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The temporal pattern of terminal buzz by captive bottlenose dolphins (*Tursiops truncatus*) approaching a target.

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Running Title

Terminal buzz of captive dolphins
Abstract

Odontocetes modulate the rhythm of their echolocation clicks to draw information from their environment. They speed up their emissions, especially when approaching prey, to increase the sampling rate of “distant touch” and to improve information updating. This general acceleration turns into a “terminal buzz” also described in bats, which is a click train with a drastic rate increase, just as they reach the prey. This study documents and analyses the echolocation activity of captive bottlenose dolphins in a man-made pool, focusing on approaches towards non-food targets. Four dolphins’ locomotor and clicking behaviors were recorded during training sessions, when they were sent to immersed objects pointed at by their trainers. Results illustrate how these dolphins spontaneously and profusely use echolocation around novel or repeatedly presented objects. Their click emissions accelerate as they approach the target, thus displaying a classic terminal buzz. However, their terminal buzz slackens off within a quarter of second before the end of the click train. Typically, they decelerate the clicking and stop completely just before touching the object, using their rostrum lower tip. They do not emit clicks during contact. In conclusion, bottlenose dolphins under human care do spontaneously use echolocation in activities directed by their caretakers. When approaching inert objects, they accelerate their clicking, as do other toothed whales or bats approaching prey. Bottlenose dolphins’ particular slackening-off profile at the end of the buzz shows that they anticipate the moment of direct contact, and they stop just before real touch takes over for the “distant touch” of the object.

Keywords

Bottlenose dolphin (*Tursiops truncatus*), echolocation, inter-modal relay, approach phase, terminal buzz, pulse rhythm, inter-pulse interval, slackening-off.
**Introduction**

Toothed whales such as dolphins, porpoises, and sperm whales are equipped with bio-sonar analogous to that of bats (Griffin, 1944), allowing navigation and detection in the dark (Thomas et al., 2004). They echolocate using broadband pulses called clicks (Herman and Tavolga, 1980; Au et al., 2000), that are repeatedly emitted in click trains. Clicks are short transitory signals: 50 to 80 $\mu$s for bottlenose dolphins (Mann et al., 1998), thus mainly ultrasonic to the human ear. The duration between two adjacent clicks or inter-click interval (ICI) is highly variable within a train as well as between two trains. Click emission is not automatic but controlled (Moore and Pawloski, 1990); the animal modulates amplitude, frequency content, and rhythm of the clicks depending on the echolocating function (e.g., navigation, target detection or discrimination, prey pursuit, social contact, etc.).

This paper focuses on the temporal aspect of click emissions, i.e. rhythm. Modulation of echolocation rhythm during foraging and prey capture was first described in bats that use ultrasonic pulses comparable to clicks. Griffin divided mosquito hunting by bats into three phases: search, approach, and terminal, associated with characteristic acoustic behaviors (Griffin, 1958; Griffin et al., 1960). The search phase consists of navigation by the predator in the environment to detect and locate potential prey. It involves ICIs of about 50-100 ms. The second phase, called prey approach, begins when prey is detected, at a distance of approximately 2-4 m (Kalko, 1995); the animal moves toward the target and pursues it if necessary. Approach is associated with an acceleration in emission rate, with ICIs of about 10-50 ms. Finally, the terminal phase, when the predator is close enough to attempt capture, is associated with a “terminal buzz”, comprised of ICIs of about 4-7 ms. The “buzz” is the sound heard from an ultrasonic converter, when successive pulses are no longer perceived as distinct clicks but as a continuously vibrating hum produced by the accelerated train.

Other echolocating species such as sperm whales (*Physeter macrocephalus*) (Miller et al., 2004) and beaked whales (*Ziphiidae*) (Madsen et al., 2005), recorded in the wild using sound and position sensors directly attached to them, display similar patterns, which can be explained by convergent evolution. During the search phase, they emit spaced and regular clicks (Mullins et al., 1988; Whitehead and Weilgart, 1991). Trains turn to buzzes or “creaks” during capture events that are inferred from recorded accelerations and rapid body movements (Mohl, 2003; Zimmer et al., 2005). For captive odontocetes, one detailed study documented
temporal echolocation click patterns during prey capture (Verfuss et al., 2009). Synchronized underwater video - and high-frequency sound - recording focused on two harbor porpoises (*Phocoena phocoena*) tracking a live trout released in their outdoor sea enclosure. Again, results show a speed-up in their clicks when the porpoises approach the prey: when the fish is inserted in the pool, ICIs are about 50 ms; they decrease to a minimum, close to 1.5 ms, when the fish is less than 1 m away.

