

## RESEARCH ARTICLE

# Modulation of Whistle Production Related to Training Sessions in Bottlenose Dolphins (*Tursiops truncatus*) Under Human Care

Juliana Lopez Marulanda,<sup>1\*</sup> Olivier Adam,<sup>1,2</sup> and Fabienne Delfour<sup>3</sup>

<sup>1</sup>Institute of Neurosciences Paris Saclay, Université Paris Sud, CNRS UMR 9197Orsay, France

<sup>2</sup>Institut Jean Le Rond d'Alembert, Sorbonne Universités, UPMC Univ Paris 06, CNRS UMR 7190Paris, France

<sup>3</sup>Laboratoire d'Ethologie Expérimentale et Comparée E.A. 4443 (LEEC), Université Paris 13, Sorbonne Paris CitéVilletaneuse, France

Bottlenose dolphins are highly social cetaceans with an extensive sound production including clicks, burst-pulsed sounds, and whistles. Some whistles, known as signature whistles, are individually specific. These acoustic signatures are commonly described as being emitted in contexts of stress during forced isolation and as group cohesion calls. Interactions between humans and captive dolphins is largely based on positive reinforcement conditioning within several training/feeding sessions per day. Vocal behavior of dolphins during these interactions might vary. To investigate this, we recorded 10 bottlenose dolphins of Parc Asterix dolphinarium (France) before, during and after 10 training sessions for a total duration of 7 hr and 32 min. We detected 3,272 whistles with 2,884 presenting a quality good enough to be categorized. We created a catalog of whistle types by visual categorization verified by five naive judges (Fleiss' Kappa Test). We then applied the SIGID method to identify the signatures whistles present in our recordings. We found 279 whistles belonging to one of the four identified signature whistle types. The remaining 2,605 were classified as non-signature whistles. The non-signature whistles emission rate was higher during and after the training sessions than before. Emission rate of three signature whistles types significantly increased afterwards as compared to before the training sessions. We suggest that dolphins use their signature whistles when they return to their intraspecific social interactions succeeding scheduled and human-organized training sessions. More observations are needed to make conclusions about the function of signature whistles in relation to training sessions. *Zoo Biol.* XX: XX–XX, 2016. © 2016 Wiley Periodicals, Inc.

**Keywords:** signature whistle; whistle; communication; dolphinarium

## INTRODUCTION

Bottlenose dolphins (*Tursiops truncatus*) are highly social cetaceans that live in a fission–fusion society where individuals associate in small groups that can vary in composition according to age, sex, reproductive status, and activity [Connor et al., 2000; Mann et al., 2000; Gibson and Mann, 2008; Tsai and Mann, 2013]. In this extremely mobile species, group members can be separated by hundreds of meters within a habitat with limited visibility [Connor et al., 1998]. Interactions based on the use of acoustic signals seem to be the most effective communication strategy under these conditions [Janik, 1999a,b].

Consequently, bottlenose dolphins display an extensive sound production including clicks or pulsed

sounds [Au, 1993; Au and Fay, 2012], burst-pulsed sounds [López and Shirai, 2009], and whistles or tonal sounds (reviewed in Janik, 2009). The term “whistle” is used to refer to a unit of one continuous contour (loop), two or more

\*Correspondence to: Juliana Lopez Marulanda, Institute of Neurosciences Paris Saclay, University Paris Sud, CNRS UMR 9197, Orsay 91405, France. E-mail: juliana.lopez-marulanda@u-psud.fr

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repeated contours (multiloops) that can be connected or separated by a period of silence lasting between 0.03 and 0.25 sec in duration (disconnected multi-loop whistle) [Esch et al., 2009a]. The term “whistle type” describes all whistles showing specific frequency modulations as determined by visual categorization [Kriesell et al., 2014].

