by lookouts or detected acoustically. In addition to this, the correlation between the movements of the whale (e.g., reduction in click intensity as the whale emerged from the water with the nose; see below) made us confident that the whale we observed on the video was the same as the one we recorded with the hydrophone.

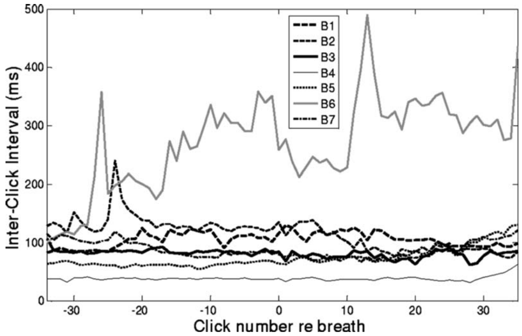

FIG. 2. Interclick intervals of clicks recorded right before until right after seven breaths (labelled B1–B7) made by a sperm whale. Breaths occur at the x value of 0 for each sequence.

III. RESULTS AND DISCUSSION

Instances of the whale ventilating were observed from the surface video recordings, shown by moist air being emitted from the blow hole. During seven such events the whale was clicking during lung ventilation. The few sudden excursions observed in the interclick intervals (ranging from 31 to 490 ms, Fig. 2) appeared to be independent of the breathing events. During ventilation of the lungs the blow hole is open and connects the left nasal passage and the lungs to the atmosphere (Raven and Gregory, 1933; Norris and Harvey, 1972; Schenkkan and Purves, 1973). There is no sphincter structure between the left nasal passage and the distal air sac (Fig. 3). Therefore it is not possible to build up pressure on the anterior side of the monkey lips while breathing. Air must be pressurized in the right nasal passage and flow anteriorly through the phonic lips into the frontal sac. This is consistent with the inferences made from anatomical observations by Norris and Harvey (1972) and analogous to the direction of airflow in other toothed whales (Cranford *et al.*, 1996).

Even though the sound generator system of sperm whales is homologous to that of other toothed whales (Cranford *et al.*, 1996) the observations made here indicate that the mechanism behind the air pressure build up for actuating the pneumatically driven sound generator might be quite different. In dolphins, click sound production is initiated by keeping the muscular sphincter around the epiglottal spout of the larynx closed and then pressurizing the bony nares by contraction of the palatopharyngeal and anteriorinternus muscles (Ridgway *et al.*, 1980; Cranford *et al.*, 1996). The pressurized air is metered past the two pairs of monkey lips [the right pair being homologous to the monkey lips of sperm whales (Cranford *et al.*, 1996)]. The internareal pressures in the two nasal passages rise and fall together during click production (Ridgway *et al.*, 1980; Amundin and Andersen, 1983). Thus the contracting palatopharyngeal and anteriorinternus muscles act on both nasal passages and dolphins are therefore not able to click and breathe simultaneously. However, sometimes during click production the two phonic lips can be actuated independently from each other (Cranford *et al.*, 2000), demonstrating some degree of separation in the control of sound production between the left and the right side.

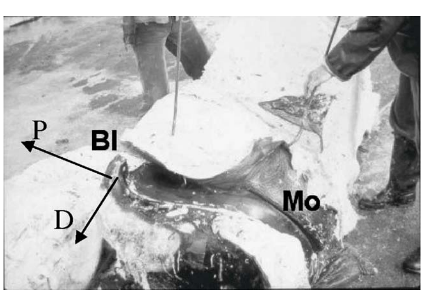

FIG. 3. Dissection of an adult male sperm whale showing the passage between the blowhole (Bl) and the monkey lips (Mo) through the distal air sac. P denotes posterior direction, D denotes dorsal direction.

The fact that the sperm whale can click and ventilate its lungs simultaneously shows that the right nasal passage can be pressurized independently of the left nasal passage which is connected to the lungs. This can either be achieved (1) if the open epiglottis inserts into the left bony naris during ventilation while the pterygopharyngeus muscle pressurizes the cavity beneath the bony nares and thereby the right nasal passage or (2) by closing the ventro-posterior entrance to the right naris disconnecting the right nasal passage from the ventilation pathway made up by the trachea, the open epiglottis, and the left nasal passage. The latter scenario is supported by the existence of a sphincter at the right bony naris (Raven and Gregory, 1933; Norris and Harvey, 1972; Schenkkan and Purves, 1973) The air pressure necessary for click production may in that case result from contracting the muscles below and above the right nasal passage [described in Schenkkan and Purves (1973) and Clark (1978)] throughout its course towards the monkey lips. The latter scenario will, however, be fundamentally different from the way air pressure for sound production is generated in other toothed whales (Ridgway *et al.*, 1980), whereby homologous structures would not serve homologous functions of actuating the sound generator among clicking toothed whales. These two conjectures remain to be tested.

When diving to great depths, the air available for sound production is seriously restricted (Madsen *et al.*, 2002b, Wahlberg, 2002). Recycling may be accomplished by opening the monkey lips and moving the air backwards into the right nasal passage through the action of the maxillonasalis and maxillolabialis muscles as well as additional muscles above and below the right nasal passage (Schenkkan and Purves, 1973; Clark, 1978; Madsen, 2002).

In the observations presented here, the peak-to-peak sound level of the clicks dropped with up to 28 dB when the whale partially raised its head out of the water surface (either to breathe or not), sometimes emerging the whole anterior area leading in to the junk. This is probably a minimum estimate, as the measurements were restricted by the low recording band width, dynamic range, and possibly also by the automatic gain control mechanism of the camera. These measurements are contradictory to Watkins and Daher's (2004) observation of a whale lifting its head completely out of the water without affecting the level nor the frequency content of the clicks.

In one of the surface video sequences analyzed here small drops of water jumped out from the emerged blowhole while the whale was clicking rapidly. This may be caused by vibrations of the nose associated with sound production. Very powerful accelerations at the front of a sperm whale nose were observed by a diver in an earlier study (Norris and Møhl, 1983).

These observations were made on a single individual observed during two independent observations. *Ad libitum* observations that we made on another individual, unfortunately without recording it, indicates that breathing while clicking is not a unique behavior of the recorded individual, nor does it seems to be a rare phenomenon.

Future work will benefit from methods telling the distance and bearing to the whale, as well as from using a calibrated sound recording system sensitive in the entire frequency range of sperm whale vocalizations. With this information the sound production of sperm whales could be even further investigated, including variations in source level and frequency content with the direction to the whale. The synchronized observations of video and audio hold promise to contribute to the understanding of possible fine-scale changes in the nasal system during sound production not observable with other methods, e.g., to understand how the nose may become slightly deformed while producing different types of clicks.

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