

BONY NARES AIR PRESSURE AND NASAL PLUG
MUSCLE ACTIVITY DURING CLICK PRODUCTION
IN THE HARBOUR PORPOISE, *PHOCOENA PHOCOENA*,
AND THE BOTTLENOSED DOLPHIN, *TURSIOPS*
TRUNCATUS

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SUMMARY

Sound production mechanisms have been studied in two delphinid species – the harbour porpoise, *Phocoena phocoena* (L.), and the bottlenosed dolphin, *Tursiops truncatus* (Montagu). It was found that, in both species, the click sound production was coupled to a considerable pressure increase in the bony nares. The maximum pressure recorded in *Phocoena* was approximately 54 kPa and in *Tursiops* close to 81 kPa; it was equal in time and amplitude in both nares. The nasal plug muscle was found to be active up to 450 ms prior to and during sound production. Sound production without such activity was not seen. The results suggest that an identical mechanism underlies click production in both species, with pressurized air being the driving force and the nasal plug muscle having some active regulating function.

Probes were inserted into the bony nares of three harbour porpoises, *Phocoena phocoena*, and one bottlenosed dolphin, *Tursiops truncatus*, in order to record air pressure variations together with sound production. Sounds were picked up by a hydrophone manually held to the forehead of the animals. In several of the *Phocoena* recordings, electromyographic activity in the nasal plug muscle was also recorded.

INTRODUCTION

Current hypotheses suggest that delphinids produce sounds in the upper nasal tract, between the dorsal apertures of the bony nares and the blowhole. (Norris, Dormer, Pegg & Liese, 1971; Evans & Maderson, 1973; Hollien, Hollien, Caldwell & Caldwell, 1976; Dormer, 1979; Ridgway *et al.* 1980).

The present hypothesis for the sound production mechanism in *Phocoena* is as follows (Fig. 1). The nasopharyngeal muscle complex protrudes into the bony nares