Some individually specific whistles are called “signature whistles” [Caldwell and Caldwell, 1965]. Signature whistles may be composed of a single or multiple loops [Caldwell et al., 1990]. The number of loops produced in a signature whistle varies according to the behavioral context and it increases with age [Caldwell et al., 1990]. It can also depend of whether it is produced by its owner or copied by another individual [King et al., 2013]. Signature whistles have been detected in dolphins as young as 1 or 2 years old [Fripp et al., 2005; Sayigh et al., 1990] and their frequency modulation pattern remains stable during the entire life of the individuals [Sayigh et al., 1990]. However, males’ signature whistles can vary throughout life as a consequence of changing social relationships [Watwood et al., 2004]. Young males may use signature whistles similar to their mother while young females are more likely to choose different frequency modulation patterns [Sayigh et al., 1990, 1995]. Signature whistles are emitted in context of forced isolation [Caldwell and Caldwell, 1965; Sayigh et al., 1990, 1995; Janik et al., 1994; Watwood et al., 2005] and as a contact or cohesion call between mothers and calves [Smolker et al., 1993] and between members of the same group [Janik and Slater, 1998]. During social interactions, signature whistles are more frequently emitted than during other behavioral contexts such as feeding or travelling [Cook et al., 2004]. These signals can also be copied [Janik, 2000; Tyack, 1986] by other individuals of the group, possibly to label a particular individual [Janik, 2000]. It has been suggested that signature whistle mimicry might be affiliative [King et al., 2014]. Finally, an increase of the signature whistle emission rate has been reported during capture-release procedures with free-ranging bottlenose dolphins, suggesting that signature whistle emission rate could be considered as a potential indicator of stress in dolphins [Esch et al., 2009b].

The management of dolphins in captivity is largely based on positive reinforcement training [Brando, 2010; Laule, 2003], and often several training/feeding sessions are held per day during which caregivers promote desired behaviors to facilitate husbandry and medical care and build a bond with the animals [Brando, 2010]. In the daily life of captive dolphins, training/feeding sessions could represent remarkable events that involve the development of cognitive skills and the modulation of the animals’ behaviors. In the case of Parc Asterix delphinarium, the dolphins are separated into sub-groups during each training session and each sub-group performs different exercises. Under these conditions, it is possible that the dolphins’ vocal repertoire and behavior may vary. For example, it has been reported that the number of whistle emissions in captive bottlenose dolphins increases

during interactions with people [Akiyama and Ohta, 2007]. Another study on a captive group of false killer whales (*Pseudorca crassidens*) reported that the highest vocalization rate was registered when animals were fed [Platto et al., 2015]. However, according to our knowledge, it remains unknown how the scheduled training/feeding sessions in bottlenose dolphins under human care modulate the emission rate of different whistles types (e.g., signature whistles).

This study aims to describe the possible effects that training/feeding sessions, have on the emission rate of non-signature and signature whistles, in a group of captive bottlenose dolphins.

## METHODS

### Study Subjects

The study was conducted in November 2014 and May 2015 at the Parc Asterix dolphinarium (Plailly, France). At the time of the study, the dolphinarium was closed to the public. The complex was first inhabited in November by nine Atlantic bottlenose dolphins (*T. truncatus*), four females aged 41, 34, 20, and 15 and years, and five males aged 32, 5, 4, 4, and 3 years. In January 2015, two males (4 and 5 years old) were transferred to another facility and one adult male (31 years old) arrived. Thus, the recordings in May were conducted on a group of eight individuals. All dolphins are subject to the same management schedule based on positive reinforcement training methods. Every day dolphins take part in at least five training sessions approximately at the same time during which their trainers feed them after they perform several exercises aimed to facilitate the husbandry and medical care procedures and to prepare for presentations to the public. Each dolphin knows around 100 behaviors to perform upon trainers’ command plus the new behaviors they are learning. Their sequence, their frequency and their duration change every day in every session. It could be underwater/aerial behaviors and solitary/group behaviors. Before and after the training sessions the trainers mainly stayed in the office and food preparation area and remained not visible but audible by the dolphins. At the beginning of each training session the trainers went out of the food preparation area at the same time carrying fish buckets and place themselves at the edge of the pool. During training sessions, the trainers divide the animals into sub-groups of the same two or three individuals. Each sub-group stays with one trainer and performs different exercises during the session which lasts around 15 min. This separation is never forced and it is achieved because animals are reinforced positively when they stay together in their assigned group. The trainers start and end their working day by feeding the dolphins ad-libitum without asking them to perform any kind of exercises.

Overall, this facility consists of one outdoor and two indoor pools not acoustically isolated. The outdoor pool has a volume of 3,246 m<sup>3</sup> and a depth that varies from 2.5 m at the

shallowest point to 4.5 m at its deepest. The indoor part of the complex, divided into two sections, has a total volume of 550 m<sup>3</sup> and a depth of 2.5 m. The dolphins have free access between the pools at all times.

