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1 **Postnatal development of echolocation abilities in a bottlenose dolphin (*Tursiops***
2 ***truncatus*): temporal organization**

3

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10 Short title: The ontogeny of echolocation in a bottlenose dolphin

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36 **ABSTRACT**

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38 In spite of all the information available on adult bottlenose dolphin (*Tursiops truncatus*)
39 biosonar, the ontogeny of its echolocation abilities has been investigated very little. Earlier
40 studies have reported that neonatal dolphins can produce both whistles and burst-pulsed sounds
41 just after birth and that early-pulsed sounds are probably a precursor of echolocation click
42 trains. The aim of this research is to investigate the development of echolocation signals in a
43 captive calf, born in the facilities of the Acquario di Genova.

44 A set of 81 impulsive sounds were collected from birth to the seventh postnatal week and 6
45 additional echolocation click trains were recorded when the dolphin was 1 year old. Moreover,
46 behavioral observations, concurring with sound production, were carried out by means of a
47 video camera.

48 For each sound we measured 5 acoustic parameters: click train duration, number of clicks per
49 train, minimum, maximum and mean click repetition rate. Click train duration and number of
50 clicks per train were found to increase with age. Maximum and mean click repetition rate
51 followed a decreasing trend with dolphin growth starting from the second postnatal week. The
52 calf's first head scanning movement was recorded 21 days after birth.

53 Our data suggest that in the bottlenose dolphin the early postnatal weeks are essential for the
54 development of echolocation abilities and that the temporal features of the echolocation click
55 trains remain relatively stable from the seventh postnatal week up to the first year of life.

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57 **Keywords:** biosonar, ontogeny, bioacoustics

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71 **INTRODUCTION**

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73 Toothed whales are known to use echolocation for orientation in marine environment and to
74 capture prey (Evans, 1973). Historically, most of our knowledge in this field comes from
75 studies carried out on killer whales (*Orcinus orca*), false killer whales (*Pseudorca crassidens*)
76 and, above all, the bottlenose dolphin (*Tursiops truncatus*) (Au, 1993). In the last 30 years,
77 several Authors extensively investigated the mechanisms of sound production, transmission and
78 perception in the bottlenose dolphin sonar system as well as its detection and target
79 discrimination capabilities (for a review, see Au and Hastings, 2008). However, nearly all of
80 these researches has been carried out on adult individuals. As a consequence, in spite of all the
81 information available on mature dolphins biosonar, not much has been reported on its ontogeny.
82 To fulfill this lacuna it is potentially very important because it can lay the foundation to fully
83 understand the echolocation behavior in the adult. Earlier studies (Killebrew et al., 2001;
84 Morisaka et al., 2005a,b; Gnone and Moriconi 2010), carried out in captive settings,
85 investigated the vocal behavior of young bottlenose dolphins during postnatal development and
86 showed that newborn dolphins can produce both whistles and burst-pulsed sounds just after
87 birth. Unfortunately, the calf observed by Killebrew et al. (2001) and one of the two animals
88 observed by Morisaka et al. (2005a,b) died within the first five postnatal days. As a
89 consequence, the data from these dolphins are limited in their contribution. Moreover, although
90 the second calf observed by Morisaka et al. (2005a,b) was recorded at constant intervals within
91 the first 32 days of life, acoustic analyses were limited to whistle vocalizations.

92 Reiss (1988) performed behavioral observations, supported by visual inspection of acoustic
93 recordings, on two captive-born *T. truncatus* to document the development of their echolocation
94 abilities. She reported the presence of both whistle and “squawk” - defined as the pulsed
95 component of the signals - vocalizations since the animals’ first week of life. In addition, she
96 observed substantial changes occurring in the acoustic structure of pulsed sounds from birth to
97 the first forty days and suggested that early-pulsed “squawk” may play a role as precursor to
98 adult echolocation click trains. However, Reiss’s assertions lack quantitative details and
99 statistical analyses were not performed to corroborate these hypotheses.

100 Manoukian et al. (2002) carried out acoustic analyses of the pulsed vocalizations emitted by two
101 calves born in Cattolica and Rimini Delphinaria (Italy) and suggested that the study subjects
102 have spent respectively 2 and 5 months to set up their echolocation abilities. Unfortunately,
103 acoustic recordings did not start at the birth of the calves and, therefore, we do not have a full
104 picture of what happened during the entire postnatal period.

105 Finally, Carder and Ridgway (1983) reported an apparent adult-like echolocation click train
106 recorded by a sixty-day-old calf in the San Diego Bay facilities. On the contrary, Lindhard
107 (1988) described a few sonar-like clicks emitted by the dolphin Venus when only 2 weeks old,
108 although the peak energy recorded in that occasion was reported to be not as high in frequency
109 as in the adult.

