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

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Short title: The ontogeny of echolocation in a bottlenose dolphin

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ABSTRACT

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

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

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

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

**Keywords:** biosonar, ontogeny, bioacoustics
INTRODUCTION

Toothed whales are known to use echolocation for orientation in marine environment and to capture prey (Evans, 1973). Historically, most of our knowledge in this field comes from studies carried out on killer whales (Orcinus orca), false killer whales (Pseudorca crassidens) and, above all, the bottlenose dolphin (Tursiops truncatus) (Au, 1993). In the last 30 years, several Authors extensively investigated the mechanisms of sound production, transmission and perception in the bottlenose dolphin sonar system as well as its detection and target discrimination capabilities (for a review, see Au and Hastings, 2008). However, nearly all of these researches has been carried out on adult individuals. As a consequence, in spite of all the information available on mature dolphins biosonar, not much has been reported on its ontogeny.

To fulfill this lacuna it is potentially very important because it can lay the foundation to fully understand the echolocation behavior in the adult. Earlier studies (Killebrew et al., 2001; Morisaka et al., 2005a,b; Gnone and Moriconi 2010), carried out in captive settings, investigated the vocal behavior of young bottlenose dolphins during postnatal development and showed that newborn dolphins can produce both whistles and burst-pulsed sounds just after birth. Unfortunately, the calf observed by Killebrew et al. (2001) and one of the two animals observed by Morisaka et al. (2005a,b) died within the first five postnatal days. As a consequence, the data from these dolphins are limited in their contribution. Moreover, although the second calf observed by Morisaka et al. (2005a,b) was recorded at constant intervals within the first 32 days of life, acoustic analyses were limited to whistle vocalizations.

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

Manoukian et al. (2002) carried out acoustic analyses of the pulsed vocalizations emitted by two calves born in Cattolica and Rimini Delphinaria (Italy) and suggested that the study subjects have spent respectively 2 and 5 months to set up their echolocation abilities. Unfortunately, acoustic recordings did not start at the birth of the calves and, therefore, we do not have a full picture of what happened during the entire postnatal period.
Finally, Carder and Ridgway (1983) reported an apparent adult-like echolocation click train recorded by a sixty-day-old calf in the San Diego Bay facilities. On the contrary, Lindhard (1988) described a few sonar-like clicks emitted by the dolphin Venus when only 2 weeks old, although the peak energy recorded in that occasion was reported to be not as high in frequency as in the adult.

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

METHODS

Study subject and data collection

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

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

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

The audio recordings were taken using an Offshore Acoustic spherical hydrophone (flat frequency response 10-Hz-to-100-kHz ± 2dB) placed into a fiberglass pipe 2 m below the water surface. The hydrophone output signal was amplified and recorded onto S-VHS (frequency
response 20 Hz-20 kHz ± 10 dB) and then digitized onto a PC using a SoundBlaster-32 sound card.

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

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

**Acoustical measurements**

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

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

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

RESULTS

Development of vocal behavior

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

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

Acoustical analysis

Table 1 shows the values of the acoustic parameters measured on the click trains at different stages of the dolphin’s first year of life. The Spearman’s Rho test shows that, starting from birth up to the seventh postnatal week, click train duration (CTD) and number of click per train (NCT) increase with age (CTD: Correlation Coefficient = 0.904, p < 0.001, N = 81; NCT: Correlation Coefficient = 0.890, p < 0.001, N = 81). The Mann-Whitney U test did not show statistically significant differences in the mean values of click train duration and number of clicks per train when the dolphin was respectively 7 weeks and 1 year old (CTD: Mann-Whitney U = 45, p > 0.05, ns; NCT: Mann-Whitney U = 24, p = 0.062, ns). Figure 2 shows click train duration plotted as a function of age.
The picewise regression showed that max and mean click repetition rate (CRR) increase in the first week of life (max CRR: $R^2 = 0.29$, $p = 0.001$; mean CRR: $R^2 = 0.13$, $p < 0.05$) and then decrease starting from the second postnatal week (max CRR: $R^2 = -0.25$, $p < 0.001$; mean CRR: $R^2 = -0.18$, $p < 0.005$). Figure 3 shows max click repetition rate and mean click repetition rate plotted against the dolphin age.

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

**DISCUSSION**

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

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

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

Moreover, according to Reiss (1988), the click trains recorded in those occasions were emitted in absence of head scanning movement. Indeed, by adjusting the position of its head, a dolphin can change the angle at which its clicks impact on a target. As a result, it can process returning echoes from different angles and obtain more details on the target. We suggest that the lack of these movements, of our calf, during the first two weeks after birth was indicative of its scarce ability to process the information contained in the returning echoes. In fact, the first head scanning movement was observed at the age of 21 days - 1 week before Reiss (1988) observation, 39 days before Carder and Ridgway’s (1983) observation and in accordance to Hendry (2004). This may have been related to an increasing interest by the calf in exploring its surroundings, due to the dolphin’s improved ability to process the information contained in echolocation signals.
The correlation analysis shows that the pulsed component of the early-impulsive sounds increases with age both in duration and number of pulses until it changes into an adult echolocation click train. Although it is not clear whether young dolphins obtain information from early-pulsed signals, the increase of click train duration and number of clicks per train suggests a continuous maturation process in dolphin echolocation ability during the first 49 days of life. These findings are in line with those reported by Hendry (2004) and are consistent with Reiss’s hypothesis (1988) that the early-pulsed sounds may be a precursor of the adult echolocation click trains.

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

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

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

This scenario does not seem to have affected the time necessary for the calf to develop its biosonar abilities. On the contrary, this dolphin was able to emit adult-like echolocation click
trains even earlier than calves housed in larger social units (e.g. Lindhard, 1988; Reiss, 1988).

As dolphins are known to be capable of vocal learning (Janik and Slater, 1997), and some
dolphin calves have been reported to learn whistles from the mother (Sayigh et al., 1990), it is
possible that having fewer individuals in the tank could facilitate the mother-calf learning
process.

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

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

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Table 1
Descriptive statistics of click trains (Age = days after birth; N = number of click trains analysed; CTD = click train duration; NCT = number of click per train; CRR = click repetition rate). Results are presented as mean ± standard deviation.

Table 2
Published data on the ontogeny of *Tursiops truncatus* sonar system (? = information not reported).

Figure 1
Whistle-squawk vocalization emitted by the calf during week 1. The sound is shown as (a) a waveform and (b) a spectrogram (Hamming window, FFT size 256, 50% overlap).

Figure 2
Click trains duration plotted as function of age. Circles represent the mean values and bars represent ± standard deviation.

Figure 3
Max and mean click repetition rate of the click trains plotted against age. See the results for correlations and *p*-values.