As more pulses are emitted within the same time interval, the terminal buzz represents a higher sampling rate (per time unit), and, as the beam moves around, a more precise picture in space. The subsequent faster updating of information (Britton and Jones, 1999) fulfills the need for stronger temporal and spatial resolution in order to reach a small moving target (Madsen et al., 2005; Verfuss et al., 2009). Similarly, electro-location needs explain why night-active weakly-electric fish similarly increase their rate of discharge pulses when swimming and when facing a novel object (Bauer, 1974; Avril and Graff, 2007).

An extensive population of marine mammals lives and breeds under human care (Couquiaud, 2005) in recreational resorts (“dolphinsariums”) and research centers. Some dwell in natural lagoons closed with nets, but many live in man-made pools. Little is known about the spontaneous occurrence of echolocating behavior in these animals, especially when navigating in clear waters between flat walls, and being fed without hunting. Although many behaviors observed in the wild may vanish in captivity, electric fish for instance keep discharging their electro-locating pulses continuously in aquariums, even in restrained conditions (Avril and Graff, 2007). The present study investigates the temporal echolocation patterns of the most popular marine mammal in captivity, the bottlenose dolphin (*Tursiops truncatus*, Montagu, 1821), when it is presented with inert objects. It is based on ICI duration analysis inspired by electric fish work (Graff, 1989). Unlike most investigations of captive dolphins (e.g. Harley et al., 2003), this experiment attempts to explore the echolocation behavior displayed without performance constraints, set points, or conditioning. Dolphins were not blindfolded, nor was any perceptive task imposed on them. Although they were lead to interact with objects, their use of echolocation was spontaneous. To better understand the relationship of ICI changes to the contexts in which they occur, acoustic signals were recorded simultaneously with locomotor underwater behavior. To control for contextual variables, subjects were individually called and driven by their trainers to the single inert objects. This limited the circumstances in which recording took place and standardized the conditions of movement and interaction. The animals thus received positive reinforcement for
coming over to - not for touching - the objects, and certainly not for echolocating, given that
the trainers were deaf to the clicks.

The experiment first documented the actuality of spontaneous echolocation in captive
*T. truncatus*, when there is sufficient visibility in their familiar pool and in a normal daily
context. Second, given that we were able to record abundant click trains (they were not
jammed by the echoes bouncing off of the concrete walls), their rhythms were investigated
with relation to the swimming and body movements of dolphins reacting to the pointing out
of objects dipped near them. Third, the increase in emission rate of dolphins reaching the
object was quantified for comparison with terminal phases of prey capture in bats and other
odontocetes. Finally, specific clicking parameters were defined for these representatives of the
most commonly studied and trained toothed-whale species, in the context of contact with inert
objects, be they novel or familiar.

**Method**

**Subjects and Housing**

Observation focused on four bottlenose dolphins (*T. truncatus*) housed at the Parc
Astérix dolphinarium in Plailly, France. It took place in the daytime, during seven regular
show training sessions, in February 2012. There were two females (Beauty and Baily) and
two males (Guama and Balasi), aged 40, 13, 30, and 8, respectively. The two older dolphins
were born in the wild, while the two younger ones were born at Parc Astérix. Their weight
and body length were as follows: Beauty, 245 kg and 2.75 m; Baily, 183 kg and 1.91 m;
Guama, 235 kg and 2.48 m; and Balasi, 188 kg and 2.49 m. The animals interacted at will
with six other conspecifics in three interconnected pools, two indoors and one outdoors.

Research focused on these four individuals, who could easily be separated temporarily
and tested apart from their social group; separation was never forced. Trainers commanded
them to swim alone to the recording area. The experiment took place in the largest pool (60 m
* 28 m, maximum depth 4.5 m) situated outdoors, comprising two advanced platforms
facilitating contact with trainers and an underwater window gallery facilitating video
recording.

**Experimental Context**
The experiment consisted of simultaneously recording acoustical signals and locomotor behavior or movements of individual dolphins as they reacted to the underwater presentation of initially unfamiliar objects. Objects were \textit{a priori} neutral (no food, no danger): a white PVC disc with a large hole in the middle, a white wooden disc with a large hole in the middle, and a plastic bottle filled with red-colored liquid (Fig. 1).

![Fig. 1. Presented objects. The central red vertical bar represents a length of 30 cm. A - Object #1: PVC disk, 2 cm thick, 650 g. B - Object #2: wooden disk; 2.5 cm thick, 600 g. C - Object #3: colored water in a plastic bottle, 500 g.](image)

The hydrophone used for recordings was always attached to the selected object to form an “object-hydrophone device”. This was decided upon after observations in dolphinariums and in the wild highlighted the particular interest dolphins show in electronic objects such as hydrophones or underwater cameras (Goodson et al., 1988); it was done so they would not get distracted away from the object. Moreover, clicks are directed straight ahead in a beam along the animal’s axis (Au et al., 2010), and fastening the hydrophone and object together prevented signal attenuation from occurring when acquisition took place outside of the beam (Nowacek, 1999).