110 From a bottlenose dolphin calf born in the Acquario di Genova facilities, we got the opportunity
111 to contribute to the study of the ontogeny of echolocation abilities of this species. To this end,
112 we monitored the temporal organization of the calf's echolocation signals during its first 7
113 weeks of life, and we collected additional recordings when the dolphin was 1 year old.

114

115 **METHODS**

116

117 **Study subject and data collection**

118

119 The study subject was a male born at the Acquario di Genova on August 2002. The calf was
120 housed with his mother (an adult female approximately 28 years old) in a rectangular pool
121 (25x10x5 m) with three concrete walls and one facing the visitor corridor made up of glass
122 panels, which allowed a complete vision of dolphin activity. No other dolphins were housed in
123 the same pool with the mother-calf pair.

124 All recordings were carried out without any manipulation of the individual and without the use
125 of playback stimuli. Using a focal animal sampling method (Altmann, 1974) calf's sound
126 production and relevant behavior were monitored from birth to the first year by underwater
127 video-acoustic recording collected continuously over 24-hours (see Gnone et al., 2006 for more
128 details). For the purpose of this study we considered data of the first seven postnatal weeks,
129 collected on 11 separate days, and one additional 24-hour recording session carried out when
130 the dolphin was 1 year old (Table 1).

131 The video images were captured by means of a mobile camera, connected to a S-VHS video
132 recorder (Panasonic NV-HS950). The video camera was placed in front of the pool's glass wall
133 and it was constantly focused on the mother-calf pair. As the calf began to swim alone, the
134 camera was focused on him. However, when the mother was not in video range, an observer
135 documented her position and activities.

136 The audio recordings were taken using an Offshore Acoustic spherical hydrophone (flat
137 frequency response 10-Hz-to-100-kHz \pm 2dB) placed into a fiberglass pipe 2 m below the water
138 surface. The hydrophone output signal was amplified and recorded onto S-VHS (frequency

139 response 20 Hz-20 kHz \pm 10 dB) and then digitized onto a PC using a SoundBlaster-32 sound
140 card.

141 As the low frequency components of echolocation clicks are fairly omnidirectional, we used
142 different criteria to be sure that the vocalizations analyzed belonged to the calf. Following what
143 was already reported in previous studies (Reiss, 1988; Killebrew et al., 2001; Morisaka et al.,
144 2005a,b), during the first postnatal week we identified the vocalizing calf by air bubbles stream
145 production. This behavior frequently occurs with phonation in infants (McCowan and Reiss,
146 1995) and *T. truncatus* calves have been reported to produce bubblestream whistles ten times as
147 many as adults (Fripp, 2005). However, bubblestream vocalizations are non representative of
148 the whole bottlenose dolphin vocal repertoire (Fripp, 2005), and this technique can not be used
149 as the sole method for identifying which dolphin in a group is vocalizing (Fripp, 2005).
150 Therefore, as the calf became more independent, we mainly used the concomitant occurrence of
151 the head scanning movements to label click vocalizations according to the emitter. Moreover,
152 part of the click trains were recorded while the mother was resting at the surface, with her
153 blowhole above the water level.

154 Finally, we selected only sequences in which the study subject vocalized directly at the
155 hydrophone or surrounding objects and, after aural examinations of sonograms, all vocalizations
156 showing high noise level were discarded.

157

158 **Acoustical measurements**

159

160 Segments containing the selected vocalizations were edited using Adobe Soundbooth v. 2.0
161 (Adobe Systems Incorporated, San Jose CA, USA) and each click train was saved into single
162 audio files. The FFT spectrogram (size of 256 points, using a Hamming window) and waveform
163 were generated in Raven Pro v. 1.3 (Cornell Lab of Ornithology, Ithaca NY, USA), and the
164 following temporal parameters were measured: click train duration, number of clicks per train,
165 and click repetition rate - defined as the inverse of the time interval between two subsequent
166 clicks. However, since it is well documented that the time interval between clicks often changes
167 along a click train - especially for a moving dolphin (Au, 1993) - and it depends on a variety of
168 factors, including the animal's expectation of finding a specific target (Au, 1993), we
169 considered min, max and mean click repetition rate using the same measurements adopted by
170 Songhai et al. (2007).

