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

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

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21  
22 **Running Title**

23 Terminal buzz of captive dolphins

26 **Abstract**

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

46

47 **Keywords**

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

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## 55 Introduction

56

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

67

68 This paper focuses on the temporal aspect of click emissions, i.e. rhythm. Modulation  
69 of echolocation rhythm during foraging and prey capture was first described in bats that use  
70 ultrasonic pulses comparable to clicks. Griffin divided mosquito hunting by bats into three  
71 phases: *search*, *approach*, and *terminal*, associated with characteristic acoustic behaviors  
72 (Griffin, 1958; Griffin et al., 1960). The *search phase* consists of navigation by the predator in  
73 the environment to detect and locate potential prey. It involves ICIs of about 50-100 ms. The  
74 second phase, called *prey approach*, begins when prey is detected, at a distance of  
75 approximately 2-4 m (Kalko, 1995): the animal moves toward the target and pursues it if  
76 necessary. *Approach* is associated with an acceleration in emission rate, with ICIs of about 10-  
77 50 ms. Finally, *the terminal phase*, when the predator is close enough to attempt capture, is  
78 associated with a “*terminal buzz*”, comprised of ICIs of about 4-7 ms. The “buzz” is the sound  
79 heard from an ultrasonic converter, when successive pulses are no longer perceived as distinct  
80 clicks but as a continuously vibrating hum produced by the accelerated train.

81 Other echolocating species such as sperm whales (*Physeter macrocephalus*) (Miller et  
82 al., 2004) and beaked whales (*Ziphiidae*) (Madsen et al., 2005), recorded in the wild using  
83 sound and position sensors directly attached to them, display similar patterns, which can be  
84 explained by convergent evolution. During the search phase, they emit spaced and regular  
85 clicks (Mullins et al., 1988; Whitehead and Weilgart, 1991). Trains turn to buzzes or “creaks”  
86 during capture events that are inferred from recorded accelerations and rapid body movements  
87 (Mohl, 2003; Zimmer et al., 2005). For captive odontocetes, one detailed study documented

88 temporal echolocation click patterns during prey capture (Verfuss et al., 2009). Synchronized  
89 underwater video - and high-frequency sound - recording focused on two harbor porpoises  
90 (*Phocoena phocoena*) tracking a live trout released in their outdoor sea enclosure. Again,  
91 results show a speed-up in their clicks when the porpoises approach the prey: when the fish is  
92 inserted in the pool, ICIs are about 50 ms; they decrease to a minimum, close to 1.5 ms, when  
93 the fish is less than 1 m away.

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

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

121 coming over to - not for touching - the objects, and certainly not for echolocating, given that  
122 the trainers were deaf to the clicks.

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

133

## 134 **Method**

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### 136 **Subjects and Housing**

137

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

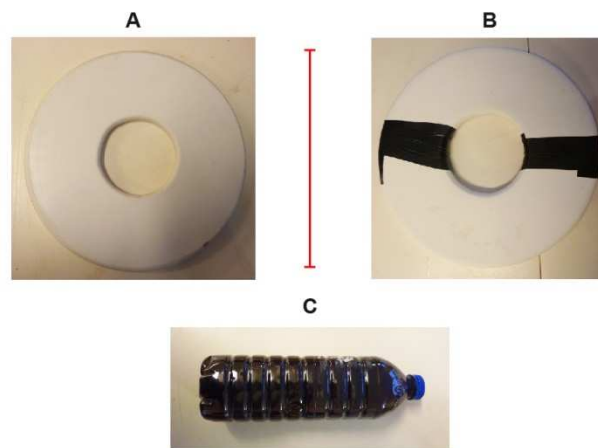
146 Research focused on these four individuals, who could easily be separated temporarily  
147 and tested apart from their social group; separation was never forced. Trainers commanded  
148 them to swim alone to the recording area. The experiment took place in the largest pool (60 m  
149 \* 28 m, maximum depth 4.5 m) situated outdoors, comprising two advanced platforms  
150 facilitating contact with trainers and an underwater window gallery facilitating video  
151 recording.

152

### 153 **Experimental Context**

154

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



160

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

164

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

173 The experiment was conducted during training sessions (including but not limited to  
 174 medical training). At the time of the experiment, sessions took place five times a day and  
 175 lasted for 20 min. We took advantage of dolphins' rapid understanding of target-pointing, an  
 176 ability observed in the wild (Pack and Herman, 2007) and exploited in captivity (Pack and  
 177 Herman, 2004) where human gestures take on major importance. For training sessions, the ten  
 178 dolphins were called in a group to the front of the outdoor beach (Fig. 2) to work with their  
 179 trainers. One of the four participant dolphins was sent off by hand gesture to the opposite side

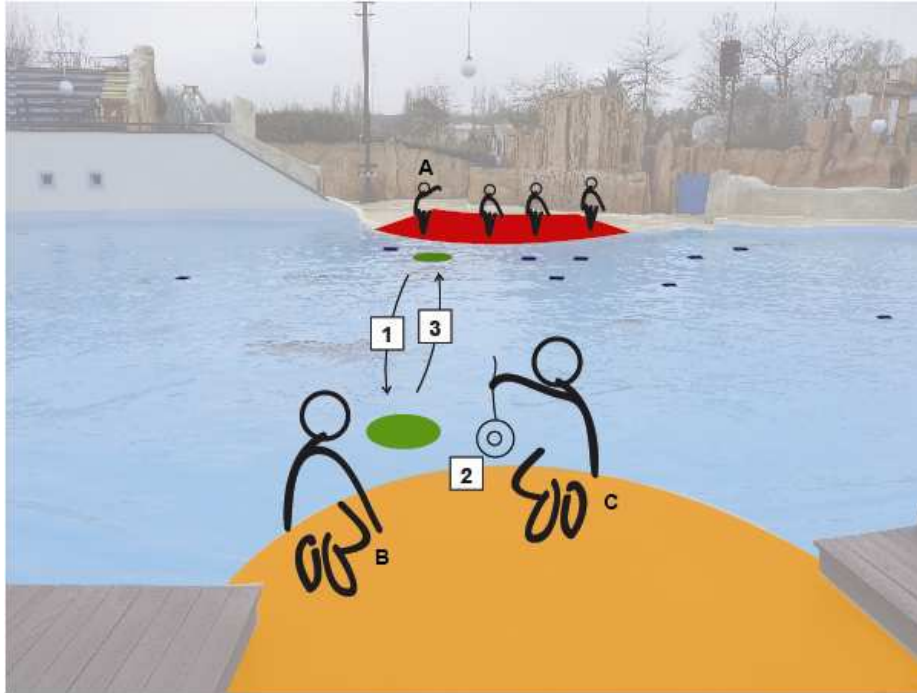
180 of the pool (as in Verfuss et al., 2009) and got close to the objects. Seclusion helped us avoid  
181 recording a mix of sounds emitted by different dolphins, without having to physically isolate  
182 the individual from its social group. When the focus dolphin arrived close to the experimental  
183 platform, a reward (food, a whistle, and/or vocal encouragement) was given by a second  
184 trainer present there. The experimenter then immersed one object-hydrophone device  
185 vertically along the pool wall, about 30 cm below the surface, so that it was presented in front  
186 of the window facing the camera, for approximately 20 to 30 s. From above the surface, the  
187 trainer pointed an index finger to the object under water.