The experiment was conducted during training sessions (including but not limited to medical training). At the time of the experiment, sessions took place five times a day and lasted for 20 min. We took advantage of dolphins’ rapid understanding of target-pointing, an ability observed in the wild (Pack and Herman, 2007) and exploited in captivity (Pack and Herman, 2004) where human gestures take on major importance. For training sessions, the ten dolphins were called in a group to the front of the outdoor beach (Fig. 2) to work with their trainers. One of the four participant dolphins was sent off by hand gesture to the opposite side.
of the pool (as in Verfuss et al., 2009) and got close to the objects. Seclusion helped us avoid
recording a mix of sounds emitted by different dolphins, without having to physically isolate
the individual from its social group. When the focus dolphin arrived close to the experimental
platform, a reward (food, a whistle, and/or vocal encouragement) was given by a second
trainer present there. The experimenter then immersed one object-hydrophone device
vertically along the pool wall, about 30 cm below the surface, so that it was presented in front
of the window facing the camera, for approximately 20 to 30 s. From above the surface, the
trainer pointed an index finger to the object under water.

The protocol was part of a pilot study on reaction to novelty and familiarity. Dolphins
repeatedly encountered reference Object #1 and an alternative object. During each session, the
reference object was presented first, and more often (M+/- SD = 11.5+/-3.8 times) than the
other one (3.8+/-0.5 times). For three subjects, the alternative object was Object #2. Balasi
participated in one session only, using alternative Object #3 because of previous encounters
with the two other ones. It often happened that several dolphins responded and arrived
together at the presenting spot. Their unexpected spontaneous individual and social behaviors
precluded better control of encounters, which would have been required to test for specific
effects of objects or object change.

Dolphins were free to examine the device, touch it, play with it, or to swim away. We
avoided imposing any constraints on the animals, and respected an ethological approach as
much as possible. When each trial ended, the device was removed, and the animal was sent
away to make way for another dolphin and a new trial. This procedure was repeated as often
as possible, to obtain a maximum number of trials for each dolphin and for each presented
object. Successive trials for the same individual in the same session ended up being about 5
min. apart, on average.
Figure 2. Experimental set-up: (1) Trainer A on the remote platform uses a hand gesture to send one dolphin over to the opposite side of the pool, where s/he is received by Trainer B on the experimental platform. (2) Experimenter C immerses the object-hydrophone device for about 30 s while Trainer B points to it. (3) The dolphin is sent back to the remote platform. Green ellipses represent the focus dolphin and blue squares the others.

Recording

Clear visibility was offered from a window of the underwater viewing gallery situated just under the experimental platform. Each training session was filmed in its entirety through the window, using a stationary camera (Lumix DMC-FZ38, Panasonic, Osaka, Japan; frame rate: 33 fps), allowing acute behavioral observation while the dolphin emitted sounds and interacted with the object. Sound signal acquisition was carried out through the hydrophone (C54XRS, Cetacean Research Technology, Seattle WA, USA) attached to the objects. The hydrophone was connected to an analog-to-digital converter (HD-P2, Tascam/TEAC, Tokyo, Japan) with an integrated adjustable preamplifier. Preliminary tests resulted in a gain adjustment of 4.5, and it was kept that way for the entire experiment. The converter saved the sampled signal in .WAV format on a SD card at a 44.1 KHz sampling rate and 16-bit coding. Bumps and impacts, especially on the hydrophone, were also audible on the camera soundtrack, facilitating audio-video matching of locomotor and acoustic behavior (See annex Movie 1). The duration of video and audio recording sequences reached 86 minutes over two days.
Behavioral Observations

We distinguished two types of behavior associated with echolocation in our experiment. The first, exploration, is defined as a distant scan of the object, not ending with any physical contact. The second, approach, occurs when the dolphin moves towards the object-hydrophone device and touches it, whether the contact is brief or lasting. Dolphins usually did not readily touch the object the first time it was presented to them, but did so after familiarization and further pointing by the trainers. In pilot studies however, contact with the hydrophone sometimes occurred spontaneously. Our report focuses on the approach behavior, as it has been recently investigated in porpoises (Atem et al., 2009; Verfuss et al., 2009).

Indeed, an extensive set of data could be observed and recorded for approach, because pointing to the object by the trainer unintentionally but repeatedly gave the animal instructions for contact with and positioning up against the target.

Behavioral Analysis

The first task then consisted in listing all approaches that occurred during the recording sessions, by carefully viewing videos. A total of 73 approaches were satisfactorily filmed with a usable soundtrack.

