Buzzing during biosonar-based interception of prey in the delphinids *Tursiops truncatus* and *Pseudorca crassidens*

Wisniewska D.M.*[1,2], Johnson M.[3], Nachtigall P.[4] and Madsen P.T.[2]

1) Marine Mammal Research, Bioscience, Aarhus University, Denmark

2) Zoophysiology, Bioscience, Aarhus University, Denmark

3) Scottish Oceans Institute, University of St Andrews, Scotland

4) Marine Mammal Research Program, HIMB, Hawaii, USA

* danuta.wisniewska@biology.au.dk

Short title: *Delphinids buzz for prey interception*

Abstract

Echolocating bats and toothed whales probe their environment with ultrasonic sound pulses, using returning echoes to navigate and find prey in a process that appears to have resulted from a remarkable convergence of the two taxa. Here we report the first detailed quantification of echolocation behaviour during prey capture in the most studied delphinid species, a false killer whale and a bottlenose dolphin. Using acoustic DTAGs, we demonstrate that just prior to prey interception these delphinids change their acoustic gaze dramatically by reducing inter-click intervals and outputs >10-fold in a high-repetition-rate, low output buzz. Buzz click rates of 250-500 Hz for large, but agile animals, suggest that sampling rates during capture are scaled with the whales' manoeuvrability. These observations support the growing notion that fast sonar sampling accompanied by low output level is critical for high-rate feedback to inform motor patterns during prey interception in all echolocating toothed whales.

Keywords: echolocation, buzz, convergent evolution, prey capture, delphinid, DTAG

Introduction

Echolocating bats and toothed whales emit powerful sound pulses and listen for returning echoes to navigate and capture prey under poor lighting (Griffin et al., 1960; Au, 1993). The pulse repetition rate and the output energy together delimit the depth of an echolocator’s acoustic gaze for unambiguous echo ranging (Wisniewska et al., 2012; Madsen and Surlykke, 2013). Early on, Griffin et al. (Griffin et al., 1960) identified distinct acoustic behaviours of bats that define the three foraging phases of search, approach and capture. In the search phase, most aerial hunting bats emit long and powerful cries. Upon the detection of a prey item, bats initiate the approach phase in which they call faster and gradually reduce call levels as they close in on prey. Just before capture, bats enter the terminal phase in which they emit a fast-repetition-rate buzz of short cries at low output levels. Thus, bats manipulate the rate and level of their calls to achieve dramatic acoustic gaze changes that accommodate the changing spatial relationship with their prey during capture attempts.

Although toothed whales must go through the same echo-guided tasks of search, approach and capture when hunting with echolocation, much less is known about the biosonar behaviour of most species during foraging. Early work (Norris et al., 1961; Morozov et al., 1972) showed that an echolocating bottlenose dolphin would reduce its inter-click intervals (ICIs) as it approached a dead fish, producing click repetition rates of some 300 Hz when close to the fish, but no functional links were made to buzzing in bats and this clicking mode received little further attention in captive studies. The next decades of biosonar research on dolphins had a strong biomimetic focus in order to understand the remarkable performance of toothed whale echolocation that may surpass that of man-made sonars (Au, 1993). All of the basic concepts and biosonar parameters used today stem from this research effort (Au, 1993). However, most of these studies involved a stationed delphinid performing an echolocation task with man-made targets at relatively long and static ranges. Remarkably, to our knowledge, no studies have been conducted to uncover in detail how a dolphin would use its sonar to do what it actually evolved for: to find and catch prey.

Contemporaneously with these captive studies, acoustic observations of narwhals in the wild producing fast click series prompted Miller et al. (Miller et al., 1995) to make a functional connection with the buzz of bats. However, it was not until the development of sound recording tags that this interpretation could be substantiated. It is now clear that buzzes are associated with prey capture attempts in sperm whales (Miller et al., 2004), beaked whales (Johnson et al., 2004), pilot whales (Aguilar de Soto et al., 2008), porpoises (De Ruiter et al., 2009) and belugas (Ridgway et al., 2014).