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

197 Dolphins were free to examine the device, touch it, play with it, or to swim away. We  
198 avoided imposing any constraints on the animals, and respected an ethological approach as  
199 much as possible. When each trial ended, the device was removed, and the animal was sent  
200 away to make way for another dolphin and a new trial. This procedure was repeated as often  
201 as possible, to obtain a maximum number of trials for each dolphin and for each presented  
202 object. Successive trials for the same individual in the same session ended up being about 5  
203 min. apart, on average.

204





205

206 Figure 2. Experimental set-up: (1) Trainer A on the remote platform uses a hand gesture to send one  
 207 dolphin over to the opposite side of the pool, where s/he is received by Trainer B on the experimental  
 208 platform. (2) Experimenter C immerses the object-hydrophone device for about 30 s while Trainer B  
 209 points to it. (3) The dolphin is sent back to the remote platform. Green ellipses represent the focus  
 210 dolphin and blue squares the others.

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## 212 **Recording**

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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.

## 228 **Behavioral Observations**

229 We distinguished two types of behavior associated with echolocation in our  
230 experiment. The first, *exploration*, is defined as a distant scan of the object, not ending with  
231 any physical contact. The second, *approach*, occurs when the dolphin moves towards the  
232 object-hydrophone device and touches it, whether the contact is brief or lasting. Dolphins  
233 usually did not readily touch the object the first time it was presented to them, but did so after  
234 familiarization and further pointing by the trainers. In pilot studies however, contact with the  
235 hydrophone sometimes occurred spontaneously. Our report focuses on the *approach* behavior,  
236 as it has been recently investigated in porpoises (Atem et al., 2009; Verfuss et al., 2009).  
237 Indeed, an extensive set of data could be observed and recorded for *approach*, because  
238 pointing to the object by the trainer unintentionally but repeatedly gave the animal  
239 instructions for contact with and positioning up against the target.

240

## 241 **Behavioral Analysis**

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

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

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

259

## 260 **ICI Processing**

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

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

290 After detecting the clicks, the program yielded the list of ICIs in milliseconds. Some  
291 primary detection errors by the program were caused by substantial click variations and  
292 ambient noise, with omissions (a click is present but is not detected) and false alarms  
293 (program detects a click whereas there is none). Such defects were either characterized and  
294 corrected where possible, or the sequence was discarded. Finally, sequences were converted

295 into chronograms, to visualize the evolution of ICI (Y-axis) over time (X-axis) for each click  
296 train. Some visible defects (see Appendix 1) remained in a few sequences used for analysis,  
297 but they were tolerated because they did not affect the final results. The moment of contact  
298 with the device was also plotted on the graph.

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

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

327 When a phenomenon was observed *abundantly* in a given situation, its frequency was  
328 assessed with a binomial test to see if it exceeded a 50%-50% distribution, to attest that it

329 occurs in most cases (more than half). When it was *generally* observed in a situation, the  
330 binomial test was conducted against a 75%-25% distribution to attest that it occurred in a vast  
331 majority of cases.

332

## 333 **Results**

334

### 335 **Use of Echolocation**

336 The first result we found is that dolphins in their pool used echolocation profusely, at  
337 least in the area where objects were immersed and pointed out by the trainer. Eighty-six  
338 minutes of recording provided an extensive number of echolocation sequences containing  
339 hundreds of click trains, many more of which were also observed during preliminary tests. All  
340 10 dolphins present in the pool came over to scan the presented object at least once, and all of  
341 them emitted clicks.

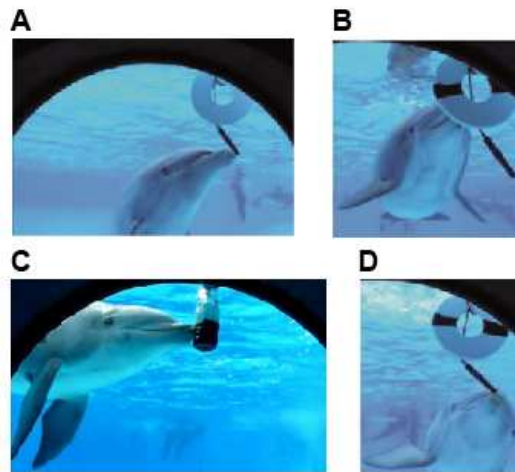
342

### 343 **Behavioral Observations**

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

359 Physical contact always involved the tip of the rostrum; no contact with any other  
360 body part was observed during the course of the experiment. Specifically, a limited area of the  
361 lower part of rostrum was involved, except for Guama, who sometimes lifted the hydrophone  
362 a few centimeters with the upper part (Fig. 3). Each dolphin positioned his or her rostrum

363 against a given point of the experimental device, yet some touched the object and others  
 364 touched the hydrophone, depending on the individual. Once a dolphin had positioned his or  
 365 her rostrum against one part of the device, s/he generally did so against the same one in  
 366 following trials.