### Whistle Recordings

Whistles were recorded approximately 15 min before, during and 15 min after ten training sessions that took place on 6 days: five recording sessions were conducted over 4 days in November 2014 and five more over 2 days in May 2015. The recordings were carried out using a CRT hydrophone C54XRS (frequency response: 0.016–44 kHz  $\pm$  3 dB) plugged in to a TASCAM HDP2 recorder at the acquisition rate of 96 kHz and samples were coded on 24 bits. In order to prevent the dolphins touching and grabbing the hydrophone, it was placed in a flexible floating tube inside an 18.9 L polycarbonate bottle with multiple perforations. The apparatus was fixed to a wooden stick at a distance of 50 cm from the edge of the pool and 50 cm deep near the small beach area (Fig. 1).

### Visual Categorization Process

To create a whistle catalogue, spectrograms (FFT size: 1024, overlap 50%, Hanning window) of the recorded whistles were analyzed using Audacity 2.06 software (GNU General Public License, The Audacity Team, Pittsburg, PA). Graphs with standardized *x*- and *y*-axes (1 sec long, with a frequency range of 0 Hz to 48 kHz) of the frequency modulation of each whistle were used to prevent distortion of whistles caused by axes differing in length as this would have influenced the visual categorization process.

Whistles with a negative signal-to-noise ratio or overlapping with other whistles were registered but not included in the categorization. Once each whistle spectrogram was registered, a visual categorization of whistle types was carried out. We applied the SIGID method [Janik et al., 2013] to identify signature whistles within our catalog of whistle types based on two criteria: firstly, signature whistles were whistle types repeated at least four times in a recording session, and secondly, at least on one occasion the whistles were produced in a sequence in which 75% or more repetitions occur within 1–10 sec of one other. The whistle types that were not cataloged as signature whistle types using this method were cataloged as non-signature whistle types.

To verify the reliability of our classification method, five experts, all affiliated to the acoustic communication team of NeuroPSI laboratory (Orsay, France) and working on bioacoustics in classification of birds or cetacean sounds, performed two visual classification tasks using the identified signature whistles of our dataset [see Kriesell et al., 2014]. For each signature whistle type, six whistle repetitions were randomly selected: 1 to act as a template and 5 to be classified by the experts. Each signature whistle repetition was surrounded by the signature whistle templates and was presented to each expert on a Microsoft Power Point slide. In the first task, the experts were asked to compare each whistle repetition with each template and to rate the similarity in a scale from 1 (very different) to 5 (very similar). The second task was to assign to each whistle repetition the most similar template category. The ratings were compared between experts using Fleiss' Kappa statistic [Siegel and Castellan, 1988] to determine inter-observer agreement in whistle classification and consistency in categorization (with and

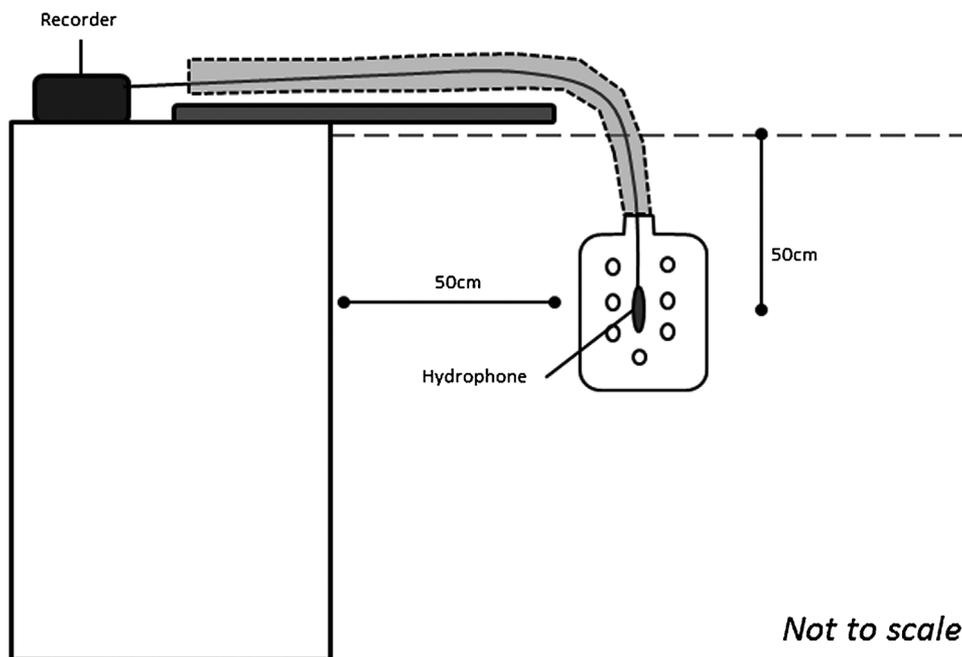


Fig. 1. Position of the recording set-up in the pool. Not to scale.

without authors' classifications). When experts are in complete agreement Fleiss' Kappa statistics ( $k$ ) is equal to 1 [Landis and Koch, 1977]. If agreement between experts is the same as expected by chance, then  $k$  is equal to 0.