Recorded approaches were first subject to qualitative sound description: if the dolphin clicked while approaching, if s/he stopped clicking at the onset of contact, or if s/he started clicking again during contact. For further, extensive quantitative analysis of ICIs (as in Verfuss et al., 2009), thirty-seven of them were conservatively excluded, a soon as 1) signal-to-noise ratio dropped too much or 2) several dolphins clicked simultaneously at the object.

For the 36 remaining high-quality trains, the ICI sequences were subjected to a more detailed analysis. Where possible, the exact instant of contact with the device was noted; this was the case in all trials where the dolphin touched a part of the hydrophone (cable or tip) instead of the attached object because physical contact is then audible on the recording. When the exact moment of contact was impossible to determine, because it was not audible in the sound file, we used the video record to define the range in which it had to fall. Such ranges remained inaccurate whenever the point of impact was behind the object and therefore hidden from the camera, and also because of the limited precision of the slow-motion capacities of our video software.

ICI Processing
The raw signal of selected sequences in .WAV format was first processed using open-source audio software (Audacity 1.2.3, SourceForge.net). It was high-pass filtered at adjusted parameters (up to the highest cutoff frequency) to sort the ultrasonic clicks and cancel most sounds from water, along with animal or human vocalization and activity. Amplification was adjusted to further prepare the click amplitude level occurring above background noise. Clicks distinctly appeared on the high-pass filtered and adjusted digitized wave track. The ICI temporal structure could be then extracted with computer assistance.

A custom-built detection program written in Matlab processed the wave track signal starting from its (time;amplitude) sample points. Clicks were primarily detected by a trigger based on amplitude (absolute values), then selected and characterized with additional comparison parameters according to biologically relevant criteria. First, putative clicks were attributed to points where the amplitude stands out with respect to the mobile arithmetic mean and standard deviation: amplitude values were compared within a 1500-sample point sliding window, thus the focus sample point was in the center of a portion lasting 34 ms. In such a small time interval, amplitude was not likely to be affected by changes in position of the source with respect to the hydrophone, either in terms of distance or orientation. Second, among neighboring detected sample points (amplitude exceeding the mean by more than 2.5 to 4.5 times the standard deviation), the abscissa of the point of highest amplitude was chosen as the position in time of its corresponding peak; high-amplitude detected points were matched with the next sample points closer than 15 steps away, i.e. within 0.34 ms of one another, which is approximately the duration of our recorded and filtered clicks. Third, a peak was recognized as a click only if its amplitude was comparable to that of the three preceding clicks. A weight of 5/11 for the last click amplitude and of 3/11 for that of the second- and third-to-last clicks yielded a weighted-mean amplitude that the candidate peak should not deviate from by more than 30%, as cetaceans never abruptly change their signal amplitude within a train. Fourth, after an assessed click, no other click was expected during a refractory phase; the corresponding delay (55 to 75 samples, i.e. 1.25 to 1.7 ms), was chosen based on observed ICIs, to be long enough to prevent repeated detection of the same click, and short enough to prevent us from ignoring the following one.

After detecting the clicks, the program yielded the list of ICIs in milliseconds. Some primary detection errors by the program were caused by substantial click variations and ambient noise, with omissions (a click is present but is not detected) and false alarms (program detects a click whereas there is none). Such defects were either characterized and corrected where possible, or the sequence was discarded. Finally, sequences were converted.
into chronograms, to visualize the evolution of ICI (Y-axis) over time (X-axis) for each click train. Some visible defects (see Appendix 1) remained in a few sequences used for analysis, but they were tolerated because they did not affect the final results. The moment of contact with the device was also plotted on the graph.

Chronograms with a logarithmic Y-scale immediately provided a clear visual image of the temporal clicking structure based on raw ICI data. Terminal buzzes obviously appeared during approach phases. However, an unexpected profile of ICI lengthening became visible towards the end of the buzzes. Data were therefore standardized using the end of the train, close to the moment of contact, as the zero of the time axis (abscissa), a procedure similar to the pre-triggering technique on an oscilloscope. ICI train profiles were then compared, qualitatively on chronograms, and quantitatively using parametric and non-parametric statistics. A more thorough comparison of 36 selected sequences was prepared, standardizing the data by going backwards, starting with the last ICI, then using second-to-last, etc.

