

RESEARCH ARTICLE

Nasal sound production in echolocating delphinids (*Tursiops truncatus* and *Pseudorca crassidens*) is dynamic, but unilateral: clicking on the right side and whistling on the left side

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SUMMARY

Toothed whales produce sound in their nasal complex by pneumatic actuation of phonic lip pairs within the blowhole. It has been hypothesized that dual actuation of the phonic lip pairs can generate two pulses that merge to form a single echolocation click with a higher source level, broader bandwidth and larger potential for beam steering than if produced by a single pair of phonic lips. Here, we test that hypothesis by measuring the sound production of five echolocating delphinids using hydrophones around the animals and imbedded in on-animal suction cups. We show that the studied animals click with their right pair of phonic lips and whistle with their left pair. We demonstrate that, with just a single pair of phonic lips, they can change the click energy levels over five orders of magnitude, change the click centroid frequencies over more than two octaves, and modulate the sound radiation from the melon for beam steering. We conclude that all of the click dynamics ascribed to dual actuation of two phonic lip pairs can be achieved with actuation of just the right pair of phonic lips, and we propose that the large dynamic range of source outputs is achieved by highly controlled modulation of the pneumatic driving pressure, the tension of the phonic lip labia and the conformation of the fatty melon and associated air sacs.

Key words: toothed whale, dolphin, sound production, click, echolocation.

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INTRODUCTION

Toothed whales employ a rich repertoire of clicks and tonal sounds for echolocation and communication. These sounds are not produced in the larynx, like in terrestrial mammals, but rather in a complex nasal system of air sacs, connective tissue and fat compartments situated on the rostrum (Norris, 1968; Cranford et al., 1996; Cranford and Amundin, 2003). The peculiar anatomy of this nasal complex and the wide range of sounds with varying but finely controlled (Janik et al., 2006; Johnson et al., 2006; Moore et al., 2008) properties have drawn substantial scientific attention to the problem of how toothed whales produce sounds. Early work by Norris and colleagues (Norris, 1964) showed that sounds emanated from a source above the rostrum in clicking dolphins, and that finding was corroborated by Diercks et al. (Diercks et al., 1971), who used an array of suction cup hydrophones to acoustically localize the sound source to a location within the blowhole. Using cinoradiographic techniques (Norris et al., 1971; Dormer, 1979), electromyographic electrodes and pressure catheters (Ridgway et al., 1980; Amundin and Andersen, 1983), it was subsequently demonstrated that toothed whale sound production is driven pneumatically by a pressure build-up from contraction of the palatopharyngeal muscles, the nasal plug muscles and internus muscles (Ridgway and Carder, 1988), moving air dorsally past the two nasal plugs and phonic lips and into the vestibular air sacs.

It was thus clear that the sound source had to be found above the bony nares, and several candidates for the actual sound source were proposed, mainly from anatomical work; the diagonal membrane

(Mead, 1975), the nasal plugs (Evans and Prescott, 1962), the air sacs (Lilly, 1962) and the blowhole ligament within the posterior phonic lips (Heyning, 1989). A common problem, however, was that their operation could not be reconciled with physiological measurements or with the parsimonious presumption that the monophyletic suborder of toothed whales would use homologous sound producing structures. That problem was solved with the publication of a seminal paper by Cranford and colleagues (Cranford et al., 1996) identifying a homologous anatomical structure across a wide range of toothed whale species with a purported function that was consistent with the physiological measurements. This structure was first coined the monkey-lips–dorsal-bursae (MLDB) complex, but it is now known as the phonic lip (Cranford, 2000). It is found in two pairs in all toothed whale species, except the sperm whales, and it is situated in each of the soft nares on the ventral side of the vestibular air sacs, just below the blowhole. The identification of two potential sound sources in most toothed whale species has helped to explain reports that some toothed whales can click and whistle simultaneously (Evans, 1973; Lilly, 1978; Brill and Harder, 1991; Murray et al., 1998). Further, both left and right side nasal muscles contract during phonations, and the air pressure rises in both the left and right nasal cavities during these contractions (Ridgway et al., 1980).

Based on initial speculations (Lilly, 1962; Norris et al., 1971), Cranford and colleagues (Cranford et al., 1996; Cranford and Amundin, 2003; Cranford et al., 2011) took the idea of dual sound production a step further by suggesting that the two pairs of phonic

lips can be actuated simultaneously to generate two pulses that interfere to form a single click with a higher power output and broader bandwidth. This idea offered an explanation for why toothed whales with similar sized pairs of phonic lips (porpoises and *Cephalorhynchus* spp.) produce long, narrow band, high frequency clicks, while toothed whales with asymmetrically sized phonic lip pairs produce short clicks of much broader bandwidths (Cranford et al., 1996; Cranford, 2000; Cranford et al., 2011). In the latter case, the larger right pair of phonic lips is envisaged to produce the low frequency peaks and the smaller left pair is believed (Cranford, 2000; Cranford et al., 2011) to produce the high frequency peaks often seen in high level dolphin clicks (Au, 1993; Houser et al., 1999). It has also been suggested that very acute controlled timing of the two pairs of phonic lips may be used for beam steering in the horizontal plane *via* delay adjustments (Moore et al., 2008; Starkhammar et al., 2011; Cranford et al., 2011). While these virtues of dual sound production are functionally attractive, some of them are mutually exclusive: beam steering and increased peak power output call for complete spectral overlap in the two pulses, while higher click bandwidth can only be achieved if there is little spectral overlap. Common to the virtues of dual actuation of two sources to form a single click is that they require a motor neural timing of the order of a microsecond to work (Madsen et al., 2010). Such timing is to our knowledge unprecedented in mammalian motor circuits, but provides an interesting and thought-provoking working hypothesis for testing how the two phonic lip pairs operate to generate both clicks and whistles with widely variable source parameters (Moore and Pawloski, 1990; Houser et al., 1999; Au et al., 1995; Madsen et al., 2004a; Madsen et al., 2004b; Madsen et al., 2012).

Given the challenges of understanding how the two phonic lip pairs can be actuated simultaneously, it was most intriguing when Lammers and Castellote reported data in support of the dual actuation hypothesis using two-hydrophone recordings in the far-field of a clicking white whale (Lammers and Castellote, 2009). They observed that a single click recorded on-axis with one hydrophone was breaking up into two pulses with increasing delay as another hydrophone was moved off-axis. They interpreted this pattern to arise from two pulses produced simultaneously by each of the two phonic lip pairs, while acknowledging that the resulting time delays at 90 deg off-axis were much longer than what could be explained by the spatial separation between the two pairs of phonic lips. In a later study, using a similar setup with an echolocating bottlenose dolphin, it was also found that a single click would split into two pulses when recorded off-axis (Au et al., 2012). However, Au and colleagues found that the two off-axis pulses had a frequency structure where the first arriving click contained energy at lower frequencies than the second pulse no matter whether they were recorded on the left- or right-hand side of the animal. This observation is inconsistent with an off-axis pulse pattern generated by two simultaneously actuated pairs of phonic lips of different sizes, because the low frequency pulse in this model should arrive first on the right-hand side, but second on the left-hand side.

In an attempt to investigate whether echolocating porpoises actuate two sources simultaneously for clicking, we (Madsen et al., 2010) used three suction cup hydrophones on the nasal complex of three porpoises to show that they consistently clicked with their right pair of phonic lips, as has been reported from many studies on both porpoises (Amundin and Andersen, 1983; Au et al., 2006) and delphinids (Norris et al., 1971; Dormer, 1979; Mackay and Liaw, 1981; Amundin and Andersen, 1983; Au et al., 2010; Dubrovskiy and Giro, 2004). The melon recordings that we obtained (Madsen

et al., 2010) also strongly suggested that porpoises can modulate their sound beams with just one source active, presumably by changing the conformation of the nasal soft structures and air sacs. This work was subsequently criticized by Cranford (Cranford, 2011; but see Madsen et al., 2011) for not being able to demonstrate that the porpoises were in fact echolocating.

Thus, some functional studies seem to lend circumstantial support to the dual actuation hypothesis for toothed whales (Moore et al., 2008; Lammers and Castellote, 2009; Starkhammar et al., 2011) while other are inconsistent with it (Amundin and Andersen, 1983; Au et al., 2012; Madsen et al., 2010). However, progress on this matter is confounded by a lack of comparable methods on different species in various contexts where echolocation may or may not take place. In an attempt to alleviate these problems, we designed a target detection experiment with echolocating delphinids with a sufficient number of suction cup (Diercks et al., 1971) and far-field hydrophones to quantify the number of active sound sources along with click parameters on and off the acoustic axis. Here, we report data to test the dual actuation hypothesis (Cranford et al., 2011), proposing that it requires two sources for modulating the sound beam, source levels and bandwidths of delphinid echolocation clicks. We show that the five delphinids studied consistently click with their right pair of phonic lips and whistle with their left pair. We reject the dual actuation hypothesis by showing that the studied animals can change their click energy output by five orders of magnitude, alter the centroid frequencies by more than two octaves and modulate their sound beams with just one click source active. We conclude that delphinids primarily click with their right pair of phonic lips and whistle with their left pair, and propose that dynamic source outputs are achieved by highly controlled modulation of the pneumatic driving pressure, the tension of the phonic lip labia and the conformation of the fatty melon and associated air sacs.

MATERIALS AND METHODS

Three experiments were conducted on four bottlenose dolphins, *Tursiops truncatus* Gervais 1855, and one false killer whale, *Pseudorca crassidens* (Owen 1846). Experiment I was a go/no-go target detection experiment with one bottlenose dolphin, BJ, and one false killer whale, Kina. Experiment II involved the same animals as in experiment I, but with a focus on whistle production. Experiment III involved three bottlenose dolphins, Liho, Kolohe and Noah, trained to station while echolocating *ad libitum* on different objects introduced in front of them. All experiments were conducted under University of Hawaii IACUC protocol 09-712 and US Marine Mammal Permit no. 978-1567 issued to Paul Nachtigall.