Here we report the biosonar behaviour during prey interception in two trained specimens of the most studied delphinid species, a false killer whale (*Pseudorca crassidens* Owen, 1846) and a bottlenose dolphin (*Tursiops truncatus* Montagu, 1821) and test the hypothesis that fast repetition rate buzzing is an integral part of echolocation for prey in these species. We show that these delphinids employ range-dependent output changes when approaching prey as found in non-prey target experiments (Au and Benoit-Bird, 2003). But most prey capture attempts occur with a radical output change in the form of a high-repetition-rate, low-output buzz, suggesting a universal and strong functional convergence in the biosonar of bats and toothed whales.

Results and discussion

A total of 116 (63 herring, 53 capelin) prey capture trials with a false killer whale, Kina, and 103 (42 herring, 61 capelin) trials with a bottlenose dolphin, BJ, were recorded over the course of four recording sessions per animal. Of those, 40 (20 herring, 20 capelin) trials for Kina and 72 (33 herring, 61 capelin) trials for BJ generated echograms (see Material and methods and (Johnson et al., 2004)) with discernible prey echoes (Fig. 1). In general, the ability to record echoes on a tag will depend on the placement of the tag with respect to the axis of the animal's sonar beam and the sound-shading structures of its body. A false killer whale has a larger melon than does a bottlenose dolphin (see Fig. S1 in supplementary material) and this may have impacted the quality of the recordings. A number of other factors may have contributed to the variable quality of the received echo signals including: the amount of air inside the fish, and hence its target strength; the angle of approach; the proximity of the fish to other targets and the water surface, and hence the signal-to-clutter ratio. Finally, the net-pen was not separated in any way from the natural environment of Kaneohe Bay, which is abundant in snapping shrimps. The signal-to-noise ratio between sessions, or trials, could have therefore varied.

When discernible, the echoes could be tracked until the prey were 45-55 cm ahead of the blowhole for the false killer whale, and 25-40 cm for the bottlenose dolphin (Fig. 1), corresponding approximately to the tip of the rostra of the animals (see Fig. S1 in supplementary material), and allowing verification of the exact time of prey interception. As in free-ranging beaked whales (Johnson et al., 2004), prey engulfment by the delphinids was accompanied by a rapid change in acceleration (Fig. 1) that most likely reflected movements of the musculature in the gular region, giving rise to a high-magnitude jerk signature (Ydesen et al., 2014). The signature was used to pinpoint the exact time of prey interception in trials with no discernible prey echoes in the echograms.

Roughly half of prey interceptions (56% and 39% of trials with Kina and BJ, respectively) were followed by distinct, isolated sequences of rapid pulsed sounds. These were short click trains of low (~2 ms for BJ and 2-5 ms for Kina), nearly constant or slightly increasing ICIs (Fig. 1) that may be analogous to the recently described victory squeals (VS) produced by trained belugas and bottlenose dolphins elsewhere (Ridgway et al., 2014). Because of their post-capture occurrence and their apparent communicative, rather than echolocation function, the VS were disregarded in further ICI analyses (e.g. Figs 2, and S2-S3 in supplementary material).

Both delphinids went through a series of acoustic gaze changes whilst approaching prey, culminating in a transition from regular clicking to a high-click-rate, low output buzz during the terminal approach and capture (Figs 1 and 2, and S2 in supplementary material). In 23 of the trials with Kina (15 with herring, 8 with capelin), the whale did not produce any buzz clicks (ICI<14 ms; see Fig. S3 in supplementary material) within a body length of the prey (i.e. up to 2.4 s prior to jerk peak under the assumption of Kina moving at a normal odontocete swimming speed of 2 m/s (Madsen and Surlykke 2013)). Similarly, on 12 occasions, four with herring and eight with capelin, BJ captured a fish without transitioning into a buzz within 1.2 m from jerk peak. However, the majority (>75%) of prey interceptions in both animals were accompanied by buzzing.

Acoustic gaze adjustments in the approach phase

During most prey approaches, both the bottlenose dolphin and the false killer whale gradually reduced their ICIs and output levels roughly proportionate with reducing target range (Figs 1 and 2, and S2 in supplementary material), as has been seen for free-ranging delphinids approaching hydrophone arrays (Au and Benoit-Bird, 2003). Thus, the concept of automatic gain control to compensate for a reduced transmission loss with decreasing target range also seems to be applicable to some degree in delphinids approaching small prey items. Yet, both animals exercised a degree of flexibility in their biosonar sampling; either they gradually decreased ICI with decreasing target range, like harbour porpoises (Fig. 2; (Madsen and Surlykke, 2013)), or kept a wide auditory scene by maintaining relatively constant clicking rates prior to buzzes, akin to beaked whales (Fig. 2;

(Madsen and Surlykke, 2013)). This suggests that ICI adjustments in the approach may not always be necessary or advantageous. These delphinids, and perhaps all toothed whales, seem to have a preferred strategy, but they may switch between, and perhaps combine, different degrees of adjustments, depending on the environment and the echolocation task at hand.