A general image was also obtained by breaking down trains into segments. For each individual train, ICIs were pooled together in successive groups of 32, beginning with the last ICI in the train and going backwards to the first ICI in the sequence. N=32 ICIs was arbitrarily chosen because it exceeds the sample size which allows most statistics to be interpolated (see tables in Sokal and Rohlf, 1973). A median duration was then computed for the 32 ICIs of each train segment. The general image of the 36 approach sequences was portrayed by computing, for the eight last successive steps, the minimum, first quartile, median, third quartile, and maximum of the segment’s median ICI. Note that the number of segment medians (sample size) used for this image decreases from the very last segment, to the second-, third-, (…), and eighth-to-last one, because the number of segments varies for each click train according to the total number N of ICIs in the corresponding sequence. Thus, some sequences with 32<N<64 only had one complete segment, i.e., the “last one”, closest to the end. This last segment, number 1, was the only segment present in all 36 sequences, whereas the longest sequences had up to 20 segments (as N=20*32 ICIs), that were not all taken into consideration. Indeed, medians were not computed from all the sequence segments starting with the initial ICI of all sequences; only those of the last eight segments (N>256, present in 18 sequences) were taken into consideration. Beyond this limit, data were not present in most trains, which were too short. Medians and other nonparametric rank statistics were privileged in order to discard other artifact and outlier effects.

When a phenomenon was observed abundantly in a given situation, its frequency was assessed with a binomial test to see if it exceeded a 50%-50% distribution, to attest that it
occurs in most cases (more than half). When it was generally observed in a situation, the binomial test was conducted against a 75%-25% distribution to attest that it occurred in a vast majority of cases.

Results

Use of Echolocation

The first result we found is that dolphins in their pool used echolocation profusely, at least in the area where objects were immersed and pointed out by the trainer. Eighty-six minutes of recording provided an extensive number of echolocation sequences containing hundreds of click trains, many more of which were also observed during preliminary tests. All 10 dolphins present in the pool came over to scan the presented object at least once, and all of them emitted clicks.

Behavioral Observations

When they were sent over by their trainer, the four experimental dolphins exhibited behavior which indicated they were expecting an instruction. Their locomotor behavior somehow differed from that of other dolphins that came over and clicked without being called. After performing a quick exploration when the device was immersed, selected dolphins clearly showed signs indicating that they were waiting for something: they glanced at their trainer from under the surface or with their head out of the water, for example. As the trainer kept pointing to the device, they eventually positioned their rostrum against it. This position was maintained for a duration that depended on the animal; sometimes contact was very brief, and sometimes they maintained static positioning for up to ten seconds. Contact with the device was observed for each of the four dolphins and always occurred the first or second time it was presented, generally after an observation phase from a distance. During long static positioning against the device, a dolphin sometimes briefly lost contact because the object was moved by the pool wavelets. In those particular cases, a kind of new approach started; we call it repositioning. Repositioning movements were of lower amplitude, and can be considered minor adjustments.

Physical contact always involved the tip of the rostrum; no contact with any other body part was observed during the course of the experiment. Specifically, a limited area of the lower part of rostrum was involved, except for Guama, who sometimes lifted the hydrophone a few centimeters with the upper part (Fig. 3). Each dolphin positioned his or her rostrum
against a given point of the experimental device, yet some touched the object and others
touched the hydrophone, depending on the individual. Once a dolphin had positioned his or
her rostrum against one part of the device, s/he generally did so against the same one in
following trials.

Fig. 3. Examples of positioning against the object/hydrophone device, as recorded through a window
from the underwater viewing gallery. Panel A and D are of Guama, Panel B is of Beauty, and C of
Balasi. Contact involved the lower rostrum, except in Panel D where Guama lifts Object #2's
hydrophone.

Echolocation During Approach

Use of Echolocation During Approach. The 73 approach sequences identified on
video were subdivided into 56 normal approaches (i.e. no repositioning) and 17 repositioning
approaches. Of 56 normal approaches, 50 (89.29 %) involved a click train, which suggests
that during training, dolphins generally use echolocation to reach a target. Conversely, clicks
occurred in only 2 of the 17 repositioning approaches. Thus, the presence of clicks
significantly depended on the type of approach ($\chi^2$ test (1, N= 73) = 38.25, p < .05),
suggesting that echolocation was no longer used for minor adjustments once the target was
reached.

Acceleration in the Approach Phase. For each of the 36 sequences usable for ICI
rhythm analysis, a chronogram was plotted to show ICI duration with respect to the date it
occurred (Appendix 1), set with the train end as zero. For each chronogram, a linear trendline
was adjusted to it in order to determine the evolution of emission rhythm. Of 36 trendlines, 31
show a negative slope, meaning that the animals accelerate their click emissions when they
get close to the target in 86.11 % of the cases, a significant majority (binomial test (.5, N=36)
Not all linear trendlines fit the data well (mean $R^2 = .36; \ SD = .27$) because, during approach, the click train generally included two or more accelerations, and some decelerations. The negative trendline can be attributed to stronger acceleration as it gets closer to the end of the click train (see examples in Fig. 4), as observed in 34 individual chronograms out of 36. These 94.4% of cases represent a significantly large majority (binomial test (.75, N=36) $p < .05$). Thus, dolphins usually accelerated their click emissions while approaching objects, and the shorter ICIs occurred closer to the end of the train. However, the acceleration was not linear because the trend was mitigated by frequent decelerations before the extreme, final speed-up, but also (as will be shown later) by some slackening off before the train ended.

