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

26   **<u>Abstract</u>**

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.

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47   **<u>Keywords</u>**

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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 µs 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

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 **<u>Method</u>**

135

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).
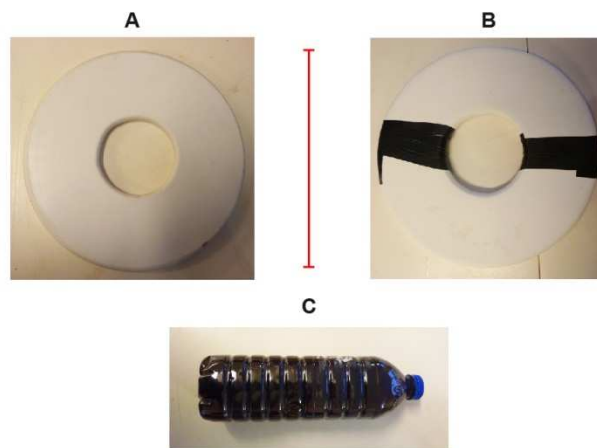

160

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+/- SD = 11.5+/-3.8 times) than the

191   other one (3.8+/-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
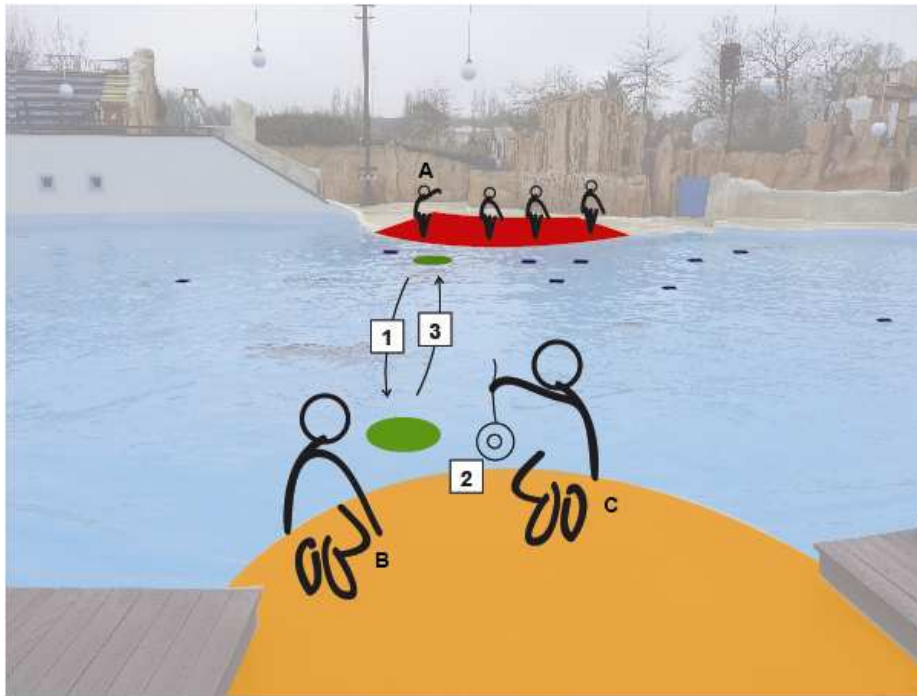
203   min. apart, on average.

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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.

211

212 **Recording**

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

227

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, a 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 **<u>Results</u>**

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
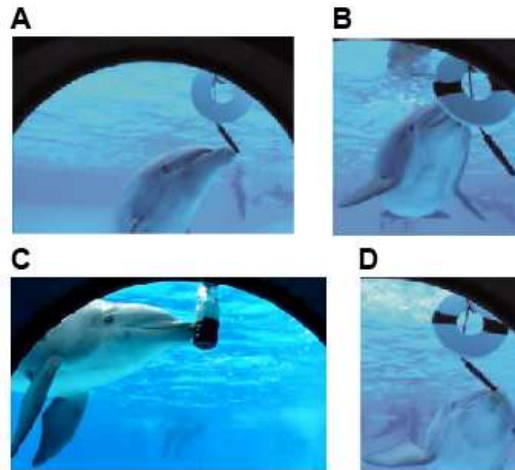366 following trials.