### Whistle Emission Analysis

Statistical tests were conducted using R statistical software version 3.02 [R Core Team, 2013]. Mean values of whistles emission rate and signature whistle emission rate per minute were calculated for the recordings before, during and after each training session. The Friedman Rank Test was used to compare the non-signature whistle emission rate and the signature whistle emission rate before, during and after each training session. Post hoc tests were performed to examine the variation in the tested variables.

## RESULTS

A total of 7 hr 32 min (Table 1) were recorded among the ten training sessions (154 min before, 147 min during training sessions and 152 min after) in which 3,272 whistles were identified: 309 (9.44%) were classified as having too low signal-to-noise ratio whistles to be considered in this study and 79 (2.41%) were classified as overlapping whistles, the remaining 2,884 (88.14%) were classified in signature or non-signature whistle types. Most of the identified whistles were recorded during the first five recording sessions with nine individuals ( $n = 1,946$ ; before training: 288, during training: 743, and after training: 915) while less of half of whistles was recorded during the last five recording sessions with eight individuals ( $n = 938$ ; before training: 192; during training: 329, and after training: 417).

According to SIGID method, 279 (9.67%) signature whistles were identified belonging to four different signature whistles types (Fig. 2). The remaining 2,605 (90.32%) were classified as non-signature whistle types. The four signature whistles were present in the first five recording

sessions in November with nine individuals and in the last five recording sessions in May with eight individuals. We detected the occurrence of 210 signature whistles during the first recording sessions and the occurrence of 69 signature whistles during the last recording sessions.

The two visual classification tasks tested reliability of identifying whistle types. The first task showed a low inter-observer agreement (Fleiss' kappa statistic without author as judge:  $k = 0.388$ ,  $n$  judges = 5,  $z = 18.7$ ,  $P = 0.00001$ ; with author as judge:  $k = 0.408$ ,  $n$  judges = 6,  $z = 24.2$ ,  $P = 0.00001$ ). During the second task, the experts repeatedly chose the highest similarity rating for the first task as the most similar whistle to the template category. The inter-observer agreement was high in the second task (Fleiss' kappa statistic:  $k = 0.956$ ,  $z = 28.7$ ,  $P = 0.00001$ ). These results show that clearly defined whistle types exist in the repertoire of Parc Asterix bottlenose dolphins and support the authors' visual categorization of the dataset.

The overall whistle emission rate during our recordings was 7.48 whistles per minute. We calculated this rate (including signature and non-signature whistles) by averaging the ten sessions before, during and after the training sessions. The rate did not change significantly from  $4.72 \pm 3.32$  whistles per minute before the training sessions, to  $8.14 \pm 2.74$  whistles per minute during the training sessions and  $9.84 \pm 7.44$  whistles per minute after the training sessions (Friedman Rank Test:  $\chi^2 = 2.6$ ,  $df = 2$ ,  $P = 0.2725$ ) (Fig. 3).

When comparing non-signature and signature whistles separately, we found that dolphins emitted more non-signature whistles during and afterwards (respectively Wilcoxon signed Rank Test:  $V = 4$ ,  $P = 0.0137$  and  $V = 2$ ,  $P = 0.0058$  with Bonferroni-adjusted significance level of  $P < 0.0167$ ) than before the training sessions. No significant differences were found between the non-signature whistle emission rate during and after the training sessions (Wilcoxon signed Rank Test:  $V = 25$ ,  $P = 0.8457$  with Bonferroni-adjusted significance level of  $P < 0.0167$ ) (Fig. 4).