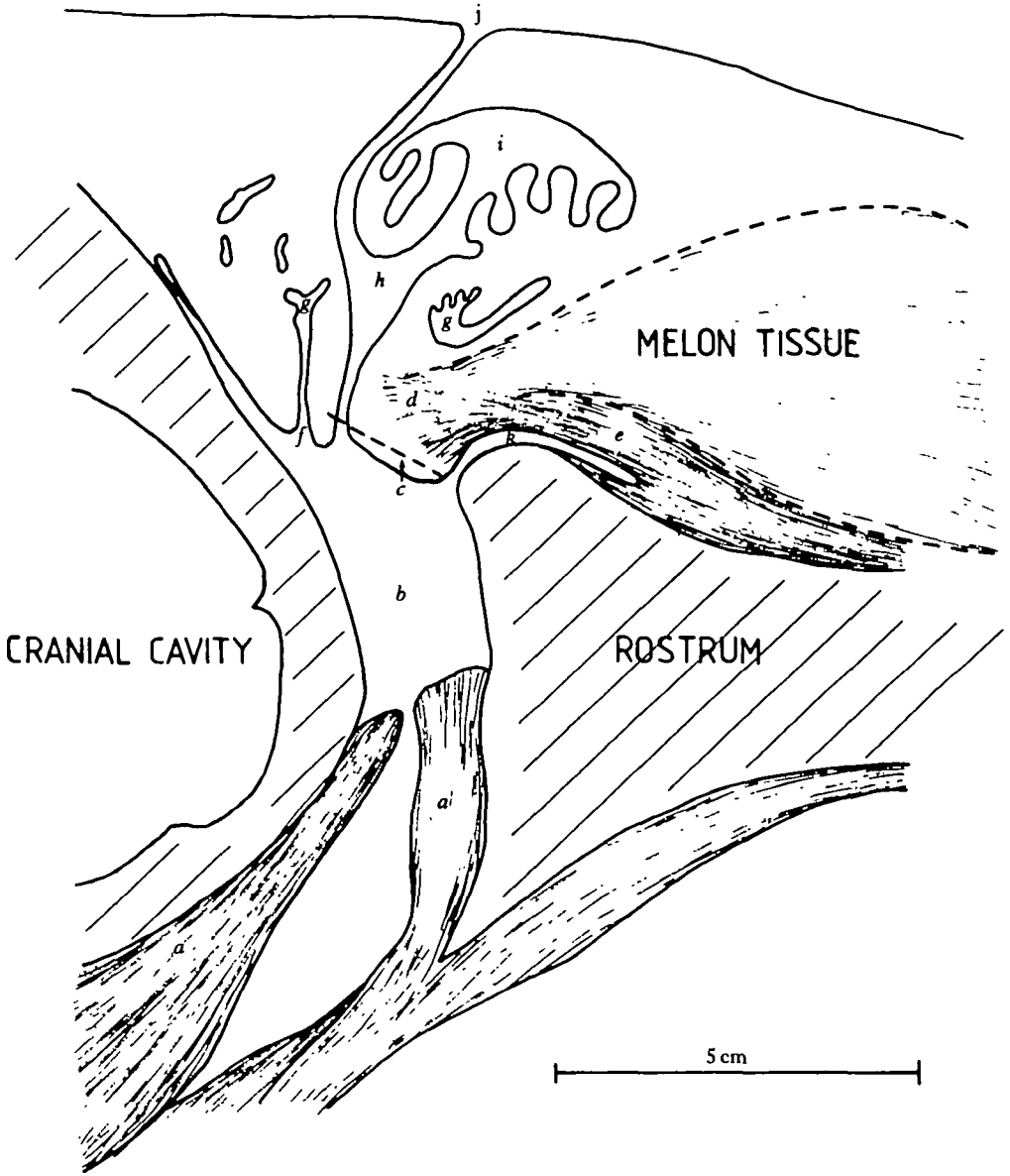


Fig. 1. Semidiagrammatic sketch of a sagittal section through the right bony nares in a harbour porpoise, *Phocoena phocoena*. *a*, nasopharyngeal muscle complex; *b*, upper part of right bony nares; *c*, level of bony nasal aperture; *d*, nasal plug; *e*, nasal plug muscle; *f*, entrance to right tubular sac; *g*, right tubular sac; *h*, upper nasal passage (vestibulum); *i*, right vestibular sac; *j*, blowhole; *k*, right premaxillary sac.

forming a thick lining of its ventral parts. When these muscles contract, the volume of the nares decreases as the air enclosed by them is squeezed into the upper parts of the nares, just ventral to the apertures of the nares. This action results in an increased pressure in the bony nares, which are sealed by an elastic connective tissue structure – the nasal plug – that fits tightly along the latero-caudal rims of the apertures of the bony nares. The nasal plug is prevented from being displaced dorsally by means of

several muscle complexes (cf. Green, Ridgway & Evans, 1980). Further, the increased pressure in the bony nares causes an identical increase in pressure in the tubular sacs, which at their entrance communicate freely with the bony nares. Together, the semi-circular paired tubular sacs surround the upper nasal passage. Because of the increased pressure they inflate, thereby sealing the passage. The nasal plug can be pulled rostrally by means of the nasal plug muscle, which inserts on the premaxillary bones just rostrally to the small premaxillary sacs. Brief and weak contractions of the nasal plug muscle will allow pressurized air from the bony nares to escape past the pneumatic lock of the tubular sacs, producing sounds in the process. The used air is collected in the vestibulum and the highly distensible vestibular sacs. This air volume can be recycled by withdrawal of the nasal plug and relaxation of the nasopharyngeal muscle complex.

This hypothesis is supported by studies of two bottlenosed dolphins species: *Tursiops truncatus* and *T. gilli* and a *Stenella longirostris* which all produce both clicks and whistles.

In this paper, the model is tested primarily on the harbour porpoise, *Phocoena phocoena*, which exclusively produces clicks. The following were measured: the pressure events in the bony nares, the direction of the air flow in the upper nasal passage, and the activity in the nasal plug muscle – all during production of click sounds. Additionally, the pressure events in the bony nares of a clicking bottlenose dolphin are presented.

MATERIALS AND METHODS

Three subadult harbour porpoises, *Phocoena phocoena*, and a fully grown bottlenosed dolphin, *Tursiops truncatus*, were used as subjects for this research. During recordings the animals were either floating on the surface, resting on a stretcher, or beached.

Sound recordings

A six-channel Elema-Schoenander type 81 Mingograph was used to make simultaneous recordings of dolphin sounds, pressure and muscle activity. Since the main energy of the harbour porpoise click is between 110 and 150 kHz (Møhl & Andersen, 1973), we chose to record periods of phonation as follows. Sound was picked up by a Brüel & Kjaer Type 8100 hydrophone manually held to the forehead (melon). A Brüel & Kjaer Type 2607 measuring amplifier with an external Brüel & Kjaer Type 1614, $\frac{1}{3}$ octave filter centred at 125 kHz delivered a signal that triggered a Wavetake Type 105 tone generator to produce 2 kHz pulses in response to the animals high frequency click emission.