367  
 368 Fig. 3. Examples of positioning against the object/hydrophone device, as recorded through a window  
 369 from the underwater viewing gallery. Panel A and D are of Guama, Panel B is of Beauty, and C of  
 370 Balasi. Contact involved the lower rostrum, except in Panel D where Guama lifts Object #2's  
 371 hydrophone.

372

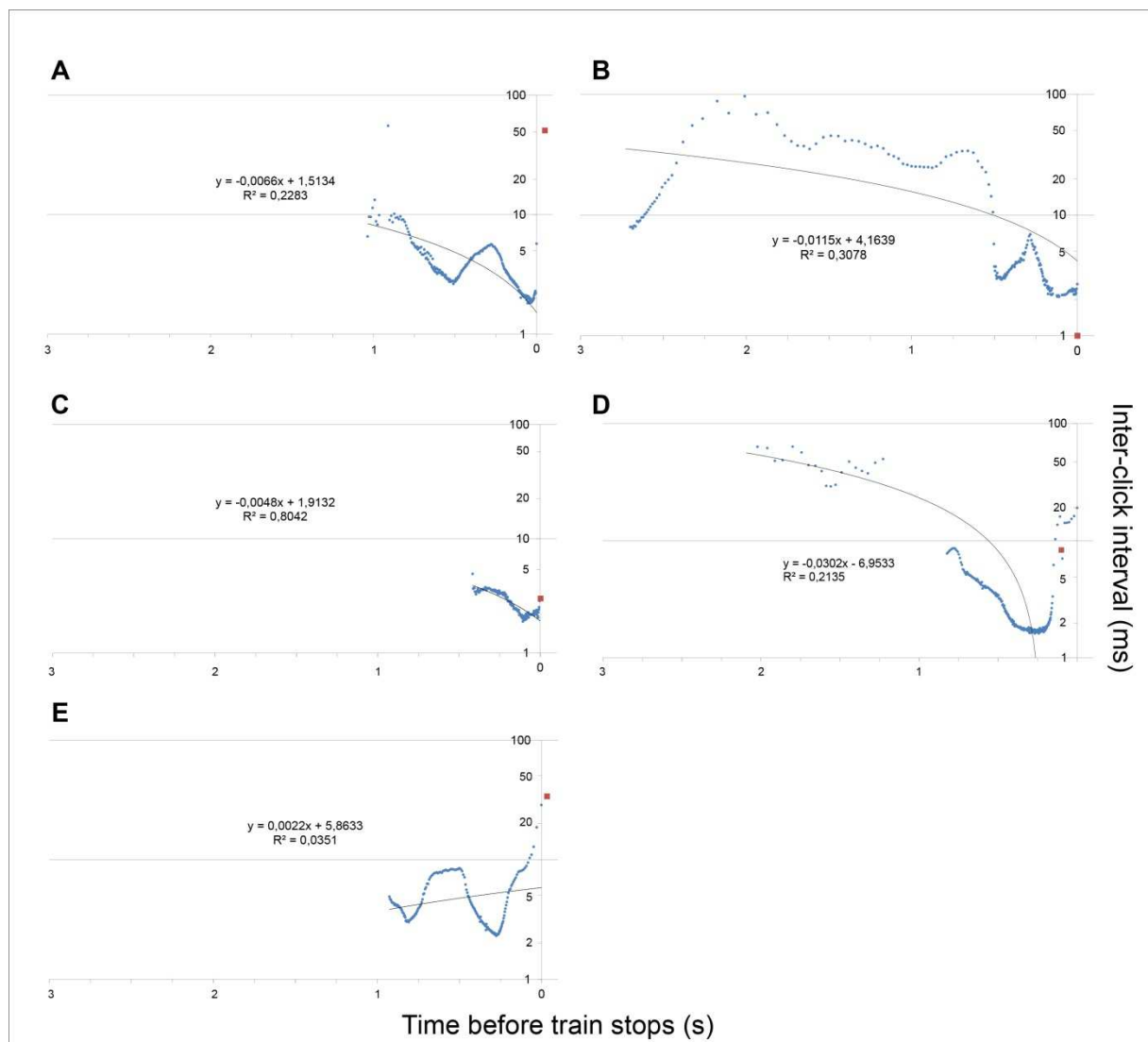
### 373 **Echolocation During Approach**

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

383 **Acceleration in the Approach Phase.** For each of the 36 sequences usable for ICI  
 384 rhythm analysis, a chronogram was plotted to show ICI duration with respect to the date it  
 385 occurred (Appendix 1), set with the train end as zero. For each chronogram, a linear trendline  
 386 was adjusted to it in order to determine the evolution of emission rhythm. Of 36 trendlines, 31  
 387 show a negative slope, meaning that the animals accelerate their click emissions when they  
 388 get close to the target in 86.11 % of the cases, a significant majority (binomial test (.5, N=36)

389  $p < .05$ ). Not all linear trendlines fit the data well (mean  $R^2 = .36$ ;  $SD = .27$ ) because, during  
 390 approach, the click train generally included two or more accelerations, and some  
 391 decelerations. The negative trendline can be attributed to stronger acceleration as it gets closer  
 392 to the end of the click train (see examples in Fig. 4), as observed in 34 individual  
 393 chronograms out of 36. These 94.4 % of cases represent a significantly large majority  
 394 (binomial test (.75,  $N=36$ )  $p < .05$ ). Thus, dolphins usually accelerated their click emissions  
 395 while approaching objects, and the shorter ICIs occurred closer to the end of the train.  
 396 However, the acceleration was not linear because the trend was mitigated by frequent  
 397 decelerations before the extreme, final speed-up, but also (as will be shown later) by some  
 398 slackening off before the train ended.