**TABLE 1. Time of recording of the 10 sessions: Before, during and after the training**

Session and social grouping	Duration (hh:mm:ss)			Total
	Before	During	After	
1st social grouping, session 1	00:02:09	00:24:21	00:14:32	00:41:02
2	00:04:17	00:20:42	00:15:59	00:40:58
3	00:06:49	00:17:50	00:14:26	00:39:05
4	00:16:23	00:13:18	00:14:29	00:44:10
5	00:15:00	00:11:08	00:16:33	00:42:41
Sub-total	00:44:38	01:27:19	01:15:59	03:27:56
2nd social grouping, session 1	00:30:07	00:13:29	00:15:00	00:58:36
2	00:35:39	00:15:33	00:15:08	01:06:20
3	00:14:58	00:11:18	00:15:00	00:41:16
4	00:12:38	00:11:30	00:15:00	00:39:08
5	00:16:01	00:08:13	00:15:00	00:39:14
Sub-total	01:49:23	01:00:03	01:15:08	04:04:34
Total	02:34:01	02:27:22	02:32:07	07:32:30

The first five recording sessions were carried out with the first social group (nine animals) and the last five recording sessions were carried out with a second social group (eight animals).

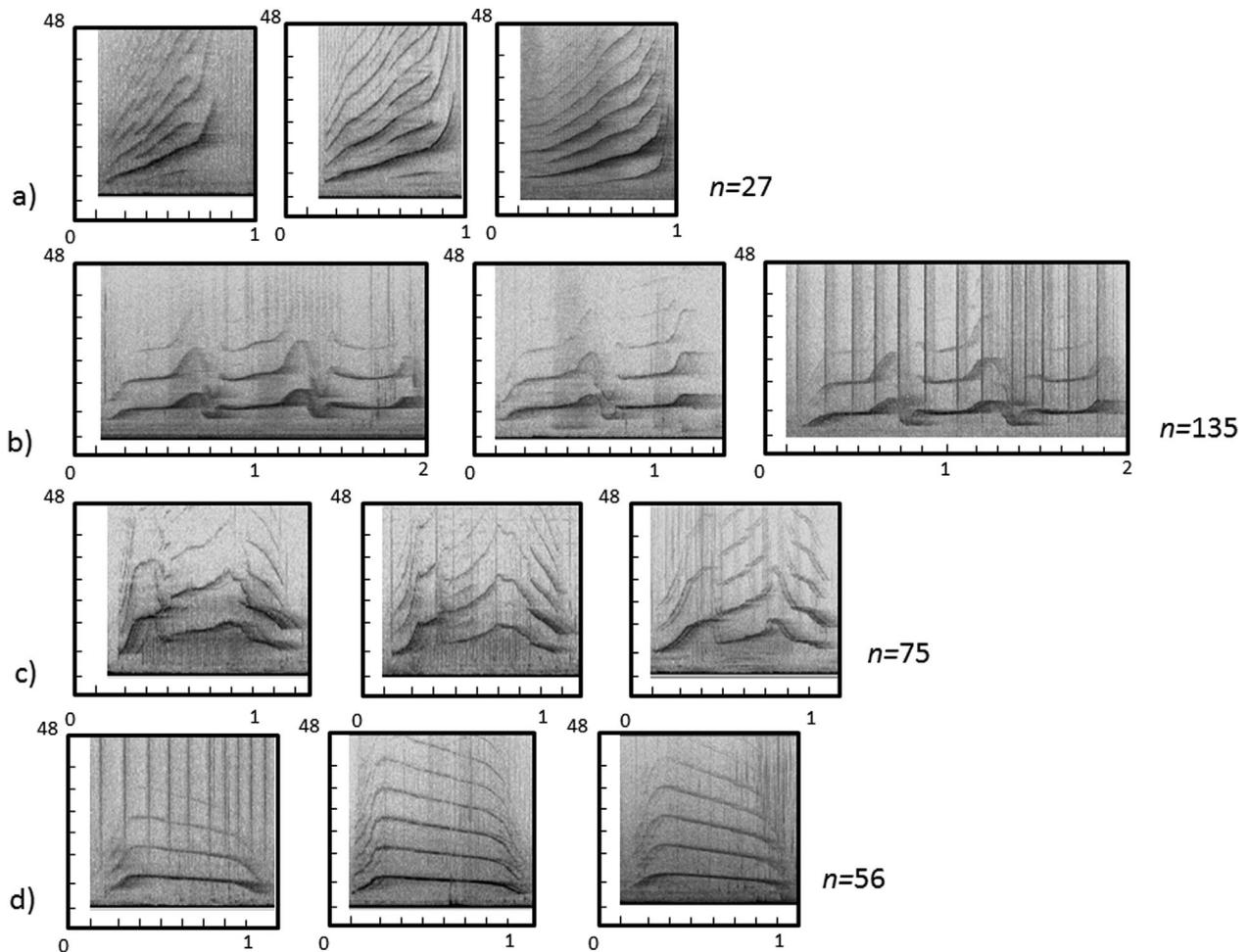


Fig. 2. Three randomly chosen spectrograms of each of the identified signature whistles emitted by Parc Astérix bottlenose dolphins (Plailly, France): (a) Signature whistle type 1 (SW1); (b) Signature whistle type 2 (SW2) which can be identified as variably loopy based on the final loop which is consistent from whistle to whistle; (c) Signature whistle type 3 (SW3); (d) Signature whistle type 4 (SW4). The numbers in the right are the total occurrences of the whistle type found in the acoustic recordings ( $n=293$  signature whistles). Spectrograms are all presented in the same scaling. Frequency (kHz) is on the y-axis and ranges from 0 to 48 kHz. Time (s) is on the x-axis. FFT 1,024, Hanning window, overlap 50%.

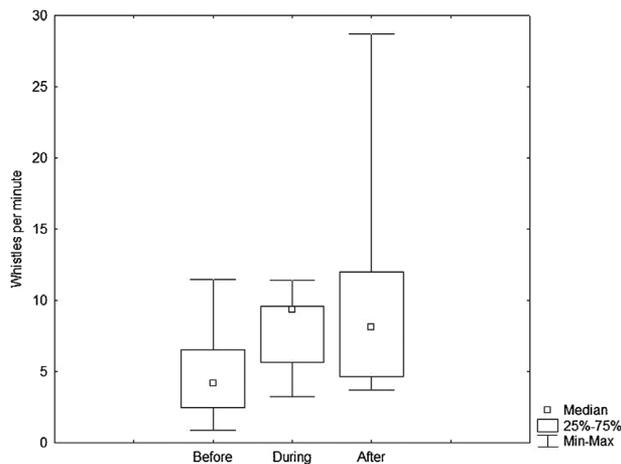


Fig. 3. Boxplot of bottlenose dolphins' whistle (all types) emission rate before, during and after training sessions ( $n=10$ ). Friedman Rank Test:  $\chi^2=2.6$ ,  $df=2$ ,  $P>0.05$ .