Experiment I

Animals and setup

Experiment I was conducted at the Coconut Island Marine Mammal Facility off Oahu, Hawaii, with two trained delphinids; a 28 year old female Atlantic bottlenose dolphin, BJ, and a >30 year old female false killer whale, Kina. Both animals were trained to participate in go no-go target detection experiments with targets consisting of three cylinders (o.d.=38 mm, i.d.=25 mm); 22, 69 or 180 mm long with measured target strengths of -40, -36 and -32 dB (Table 1). Each animal was trained to station in a hoop at 1 m depth and echolocate through an acoustically transparent PVC screen, and then subsequently either press a response paddle to indicate target present or remain on station to indicate target absent (for details, see Kloepper et al., 2010). The target was presented from a position behind the animal and lowered *via* a pulley system to 1 m depth 2.65 m ahead of the hoop (Fig. 1A).

Table 1. Click properties in experiment I

Session	No. of trials	Target size (S/M/L)	%Correct	Mean no. clicks trial ⁻¹	Mean no. clicks on-axis trial ⁻¹	Mean SL (pp, dB re. 1 μ Pa)	Mean f_c (kHz)	Mean f_p (kHz)	Mean r.m.s. bandwidth (kHz)
BJ1_A	10	L	90	37.9	25.7	197.1 \pm 1.9 (194.2–200.6)	61.3 \pm 2.7 (58.3–66.3)	43.6 \pm 2.5 (41.5–49.9)	27.2 \pm 2.0 (23.8–31.0)
BJ2_A	20	L	100	38.5	21.8	194.5 \pm 3.7 (187.6–203.2)	59.7 \pm 4.7 (53.6–71.2)	48.9 \pm 4.3 (42.1–57.5)	25.9 \pm 2.3 (21.6–32.2)
BJ3_A	20	L	95	36.3	30.5	198.5 \pm 1.9 (193.3–200.6)	59.3 \pm 3.2 (54.0–66.1)	41.6 \pm 0.4 (40.9–42.2)	27.2 \pm 1.9 (24.3–30.8)
BJ4_A	20	L	100	20.7	18.2	196.0 \pm 3.1 (190.5–201.1)	58.4 \pm 5.2 (50.3–67.0)	42.0 \pm 1.3 (40.0–44.5)	27.4 \pm 2.8 (21.9–31.4)
BJ5_A	20	L	100	50.8	41.2	196.5 \pm 3.8 (188.6–203.3)	60.0 \pm 4.7 (52.6–68.2)	40.6 \pm 0.7 (38.7–42.2)	28.5 \pm 2.3 (24.3–32.0)
BJ6_A	21	M/S	100	51.7	42.1	199.0 \pm 2.1 (193.8–202.4)	64.2 \pm 4.3 (56.0–73.7)	41.3 \pm 0.7 (39.9–42.7)	31.0 \pm 2.4 (27.6–35.7)
BJ7_A	24	S	100	45.0	37.0	197.5 \pm 2.5 (192.3–201.7)	58.8 \pm 3.7 (49.8–66.6)	40.6 \pm 0.4 (39.7–41.3)	28.7 \pm 2.9 (22.5–34.2)
BJ8_B	20	L	100	29.1	28.8	191.8 \pm 2.1 (187.7–194.3)	46.5 \pm 5.1 (40.6–57.9)	40.1 \pm 2.2 (36.2–41.8)	22.7 \pm 3.6 (19.1–30.7)
BJ9_B	20	L	100	21.9	21.1	194.5 \pm 2.2 (190.7–198.4)	46.6 \pm 4.1 (36.7–52.1)	38.5 \pm 3.8 (29.5–44.4)	23.2 \pm 1.9 (17.2–25.9)
Kina1_A	8	L	100	22.9	22.8	196.9 \pm 2.2 (193.0–200.2)	44.2 \pm 4.2 (37.1–55.8)	39.7 \pm 1.5 (36.0–41.3)	21.1 \pm 3.0 (17.4–28.8)
Kina2_A	21	L	90.5	21.9	21.6	195.5 \pm 1.4 (192.8–197.4)	42.8 \pm 3.6 (36.2–47.0)	38.4 \pm 3.0 (31.1–42.0)	20.1 \pm 3.1 (14.7–26.3)
Kina3_A	20	L	90	19.4	19.4	196.6 \pm 1.9 (192.8–199.7)	44.6 \pm 2.8 (40.4–49.6)	40.0 \pm 1.1 (37.0–41.4)	19.1 \pm 2.1 (15.6–24.6)
Kina4_A	18	L	100	11.5	11.5	200.9 \pm 2.6 (196.1–205.5)	46.7 \pm 4.2 (39.5–54.1)	40.3 \pm 1.4 (37.4–42.1)	21.1 \pm 2.1 (17.3–25.2)
Kina5_A	20	L	100	32.4	32.0	199.0 \pm 1.4 (196.0–200.9)	45.9 \pm 2.1 (41.4–49.0)	39.8 \pm 0.7 (38.3–41.4)	20.4 \pm 1.7 (17.8–23.6)
Kina6_A	22	M/S	81.8	37.9	25.7	197.1 \pm 1.9 (194.2–200.6)	61.3 \pm 2.7 (58.3–66.3)	43.6 \pm 2.5 (41.5–49.9)	27.2 \pm 2.0 (23.8–31.0)
Kina7_A	24	S	100	38.5	21.8	194.5 \pm 3.7 (187.6–203.2)	59.7 \pm 4.7 (53.6–71.2)	48.9 \pm 4.3 (42.1–57.5)	25.9 \pm 2.3 (21.6–32.2)
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Session for BJ (a bottlenose dolphin) and Kina (a false killer whale) indicates the A or B suction cup configuration of the hydrophones (see Fig. 1). Target size is small (S), medium (M) or large (L). Mean values in the final four columns are given \pm s.d.; minimum and maximum values are given in parentheses. SL, source level; pp, peak–peak f_c , centroid frequency; f_p , peak frequency; r.m.s. bandwidth, root mean square bandwidth.

Target absent and target present were alternated according to a Gellermann pseudo-random schedule. Five hydrophones were suspended on 0.5 mm monofilament lines between a wooden beam and 1 kg weights in two different configurations around the animal (Fig. 1A). Common to both of these were a hydrophone placed 0.3 m in front of the target, two hydrophones placed 15 deg to the left and the right of the center hydrophone, and a fourth hydrophone 90 deg to the right of the hoop at a distance of 0.95 m. A fifth hydrophone was then either placed 45 deg (recording setup

1A) or 90 deg (recording setup 1B) to the left of the animal (Fig. 1A). In addition, three suction cup hydrophones with 5 m long cables were attached underwater in either of two different configurations: two cups placed either side of the head in line with the blowhole and the third placed on the middle of the melon (configuration A, Fig. 1B,D; Table 1) or two cups next to each other on either side of the melon, and the third anterior to those on the melon midline (configuration B, Fig. 1C,E; Table 1). The suction cups were color coded for photo documentation before each session

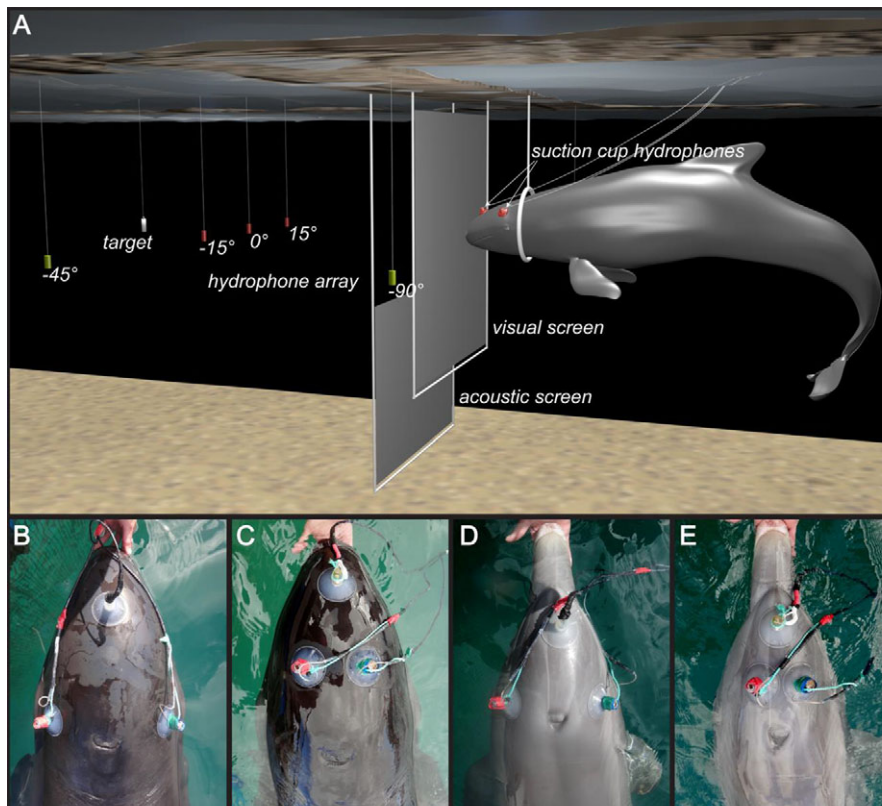


Fig. 1. (A) Setup of experiment I with a false killer whale stationed in a hoop echolocating for the target through a visual screen while the acoustic screen is lowered. Three hydrophones are ahead of the animal at 0 and \pm 15 deg from the target. A fourth hydrophone is located at either 45 deg (recording configuration 1) or 90 deg (recording configuration 2) to the left of the animal, and the fifth hydrophone is located 90 deg to the right of the animal. (B,D) Hydrophone placement in suction cup configuration A on Kina (a false killer whale) and BJ (a bottlenose dolphin), respectively. (C,E) Hydrophone placement in suction cup configuration B for BJ and Kina, respectively.

and swapped in terms of head location between sessions to counter any unknown cup-specific biases in delay or sensitivity.