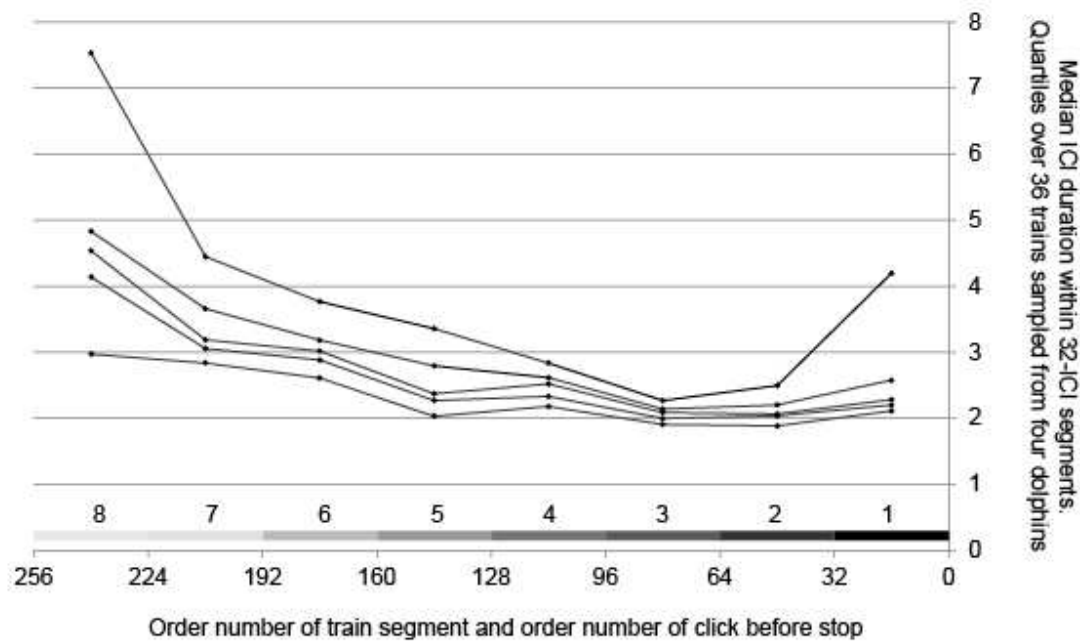


399  
 400 Fig. 4. Examples of chronograms for each individual dolphin: ICI duration in milliseconds (log scale) as  
 401 a function of countdown time from train stop in milliseconds. Linear trendlines show overall  
 402 acceleration for Panel A (Guama), B (Baily), C (Beauty), and D (Balasi), but not for Panel E (Balasi)  
 403 because of the final deceleration. Note that linear trendlines appear curved because of the logarithmic

404 Y-scale. The red square represents the onset of contact with the object; its height shows how long  
 405 after the preceding click it occurred (Y-axis).

406

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



413

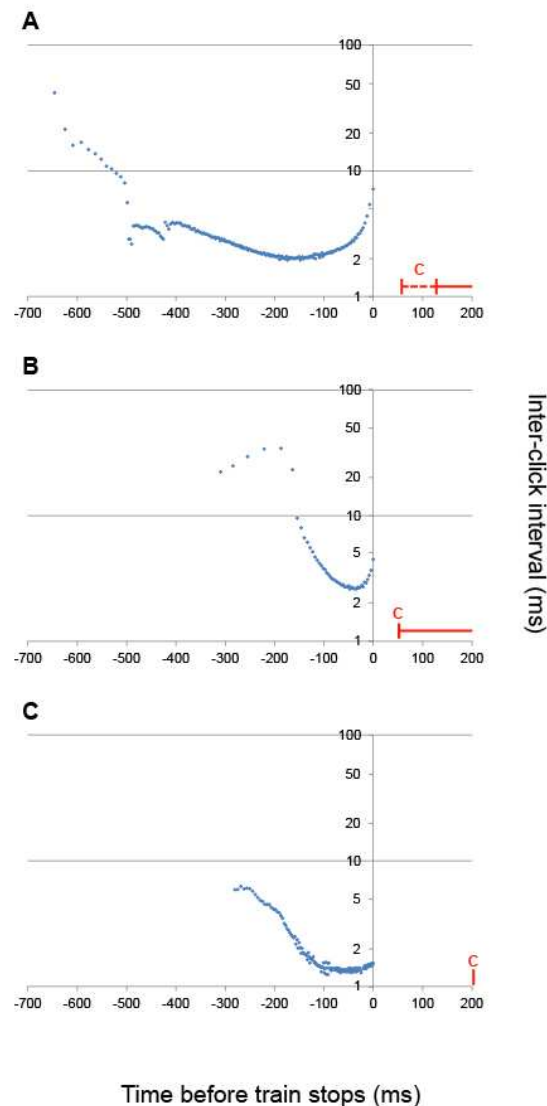
414 Fig. 5. General profile of clicking behavior when arriving close to the objects. From top to bottom: the  
 415 maximum, third quartile, median, first quartile, and minimum values of N = 36 sequences' median ICI  
 416 duration of segments grouping 32 sample ICIs. The segments - and cut-off point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

418

419 Indeed, dolphins decelerated (ICIs increased) just before ending their click trains. The  
 420 segment of shortest median ICI, about 2 ms, was typically the third or second one before the  
 421 end (32<sup>nd</sup>-to-last to 96<sup>th</sup>-to-last ICI). This pattern seemed characteristic of our dolphins'  
 422 terminal buzz. As illustrated in Figure 6, it was not an artifact due to data pooling. In 32 out of  
 423 36 cases (see Appendix 1), in the last quarter-second before the end, chronograms fell to a  
 424 minimum, after which trains ended with an increase in ICIs. Thus, this end pattern of the click  
 425 train was visible in 89.89 % of cases, a significantly large majority (binomial test, (.75, N=36)  
 426  $p < .05$ ). The shortest ICI was therefore not the last one; it generally occurred 0.25 to 0.05



427 seconds before the end (Q3, median, Q1 = 240, 130, 54 ms respectively). When swimming  
 428 closer to an object, the dolphin typically accelerated its click train; however it decelerated and  
 429 stopped at the last moment, when it reached the target.