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**

374

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 (χ^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
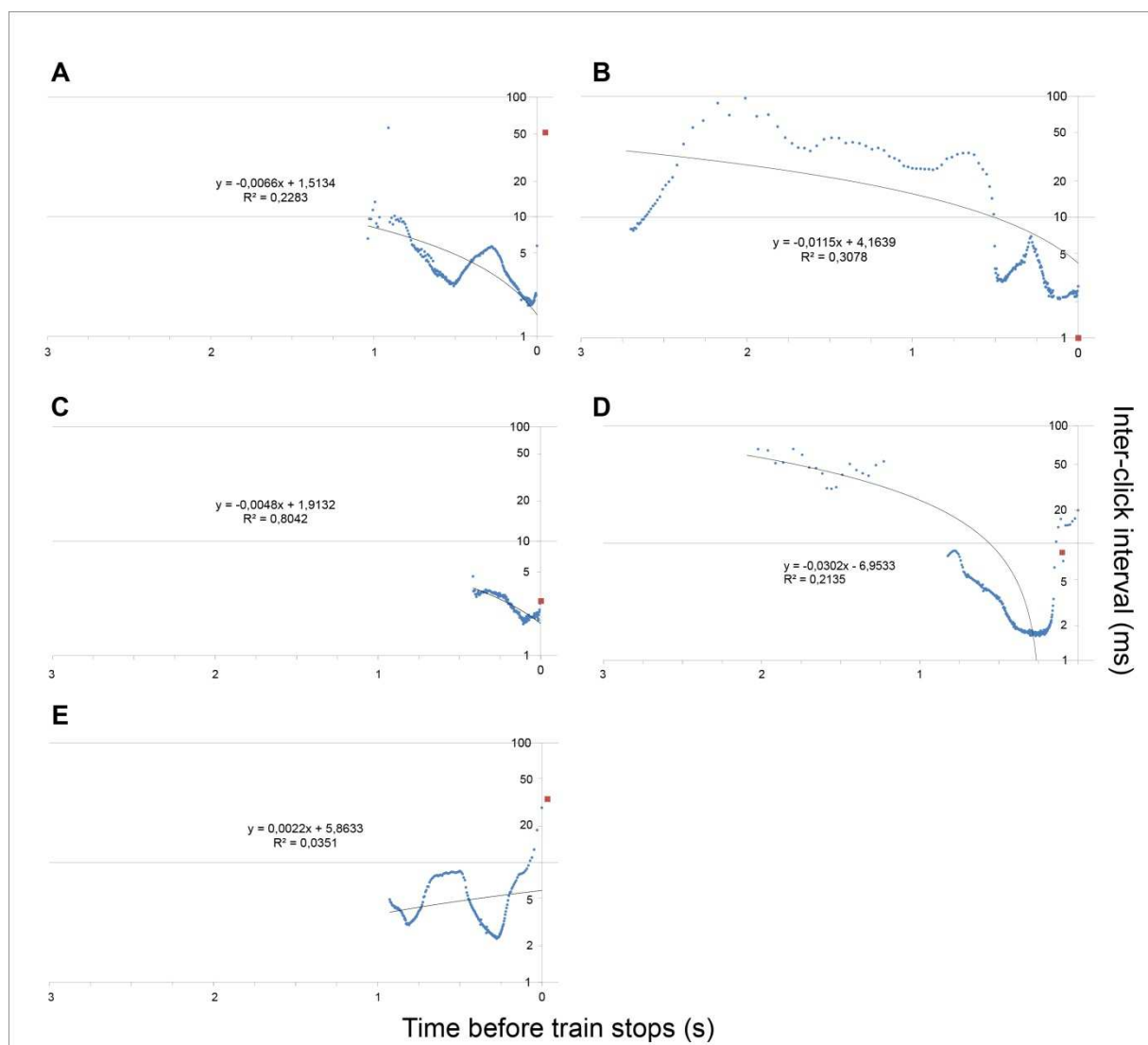
400   Fig. 4. Examples of chronograms for each individual dolphin: ICI duration in milliseconds (log scale) as