171

172 **Statistical analysis**

173

174 Data distribution was assessed using the Kolmogorov-Smirnov test. Since the assumptions for
175 parametric analyses were not met for click train duration and number of clicks per train,
176 inference on these parameters was made from non-parametric statistical technique following
177 Weber (1972). The Spearman's Rho test was then applied to determine whether significant
178 correlation could be found with dolphin age. Moreover, the Mann-Whitney U test was used to
179 ascertain significant differences between click train duration and number of clicks per train at
180 the age of 7 weeks and 1 year respectively. Finally, a piecewise regression was performed to
181 evaluate the trend between min, max and mean click repetition rate and dolphin age.

182 All tests were performed in SPSS v. 17 (SPSS Inc., Chicago IL, USA) for Macintosh.

183

184 **RESULTS**

185

186 **Development of vocal behavior**

187

188 Two days after birth the calf was already able to emit "whistle-squawks" vocalizations where
189 the pulsed component usually occurred at the beginning or at the end of the signal (Figure 1)
190 and showed an Inter Click Interval (ICI) of less than 10 milliseconds. According to Lammers et
191 al. (2003), these vocalizations were believed to play a role in social interactions.

192 At days four and seven, the pulsed component was frequently observed to occur alone.
193 Moreover, it began to increase both in duration and number of clicks. The first head scanning
194 movement was observed at day 21. The click train recorded in that occasion lasted 3.6 seconds
195 and, from that moment, the scanning movement was always observed to occur together with the
196 production of the echolocation click trains.

197

198 **Acoustical analysis**

199

200 Table 1 shows the values of the acoustic parameters measured on the click trains at different
201 stages of the dolphin's first year of life. The Spearman's Rho test shows that, starting from birth
202 up to the seventh postnatal week, click train duration (CTD) and number of click per train
203 (NCT) increase with age (CTD: Correlation Coefficient = 0.904, $p < 0.001$, $N = 81$; NCT:
204 Correlation Coefficient = 0.890, $p < 0.001$, $N = 81$). The Mann-Whitney U test did not show
205 statistically significant differences in the mean values of click train duration and number of
206 clicks per train when the dolphin was respectively 7 weeks and 1 year old (CTD: Mann-
207 Whitney U = 45, $p > 0.05$, ns; NCT: Mann-Whitney U = 24, $p = 0.062$, ns). Figure 2 shows
208 click train duration plotted as a function of age.

209 The piecewise regression showed that max and mean click repetition rate (CRR) increase in the
210 first week of life (max CRR: $R^2 = 0.29$, $p = 0.001$; mean CRR: $R^2 = 0.13$, $p < 0.05$) and then
211 decrease starting from the second postnatal week (max CRR: $R^2 = -0.25$, $p < 0.001$; mean CRR:
212 $R^2 = -0.18$, $p < 0.005$). Figure 3 shows max click repetition rate and mean click repetition rate
213 plotted against the dolphin age.

214 On the contrary, min click repetition rate was not related with the dolphin's age both in the first
215 week of life ($R^2 = 0.1$, $p > 0.05$) and from day 14 to 49 ($R^2 = -0.08$, $p > 0.05$).

216

217 **DISCUSSION**

218

219 The present research investigated the organization of the temporal features of the echolocation
220 click trains in a captive-born bottlenose dolphin occurring in its first year of life. This was
221 described by means of acoustic analysis and related behavioral observation.

222 Table 2 collates data published over the last 30 years on the ontogeny of *Tursiops truncatus*
223 sonar system.

224 Our findings suggest that, in the study subject, the first pulsed signals with sonar-like structure
225 appeared approximately 14 days after birth. However, the signals recorded in that occasion were
226 shorter in duration and were made up of less pulses if compared to adults'. Unfortunately, the
227 sensitivity of the entire recording system was linear up to 20 kHz and we were not able to detect
228 the dominant frequency of the clicks. However, following the reports by Lindhard (1988) for
229 the calf "Venus" at the age of two weeks, we could imagine a similar scenario where the shorter
230 duration and less number of pulses were concomitant with a lower peak frequency of the clicks
231 compared to adults'. Further investigation, without frequency limits of the recording array, are
232 needed to confirm this hypothesis.

233 Moreover, according to Reiss (1988), the click trains recorded in those occasions were emitted
234 in absence of head scanning movement. Indeed, by adjusting the position of its head, a dolphin
235 can change the angle at which its clicks impact on a target. As a result, it can process returning
236 echoes from different angles and obtain more details on the target. We suggest that the lack of
237 these movements, of our calf, during the first two weeks after birth was indicative of its scarce
238 ability to process the information contained in the returning echoes. In fact, the first head
239 scanning movement was observed at the age of 21 days - 1 week before Reiss (1988)
240 observation, 39 days before Carder and Ridgway's (1983) observation and in accordance to
241 Hendry (2004). This may have been related to an increasing interest by the calf in exploring its
242 surroundings, due to the dolphin's improved ability to process the information contained in
243 echolocation signals.