Fig. 4. Examples of chronograms for each individual dolphin: ICI duration in milliseconds (log scale) as a function of countdown time from train stop in milliseconds. Linear trendlines show overall acceleration for Panel A (Guama), B (Baily), C (Beauty), and D (Balasi), but not for Panel E (Balasi) because of the final deceleration. Note that linear trendlines appear curved because of the logarithmic
Y-scale. The red square represents the onset of contact with the object; its height shows how long after the preceding click it occurred (Y-axis).

**Terminal Buzz Slackens Off.** Despite much inter-and intra-individual variability, the graph obtained by breaking down click levels into 32 ICI segments (defined according to the termination of the approach, Figure 5) also illustrates the general acceleration (ICI decrease). From the eighth-to-last to the last segment, the rhythm got more than twice as fast, i.e. median IPI was reduced by more than half. However, the graph also shows that the shortest ICIs were not emitted during, but before, the last segment.

![Graph showing terminal buzz slackens off](image)

Fig. 5. General profile of clicking behavior when arriving close to the objects. From top to bottom: the maximum, third quartile, median, first quartile, and minimum values of N = 36 sequences’ median ICI duration of segments grouping 32 sample ICIs. The segments - and cut-off point ICIs - are reverse-numbered starting with the end of the trains.

Indeed, dolphins decelerated (ICIs increased) just before ending their click trains. The segment of shortest median ICI, about 2 ms, was typically the third or second one before the end (32\(^{nd}\)-to-last to 96\(^{th}\)-to-last ICI). This pattern seemed characteristic of our dolphins’ terminal buzz. As illustrated in Figure 6, it was not an artifact due to data pooling. In 32 out of 36 cases (see Appendix 1), in the last quarter-second before the end, chronograms fell to a minimum, after which trains ended with an increase in ICIs. Thus, this end pattern of the click train was visible in 89.89 % of cases, a significantly large majority (binomial test, (.75, N=36) p < .05). The shortest ICI was therefore not the last one; it generally occurred 0.25 to 0.05
seconds before the end (Q3, median, Q1 = 240, 130, 54 ms respectively). When swimming closer to an object, the dolphin typically accelerated its click train; however it decelerated and stopped at the last moment, when it reached the target.

Fig. 6. Examples of terminal buzz pattern in relation to the onset of contact, for Guama (A and B) and Balasi (C). The X-axis is countdown time from train end, in milliseconds; the Y-axis is ICI duration in milliseconds (log scale). Red bars represent the beginning of contact with the object/hydrophone device, with a red “C” indicating the onset of contact, either precisely (Panel B and C), or within a range (Panel A).

**Touch Relays Echolocation**

**Click Train Ends Before Contact.** This deceleration and subsequent stop were not due to contact, but in anticipation of it. Out of the 52 times dolphins clicked during the approach phase, their click train ended before the moment of contact 39 times, ended afterwards 6 times, and the contact-to-stop interval was unknown for the remaining 7.
Therefore, their clicking stopped before they touched the object in 87% of the non-questionable cases, a significantly large majority (*binomial test* (.75, N=45) *p* < .05). In those cases, the click train stopped for a maximum 1030 ms before contact (N = 39; M = 233 ms; SD = 331.6). For those who did not stop clicking before contact, the click train continued for a maximum 185 ms afterwards (N= 6; M = 87 ms; SD = 67.4). Overall, trains generally terminated a tenth to a hundredth of a second before contact (Q1-, median-, Q3-delay = 9, 46, 137 ms respectively).

To sum up, dolphins usually stopped clicking just before touching the target with their rostrum, and more rarely, did so very shortly afterwards. The interval between the last click and contact was always (except for 1 sequence out of 39) greater than the ICI just before it. Dolphins did not decide to instantly stop clicking once contact occurred; they definitely seemed to anticipate the moment of contact.

**No Clicking While Contact Lasts.** The end observed in the 52 approach click trains was usually definitive whether it occurred before, or exceptionally, shortly after, the onset of contact; dolphins resumed clicking before the end of *positioning* in six cases only; in 42 cases, the dolphins remained silent the entire time contact was maintained; the 4 other cases are undetermined. Therefore, for the trains we are sure of, they did not emit clicks while touching the object in 87.5% of them, *i.e.*, a significantly large majority (*binomial test* (.75, N=48) *p* < .05). Dolphins did not use echolocation and touch simultaneously.