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.
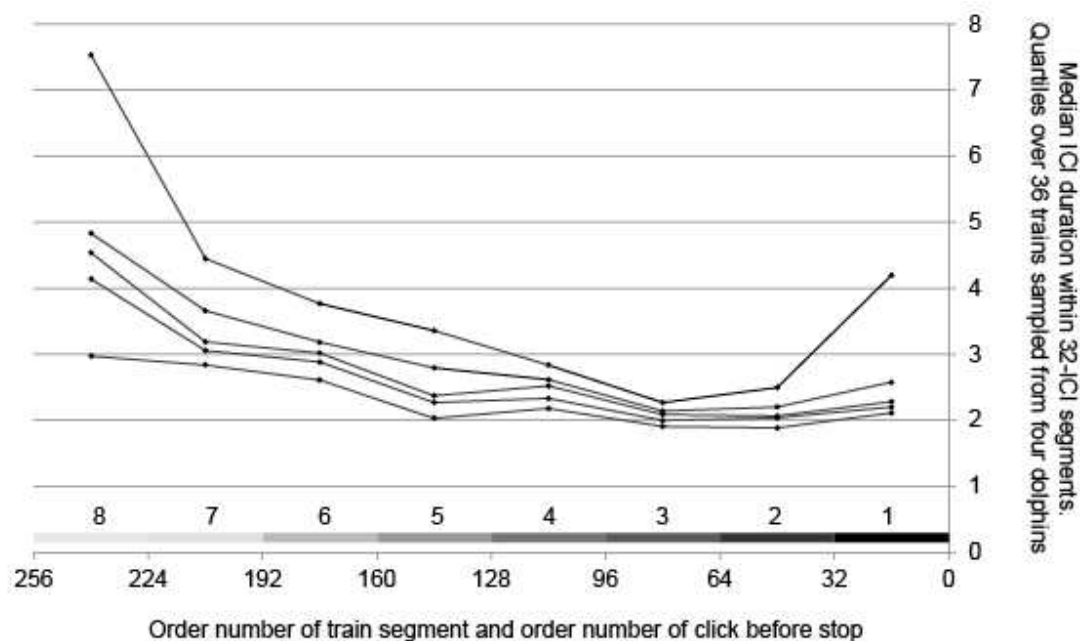

413
414 Fig. 5. General profile of clicking behavior when arriving close to the objects. From top to bottom: the
415 maximum, third quartile, median, first quartile, and minimum values of N = 36 sequences' median ICI
416 duration of segments grouping 32 sample ICIs. The segments - and cut-off point ICIs - 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 (32nd-to-last to 96th-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.
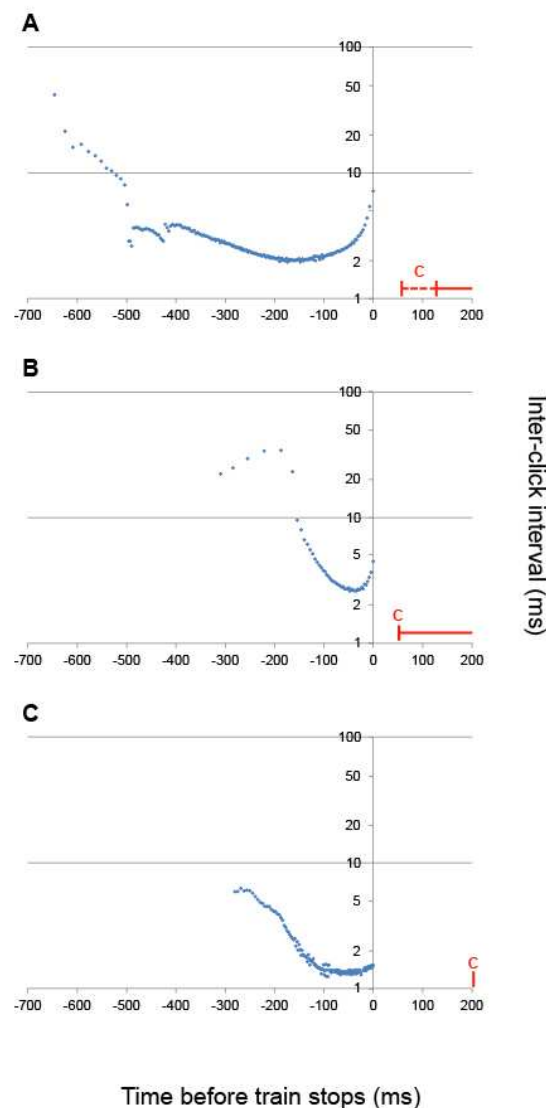