Recording gear and calibration

Recordings were made with an eight-channel National Instruments (USB-6356; Austin, TX, USA) box simultaneously sampling at 500kHz per channel with 16bit resolution. The eight recording channels were connected to the five far-field hydrophones in two different recording setups (1 and 2) and the three suction cup hydrophones placed in either of two configurations on the melon (Fig. 1B–E). To minimize reflections, we used custom-built hydrophones consisting of a single small 4×6mm prolate spheroid piezoceramic element with a polyurethane coating. The hydrophones were calibrated before and after the experiments relative to a Reson TC4014 hydrophone (Slangerup, Denmark), and displayed a nominal sensitivity of $-211\text{ dB re. } 1\text{ V}\mu\text{Pa}^{-1}$. The suction cup hydrophones (diameter of 60mm) were custom built with either spherical or cylindrical piezoceramic elements molded in a silicone resin. They were also calibrated relative to a Reson TC4014 hydrophone before and after experiments to show sensitivities of -210 and $-208\text{ dB re. } 1\text{ V}\mu\text{Pa}^{-1}$. All hydrophones were connected to custom-built conditioning boxes with adjustable gains between 10 and 50dB depending on placement and aspect to the clicking animal, and band-pass filters between 1 and 200kHz (Butterworth, one pole high-pass, four poles low-pass).

Analysis

Recordings were stored as eight-channel pcm *.wav files. Click extraction was carried out *via* a combination of automation and visual inspection to identify the click train recorded on the center hydrophone in line with the target and the melon of the animal. To ensure that only clicks close to or on the acoustic axis were included in the analysis of spectrum, source level and centroid frequency, clicks on the center hydrophone had to be more than 3dB higher than those on either of the two hydrophones 15 deg to the left and right of the center hydrophone. For each session we then identified the lowest threshold that allowed for inclusion of all on-axis clicks used by the animal to probe the target for presence/absence. For each of the two animals, BJ and Kina, all eight channels of the clicks being on-axis on the center hydrophone were saved into a Matlab structure (7.5, MathWorks, Natick, MA, USA), making it convenient to extract parameters for subsequent analysis. For each trial, information was stored on file name, target size and target presence, and correctness of response. For each click registered on the target hydrophone as on-axis, the corresponding waveforms recorded on the suction cup hydrophones were evaluated by peak-to-peak amplitude and delay to the other suction cup hydrophones. The delay was measured as the difference between the last sample before the first -10 dB points of the peaks of the signal envelopes (absolute value of the Hilbert transformed signal). Click spectra were calculated as 512 point fast Fourier transforms (FFTs). The signals were windowed with a 300 μs long Tukey window (30 μs slope, 240 μs uniform, 30 μs slope) centered on the peak sample. We computed the centroid frequency (f_c) as the frequency that divided the energy spectrum into two equally sized halves on a linear scale, and the root mean square (r.m.s.) bandwidth as the spectral standard deviation around the centroid.

Experiment II

Whistling

For each animal, Kina and BJ, one session was run where the animal was trained to whistle following the procedures of Ridgway and

Carder (Ridgway and Carder, 1988). For this experiment we only used two laterally placed suction cups on either side of the blowhole (Fig. 1B,D). The animal was trained to station at 0.5m depth and subsequently to produce a series of whistles before returning to the surface. The suction cup hydrophone outputs were amplified by 50dB and band-pass filtered between 1 and 50kHz (Butterworth, four pole) before being recorded on an M-Audio, Microtrack II device (Cumberland, RI, USA), sampling at 96kHz, 16bit. We identified and analyzed all whistles with signal-to-noise ratios (SNR) better than 20dB. Time delays between the two hydrophones were determined by cross-correlating the two channels against each other (right side against left side) and measuring the delay of the peak sample.

Experiment III

Animals, setup, recordings and analysis

Data were obtained from three male Atlantic bottlenose dolphins named Noah (13 years), Liho (16 years) and Kolohe (16 years), housed in an artificial lagoon complex at the Dolphin Quest facility at the Kahala Hilton in Honolulu, Hawaii. Each animal was trained to hold station with its rostrum through a 5 cm diameter hoop placed 1 m below the water surface while wearing eyecups and suction cup hydrophones on the head. Two suction cup hydrophones were placed 8 cm forward and to either side of the center of the blowhole while the third was placed on the animal's melon, 20 cm forward of the blowhole. Each suction cup hydrophone had a sensitivity of $-220\text{ dB re. } 1\text{ V}\mu\text{Pa}^{-1}$. Hydrophone outputs were amplified by a custom-built (W. Au) multi-channel variable gain amplifier. The signal from each hydrophone was digitized using a four-channel Measurement Computing A/D board (PCIDAS4020/12; Norton, MA, USA), sampling at 500kHz (12 bit) that was operated from a 12 V battery-powered Pentium 850MHz 'lunchbox' computer. A custom-written (M. Lammers) LABVIEW 6i program performed the data acquisition and storage process. A recording trial was initiated once the animal was instrumented with the suction cup hydrophones and at the stationing hoop underwater. To stimulate echolocation by the animal, a variety of metal objects (e.g. the element from a range, a shelf bracket, a metal dish rack, etc.) were suspended underwater at a distance of $\sim 20\text{ m}$. Recordings from the hydrophones were obtained in 6 s increments over the course of $\sim 1\text{--}2\text{ m}$ until the animal was released from the task by the trainer. The length of each experimental session varied between 20 and 45 min. As in Experiment I, the suction cup hydrophones were color coded and the two hydrophones lateral to the blowhole were swapped for each session to counter any unknown cup-specific biases in delay or sensitivity. The data were analyzed for delay and amplitude differences by identifying clicks on the central suction cup hydrophone (*sensu* Madsen et al., 2010). The delay between click arrivals on the two lateral hydrophones was measured in the same way as for Experiment I.

RESULTS

The parts of experiment I with suction cup configuration A (Fig. 1B,D) involved seven sessions for Kina and BJ consisting of 134 trials. During these, BJ produced a total of 4987 detected clicks while the screen was lowered and 3883 of those were classified as on-axis (Table 1). Kina produced 2728 on-axis clicks out of 2763 clicks with the screen lowered. For all of the 7750 clicks analyzed from configuration A of both animals, the right side cup received the click first (Figs 2, 3) with a mean (\pm s.d.) delay to the left cup of $26.0\pm 6.0\mu\text{s}$ for BJ and $24.3\pm 11.7\mu\text{s}$ for Kina (Fig. 4A,C). The received levels on the right suction cup were also on average higher

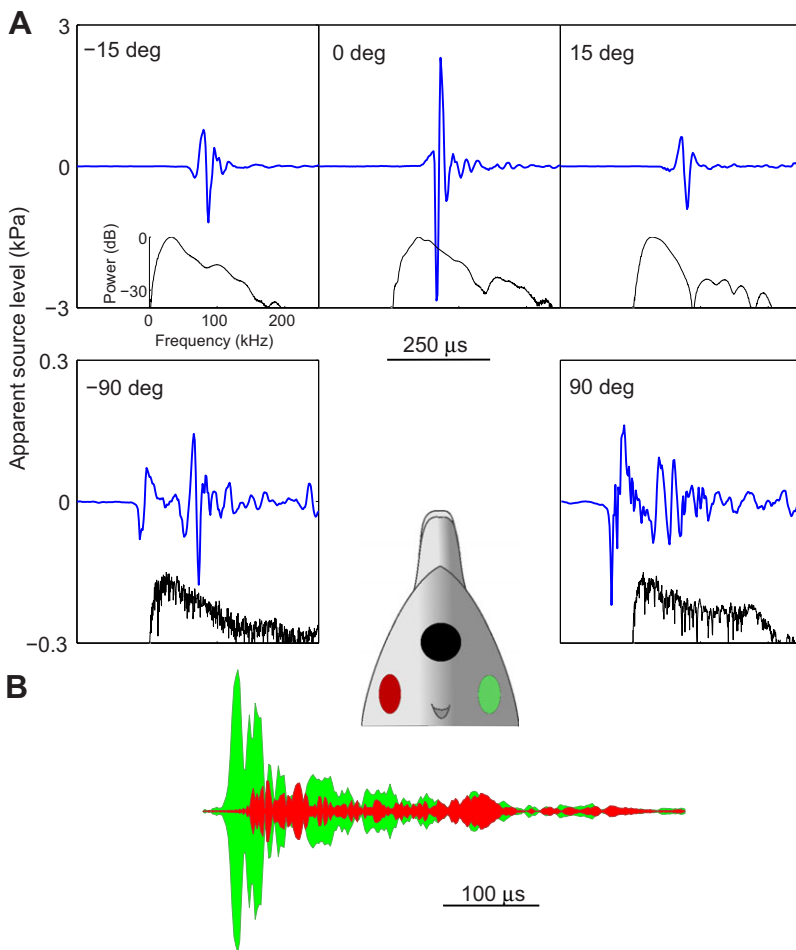


Fig. 2. (A) Waveforms of the same click from BJ, the bottlenose dolphin, recorded at different angles with respect to the acoustic axis. Note how the levels taper off with angle away from the on-axis, and that the clicks break up into several pulses at ± 90 deg with delays of some 100 μ s between the two first pulses. (B) Colored waveforms, from the left (red) and right (green) suction cups placed as indicated on the dolphin head, show that the produced click arrives first on the green suction cup hydrophone on the right side of the blowhole and some 26 μ s later on the red suction cup hydrophone on the left side of the blowhole.

than those on the left cup by 17.5 ± 5.3 dB on average for BJ and 6.2 ± 7.1 dB for Kina in configuration A (Figs 2, 3 and Fig. 4B,D). Comparable delays and received level differences between the right and the left side suction cup hydrophones were found for the 3476 clicks produced by the three other bottlenose dolphins in experiment III during two sessions consisting of three trials for each of the animals (Fig. 5). Thus, all five animals consistently used their right pair of phonic lips when producing clicks for echolocation.