When we pooled the four types of signature whistles, we found that signature whistle emission rate varied significantly before, during and after training sessions (Friedman Rank Test:  $\chi^2=12.2$ ,  $df=2$ ,  $P=0.0022$ ): dolphins emitted significantly more signature whistles afterwards than before the training sessions (Wilcoxon signed Rank Test:  $V=0$ ,  $P=0.0019$  with Bonferroni-adjusted significance level of  $P<0.0167$ ), but the animals' signature whistle emission rate before and during the training sessions did not show any significant variation (Wilcoxon signed Rank Test:  $V=30$ ,  $P=0.8457$  with Bonferroni-adjusted significance level of  $P<0.0167$ ) nor between periods during and after the training sessions (Wilcoxon signed Rank Test:  $V=0$ ,  $P=0.0195$  with Bonferroni-adjusted significance level of  $P<0.0167$ ) (Fig. 5).

The four different signature whistle types were not present in all the recording sessions making it impossible to statistically compare the whistle emission rate of each kind of

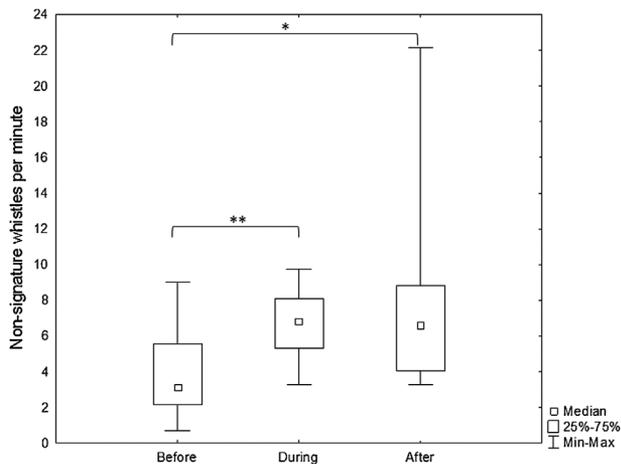


Fig. 4. Boxplot of bottlenose dolphins' non-signature whistle emission rate before, during and after training sessions ( $n = 10$ ). \*Wilcoxon signed Rank Test:  $V = 2$ ,  $P < 0.0167$  (with Bonferroni correction). \*\*Wilcoxon signed Rank Test:  $V = 4$ ,  $P < 0.0167$  (with Bonferroni correction).

signature whistle between the sessions. However, we calculated the emission rate of each signature whistle type for the 10 sessions before, during and after the training. Whistle rate increased after the training sessions for signatures whistles type 1 (SW1), type 2 (SW2), and type 3 (SW3). The whistle emission rate of the signature whistle type 4 (SW4) was higher before than after the training sessions (Fig. 6).