Buzzing during prey captures

A much more dramatic change in the acoustic gaze, featuring increased click repetition rates and >10-fold output level reduction, occurred at the transition to a buzz (Fig. 2), which was initiated at a median range of 0.6 (IQR, 0.4-0.1, Kina) and 1.5 (IQR, 0.8-1.9, BJ) meter from the prey (assuming an upper ICI limit for the onset of buzz of 14 ms for Kina and 16 ms for BJ (see Fig. S3 in supplementary material) and correcting for distance between the sound source and the tip of the rostrum). Both delphinids buzzed with click repetition rates on the order of 250-500 clicks/second (Figs 2 and S2), and used short buzz durations of 1 (0.6-1.5) and 0.6 (0.1-1.3) second for BJ and Kina, respectively, with a tendency toward longer buzzes in trials with preceding gradual ICI changes (Fig. 2). The high sampling rates during the buzz are comparable to the high-rate click trains, variously coined mews or creaks, reported in early studies (Norris et al., 1961; Morozov et al., 1972). These rates are similar to those found in buzzing porpoises (De Ruiter et al., 2009) but slightly faster than those of similar-sized beaked whales (Fig. 2). They therefore deviate from a simple size scaling, but support the recently-proposed hypothesis that biosonar sampling rates during capture are scaled with manoeuvrability of toothed whales (Madsen and Surlykke, 2013) as well as perhaps the agility of their preferred prey.

Both during the approach and capture phases, the ICIs were consistently longer than the two-way-travel time to the prey, but in the buzz the lag time, i.e., the time between the arrival of the prey echo and the subsequent click, was reduced to 1.5-4 ms just before target interception (Fig. 2). This suggests that ICI is adjusted throughout the buzz to avoid target echo ambiguity (Madsen and Surlykke, 2013). Such adjustments reveal an acute vocal-motor control that is finely tuned to the echo delays to targets of interest (Wisniewska et al., 2012). The ICI dynamics shown here (Fig. 2) further imply that the concept of a fixed lag time of approximately 20 ms for echo processing, found for stationed dolphins performing target detection tasks (Au, 1993), is unsupported for free-swimming delphinids targeting prey. The very short lag times found during buzzes and their wide variability suggest that the lag time may have little connection with cognitive processing time in a buzz.

Universality of buzzing in toothed whales?

Despite having been in captivity for many years and being faced with an easy task of intercepting a dead fish in the well-lit waters of a familiar net-pen, the trained delphinids studied here displayed stereotyped buzz behaviour very similar to that reported from diverse toothed whale species when catching prey in the wild. This suggests that high-rate biosonar sampling is a deeply integrated part of close-range target interception in a toothed whale. We propose that buzzing, although hitherto largely overlooked in captive animals, is a universal and critical key to biosonar-based interception of prey in toothed whales, as is the case for bats hunting prey on the wing.

Materials and methods

Experiments were conducted in a 12x12 m net-pen at the University of Hawaii Marine Mammal Facility with a 28-year-old female bottlenose dolphin, BJ, and a >26–year-old, female false killer whale, Kina. Animals were trained to wear a DTAG-3 multi-sensor tag (Woods Hole Oceanographic Institution, Woods Hole, MA, USA) that simultaneously records stereo sound at a sampling rate of 500 kHz (16-bit resolution, 178 dB re 1µPa clip level) and samples tri-axial accelerometers at 500 Hz. The suction-cup attached tag was placed dorsally behind the blowhole (Fig. S1) to ensure good quality recordings of outgoing clicks and to maximize the chance of recording faint echoes. Each session started with the animal stationed at the trainer after which three dead fish (10-15cm capelin or 20-25cm herring, estimated target strength of -35 to -40 dB) were introduced in opposite ends of the pen. The tagged animal was then sent towards the fish for interception at depths between 0.5 and 2m. Each session was filmed using an in-air Sony camcorder, synchronized with the DTAG-3 by tapping the tag hydrophones in front of the camera, allowing for visual verification of the time of prey ingestion on the DTAG-3 with <1 second of error.