In experiment I, both BJ and Kina were highly focused on the detection task with a percentage of correct answers between 90 and 100% for BJ and between 82 and 100% for Kina (Table 1). Consequently, a large proportion of the clicks produced were directed towards the target location, giving rise to a high percentage of on-axis clicks out of the total number of clicks produced (Table 1). BJ used on average between 22 and 57 clicks to solve the detection task, while Kina used between 12 and 34 clicks to do the same (Table 1). In an attempt to induce a change in source parameters, we used a small (S, 22 mm long) and a medium (M, 69 mm long) cylinder in two sessions rather than the standard large (L, 180 mm long) cylinder used in five sessions for each animal (Table 1). A permutation test on the average levels within the trials revealed small, but statistically significant ($P < 0.01$, BJ and $P < 0.001$, Kina) increases in source levels (SLs) for both animals, but with no significant changes in centroid frequency (f_c). The source sound pressure levels varied over more than two orders of magnitude (five orders of magnitude in energy) from 160 to 210 dB re. 1μ Pa (peak–peak, pp) for BJ and from 160 to 209 dB re. 1μ Pa (pp) for Kina (Table 1; Fig. 6). The click f_c varied over more than two octaves

from 22 to 77 kHz for BJ and from 21 to 85 kHz for Kina (Fig. 6A,C). For both animals, the f_c were positively correlated with the SLs (Fig. 6A,C). To visualize the relationship between SLs and the spectral composition of the clicks, we sorted the clicks by amplitude and plotted their stacked spectra with signal energy color coded in Fig. 6B,D. It can be seen that the peak frequencies for both animals are centered on 40 kHz (Fig. 6B,D; Table 1), but with increasing amounts of high frequency energy with increasing SLs, giving rise to a second frequency peak above 100 kHz for high SL clicks (Fig. 6B,D).

The far-field signatures of the produced clicks are plotted in Fig. 2A for BJ and Fig. 3A for Kina. The clicks display all the common directionality features for delphinid clicks reported in previous studies (Au, 1993): on-axis, the clicks are short with the most high frequency energy, but when moving off-axis, the levels and high frequency energy drop off dramatically (Fig. 2A and Fig. 3A). At ± 90 deg off-axis, the clicks of BJ break into several discrete pulses with a delay between the two dominant pulses of some 100 μ s (Fig. 2). For Kina, a similar multi-pulsed pattern is observed (Fig. 3) with delays between the two dominant pulses of some 200 μ s. To study beam dynamics, we conducted two additional sessions with BJ and one additional session with Kina using suction cup hydrophone configuration B in experiment I (Fig. 1C,E and Fig. 7). This configuration allowed us to study fluctuations in received levels on either side of the melon (see Au et al., 2010; Madsen et al., 2010) as a proxy for beam changes. Fig. 7 displays two examples from Kina (Fig. 7A) and BJ (Fig. 7C) where relative changes in received levels on the left and right suction cup

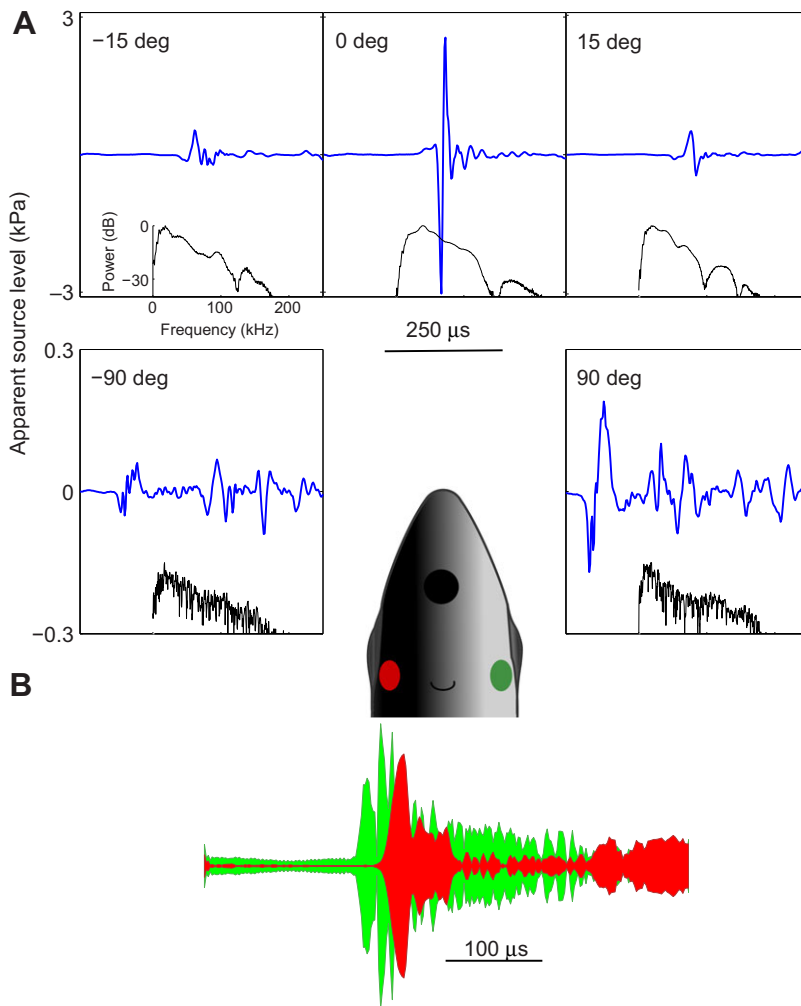


Fig. 3. (A) Waveforms of the same click from Kina, the false killer whale, recorded at different angles with respect to the acoustic axis. Note how the levels taper off with angle away from the on-axis, and that the clicks break up into several pulses at ± 90 deg with delays of some 200 μ s between the two first pulses. (B) Colored waveforms show that the produced click arrives first on the green suction cup hydrophone on the right side of the blowhole and some 24 μ s later on the red suction cup hydrophone on the left side of the blowhole.

hydrophones are shown to fluctuate over the course of a single click train. It can be seen that the received levels in general are higher on the right side than on the left side by about 4 dB (Fig. 7B,D), but that the level differences may occasionally change so that they are higher on the left than on the right side (Fig. 7A,C), despite the fact that the clicks arrive first on the suction cup on the right side. Similar variations in output across the nasal structures are also indicated by the relative level fluctuations between the right and left suction cup hydrophones seen for all animals using configuration B in experiments I (Fig. 4) and III (Fig. 5).

To study whistle production, we conducted experiment II, where BJ and Kina were trained to station at 0.5 m depth wearing two laterally placed suction cups in configuration A (Fig. 1B,D). During the course of a single session we recorded 41 whistles from BJ and 69 from Kina with SNRs better than 20 dB (Fig. 8). We cross-correlated the two hydrophone channels to get time of arrival differences between the two hydrophones. The data provide a median delay of 4.5 μ s for BJ (Fig. 8A) and 14.4 μ s for Kina (Fig. 8B), showing that the whistles were produced by the left pair of phonic lips with the possible production of a few whistles on the right side (Fig. 8).

DISCUSSION

Here, we tested the dual actuation hypothesis proposing that echolocating toothed whales can actuate two pairs of phonic lips simultaneously to form a single click (Cranford et al., 2011). We show that all the five echolocating delphinids tested in this study

click with their right pair of phonic lips (Figs 2–5) and whistle with their left pair of phonic lips (Fig. 8) with no evidence of dual actuation of two pairs of phonic lips to produce a single click. This finding is in line with observations from porpoises (Madsen et al., 2010; Amundin and Andersen, 1983), and previous studies on bottlenose dolphins using direct measurements (Norris et al., 1971; Dormer, 1979; Mackay and Liaw, 1981; Amundin and Andersen, 1983; Au et al., 2010; Dubrovskiy and Giro, 2004), modeling (Aroyan et al., 1992; Aroyan et al., 2000) and anatomical inferences (Mead, 1975; Heyning, 1989; Harper et al., 2008; McKenna et al., 2012). The clicks recorded here consistently arrive from a source to the right of the medial nasal midline of the studied animals (Figs 4, 5), but the delays vary between 5 and ~ 50 μ s, with means of around 26 μ s for the bottlenose dolphins and 24 μ s for the false killer whale. Such variation may in part stem from slightly different suction cup placements between sessions and animals but also from the fact that dolphins can actuate various parts of the phonic labia for sound production (Cranford et al., 2011). Actuation of the right pair of phonic lips is further corroborated by the on average higher received levels for the suction cups on the right-hand side (Figs 2–5, 7) as also found for other bottlenose dolphins (Au et al., 2010) and for porpoises (Au et al., 2006; Madsen et al., 2010).

Multi-pulsed patterns off-axis stem from multi-path propagation and not two sources

Despite the finding of just one active pair of phonic lips, we did observe the multi-pulsed pattern at ± 90 deg (Figs 2, 3) that was

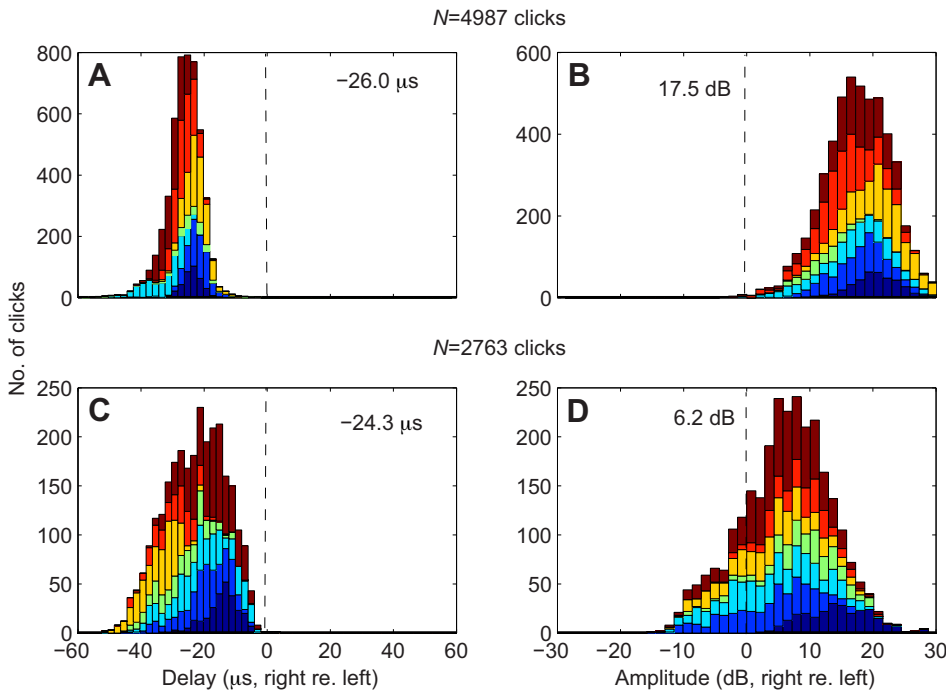


Fig. 4. (A) Distribution of time delays between the left and right suction cup hydrophones on BJ using hydrophone configuration A. (B) Distribution of amplitude differences between the left and right suction cup hydrophones on BJ. (C) Distribution of time delays between the left and right suction cup hydrophones on Kina using hydrophone configuration A. (D) Distribution of amplitude differences between the left and right suction cup hydrophones on Kina. Different colored bars denote different sessions (see Table 1). The mean difference is shown at the top of each panel.