244 The correlation analysis shows that the pulsed component of the early-impulsive sounds
245 increases with age both in duration and number of pulses until it changes into an adult
246 echolocation click train. Although it is not clear whether young dolphins obtain information
247 from early-pulsed signals, the increase of click train duration and number of clicks per train
248 suggests a continuous maturation process in dolphin echolocation ability during the first 49 days
249 of life. These findings are in line with those reported by Hendry (2004) and are consistent with
250 Reiss's hypothesis (1988) that the early-pulsed sounds may be a precursor of the adult
251 echolocation click trains.

252 The wide range of min, max and mean click repetition rate values recorded in the early-period
253 of life are consistent to the 2 to 70 ms inter click interval reported by Lindhard (1983) for the
254 calf Venus when 2 weeks old. Moreover, max and mean click repetition rate showed an
255 increasing trend within the first 7 days of life and then gradually decreased starting from the
256 second week after birth. These findings further suggest an ongoing maturation process in the
257 study subject sensory system within the first 7 weeks of life, and they are in line with the trend
258 of the inter click interval reported by Hendry (2004) in 5 bottlenose dolphin calves.

259 Although the bottlenose dolphin is considered a precocial species (Dearolf et al., 2000), a
260 postnatal development period is necessary to accomplish maturation of physiological
261 characteristics that support vocal and echolocation abilities (Killebrew et al., 2001). The length
262 of this period may vary from case to case and it is supposed to depend on a combination of
263 factors including: the group composition, the presence of other calves, and the environmental
264 stimuli (Hendry, 2004). In the present study, the click train duration and number of clicks per
265 train of dolphin's echolocation signals were not significantly different between 7 weeks and one
266 year of age, as indicate by the Mann-Whitney U test. This result suggests that, in the study
267 subject, the period to complete the temporal organization of the echolocation click trains was
268 roughly seven weeks. This time period is almost the same observed by Manoukian et al. (2002)
269 for the calf Daphne. However, it should be considered that both studies were carried out on
270 dolphins born in captivity, so controlled conditions may affect the speed at which echolocation
271 becomes effectively functional (Songhai et al., 2007). However, to corroborate this hypothesis,
272 further studies should be carried out in natural settings with a larger number of individuals.

273 Manoukian et al. (2002) report that vocal learning play a role in the ontogeny of echolocation in
274 the bottlenose dolphin, since the acoustic nature of echolocation signals is modifiable with
275 exposure to auditory stimuli from conspecifics. In the case study, the calf was not housed in a
276 community pool and social interaction took place only with the mother.

277 This scenario does not seem to have affected the time necessary for the calf to develop its
278 biosonar abilities. On the contrary, this dolphin was able to emit adult-like echolocation click

279 trains even earlier than calves housed in larger social units (e.g. Lindhard, 1988; Reiss, 1988).
280 As dolphins are known to be capable of vocal learning (Janik and Slater, 1997), and some
281 dolphin calves have been reported to learn whistles from the mother (Sayigh et al., 1990), it is
282 possible that having fewer individuals in the tank could facilitate the mother-calf learning
283 process.

284 In conclusion, the data presented here suggest that in the first 7 postnatal weeks significant
285 changes occur in the sensory system of dolphins born in captivity, therefore, this period is
286 important for the development of accurate echolocation abilities.

287 Certainly much remains to be learnt about ontogeny of echolocation in the bottlenose dolphin
288 and many aspects deserve further investigation. We hope that the present study will pave the
289 way for further research.

290

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292

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298

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352

353 **TABLE LEGENDS**

354

355 Table 1

356 Descriptive statistics of click trains (Age = days after birth; N = number of click trains analysed;

357 CTD = click train duration; NCT = number of click per train; CRR = click repetition rate).

358 Results are presented as mean \pm standard deviation.

359

360 Table 2

361 Published data on the ontogeny of *Tursiops truncatus* sonar system (? = information not
362 reported).

363

364 **FIGURE LEGENDS**

365

366 Figure 1

367 Whistle-squawk vocalization emitted by the calf during week 1. The sound is shown as (a) a

368 waveform and (b) a spectrogram (Hamming window, FFT size 256, 50% overlap).

369

370 Figure 2

371 Click trains duration plotted as function of age. Circles represent the mean values and bars

372 represent \pm standard deviation.

373

374 Figure 3

375 Max and mean click repetition rate of the click trains plotted against age. See the results for

376 correlations and *p*-values.