**Exemplified Synthesis of the General Pattern.**

To summarize, Figure 7 displays a representative case. It highlights typical clicking behavior in a majority of the cases where any of the four dolphins swam over to an object. The clicking accelerated more than it decelerated as the animal approached. When s/he got very close to the target, it accelerated to a maximum (minimum ICI), then slackened off and stopped for good just before contact. Clicking did not resume as long as contact was maintained.
Fig. 7. Example of a click train showing the most prevalent temporal pattern during approach. The X-axis is the countdown time from the end of the click train in seconds, and the Y-axis is ICI duration in milliseconds (log scale).

Discussion

Bottlenose Dolphins in Human Care Also Click

First, it appears that captive bottlenose dolphins may well spontaneously and profusely emit echolocation clicks in their man-made pools. This basic result is worth mentioning. On one hand, because the fact has been omitted or neglected in scientific reports, which essentially deal with recordings of spontaneous clicking in the sea or study induced clicking in experimental contexts specifically testing for echolocation skills. On the other hand, professional trainers and caregivers are not attuned to the mostly ultrasonic clicks. Before undertaking sound acquisition, we could not exclude the possibility that dolphins click only in the wild or in specific, behaviorally constrained conditions. Animals could have been disturbed enough to limit their emissions by the reverberation of their clicks off of pools’ flat concrete walls. Such reverberations could also have jammed our signal acquisition, which would have required additional filtering. Fortunately, interfering echoes were barely detected by our conventional recording set-up. The captive dolphins used echolocation plentifully, even though it is usually considered an adaptation to conditions of reduced visibility (i.e.,
turbid waters, ocean depths, nighttime activity) and the study took place during daytime in clear water. Although they were in their most familiar environment and context, they all clicked when more or less novel objects were proposed, and also when objects had become familiar after repeated encounters. We conclude that Beauty, Baily, Guama, Balasi, and probably other dolphins living in man-made pools, take advantage of bio-sonar in their daily activities, especially when approaching a target and positioning themselves against it, despite the absence of voluntary or noticeable reinforcement by their trainers.

For comparison with other *T. truncatus* studies, only fragmented data seem to be available, and they generally do not take behavioral context into consideration. Akamatsu et al., (1998) report a 4-6 ms mode in the ICI distribution of three individuals confined in a 12-m diameter pool, contrasting with a 26-28 ms mode for blind records of wild *T. truncatus*. Our dolphins exhibited a wider ICI range covering their two sample categories. This suggests that these authors recorded the search phases of free-roaming bottlenose dolphins in open waters and compared them to buzzes of captive ones kept close to their conspecifics or to the walls of their small pool.

**Dolphins Emit Terminal Buzz during Target Approach**

Second, we observed a prevalent terminal buzz pattern of clicking when dolphins swam towards objects. As far as we know, this is the first scientific report providing quantitative results on this characteristic temporal pattern behavior of *Tursiops sp.* The ICI sequence during the *approach* phase (moving towards a target) and during the *terminal* phase (right before contact) is comparable to those described for other taxa, chiropters hunting in the air and other odontocetes in the sea. When heading towards an inert target, our dolphins displayed acceleration comparable to bats, harbor porpoises, and beaked and sperm whales capturing prey (Griffin et al., 1960; Miller et al., 2004; Madsen et al., 2005; Verfuss et al., 2009). However, the preceding *searching* phase, during which targets or prey are sought out from farther away, appeared difficult to investigate while keeping the animals in their most familiar context, as we chose to do here. This phase may be studied, with additional means, in future data sampling designs, to complete the classic three-phase configuration.

Functional explanations for the observed pattern are similar to those applied to other species. Overall acceleration in emissions increases the sampling rate, and therefore the amount of collected data in a given portion of time. Data may relate to an object’s position (hence the term “echolocation”) but also to its shape, movement, and even make-up (Harley et al., 2003). In the wild, a rapid update of small prey’s trajectory compensates for the lack of
Dolphins also need accuracy in non-feeding situations to position their rostrum on a limited area, such as the tip of the hydrophone in our conditions. A high degree of precision is required to avoid violent skin contact with a target, or an obstacle such as a rocky outcropping at the bottom of the sea, because the rostrum is so sensitive (Mauck et al., 2000).

In short, various animals heading towards an object or tracking prey through echolocation pulses need a higher emission rate, and terminal buzz provides rapid and accurate updating. In our captive animals, locating and moving was explicitly induced by trainers’ pointing gestures at man-made targets, a very common form of interaction between humans and dolphins under their care. This practice most likely emerged because dolphins are prone to understanding finger – and eye – pointing, not just in captivity (Pack and Herman, 2004) but also in the wild (Pack and Herman, 2007).

The observation that individuals usually kept clicking when positioning themselves against a previously-encountered object, but not when repositioning themselves against the same object after a brief loss of contact, suggests that echolocation 1) is not limited to special or novel situations, but that 2) echolocation parameters may be stored in their short-term memory. This opens the possibility of testing dolphins for object discrimination with the habituation/novelty paradigm already applied to other species (e.g. Saayman et al., 1964; Halm et al., 2006; Racca et al., 2010).