interpreted by Lammers and Castellote to stem from each of two active phonic lip pairs (Lammers and Castellote, 2009). Thus, the increasing delays between two pulses when moving off axis in echolocating delphinids can be generated by just a single active source in their nasal complex. One explanation that can reconcile this fact with the longer than expected delays reported by Lammers and Castellote (Lammers and Castellote, 2009), as also found here, may be that sound energy escapes the head *via* at least two different exits: we propose that the first pulse arrives directly from the right phonic lip pair while the second pulse is radiated from the front of

the melon (Au et al., 2006; Au et al., 2010) to ensonify the hydrophones off axis at ± 90 deg. This would be consistent with the observations of Au and colleagues (Au et al., 2012) that the first pulse has a lower frequency than the second pulse, which under this scenario has been propagating in the melon (Varanasi et al., 1975). Delays of some $100 \mu\text{s}$ (Fig. 2) and $200 \mu\text{s}$ (Fig. 3) between the two main pulses would then correspond to a melon propagation path of some 15 cm for BJ and 30 cm for Kina, and a delay of about $250 \mu\text{s}$ corresponds to some 38 cm for the white whale in the study by Lammers and Castellote (Lammers and Castellote, 2009), assuming

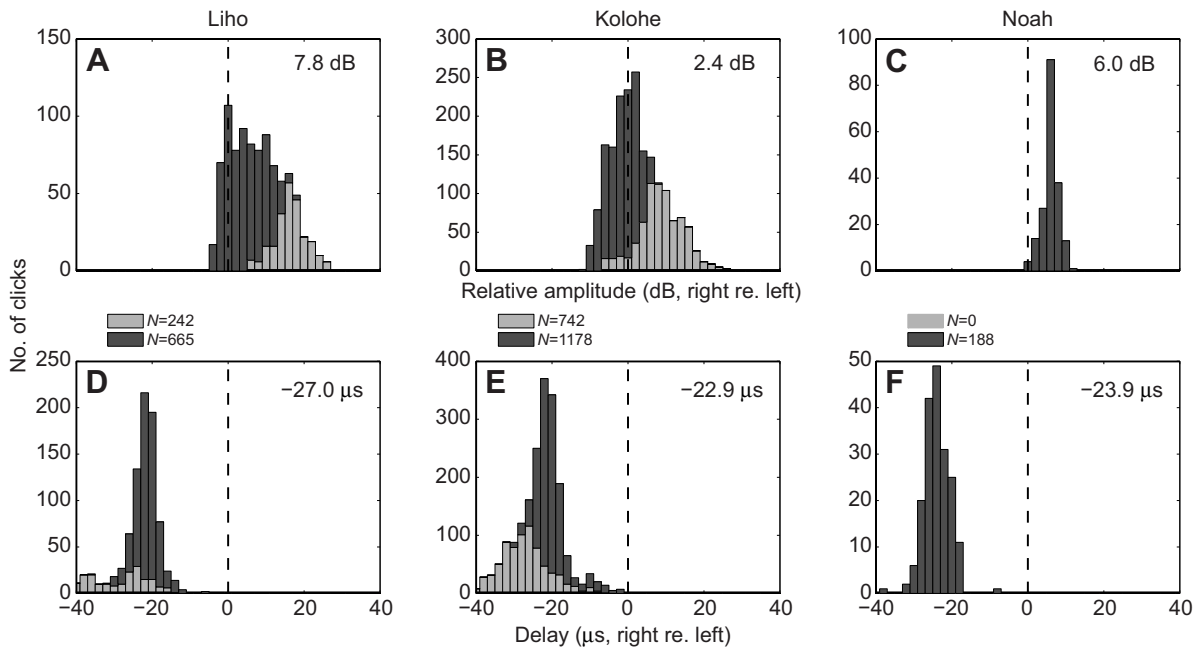


Fig. 5. (A–C) Distributions of amplitude differences between the right and left suction cup hydrophones of the three bottlenose dolphins in experiment III. (D–F) Distributions of time delays between the right and left suction cup hydrophones of the three bottlenose dolphins in Experiment III. The mean difference is shown at the top right of each panel.

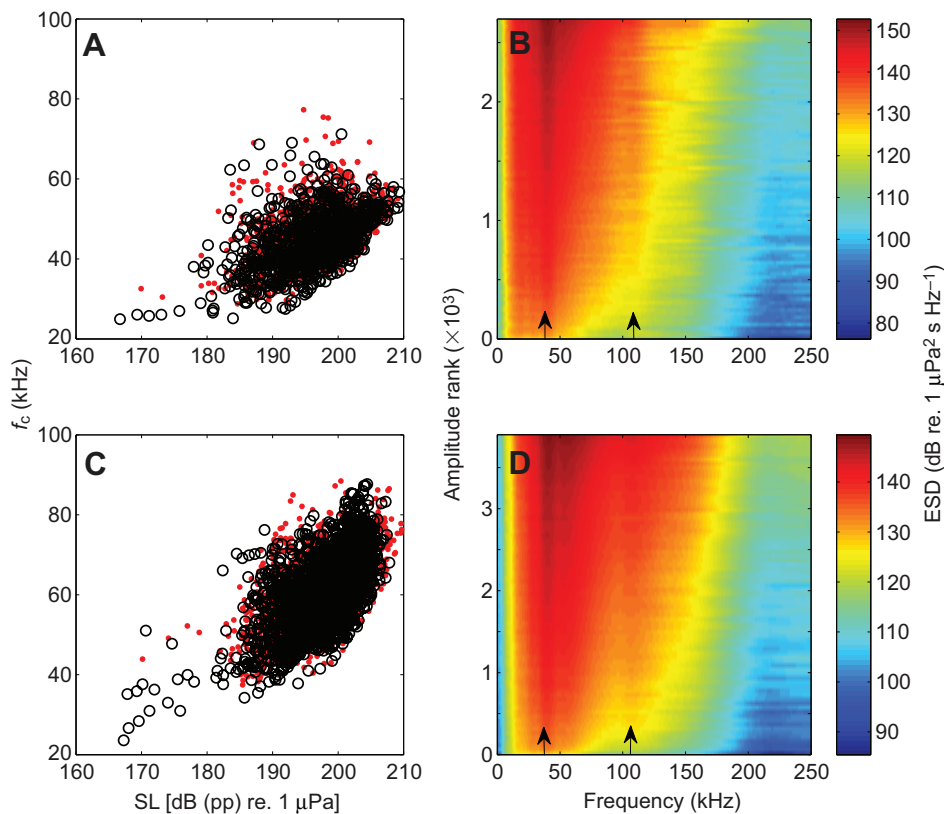


Fig. 6. (A) Correlation between source level (SL) and centroid frequency (f_c) for the on-axis clicks of BJ. Black circles are clicks from trials with target absent and red dots are from trials with target present. (B) Stacked click spectra from BJ sorted by SL with energy spectral density (ESD) color coded. (C) Correlation between SL and f_c for the on-axis clicks of Kina. (D) Stacked click spectra from Kina sorted by SL with ESD color coded.

a sound speed in tissue of $1.5 \text{ mm } \mu\text{s}^{-1}$. Such estimated sound paths are consistent with the dimensions of the melons in these three delphinid species of different sizes. This dual path propagation may also explain why the delays between the multi-pulses to the right side of the white whale on average are $50 \mu\text{s}$ shorter than those to multi-pulses to the left side (Lammers and Castellote, 2009): if the clicks are produced by the right pair of phonic lips in the white whale as well, the delay between the direct and the melon-propagated pulses at 90° to the right of the animal should be shorter than if they were recorded on the left side. Movements by the animals within the hoop precluded such analysis for the animals of the present study.

High click rates with one source active

In their comprehensive treatise, Cranford and colleagues (Cranford et al., 2011) list a range of remarkable click properties that lend apparent support to the dual actuation hypothesis: (i) two active sources can generate higher click repetition rates, (ii) constructive interference by pulses from two sources can lead to higher SLs, (iii) pulses from two sources of different size can interfere to generate a click of broader bandwidth, and (iv) by adjusting the timing of the two pulses, echolocating toothed whales can steer their sound beams. The highest click rates measured here reached $430 \text{ clicks s}^{-1}$, which along with the $600 \text{ clicks s}^{-1}$ for porpoises (Madsen et al., 2010) shows that toothed whales, with just a single sound source, can generate clicks fast enough to support the very short inter-click intervals required during buzzing when capturing prey (Madsen et al., 2005; Deruiter et al., 2009; Madsen et al., 2010). In addition, if the two phonic lip pairs with different tissue resonances take turns in producing a click in high-rate clicking, every other click should have spectra that are consistently higher or lower than those of the following click. We did not find that, but rather that a given click is very similar to the previous and following clicks. Finally,

Cranford and colleagues (Cranford et al., 2011) point to the study of Weir and colleagues (Weir et al., 2007) reporting that sperm whales with a single phonic lip pair apparently can click at rates of up to $1600 \text{ clicks s}^{-1}$. Further, it seems that delphinid whistles are in fact a form of very fast clicking (Madsen et al., 2011). The notion that two active phonic lip pairs are required to generate high repetition rates is therefore unsubstantiated.