430  
 431 Fig. 6. Examples of terminal buzz pattern in relation to the onset of contact, for Guama (A and B) and  
 432 Balasi (C). The X-axis is countdown time from train end, in milliseconds; the Y-axis is ICI duration in  
 433 milliseconds (log scale). Red bars represent the beginning of contact with the object/hydrophone  
 434 device, with a red “C” indicating the onset of contact, either precisely (Panel B and C), or within a  
 435 range (Panel A).

436

### 437 Touch Relays Echolocation

438 **Click Train Ends Before Contact.** This deceleration and subsequent stop were not  
 439 due to contact, but in anticipation of it. Out of the 52 times dolphins clicked during the  
 440 approach phase, their click train ended before the moment of contact 39 times, ended  
 441 afterwards 6 times, and the contact-to-stop interval was unknown for the remaining 7.

442 Therefore, their clicking stopped before they touched the object in 87% of the non-  
443 questionable cases, a significantly large majority (*binomial test* (.75, N=45)  $p < .05$ ). In those  
444 cases, the click train stopped for a maximum 1030 ms before contact (N = 39; M = 233 ms;  
445 SD = 331.6). For those who did not stop clicking before contact, the click train continued for  
446 a maximum 185 ms afterwards (N= 6; M = 87 ms; SD = 67.4). Overall, trains generally  
447 terminated a tenth to a hundredth of a second before contact (Q1-, median-, Q3-delay = 9, 46,  
448 137 ms respectively).

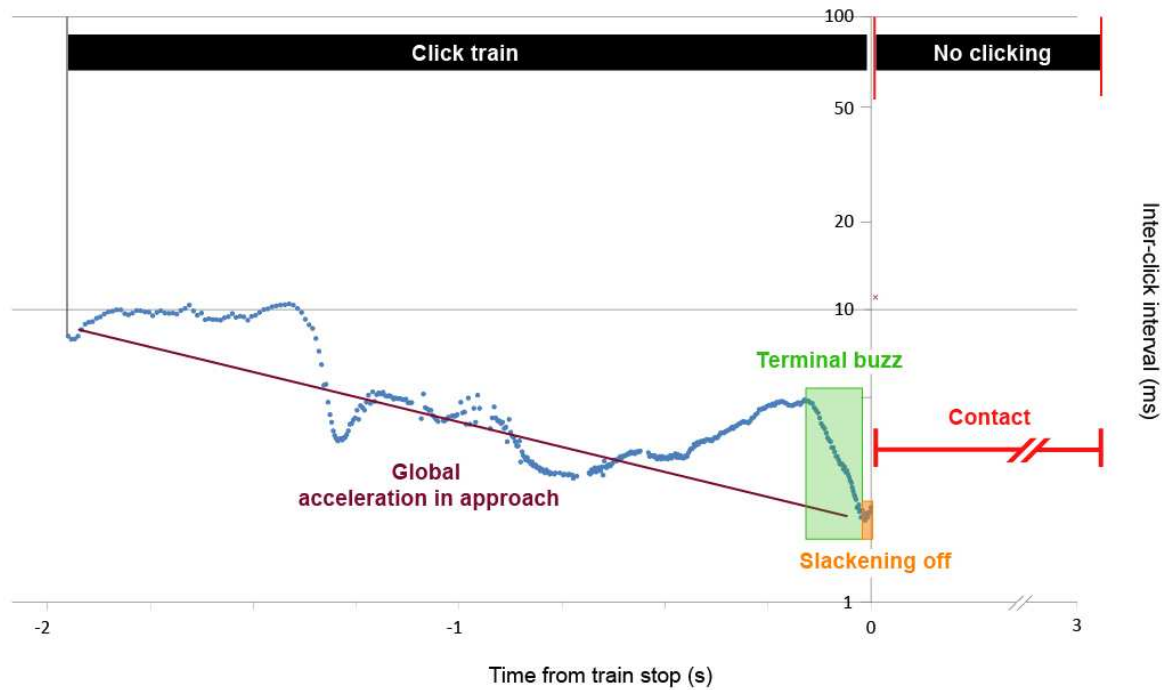
449 To sum up, dolphins usually stopped clicking just before touching the target with their  
450 rostrum, and more rarely, did so very shortly afterwards. The interval between the last click  
451 and contact was always (except for 1 sequence out of 39) greater than the ICI just before it.  
452 Dolphins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

454 **No Clicking While Contact Lasts.** The end observed in the 52 *approach* click trains  
455 was usually definitive whether it occurred before, or exceptionally, shortly after, the onset of  
456 contact; dolphins resumed clicking before the end of *positioning* in six cases only; in 42 cases,  
457 the dolphins remained silent the entire time contact was maintained; the 4 other cases are  
458 undetermined. Therefore, for the trains we are sure of, they did not emit clicks while touching  
459 the object in 87.5 % of them, *i.e.*, a significantly large majority (*binomial test* (.75, N=48)  $p <$   
460  $.05$ ). Dolphins did not use echolocation and touch simultaneously.

461

#### 462 **Exemplified Synthesis of the General Pattern.**

463 To summarize, Figure 7 displays a representative case. It highlights typical clicking  
464 behavior in a majority of the cases where any of the four dolphins swam over to an object.  
465 The clicking accelerated more than it decelerated as the animal approached. When s/he got  
466 very close to the target, it accelerated to a maximum (minimum ICI), then slackened off and  
467 stopped for good just before contact. Clicking did not resume as long as contact was  
468 maintained.



469

470 Fig. 7. Example of a click train showing the most prevalent temporal pattern during approach. The X-  
 471 axis is the countdown time from the end of the click train in seconds, and the Y-axis is ICI duration in  
 472 milliseconds (log scale).