Analyses were performed using Matlab (Mathworks, Natick, MA, USA). Clicks from tag recordings were extracted with a supervised click detector. Relative apparent output level (RAOL) of the clicks (Wisniewska et al., 2012) was computed as peak-peak received level in dB re maximum level in the trial, and ICIs were calculated as time intervals between each click and the preceding click. For each species, we used a change in the distributions of ICIs of all trials as the border value between buzz and regular clicks (see Fig. S3 in supplementary material). Clicks with ICIs <14ms for Kina and <16ms for BJ were accordingly classified as being part of a buzz. Time-range echograms (Johnson et al., 2004) were formed by time-aligning the signal recorded in a time window from -0.5ms to +6.5ms around each click, and subsequent color-coding by intensity. The width of each time bin in the echogram was adjusted to the ICI of that click to provide a time resolution matching the animal's sampling rate and to form a time axis compatible with the video recording (Johnson et al., 2004). Echo range was computed as half the time delay between the emitted click and the returning echo divided by a sound speed of 1534 m/s. To investigate possible change in the animals' movement patterns accompanying prey interception, we computed acceleration rate, or jerk, of the whales for the duration of the trials (Ydesen et al., 2014). The accelerometer data were low-pass filtered at 30 Hz (6^{th} order Butterworth filter) and the total jerk was computed at each time instant as the norm of the differential of the acceleration for each axis (Ydesen et al., 2014).

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Competing interests

The authors declare no competing interests.

Author contributions

DMW, PTM and PN planned and performed the experiments. DMW and MJ provided analytical tools. DMW analyzed the data. All authors contributed to the interpretation of the data. PTM and DMW wrote the manuscript. All authors edited the manuscript prior to submission.

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Figure legends

Figure 1. Echolocation of prey by a false killer whale (A,B,C) and a bottlenose dolphin (D,E,F). (A,D) Echograms (Johnson et al., 2004) displaying sonar clicks and echoes recorded by a DTAG-3. y-axis indicates time elapsed from emitted clicks to returning echoes expressed as target range. Clicks emitted at ICIs shorter than the 6.5-ms time window presented here are displayed repeatedly in the vertical axis. The colour scale indicates signal energy from blue (faint) to red (intense). (B,E) Inter-click intervals colour-coded for relative apparent output level of signals. VS marks victory squeals. (C,F) Jerk, or rate of change of acceleration as recorded by the DTAG.

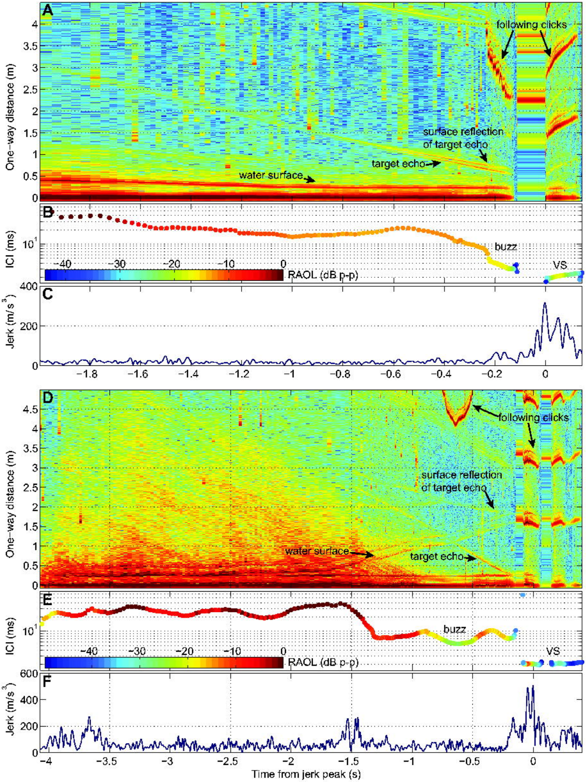
Figure 2. Delphinid echolocation behaviour during prey capture. Inter-click intervals (ICIs) of the false killer whale (A), the bottlenose dolphin (B), and three other toothed whale species (adapted from (Madsen and Surlykke, 2013)) (C). ICIs are colour-coded for relative apparent output level of signals. Dashed and dotted lines at the bottom of each plot mark target ranges (shown by the right-hand y-axis) estimated from the echograms (Fig. 1) for trials with the lowest ICI values in the buzz (drawn with matching line styles). Pooled ICI and RAOL data from all trials for Kina (A) and BJ (B) (see Fig. S2 in supplementary material) have been grouped into logarithmically increasing time bins (time from jerk peak) to form box plots, showing the 25th, 50th (median) and 75th percentiles (lower, mid and upper lines in the box) of the respective parameters within each time bin. Whiskers extend to the most extreme data points within 1.5 interquartile ranges. Values outside of those ranges are marked with crosses.