Source level dynamics with one source active

If two identical pulses from two simultaneously actuated phonic lip pairs interfere constructively, the resulting SL may maximally be 6 dB higher than if the click was produced by a single source. If pulses with little spectral overlap from two pairs of phonic lips of different sizes interfere incoherently, the resulting SL can maximally be 3 dB higher than if the click was produced by a single source. Thus, the SL gain from actuating two phonic lip pairs simultaneously is very limited, and much lower than the dynamic range of toothed whale clicks, $\sim 160\text{--}228 \text{ dB re. } 1 \mu\text{Pa (pp)}$ (Au, 1993). In the present study we found SL differences of 50 dB from about 160 to 210 dB re. $1 \mu\text{Pa (pp)}$ for both animals in experiment I (Fig. 6). Despite the small increases in SL to smaller targets, it is clear that the animals faced a fairly easy detection task (Table 1), which likely explains the relatively low SLs compared with the maximum recorded for these species both in captivity and in the wild of some 228 dB re. $1 \mu\text{Pa (pp)}$ (Au et al., 1974; Au et al., 1995; Madsen et al., 2004b; Wahlberg et al., 2011). Further, both BJ and Kina may have adjusted their sound production to their reduced frequency range of functional hearing (Ibsen et al., 2007; Kloepper et al., 2010), but they nevertheless both generated the second spectral peak for higher SLs (Fig. 6B,D, see arrows). We have thus not explored the maximum capabilities of their sonar systems in terms of output, but the large dynamic range of SLs demonstrated here with just one source active compared with the maximal gain that may result from actuating two

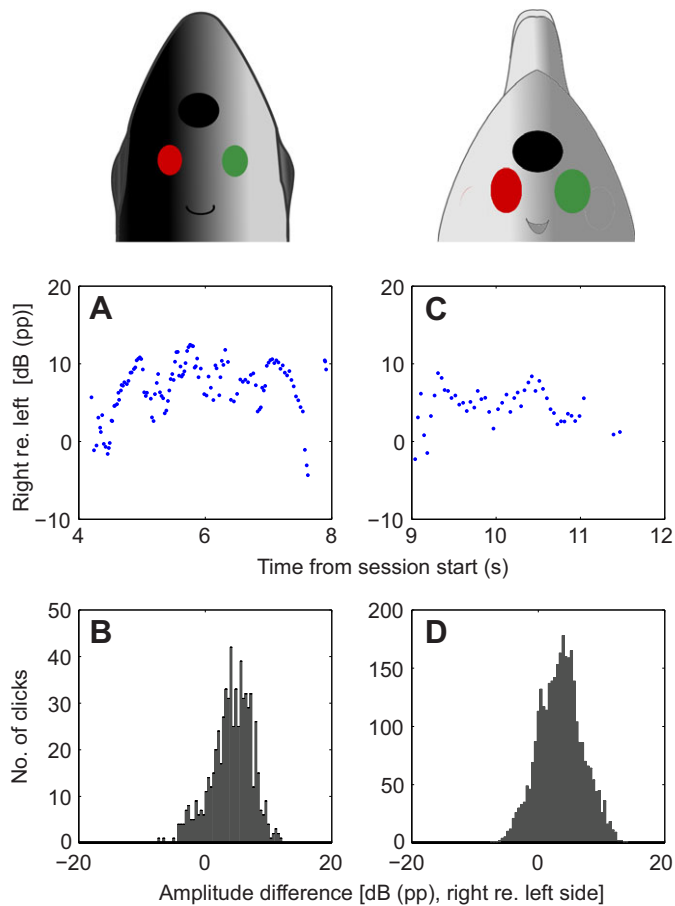


Fig. 7. Recordings from suction cup hydrophone configuration B (shown at the top of the figure). (A) Example of a click train from Kina where the received level between the left (red) and right (green) hydrophones fluctuates rapidly, indicating beam modulation. (B) Distribution of amplitude differences between the left and right hydrophone of all clicks from Kina. (C) Example of a click train from BJ where the received level between the left and right hydrophones fluctuates rapidly, indicating beam modulation. (D) Distribution of amplitude differences between the left and right hydrophone of all clicks from BJ.

sources exactly simultaneously of only 6 dB makes it clear that the vast majority if not all of SL regulation in toothed whale clicks must take place at the level of an individual pair of phonic lips by adjusting the driving air pressure and tension of the phonic lip labia.

Dynamic bandwidths with one source active

The spectral properties of the clicks recorded here from both species (Figs 2, 3, 6; Table 1) are comparable to published spectra in the same SL range for both free-ranging and captive bottlenose dolphins and false killer whales (Au et al., 1974; Au et al., 1995; Ibsen et al., 2009; Kloepper et al., 2010; Madsen et al., 2004a). A common feature in broad-band echolocation clicks of toothed whales is a positive correlation between the SL and the f_c , both for species with two possible sound sources (Au et al., 1974; Au et al., 1995) and for sperm whales, which carry a single sound source (Madsen et al., 2002). We found a similar relationship between SL and f_c for both BJ and Kina in the present experiment, where the f_c varied by more than two octaves as a function of SL (Fig. 6A,C). In line with that, Cranford and colleagues (Cranford et al., 2011) report the occurrence of two distinct bands of peak frequencies in delphinid clicks; one around 40 kHz and another around 110 kHz. Both peak

frequency bands are shifted upwards with increasing SLs and the high frequency band only appears for high SLs (Cranford et al., 2011), giving rise to the SL- f_c relationship. Cranford and colleagues (Cranford et al., 2011) and others (Houser et al., 1999; Moore et al., 2008) interpret these patterns to arise from the actuation of two differently sized pairs of phonic lips; the low frequency band of peak frequencies is generated by the large right pair of phonic lips while the high frequency band stems from a pulse generated by the smaller left pair of phonic lips.

However, here we found that that the clicks of both BJ and Kina display the same phenomenon despite the fact that only the right pair of phonic lips is active: Fig. 6B,D shows click spectra sorted by SL, and it can be seen that there is a consistent peak frequency band around 40 kHz. With increasing SL the bandwidth increases and another band of peak frequencies starts to appear around 110 kHz. Thus, the two peak frequency bands are not each generated by two active phonic lip pairs, but rather by a single source that radiates more high frequency energy at high SLs. We therefore conclude that delphinids can generate broad click bandwidths with two lines of peak frequencies using just a single pair of phonic lips. What then may give rise to different SLs and frequency compositions of echolocation clicks from a single source? Harper and colleagues (Harper et al., 2008) propose that the nasal plug muscle can change the tension of the phonic lips and hence their resonance frequency by adjusting the stiffness of the bursal connective tissue sheath. Under such a scenario, it will take a higher driving pressure to actuate the tense phonic lip labia acting as a pneumatic oscillator. We propose that increased tension on the phonic lips will lead to higher source levels with more energy at higher frequencies (Fig. 6). This mechanism is consistent with the observation that dolphins can easily be trained to produce high or low source levels, but it is not possible for them to produce low source levels with high centroid frequencies nor high source levels with low centroid frequencies (Moore and Pawloski, 1990); the high pneumatic driving pressure and high tension on the phonic lips required to generate high SLs seem to result in more energy at high frequencies.

Several authors have ascribed clicks from false killer whales (Au et al., 1995; Kloepper et al., 2010) and bottlenose dolphins (Houser et al., 1999) to different categories according to their SLs, waveforms and frequency content. Such classification may in part stem from inclusion of clicks at off-axis angles, but even when applying rigid on-axis criteria, it is clear that delphinid click spectra do vary significantly in a manner that is predictable from their SLs (Fig. 6). The continuums seen in Fig. 6B,D do, however, suggest that the fixed categories proposed in earlier studies for these species (Au et al., 1995; Kloepper et al., 2010; Houser et al., 1999; Muller et al., 2008) may not be supported, as it is very difficult to unequivocally ascribe a given click to a specific category from such a continuum (Fig. 6).

Beam modulation with one source active

While many studies have successfully applied piston models with fixed apertures to explain the radiation patterns of toothed whale clicks (Au, 1993; Kyhn et al., 2010; Koblitz et al., 2012), it is increasingly clear that toothed whales can modulate both the widths and the direction of their projected sound beams (Evans, 1973; Moore et al., 2008; Madsen et al., 2010; Starkhammar et al., 2011; Wisniewska et al., 2012). In particular, the groundbreaking study by Moore and colleagues (Moore et al., 2008) provided convincing evidence for the fact that dolphins can steer their beams as part of an acoustic gaze control. Moore and colleagues proposed that one explanation for such beam steering is that it could stem from dual

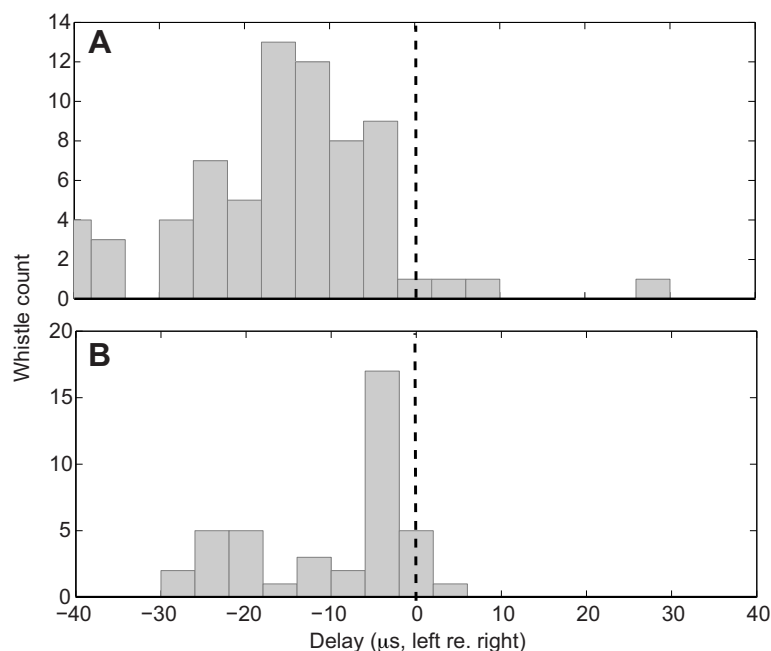


Fig. 8. Distribution of whistle delays between the left and right suction cup hydrophones in experiment II for (A) BJ and (B) Kina.

actuation of the two phonic lip pairs with acutely timed delays (Moore et al., 2008). Such beam steering will, however, only work if the two pulses from each of the phonic lip pairs have a large spectral overlap. Here, we show that the sound patterns in the near-field of the melon complex of both BJ and Kina can change rapidly over the course of a click train even with just a single source active (Fig. 7A,C). We could not in this experiment test whether such variations in fact also caused beam changes in the far-field, but it is hard to imagine that they would not (Madsen et al., 2010). It is therefore implied that while the overall directionality may be set by the cranial structures (Aroyan et al., 2000), beam changes can be achieved with one pair of phonic lips active through conformation changes in the nasal soft structures and air sacs (Dormer, 1979; Harper et al., 2008; McKenna et al., 2012).