473

## 474 Discussion

475

### 476 **Bottlenose Dolphins in Human Care Also Click**

477 First, it appears that captive bottlenose dolphins may well spontaneously and profusely  
 478 emit echolocation clicks in their man-made pools. This basic result is worth mentioning. On  
 479 one hand, because the fact has been omitted or neglected in scientific reports, which  
 480 essentially deal with recordings of spontaneous clicking in the sea or study induced clicking  
 481 in experimental contexts specifically testing for echolocation skills. On the other hand,  
 482 professional trainers and caregivers are not attuned to the mostly ultrasonic clicks. Before  
 483 undertaking sound acquisition, we could not exclude the possibility that dolphins click only in  
 484 the wild or in specific, behaviorally constrained conditions. Animals could have been  
 485 disturbed enough to limit their emissions by the reverberation of their clicks off of pools' flat  
 486 concrete walls. Such reverberations could also have jammed our signal acquisition, which  
 487 would have required additional filtering. Fortunately, interfering echoes were barely detected  
 488 by our conventional recording set-up. The captive dolphins used echolocation plentifully,  
 489 even though it is usually considered an adaptation to conditions of reduced visibility (i.e.,

490 turbid waters, ocean depths, nighttime activity) and the study took place during daytime in  
491 clear water. Although they were in their most familiar environment and context, they all  
492 clicked when more or less novel objects were proposed, and also when objects had become  
493 familiar after repeated encounters. We conclude that Beauty, Baily, Guama, Balasi, and  
494 probably other dolphins living in man-made pools, take advantage of bio-sonar in their daily  
495 activities, especially when approaching a target and positioning themselves against it, despite  
496 the absence of voluntary or noticeable reinforcement by their trainers.

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

505

### 506 **Dolphins Emit Terminal Buzz during Target Approach**

507 Second, we observed a prevalent terminal buzz pattern of clicking when dolphins  
508 swam towards objects. As far as we know, this is the first scientific report providing  
509 quantitative results on this characteristic temporal pattern behavior of *Tursiops sp.* The ICI  
510 sequence during the *approach* phase (moving towards a target) and during the *terminal* phase  
511 (right before contact) is comparable to those described for other taxa, chiropters hunting in the  
512 air and other odontocetes in the sea. When heading towards an inert target, our dolphins  
513 displayed acceleration comparable to bats, harbor porpoises, and beaked and sperm whales  
514 capturing prey (Griffin et al., 1960; Miller et al., 2004; Madsen et al., 2005; Verfuss et al.,  
515 2009). However, the preceding *searching* phase, during which targets or prey are sought out  
516 from farther away, appeared difficult to investigate while keeping the animals in their most  
517 familiar context, as we chose to do here. This phase may be studied, with additional means, in  
518 future data sampling designs, to complete the classic three-phase configuration.

519 Functional explanations for the observed pattern are similar to those applied to other  
520 species. Overall acceleration in emissions increases the sampling rate, and therefore the  
521 amount of collected data in a given portion of time. Data may relate to an object's position  
522 (hence the term "echolocation") but also to its shape, movement, and even make-up (Harley et  
523 al., 2003). In the wild, a rapid update of small prey's trajectory compensates for the lack of

524 maneuverability before attempted capture (Miller et al., 2004). Dolphins also need accuracy in  
525 non-feeding situations to position their rostrum on a limited area, such as the tip of the  
526 hydrophone in our conditions. A high degree of precision is required to avoid violent skin  
527 contact with a target, or an obstacle such as a rocky outcropping at the bottom of the sea,  
528 because the rostrum is so sensitive (Mauck et al., 2000).

529 In short, various animals heading towards an object or tracking prey through  
530 echolocation pulses need a higher emission rate, and terminal buzz provides rapid and  
531 accurate updating. In our captive animals, locating and moving was explicitly induced by  
532 trainers' pointing gestures at man-made targets, a very common form of interaction between  
533 humans and dolphins under their care. This practice most likely emerged because dolphins are  
534 prone to understanding finger – and eye – pointing, not just in captivity (Pack and Herman,  
535 2004) but also in the wild (Pack and Herman, 2007).

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

543

#### 544 **Dolphins' Terminal Buzz Slackens Off**

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

555 Although the recording and filtering conditions could not guarantee accurate  
556 measurement of every single ICI, as is visible on sample chronograms (Figures 4, 6 and 7, and  
557 Appendix 1), this lack of precision would not affect the evidence of observed and quantified

558 patterns in the temporal dimension. However, more sophisticated acquisition procedures will  
559 be necessary to assess the rate-amplitude relationship.

560 Akamatsu et al.'s paper (1998) displays a single 650-ms chronogram of a captive *T.*  
561 *truncatus*: the buzz terminates with a very slight slow-down (6 to 7.5 ms before the end of a  
562 200-ms time period), not commented on by the authors, but evocative of the slackening off we  
563 observed. For closely related species under human care, a slackening off may be considered in  
564 harbor porpoises (*P. Phocoena*) in two studies. First, DeRuiter et al. (2009) recorded multiple  
565 instances of two individuals, one after the other, catching a dead fish. Both produced buzzes  
566 with ICIs of approximately 3 ms and kept buzzing after the onset of contact; only once the  
567 fish was entirely their mouths did they decelerate; but they did not stop, as we observed in the  
568 present study. Second, Verfuss et al. (2009) recorded two trained harbor porpoises catching  
569 live prey. They produced click trains comparable to ours, with a buzzing deceleration after  
570 capture (not before), followed by a stop. The authors compared the profile with that of finless  
571 porpoises and beaked whales but did not comment on the slackening off. The profile seems  
572 absent in finless porpoises (*Neophocoena phocaenoides*), but some kind of slackening off is  
573 visible in Johnson et al.'s (2006) study on a single beaked whale (*Mesoplodon densirostris*,  
574 Blainville). Yet this species' click structure and average ICI duration put it in a different  
575 category than dolphins and porpoises.

576

### 577 **Click and Touch**

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

584 Recordings show that contact takes place with the rostrum tip, usually its lower part.  
585 This distinct posture may well favor association with sight, as eyes are oriented ventrally in  
586 cetaceans. Moreover, the lower jaw is the locus of reception for click echoes (Brill et al.,  
587 1988). This reception may be hampered by the direct contact with the object, thus rendering  
588 echolocation useless. Echolocation, like vision, is useful for extracting information at a  
589 distance; this "distant touch" may no longer be appropriate at point-blank range. Either the  
590 beam emanating from the melon (above the rostrum) can no longer reach the target (situated  
591 underneath the rostrum), or powerful sounds reflected from an object that is getting too close

592 cause aversive reverberations to the rostrum it is in direct contact with. Click vibrations  
 593 indeed provoke mechanical effects: powerful clicks can be used to caress conspecifics or even  
 594 to strike or knock out prey (Herzing, 1996; Herzing, 2004). Thus reciprocally, the  
 595 reverberations coming off of the object would disturb or jam the reception of tactile stimuli.  
 596 Stopping the clicking in anticipation of contact guarantees the integrity of tactile stimuli, and  
 597 respects the sensitivity of echolocation stimuli.