Pressure recording

Pressure was measured in the bony nares ventral to the nasal plug and dorsal to the aperture of the hollow nasopharyngeal muscle complex (Fig. 1, *b*). Two Elema-Schoenander Type EMT 35 electromanometers were used; they were equipped with waterfilled probes made from hard walled nylon tubes. The probes were 120 cm long,

with an internal diameter of 1.3 mm and were tipped with a 25 cm intravenous cannula with an internal diameter of 1.0 mm. The rise time of this recording system was 20 ms. The selected pressure reference was the ambient pressure at the level of the bony nares. The electromanometers were calibrated between 0 and 88 kPa against a mercury manometer (100 kPa = 9.8692 atm).

Electromyography (EMG)

Sterilized platinum fine-wire electrodes with a diameter of 0.05 mm were implanted into the nasal plug muscles using the method of Basmaïjan & Stecko (1962). The positions of the electrode tips were determined from anatomical measurements on the head of a dead specimen of the same body length. The electrode terminals were connected to a DISA Type 14 A 52/C 10 multichannel amplifier and the signal fed to the multichannel recorder.

RESULTS

The pressure recordings in *Phocoena* were preceded by manual palpation of the upper nasal tract. If the blowhole and the upper nasal passage were opened but the nasal plug left undisturbed, an airborne, low frequency click emission could be heard very loudly. This emission was similar to the low frequency component described by Busnel, Dziedzic & Andersen (1963) and Schvill, Watkins & Ray (1969). Simultaneously, small bubbles appeared in the moisture of the righthand corner of the nasal plug. Clear vibrations in the tissues could be felt by placing a finger at that corner; smaller vibrations could be felt when the fingers were moved towards the lefthand part of the nasal plug. Phonation could be halted by manually forcing the nasal plug rostrally and thus exposing the bony nares. That oscillations occur only in the righthand part of the nasal plug has been confirmed by this method in five harbour porpoises.

In this case, 27 click trains were recorded together with pressure measurements in either left or right bony nares. For three series, pressure recordings were obtained from both bony nares simultaneously with sound recordings. EMG recordings were successfully obtained during both unilateral and bilateral pressure recordings. In *Tursiops*, four click trains were recorded simultaneously with pressure recordings in left or right bony nares. However, the recordings of EMG activity were not successful. The results of these experiments are listed in Table 1. Typical recordings of *Phocoena* are shown in Figs 2 and 3 and of *Tursiops* in Fig. 4. In both species, click trains were always preceded by a considerable pressure increase in the bony nares, and in all three bilateral recordings, the pressure variations were of equal amplitude and timing in both nares. It was not possible to define a threshold level above which click

Table 1. *Pressure measurements during click production*

	<i>Phocoena phocoena</i>	<i>Tursiops truncatus</i>
Pressure range at click train onset	8–43 kPa	25–79 kPa
Pressure range at click train stop	7–67 kPa	25–37 kPa
Maximum pressure	54 kPa	81 kPa