Dual sound production: whistling on the left and clicking on the right

Toothed whales produce long tonal sounds for communication (Jensen et al., 2011; Jensen et al., 2012) *via* tissue vibrations in their phonic lip labia (Cranford et al., 1996; Madsen et al., 2012). Here, we corroborate previous findings (Dormer, 1979; Mackay and Liaw, 1981; Cranford et al., 2011) showing that delphinids generally whistle with their left pair of phonic lips (Fig. 8). We have also recorded instances for both bottlenose dolphins and false killer whales during the whistle trials where both clicks and whistles are produced: the clicks arrive first on the right suction cup hydrophone and the whistles arrive first on the left suction cup hydrophone. This confirms previous reports (Brill and Harder, 1991; Murray et al., 1998; Cranford et al., 2011) that delphinids can employ dual sound production by whistling and clicking at the same time, normally by whistling with the left pair of phonic lips and clicking with the right pair.

Conclusions and perspectives on toothed whale sound production

In this study, we have shown that echolocating delphinids can achieve all of the virtues of click modulation ascribed to dual source actuation (Cranford et al., 1996; Cranford et al., 2011; Moore et al.,

2008) with just their right pair of phonic lips active. We demonstrate that with just a single pair of phonic lips they can change the click energy levels over five orders of magnitude, alter the click centroid frequencies over more than two octaves, and modulate their sound radiation from the melon for beam steering. We therefore conclude that all of the click dynamics ascribed to dual actuation of two phonic lip pairs can be achieved with actuation of just the right pair of phonic lips, and we propose that the large dynamic range of source outputs is achieved by highly controlled modulation of the pneumatic driving pressure, the tension of the phonic lip labia and the conformation of the fatty melon and associated air sacs. There is every reason to think that delphinids can click with their left pair of phonic lips, but it is strongly suggested by the present data and previous studies (Norris et al., 1971; Dormer, 1979; Mackay and Liaw, 1981; Amundin and Andersen, 1983; Au et al., 2010; Dubrovskiy and Giro, 2004) that delphinids primarily click with their right pair of phonic lips for echolocation. That notion is supported by the fact that the right anterior bursa, contrary to the left anterior bursa, is connected to the melon *via* a fatty, low velocity core in delphinids (Harper et al., 2008; McKenna et al., 2012). Modeling efforts also point to the right pair of phonic lips as the source of the clicks in dolphins (Aroyan et al., 1992; Aroyan et al., 2000). Delphinids can likely also whistle with the right pair of phonic lips (as indicated by one or two whistles in Fig. 8), but our data suggest that whistles are normally produced by the left pair of phonic lips.

We cannot of course exclude the possibility that delphinids can in fact at times actuate two sources to form a single click, but we note that there are no direct measurements to show that this has ever occurred in any of the many studies on toothed whale sound production. The sperm whale has only a single right pair of phonic lips, and yet it has been shown to produce a broad repertoire of click types with SLs, bandwidths and frequency variations (Madsen et al., 2002; Møhl et al., 2000; Zimmer et al., 2005) that match those reported for toothed whales with two pairs of phonic lips. Based on available evidence, we therefore re-propose the hypothesis (Madsen et al., 2010) that toothed whales only use one phonic lip pair at a time to generate a click, and that they primarily use their right pair

of phonic lips for pneumatic production of echolocation clicks and primarily the left pair of phonic lips for pneumatic production of whistles. Future models of how toothed whales can pneumatically excite single pairs of phonic lips to produce very short, high powered ultrasonic transients and tonal whistles in a finely controlled manner will hopefully be tested by doing direct physiological measurements using cutting edge, high resolution medical imaging techniques on phonating animals. We foresee a strong synergy between detailed anatomical studies, physical modeling and physiological measurements to understand the details of how the phonic lips make a diverse repertoire of sounds.

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AUTHOR CONTRIBUTIONS

P.T.M., D.W., M.L. and K.B. conceived, designed and executed the experiments, and all authors analyzed the results and drafted and revised the article.

COMPETING INTERESTS

No competing interests declared.