To summarize, the dolphins' overall whistle emission rate did not significantly change before, during and after the training sessions. However, the non-signature emission rate was higher during and afterwards than before the training sessions and the signature whistle emission rate was significantly higher after than before the training sessions. The emission rate varied between the different

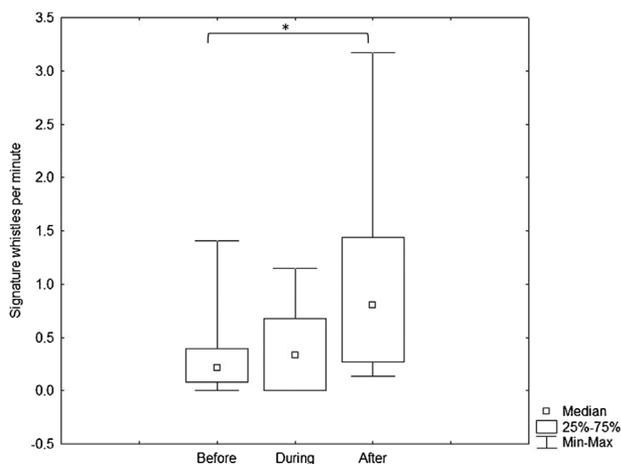


Fig. 5. Boxplot of bottlenose dolphins' signature whistle (all types) emission rate before, during and after training sessions ( $n = 10$ ). \*Wilcoxon signed Rank Test:  $V = 0$ ,  $P < 0.0167$  (with Bonferroni correction).

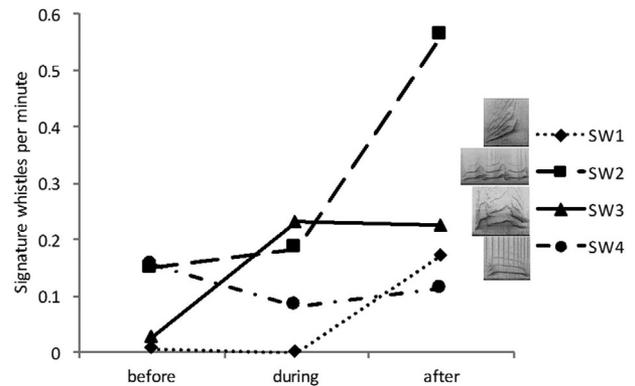


Fig. 6. Signature whistle emission rate for each type of signature whistle (SW) before, during and after the training sessions.

signatures whistles types, increasing for types 1, 2, and 3 and decreasing for type 4.

## DISCUSSION

Dolphin whistle emission rate is highly variable and depends on several parameters: groups size [Jones and Sayigh, 2002; Cook et al., 2004; Quick and Janik, 2008], group composition [Hawkins and Gartside, 2010] and behavioral context [Dos Santos et al., 1990; Jacobs et al., 1993; Acevedo-Gutiérrez and Stienessen, 2004; Cook et al., 2004]. Most of the whistles detected occurred during the first five recording sessions: in November the nine dolphins whistled and produced signature whistles two times more frequently than the eight individuals in May. It is comprehensible to have more whistles and signature whistles produced when the group size increases [Van Parijs et al., 2002], but here, the difference in occurrence of whistles was not proportional to the number of individuals. Instead, it is possible that the group composition impacted the dolphins' vocal productions, and in particular the age of the individuals might also have been an important variable. The first recording sessions in November were carried out in a group with four young dolphins out of nine individuals while the second set of recordings in May occurred in a group of two young dolphins and six adults. Mother-offspring interactions include various behaviors (i.e., teaching behaviors) [Bender et al., 2009] and involve vocalizations (i.e., during periods of separation) [Smolker et al., 1993]. The nature of the intraspecific social interactions conducted within the groups might have influenced the number of whistles and signature whistles recorded. We suggest that the presence of young dolphins might have increased the number of affiliative, play and discipline behaviors within the group and these behaviors could be correlated to a high production of whistles.