598

## 599 **Conclusion**

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

610

611

## 612 **References**

613

614 **Akamatsu, T., Wang, D., Wang, K, and Naito, Y.** (2005). Biosonar behavior of free ranging  
 615 porpoises. *Proc. Roy. Soc.* **272(1565)**, 797-801.

616

617 **Atem, A. C., Rasmussen, M. H., Wahlberg, M., Peterson, H. C., and Miller, L. A.** (2009).  
 618 Changes in click source levels with distance to targets: studies of free-ranging white-beaked  
 619 dolphins *Lagenorhynchus albirostris* and captive harbour porpoise *Phocoena phocoena*.  
 620 *Bioacoustics*. **19**, 49-65.

621

622 **Au, W. W., Popper, A. N., and Fay, R. R.** (2000). *Hearing by whales and dolphins*. New York:  
 623 Springer Handbook of Auditory Research.

624

625 **Au, W. W., Houser, D. S., Finneran, J. J., Lee, W., Talmadge, L. A., and Moore, P. W.** (2010).  
 626 The acoustic field on the forehead of echolocating Atlantic bottlenose dolphins (*Tursiops*  
 627 *truncatus*). *J. Acoust. Soc. Am.* **128(3)**, 1426-1434.

628

- 629 **Avril, A. and Graff, C.**, (2007). Active electrolocation of polarized objects by pulse-discharging  
 630 electric fish, *Gnathonemus petersii*. *J. Comp. Physiol., A*. **193(12)**, 1221-1234.  
 631
- 632 **Bauer, R.** (1974). Electric organ discharge activity of resting and stimulated *Gnathonemus*  
 633 *petersii* (Mormyridae). *Behaviour*. **50 (3/4)**, 306-323.  
 634
- 635 **Brill, R. L., Sevenich, M. L., Sullivan, T. J., Sustman, J. D. and Witt, R. E.** (1988).  
 636 Behavioral evidence for hearing through the lower jaw by an echolocating dolphin  
 637 (*Tursiops truncatus*). *Mar. Mamm. Sci.* **4**, 223-230.  
 638
- 639 **Britton, A. R., and Jones, G.** (1999). Echolocation behaviour and prey-capture success in  
 640 foraging bats: laboratory and field experiments on *Myotis Daubentonii*. *J. Exp. Biol.* **202**,  
 641 1793-180.  
 642
- 643 **Couquiaud** (2005). A survey of the environments of cetaceans in human care. *Aquat.*  
 644 *Mamm*, **31(3)**, 279-280.  
 645
- 646 **DeRuiter, S. L., Bahr, A., Blanchet M. A., Hansen, S. F., Kristensen, J. H., Madsen, P. T., Tyack,**  
 647 **P. L. and Wahlberg M.** (2009). Acoustic behaviour of echolocating porpoises during prey  
 648 capture. *J. Exp. Biol.* **212**, 3100-3107.  
 649
- 650 **Goodson, A. D., Klinowska, M. and Morris, R.** (1988). Interpreting the acoustic  
 651 pulse emissions of a wild bottlenose dolphin (*Tursiops truncatus*). *Aquat. Mamm.*  
 652 **14**, 7-12.  
 653
- 654 **Graff, C.** (1989). Firing activity of the weakly-electric fish *Marcusenius macrolepidotus*  
 655 (Mormyridae, Teleostei). Logarithmic distribution of inter-pulse intervals and sequential  
 656 inequality testing. *Behaviour*. **109**, 258-284.  
 657
- 658 **Griffin, D. R.** (1944). Echolocation by blind men, bats and radar. *Science*, **100**, 589-590.  
 659
- 660 **Griffin, D. R.** (1958). *Listening in the Dark*. New Haven, CT: Yale University Press.  
 661
- 662 **Griffin, D. R., Webster, F. A. and Michael, C. R.** (1960). The echolocation of flying  
 663 insects by bats. *Anim Behav.* **8**, 141-154.  
 664
- 665 **Halm, M. P., Poquin, D., Lestaevel, P., Chancerelle, Y. and Graff, C.** (2006). Brain and  
 666 cognitive impairment from burn injury in rats. *Burns*. **32(5)**, 570-576.  
 667
- 668 **Harley, H. E., Putman, E. A., and Roitblat, H. L.** (2003). Bottlenose dolphins perceive object  
 669 features through echolocation. *Lett. Nat.* **424**, 667-669.  
 670
- 671 **Herman, L. M., and Tavalga, W.** (1980). The communications systems of cetaceans. In  
 672 *Cetacean behavior: Mechanisms and functions* (ed. M. Herman), pp. 149–209. New York:  
 673 Wiley-Interscience.  
 674