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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 harbour porpoise, *Phocoena phocoena*, and the bottlenosed dolphin, *Tursiops truncatus*. *J. Exp. Biol.* **105**, 275-282.
- Aroyan, J. L., Cranford, T. W., Kent, J. and Norris, K. S. (1992). Computer modeling of acoustic beam formation in *Delphinus delphis*. *J. Acoust. Soc. Am.* **92**, 2539-2545.
- Aroyan, J. L., McDonald, M. A., Webb, S. C., Hildebrand, J. A., Clark, D., Laitman, J. T. and Reidenberg, J. S. (2000). Acoustic models of sound production and propagation. In *Hearing by Whales and Dolphins* (ed. W. W. L. Au, A. N. Popper and R. R. Fay), pp. 109-155. New York, NY: Springer Verlag.
- Au, W. W. L. (1993). *The Sonar of Dolphins*. New York, NY: Springer-Verlag.
- Au, W. W. L., Floyd, R. W., Penner, R. H. and Murchison, A. E. (1974). Measurement of echolocation signals of the Atlantic bottlenose dolphin, *Tursiops truncatus* Montagu, in open waters. *J. Acoust. Soc. Am.* **56**, 1280-1290.
- Au, W. W. L., Pawloski, J. L., Nachtigall, P. E., Blonz, M. and Gisner, R. C. (1995). Echolocation signals and transmission beam pattern of a false killer whale (*Pseudorca crassidens*). *J. Acoust. Soc. Am.* **98**, 51-59.
- Au, W. W. L., Kastelein, R. A., Benoit-Bird, K. J., Cranford, T. W. and McKenna, M. F. (2006). Acoustic radiation from the head of echolocating harbor porpoises (*Phocoena phocoena*). *J. Exp. Biol.* **209**, 2726-2733.
- Au, W. W. L., Houser, D. S., Finneran, J. J., Lee, W. J., Talmadge, L. A. and Moore, P. W. (2010). The acoustic field on the forehead of echolocating Atlantic bottlenose dolphins (*Tursiops truncatus*). *J. Acoust. Soc. Am.* **128**, 1426-1434.
- Au, W. W. L., Branstetter, B., Moore, P. W. and Finneran, J. J. (2012). Dolphin biosonar signals measured at extreme off-axis angles: insights to sound propagation in the head. *J. Acoust. Soc. Am.* **132**, 1199-1206.
- Brill, L. R. and Harder, P. J. (1991). The effects of attenuating returning echolocation signals at the lower jaw of a dolphin (*Tursiops truncatus*). *J. Acoust. Soc. Am.* **89**, 2851-2857.
- Cranford, T. W. (2000). In search of impulse sound sources in odontocetes. In *Hearing by Whales and Dolphins* (ed. W. W. L. Au, A. N. Popper and R. R. Fay), pp. 109-155. New York, NY: Springer Verlag.
- Cranford, T. W. (2011). Biosonar sources in odontocetes: considering structure and function. *J. Exp. Biol.* **214**, 1403-1404.
- Cranford, T. W. and Amundin, M. (2003). Biosonar pulse production in odontocetes: the state of our knowledge. In *Echolocation in Bats and Dolphins* (ed. J. A. Thomas, C. F. Moss and M. Vater), pp. 27-35. Chicago, IL: The University of Chicago Press.
- Cranford, T. W., Amundin, M. and Norris, K. S. (1996). Functional morphology and homology in the odontocete nasal complex: implications for sound generation. *J. Morphol.* **228**, 223-285.
- Cranford, T. W., Elsberry, W. R., Van Bonn, W. G., Jeffress, J. A., Chaplin, M. S., Blackwood, D. J., Carder, D. A., Kamolnick, T., Todd, M. A. and Ridgway, S. H. (2011). Observation and analysis of sonar signal generation in the bottlenose dolphin (*Tursiops truncatus*): evidence for two sonar sources. *J. Exp. Mar. Biol. Ecol.* **407**, 81-96.
- Deruiter, S. L., Bahr, A., Blanchet, M. A., Hansen, S. F., Kristensen, J. H., Madsen, P. T., Tyack, P. L. and Wahlberg, M. (2009). Acoustic behaviour of echolocating porpoises during prey capture. *J. Exp. Biol.* **212**, 3100-3107.
- Diercks, K. J., Trochta, R. T., Greenlaw, C. F. and Evans, W. E. (1971). Recording and analysis of dolphin echolocation signals. *J. Acoust. Soc. Am.* **49**, 1729-1732.
- Dormer, K. J. (1979). Mechanism of sound production and air recycling in delphinids – cineradiographic evidence. *J. Acoust. Soc. Am.* **65**, 229-239.
- Dubrovskiy, N. and Giro, L. (2004). Modeling of the click production mechanism in the dolphin. In *Echolocation in Bats and Dolphins* (ed. J. Thomas, C. Moss and M. Vater), pp. 59-64. Chicago, IL: The University of Chicago Press.
- Evans, W. E. (1973). Echolocation by marine delphinids and one species of freshwater dolphin. *J. Acoust. Soc. Am.* **54**, 191-199.
- Evans, W. E. and Prescott, J. H. (1962). Observations of the sound production capabilities of the bottlenose porpoise: a study of whistles and clicks. *Zoologica* **47**, 121-128.
- Harper, C. J., McLellan, W. A., Rommel, S. A., Gay, D. M., Dillaman, R. M. and Pabst, D. A. (2008). Morphology of the melon and its tendinous connections to the facial muscles in bottlenose dolphins (*Tursiops truncatus*). *J. Morphol.* **269**, 820-839.
- Heyning, J. E. (1989). Comparative facial anatomy of beaked whales (Ziphiidae) and a systematic revision among the families of extant Odontoceti. *Los Angeles County Museum of Natural History Contributions in Science* **405**, 1-64.
- Houser, D. S., Helweg, D. A. and Moore, P. W. (1999). Classification of dolphin echolocation clicks by energy and frequency distributions. *J. Acoust. Soc. Am.* **106**, 1579-1585.
- Ibsen, S. D., Au, W. W. L., Nachtigall, P. E., Delong, C. M. and Breese, M. (2007). Changes in signal parameters over time for an echolocating Atlantic bottlenose dolphin performing the same target discrimination task. *J. Acoust. Soc. Am.* **122**, 2446-2450.
- Ibsen, S. D., Au, W. W. L., Nachtigall, P. E. and Breese, M. (2009). Functional bandwidth of an echolocating Atlantic bottlenose dolphin (*Tursiops truncatus*). *J. Acoust. Soc. Am.* **125**, 1214-1221.
- Janik, V. M., Sayigh, L. S. and Wells, R. S. (2006). Signature whistle shape conveys identity information to bottlenose dolphins. *Proc. Natl. Acad. Sci. USA* **103**, 8293-8297.
- Jensen, F. H., Perez, J. M., Johnson, M., Aguilar Soto, N. and Madsen, P. T. (2011). Calling under pressure: short-finned pilot whales make social calls during deep foraging dives. *Proc. Bio. Sci.* **278**, 3017-3025.
- Jensen, F. H., Beedholm, K., Wahlberg, M., Bejder, L. and Madsen, P. T. (2012). Estimated communication range and energetic cost of bottlenose dolphin whistles in a tropical habitat. *J. Acoust. Soc. Am.* **131**, 582-592.
- Johnson, M., Madsen, P. T., Zimmer, W. M. X., de Soto, N. A. and Tyack, P. L. (2006). Foraging Blainville's beaked whales (*Mesoplodon densirostris*) produce distinct click types matched to different phases of echolocation. *J. Exp. Biol.* **209**, 5038-5050.
- Klopper, L. N., Nachtigall, P. E., Gisner, R. and Breese, M. (2010). Decreased echolocation performance following high-frequency hearing loss in the false killer whale (*Pseudorca crassidens*). *J. Exp. Biol.* **213**, 3717-3722.
- Koblitz, J. C., Wahlberg, M., Stiltz, P., Madsen, P. T., Beedholm, K. and Schnitzler, H. U. (2012). Asymmetry and dynamics of a narrow sonar beam in an echolocating harbor porpoise. *J. Acoust. Soc. Am.* **131**, 2315-2324.
- Kyhn, L. A., Jensen, F. H., Beedholm, K., Tougaard, J., Hansen, M. and Madsen, P. T. (2010). Echolocation in sympatric Peale's dolphins (*Lagenorhynchus australis*) and Commerson's dolphins (*Cephalorhynchus commersonii*) producing narrow-band high-frequency clicks. *J. Exp. Biol.* **213**, 1940-1949.
- Lammers, M. O. and Castellote, M. (2009). The beluga whale produces two pulses to form its sonar signal. *Biol. Lett.* **5**, 297-301.
- Lilly, J. C. (1962). Vocal behavior of the bottlenose dolphin. *Proc. Am. Philos. Soc.* **106**, 520-529.
- Lilly, J. C. (1978). *Communication Between Man and Dolphin: The Possibility of Talking With Other Species*. New York, NY: Crown Publishers, Inc.
- Mackay, R. S. and Liaw, H. M. (1981). Dolphin vocalization mechanisms. *Science* **212**, 676-678.
- Madsen, P. T., Payne, R., Kristiansen, N. U., Wahlberg, M., Kerr, I. and Möhl, B. (2002). Sperm whale sound production studied with ultrasound time/depth-recording tags. *J. Exp. Biol.* **205**, 1899-1906.
- Madsen, P. T., Kerr, I. and Payne, R. (2004a). Source parameter estimates of echolocation clicks from wild pygmy killer whales (*Feresa attenuata*). *J. Acoust. Soc. Am.* **116**, 1909-1912.
- Madsen, P. T., Kerr, I. and Payne, R. (2004b). Echolocation clicks of two free-ranging, oceanic delphinids with different food preferences: false killer whales *Pseudorca crassidens* and Risso's dolphins *Grampus griseus*. *J. Exp. Biol.* **207**, 1811-1823.
- Madsen, P. T., Johnson, M., de Soto, N. A., Zimmer, W. M. X. and Tyack, P. (2005). Biosonar performance of foraging beaked whales (*Mesoplodon densirostris*). *J. Exp. Biol.* **208**, 181-194.
- Madsen, P. T., Wisniewska, D. and Beedholm, K. (2010). Single source sound production and dynamic beam formation in echolocating harbour porpoises (*Phocoena phocoena*). *J. Exp. Biol.* **213**, 3105-3110.
- Madsen, P. T., Wisniewska, D. M. and Beedholm, K. (2011). Response to: Biosonar sources in odontocetes: considering structure and function. *J. Exp. Biol.* **214**, 1404-1405.
- Madsen, P. T., Jensen, F. H., Carder, D. and Ridgway, S. (2012). Dolphin whistles: a functional misnomer revealed by heliox breathing. *Biol. Lett.* **8**, 211-213.

- McKenna, M. F., Cranford, T. W., Berta, A. and Pyenson, N. D.** (2012). Morphology of the odontocete melon and its implications for acoustic function. *Mar. Mamm. Sci.* **28**, 690-713.
- Mead, J. G.** (1975). Anatomy of the external nasal passage and facial complex in the Delphinidea (Mammalia: Cetacea). *Smithson. Contrib. Zool.* **207**, 1-35.
- Møhl, B., Wahlberg, M., Madsen, P. T., Miller, L. A. and Surlykke, A.** (2000). Sperm whale clicks: directionality and source level revisited. *J. Acoust. Soc. Am.* **107**, 638-648.
- Moore, P. W. B. and Pawloski, D. A.** (1990). Investigations on the control of echolocation pulses in the dolphin (*Tursiops truncatus*). In *Sensory Abilities of Cetaceans: Laboratory and Field Evidence* (ed. J. A. Thomas and R. A. Kastelein), pp. 305-316. New York, NY: Plenum Press.
- Moore, P. W., Dankiewicz, L. A. and Houser, D. S.** (2008). Beamwidth control and angular target detection in an echolocating bottlenose dolphin (*Tursiops truncatus*). *J. Acoust. Soc. Am.* **124**, 3324-3332.
- Muller, M. W., Allen, J. S., 3rd, Au, W. W. L. and Nachtigall, P. E.** (2008). Time-frequency analysis and modeling of the backscatter of categorized dolphin echolocation clicks for target discrimination. *J. Acoust. Soc. Am.* **124**, 657-666.
- Murray, S. O., Mercado, E. and Roitblat, H. L.** (1998). Characterizing the graded structure of false killer whale (*Pseudorca crassidens*) vocalizations. *J. Acoust. Soc. Am.* **104**, 1679-1688.
- Norris, K. S.** (1964). Some problems of echolocation in cetaceans. In *Marine Bio-Acoustics* (ed. W. N. Tavolga), pp. 317-336. New York, NY: Pergamon Press.
- Norris, K.** (1968). The evolution of acoustic mechanisms in odontocete cetaceans. In *Evolution and Environment* (ed. E. T. Drake), pp. 297-324. New Haven, CT: Yale University Press.
- Norris, K. S., Dormer, K. J., Pegg, J. and Liese, G. T.** (1971). The mechanism of sound production and air recycling in porpoises: a preliminary report. In *Proceedings of the Eighth Conference on the Biological Sonar of Diving Mammals*, pp. 113-129. Stanford Research Institute, Menlo Park, CA, USA.
- Ridgway, S. H. and Carder, D. A.** (1988). Nasal pressure and sound production in an echolocating white whale, *Delphinapterus leucas*. In *Animal Sonar: Processes and Performance* (ed. P. Nachtigall and P. Moore), pp. 53-60. New York, NY: Plenum.
- 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* (ed. R. G. Busnel and J. F. Fish), pp. 239-250. New York, NY: Plenum Press.
- Starkhammar, J., Moore, P. W., Talmadge, L. and Houser, D. S.** (2011). Frequency-dependent variation in the two-dimensional beam pattern of an echolocating dolphin. *Biol. Lett.* **7**, 836-839.
- Varanasi, U., Feldman, H. R. and Malins, D. C.** (1975). Molecular basis for formation of lipid sound lens in echolocating cetaceans. *Nature* **255**, 340-343.
- Wahlberg, M., Jensen, F. H., Soto, N. A., Beedholm, K., Bejder, L., Oliveira, C., Rasmussen, M., Simon, M., Villadgaard, A. and Madsen, P. T.** (2011). Source parameters of echolocation clicks from wild bottlenose dolphins (*Tursiops aduncus* and *Tursiops truncatus*). *J. Acoust. Soc. Am.* **130**, 2263-2274.
- Weir, C. R., Frantzis, A., Alexiadou, P. and Goold, J. C.** (2007). The burst-pulse nature of 'squeal' sounds emitted by sperm whales (*Physeter macrocephalus*). *J. Mar. Biol. Assoc. UK* **87**, 39-46.
- Wisniewska, D. M., Johnson, M., Beedholm, K., Wahlberg, M. and Madsen, P. T.** (2012). Acoustic gaze adjustments during active target selection in echolocating porpoises. *J. Exp. Biol.* **215**, 4358-4373.
- Zimmer, W. M. X., Madsen, P. T., Teloni, V., Johnson, M. P. and Tyack, P. L.** (2005). Off-axis effects on the multipulse structure of sperm whale usual clicks with implications for sound production. *J. Acoust. Soc. Am.* **118**, 3337-3345.