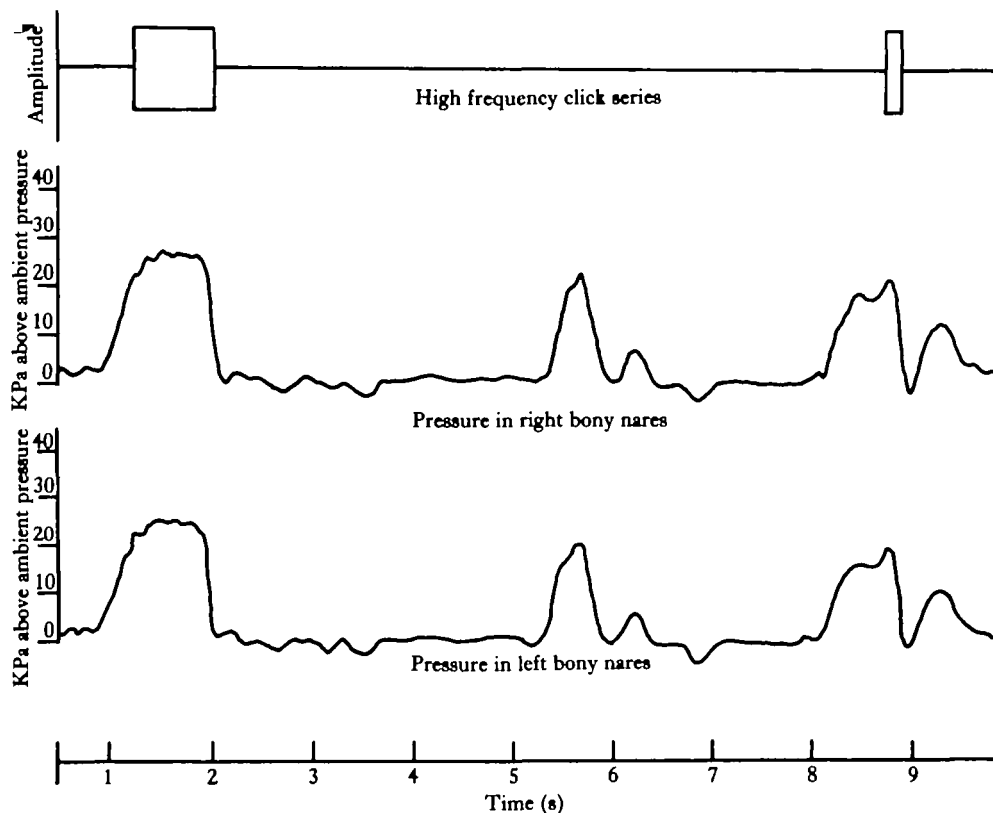


Fig. 2. Pressure events in the bony nares during high frequency click production in *Phocoena phocoena*.

trains were always emitted. On the contrary, click trains were elicited at very different pressure levels (Table 1). During periods without sounds, pressure in the bony nares could exceed the pressure recorded during click emission in both species.

In *Phocoena* the pressure peaks during phonation typically showed double maxima (Fig. 2). Moreover, EMG recordings (Fig. 3) clearly demonstrated the nasal plug muscle to be active during phonation – muscle activity commenced up to 450 ms prior to phonation – and click trains without EMG activity were not seen. It was not possible to determine (from the EMG recordings) whether the nasal plug muscle was acting as one or two functional units. Thus, these recordings provided no indication as to which side was responsible for sound production.

DISCUSSION

The hypothesis described in the Introduction appears to be supported by the present investigation. Click production in both species was coupled to a considerable pressure increase equal in time and amplitude in both bony nares. When the air pressure in the nare was bypassed by manually forcing the nasal plug rostrally, phonations in progress were halted. We conclude that the driving force behind the sound