- 675 **Herzing, D. L.** (1996). Vocalizations and associated underwater behavior of free-ranging  
 676 Atlantice spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*.  
 677 *Aquat. Mamm.* **22(2)**, 61-79.
- 678  
 679 **Herzing, D. L.** (2004). Social and nonsocial uses of echolocation in free-ranging *Stenella*  
 680 *frontalis* and *Tursiops truncatus*. In *Echolocation in Bats and Dolphins* (ed.  
 681 J. A. Thomas, C. F. Moss and M. Vater), pp. 404-410. Chicago, IL: The University of  
 682 Chicago Press.
- 683  
 684 **Johnson, M., Madsen, P.T., Zimmer, W.M.X., Aguilar de Soto, N., and Tyack, P.L.** (2006).  
 685 Foraging Blainsville's beaked whales (*Mesoplodon densirostris*) produce distinct click types  
 686 matched to different phases of echolocation. *J. Exp. Biol.* **209**, 5038-5050.
- 687  
 688 **Kalko, E.** (1995). Insect pursuit, prey capture and echolocation in pipistrelle bats  
 689 (*microchiroptera*). *Anim Behav.* **50**, 861-880.
- 690  
 691 **Kuczaj, S., Solangi, M., Hoffland, T., and Romagnoli, M.** (2008). Recognition and  
 692 discrimination of human actions across the senses of echolocation and vision in the  
 693 bottlenose dolphin: evidence for dolphin cross-modal integration of dynamic information. *Int*  
 694 *J. Comp. Psychol.* **21**, 84-95.
- 695  
 696 **Madsen, P. T., Johnson, M., Aguilar de Soto, N., Zimmer, W. M. X. and Tyack, P.**  
 697 **L.** (2005). Biosonar performance of foraging beaked whales (*Mesoplodon*  
 698 *densirostris*). *J. Exp. Biol.* **208**, 181-194.
- 699  
 700 **Mann, D. A., Lu, Z., Hastings, M. C. and Popper, A. N.** (1998). Detection of  
 701 ultrasonic tones and simulated dolphin echolocation clicks by a teleost fish, the  
 702 American shad (*Alosa sapidissima*). *J. Acoust. Soc. Am.* **104**, 562-568.
- 703  
 704 **Mauck, B., Eysel, U., and Dehnhardt, G.** (2000). Selective heating of vibrissal follicles in seals  
 705 (*Phoca vitulina*) and dolphins (*Sotalia fluviatilis guianensis*). *J. Exp. Biol.* **203**, 2125-2131.
- 706  
 707 **Miller, P. J. O., Johnson, M. P. and Tyack, P. L.** (2004). Sperm whale behaviour  
 708 indicates the use of echolocation click buzzes "creaks" in prey capture. *Proc. Biol.*  
 709 *Sci.* **271**, 2239-2247.
- 710  
 711 **Mohl, B., Wahlberg, M., and Madsen, P.** (2003). The monopulsed nature of sperm whale  
 712 clicks. *J. Acoust. Soc. Am.* **114**, 1143-1154.
- 713  
 714 **Moore, P., and Pawloski, D.** (1990). Investigations of the control of echolocation pulses in the  
 715 dolphin (*Tursiops truncatus*). In *Sensory abilities of cetaceans* (ed. J. Thomas and R.  
 716 Kastelein), pp. 305-320. New York: Plenum Press.
- 717  
 718 **Mullins, J., Whitehead, H., and Weilgart, L. S.** (1988). Behaviour and vocalizations of two  
 719 single sperm whales, *Physeter macrocephalus*, off Nova Scotia. *Can. J. Fish. Aquat. Sci.*  
 720 **45(10)**, 1736-1743.
- 721

- 722 **Nowacek, D. P.** (1999). *Sound use, sequential behavior and ecology of foraging bottlenose*  
 723 *dolphins, Tursiops truncatus*. (Unpublished doctoral dissertation), Massachusetts Institute of  
 724 Technology & Woods Hole Oceanographic Institution, Massachusetts.  
 725
- 726 **Pack, A. A., and Herman, L. M.** (1995). Sensory integration in the bottlenosed dolphin:  
 727 Immediate recognition of complex shapes across the senses of echolocation and vision. *J.*  
 728 *Acoust. Soc. Am.* **98** (2), 722-733.  
 729
- 730 **Pack, A. A., and Herman, L. M.** (2004). Bottlenose Dolphins (*Tursiops truncatus*) comprehend  
 731 the referent of both static and dynamic human gazing and pointing in an object-choice task.  
 732 *J. Comp. Psychol.* **118**(2), 160-171.  
 733
- 734 **Pack, A. A., and Herman, L. M.** (2007). The dolphin's (*Tursiops truncatus*) understanding of  
 735 human gazing and pointing: knowing what and where. *J. Comp. Psychol.* **112**(1), 34-45.  
 736
- 737 **Racca, A. R., Amadei, E., Ligout, S., Guo, K., Meints, K., and Mills, D.** (2010). Discrimination  
 738 of human and dog faces and inversion responses in domestic dogs (*Canis familiaris*). *Anim.*  
 739 *Cog.* **13**, 525-533.  
 740
- 741 **Ridgway, S. H., Elsberry, W. R., Blackwood, D. J., Kamolnick, T., Todd, M., Carder, D. A.,**  
 742 **Chaplin, M., and Cranford, T. W.** (2012). Vocal reporting of echolocation targets: Dolphins  
 743 often report before click trains end. *J. Acoust. Soc. Am.* **131**(1), 593-598.  
 744
- 745 **Saayman, G., Wardwell Ames, E., and Moffett, A.** (1964). Response to novelty as an  
 746 indicator of visual discrimination in the human infant. *J. Exp. Child. Psychol.* **(1)2**, 189–198.  
 747
- 748 **Sokal, R. R., and Rohlf, F. J.** (1973). *Introduction to Biostatistics*. San Francisco: Freeman and  
 749 Company.  
 750
- 751 **Thomas, J. A., Moss, C. F. and Vater, M.** (2004). *Echolocation in Bats and Dolphins*.  
 752 Chicago: University of Chicago Press.  
 753
- 754 **Verfuss, U. K., Miller, L. A., Pilz, P. K., and Schnitzler, H.** (2009). Echolocation by two foraging  
 755 harbour porpoises (*Phocoena phocoena*). *J. Exp. Biol.* **212**, 823-834.  
 756
- 757 **Whitehead, H., and Weilgart, L.** (1991). Patterns of visually observable behaviour and  
 758 vocalizations in groups of female sperm whales. *Behaviour.* **118**(3), 275-296.  
 759
- 760 **Zimmer, W., Tyack, P., Johnson, M., and Madsen, P.** (2005). Three-dimensional beam pattern  
 761 of regular sperm whale clicks confirms benthorn hypothesis. *J. Acoust. Soc. Am.* **117**, 1473–  
 762 1485.  
 763  
 764  
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781 **List of Abbreviations**

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783 ICI = Inter-click interval

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