Dolphins’ Terminal Buzz Slackens Off

Our study also discloses a special profile in *T. truncatus*’ terminal buzz, *i.e.* the final deceleration at the end of the click train, which had not explicitly been mentioned before, in the general pattern common to many different species. We propose an explanation of this slackening off, based on energy expenditure. Usually, terminal buzz acceleration is accompanied by a loss in amplitude (Atem et al., 2009). Most likely, a speed/amplitude trade-off compensates for the important cost in energy involved in the higher repetition rate. In the terminal buzzes we recorded, dolphins were not only emitting rapidly, but kept emitting strongly. We think that the invested energy is significant, and that the repetition mechanism cannot be stopped too abruptly (Ridgway et al., 2012). Thus, this final slackening off is observed in rate, not in amplitude.

Although the recording and filtering conditions could not guarantee accurate measurement of every single ICI, as is visible on sample chronograms (Figures 4, 6 and 7, and Appendix 1), this lack of precision would not affect the evidence of observed and quantified
patterns in the temporal dimension. However, more sophisticated acquisition procedures will
be necessary to assess the rate-amplitude relationship.

Akamatsu et al.’s paper (1998) displays a single 650-ms chronogram of a captive *T. truncatus*: the buzz terminates with a very slight slow-down (6 to 7.5 ms before the end of a 200-ms time period), not commented on by the authors, but evocative of the slackening off we observed. For closely related species under human care, a slackening off may be considered in harbor porpoises (*P. Phocoena*) in two studies. First, DeRuiter et al. (2009) recorded multiple instances of two individuals, one after the other, catching a dead fish. Both produced buzzes with ICIs of approximately 3 ms and kept buzzing after the onset of contact; only once the fish was entirely their mouths did they decelerate; but they did not stop, as we observed in the present study. Second, Verfuss et al. (2009) recorded two trained harbor porpoises catching live prey. They produced click trains comparable to ours, with a buzzing deceleration after capture (not before), followed by a stop. The authors compared the profile with that of finless porpoises and beaked whales but did not comment on the slackening off. The profile seems absent in finless porpoises (*Neophocoena phocaenoides*), but some kind of slackening off is visible in Johnson et al.’s (2006) study on a single beaked whale (*Mesoplodon densirostris*, Blainville). Yet this species’ click structure and average ICI duration put it in a different category than dolphins and porpoises.

**Click and Touch**

A focus on the instant when contact takes place, right after the buzzing ends, also highlights a cross-modal relationship between touch and echolocation for perception of the same object. Prior studies have already shed some light on cross-modal integration of sonar with vision (Pack and Herman, 1995; Kuczaj, 2008). Physical touch surely deserves attention as it is an important part of dolphins’ affiliative behavior; it is also sought by humans who are attracted by them.

Recordings show that contact takes place with the rostrum tip, usually its lower part. This distinct posture may well favor association with sight, as eyes are oriented ventrally in cetaceans. Moreover, the lower jaw is the locus of reception for click echoes (Brill et al., 1988). This reception may be hampered by the direct contact with the object, thus rendering echolocation useless. Echolocation, like vision, is useful for extracting information at a distance; this “distant touch” may no longer be appropriate at point-blank range. Either the beam emanating from the melon (above the rostrum) can no longer reach the target (situated underneath the rostrum), or powerful sounds reflected from an object that is getting too close
cause aversive reverberations to the rostrum it is in direct contact with. Click vibrations indeed provoke mechanical effects: powerful clicks can be used to caress conspecifics or even to strike or knock out prey (Herzing, 1996; Herzing, 2004). Thus reciprocally, the reverberations coming off of the object would disturb or jam the reception of tactile stimuli. Stopping the clicking in anticipation of contact guarantees the integrity of tactile stimuli, and respects the sensitivity of echolocation stimuli.

Conclusion

Bottlenose dolphins’ click accelerations and final buzz when approaching a passive target resemble strategies generally used by numerous echolocating or electro-locating species to carry out precise actions for navigation or prey capture. In our results, the rate of this “distant touch” eventually decreases as it reaches point-blank range, then stops shortly before the onset of full contact. Our simple gathering of click recordings encourages further investigation of spontaneous echolocation behavior in captive and wild dolphins. The sequence of pulse intervals can be easily and finely analyzed, based on classic tools developed for other biological pulse rhythm models (Bauer, 1974; Avril and Graff, 2007). Clicking activity can provide objective measures of dolphins’ sensitivity, cognitive abilities, or motivation.

References


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**List of Abbreviations**

ICI = Inter-click interval