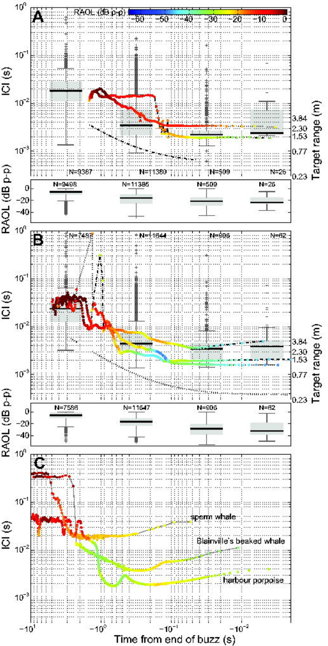
Supplementary material

Figure S1. DTAG-3 (12x2x7 cm) placement on the false killer whale (a) and the bottlenose dolphin (b) was chosen to ensure good quality recordings of outgoing clicks and to maximize the chance of recording faint echoes. The hydrophones are the two small yellow spherical elements on the front of the tag closest to the blowhole. The suction cup closest to the blowhole encases accelerometers (data not used in the present study); below which is a supporting suction cup.

Figure S2. Inter-click intervals colour-coded for relative apparent output level of signals emitted by the false killer whale (A,B) and the bottlenose dolphin (C,D) during all prey capture trials with small (capelin (A,C)) and large (herring (B,D)) fish.

Figure S3. Distribution of inter-click intervals (ICI) used by the false killer whale (Kina, A) and the bottlenose dolphin (BJ, B) during prey captures of small (capelin) and large (herring) fish. Bin width is 1 ms. The peaks centered on 2 ms for Kina and 3-4 ms for BJ correspond with the dominant ICI for buzz clicks. The plateaus between 15-25 ms (Kina) and 15-40 ms (BJ) mark the dominant ICI range for regular clicks. We used a change in the distributions of ICIs (at 14 ms for Kina and 16 ms for BJ, as marked by the dashed line) as the border value between buzz and regular clicks.


A
following clicks
surface reflection
of target echo
target echo
water surface
One−way distance (m)
B
buzz
VS
ICI (ms)
RAOL (dB p-p)
−40
−30
−20
−10
0
C
Jerk (m/s^3)
−1.8
−1.6
−1.4
−1.2
−1
−0.8
−0.6
−0.4
−0.2
0
D
following clicks
surface reflection
of target echo
water surface
target echo
One−way distance (m)
E
buzz
VS
ICI (ms)
RAOL (dB p-p)
F
Jerk (m/s^3)
−4
−3.5
−3
−2.5
−2
−1.5
−1
−0.5
0
Time from jerk peak (s)

A
RAOL (dB p-p)
-60
-50
-40
-30
-20
-10
0
10^0
10^-1
10^-2
10^-3
ICI (s)
Target range (m)
3.84
2.30
1.53
0.77
0.23
N=9387
N=11380
N=509
N=26
RAOL (dB p-p)
N=9498
N=11385
N=509
N=26
0
-20
-40
B
N=7487
N=11644
N=906
N=62
ICI (s)
Target range (m)
3.84
2.30
1.53
0.77
0.23
RAOL (dB p-p)
N=7586
N=11647
N=906
N=62
0
-20
-40
C
ICI (s)
sperm whale
Blainville's beaked whale
harbour porpoise
-10^1
-10^0
-10^-1
-10^-2
Time from end of buzz (s)