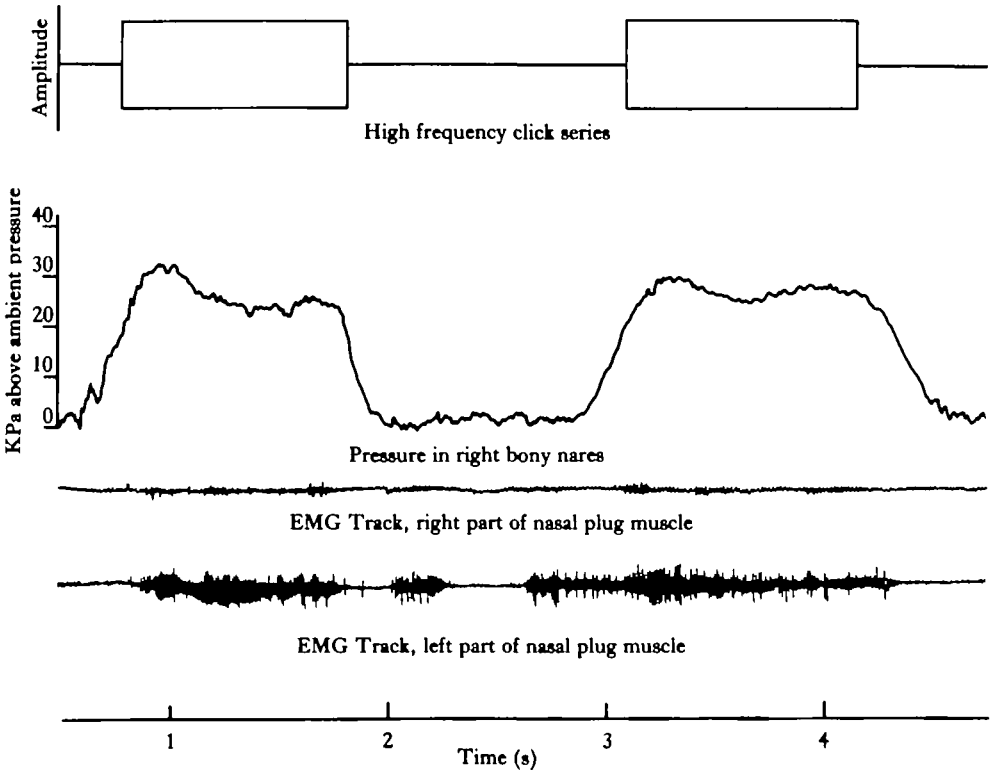


Fig. 3. High frequency click production, pressure events in the bony nares and EMG activity in the nasal plug muscle, recorded in *Phocoena phocoena*.

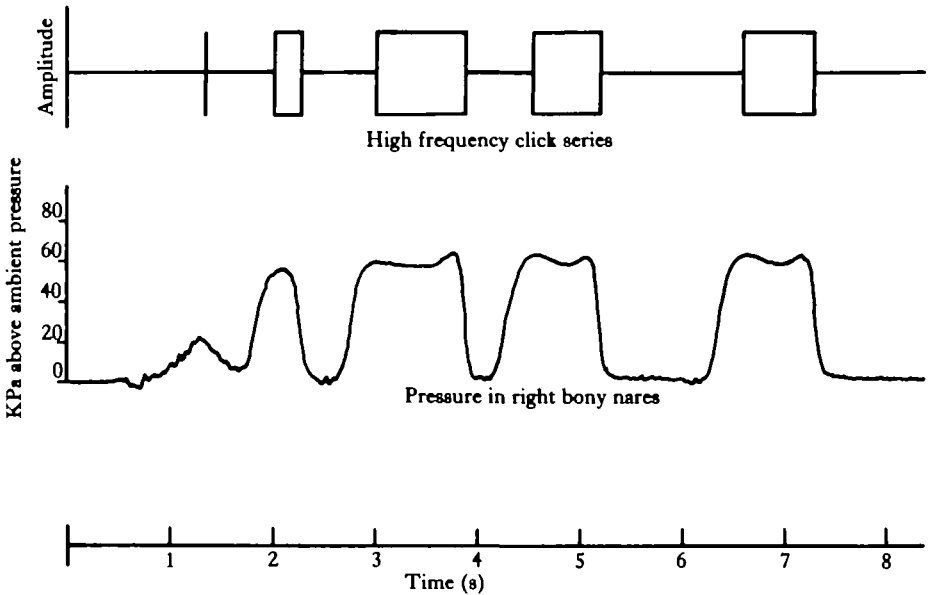


Fig. 4. Pressure events in the bony nares during click production in *Tursiops truncatus*.

generator is pressurized air in the bony nares. Identical results were reported by Ridgway *et al.* (1980) in *Tursiops*.

Air pressure shifts *per se* obviously could not initiate phonation, as a prefixed level above which clicks were always elicited could not be specified. Instead, the precise initiation of click trains, even very short ones, at very different pressure levels, suggests a neuromuscular control. This idea was confirmed by our EMG recordings in *Phocoena*, which showed that the nasal plug muscle was synchronously active with phonations. It is highly likely that the action of this muscle allows small portions of pressurized air to be metered past the tubular sac pneumatic lock, and to be released into the vestibule and vestibular sacs. At this pressure release, small bubbles could be seen forming in the righthand corner of the nasal plug in synchrony with the click sounds, thus indicating the direction of the air flow. Manual palpations on the same site during click production revealed vibrations in the nasal plug tissues; they were stronger on the righthand side than on the left. These observations further support the idea of a relaxation oscillation mode of click production.

Evans & Maderson (1973) suggested a 'friction-striction', mechanical method of click production in *Tursiops*. This hypothesis would imply considerable nasal plug movement during vocalization. Our palpations and visual inspections through the opened blowhole during click production revealed no such movements in either *Phocoena* or *Tursiops*. The same conclusion was reached by Dormer (1979) for *Tursiops*. Indeed, as judged from the palpations, clicking apparently took place on the righthand side of the nasal plug. In *Tursiops* there are several observations indicating a bilateral sound source, with clicks assigned to the righthand side of the air passage and whistles to the left (e.g. Mead, 1971, 1972; Dormer, 1979). It is interesting to note that the non-whistling *Phocoena* obviously does not utilize its lefthand side for sound production of any type.

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