430
431   Fig. 6. Examples of terminal buzz pattern in relation to the onset of contact, for Guama (A and B) and
432   Balasi (C). The X-axis is countdown time from train end, in milliseconds; the Y-axis is ICI duration in
433   milliseconds (log scale). Red bars represent the beginning of contact with 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

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
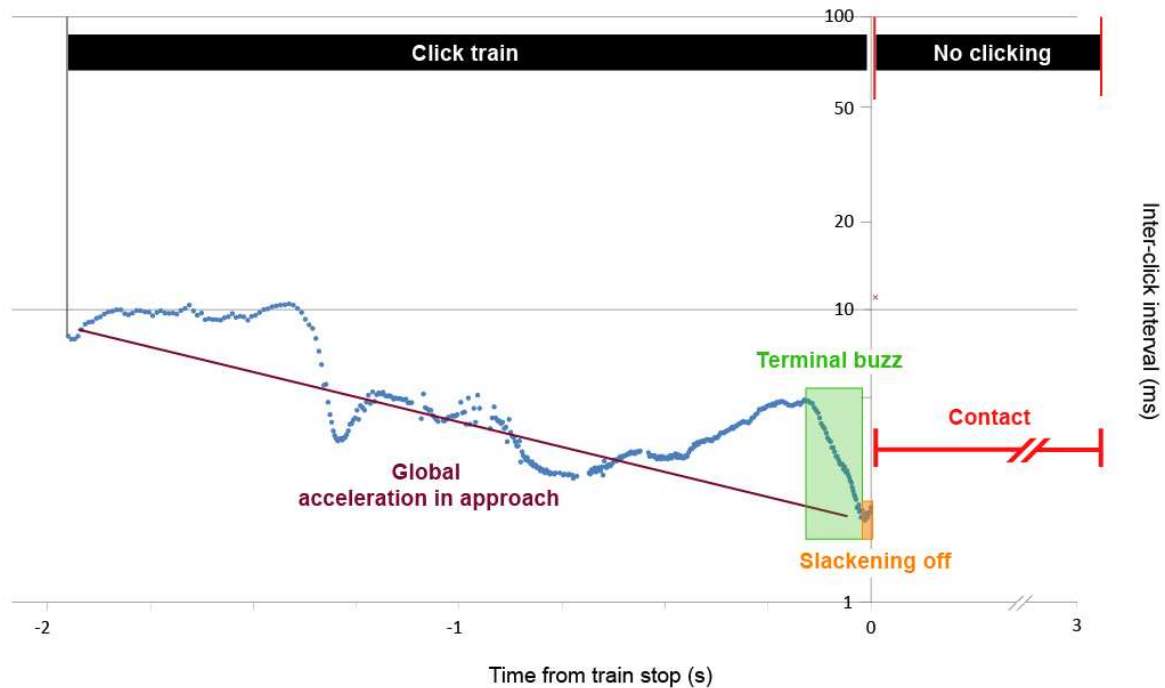468   maintained.

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

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

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

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771 **Acknowledgements**

772

781 **List of Abbreviations**

782

783 ICI = Inter-click interval

784