The SIGID method [Janik et al., 2013] allowed us to identify four signature whistles within the bottlenose dolphins at Parc Asterix dolphinarium. If signature whistles are individually specific [Caldwell et al., 1990] we could

expect to find nine signature whistles in the first half of our recording sessions and eight in the second half. However, the SIGID method was conceived to be very conservative so that false positives were eliminated. This precaution means the SIGID method did not consider about half of the signature whistles present in the sample [Janik et al., 2013]. We recorded a total of 7 hr and 32 min. It is probable that signature whistles of all the individuals were present in our samples but we only identified less than 50% of them using the SIGID method. In this case, some of the non-signature whistles that were used in our analyses are signature whistles that were not detected by the method and in this terms the results we obtained on the non-signature whistle emission rate are influenced by the signature whistle emission rate. However, the emission of signature whistles in captivity is very scarce and for some individuals can be less than 1% of whistle emission rate [Janik and Slater, 1998]. Thus, it is highly probable that signature whistles of all the individuals were not present in our acoustic recordings. It would be necessary to record the animals during forced [Esch et al., 2009a] or voluntary isolation [Janik and Slater, 1998] or using a hydrophone array [López-Rivas and Bazúa-Durán, 2010], to link the whistle emission to individual dolphins in order to find the signature whistle for each member of the group.

The first classification task allows our study to be comparable to previous studies that use visual categorization of bottlenose dolphins' whistles as Janik [2000] and Kriesell et al. [2014]. The low inter observer agreement obtained on the first classification task has also been reported by these authors and might be due to the fact that we asked judges to classify whistles on a scale of discrimination that is too fine and leads to subjectivity. In fact when one of the authors redid the first classification task several months later, the inter observer agreement with herself was low ( $K = 0.133$ ,  $z = 1.9$ ,  $P = 0.0581$ ). However, the second classification task that asked the judges to choose the most similar whistles showed a high inter observer agreement, which supports the author's visual categorization of the data set.

When we compared signature and non-signature whistles, the total emission rate did not significantly change before, during and after the training sessions. Our results differ from previous findings on other groups of cetaceans under human care: for instance, bottlenose dolphins increased whistle production during interactions with humans [Akiyama and Ohta, 2007; Therrien et al., 2012]. Akiyama and Ohta [2007] measured the number of whistles emitted by three captive bottlenose dolphins (one male and two females, all less than 8 years old) during several situations in a facility in Muroto (Japan): immediately before feeding, during feeding, during the animals' free-time without the presence of people, and during interactions with people on a float and in the water. They found that most of the whistles were emitted during the period preceding feeding (which is analog to the period before trainings in our study), and whistle emission was higher during various interactions with humans (including feeding) than during

their free-time in absence of people (which is analog to the period after training session in our study). Therrien et al. [2012] measured the whistle production of a group of eight bottlenose dolphins (four adult females, two adult males, and two young males) and found increased whistle production to coincide with increased interactions with humans during feeding/training sessions. Recently, a study carried out on five captive false killer whales (*P. crassidens*) (three adult females, one adult male, and one male calf) also found an increase in their acoustic emissions (including whistles) upon trainers' arrival [Platto et al., 2015]. The high rate was maintained during feeding sessions and reduced immediately after the animals were fed. In contrast, we found that non-signature whistles increased during the training sessions but their rate was higher afterwards, and signature whistle rate was higher after the training sessions compared to before.

Dolphins' behaviors and vocalizations can be modulated by trainings [Kuczaj and Xitco, 2002]. Since no information could be found about the influence of the nature and content of trainings in the related papers, we cannot comment on the impact they have on whistle emission rate. Moreover, in Akiyama and Ohta's [2007] study, dolphins spent less than 2 years under human care; this is in contrast to Parc Astérix dolphins, where six out of nine dolphins are born in the dolphinarium and the other three have been in captivity for over 2 decades. It has been shown that free-ranging dolphins increase their whistle emission rate during feedings probably to recruit more members to the group [Acevedo-Gutiérrez and Stienessen, 2004], and this behavior is likely not necessary, or less present, in captivity where feeding is less cooperative than in the wild. In Akiyama and Ohta's [2007] study, the dolphins might interact (e.g., to cooperate) while feeding. Unfortunately, Therrien et al. [2012] and Platto et al. [2015] do not specify for how long their studied animals have been in captivity.

Our study shows that overall, signature whistle emission significantly increased after the training sessions. However this was not the case for all the signature whistles types we detected, suggesting that depending upon the situation dolphins' signature whistles production varies, and consequently they might be used for various functions. Context of emissions of signature whistles varies from stress calls during forced isolation [Esch et al., 2009a] to cohesion calls [Smolker et al., 1993; Janik and Slater, 1998; Quick and Janik, 2012]. In Parc Asterix, during training sessions the trainers divide the animals into groups of the same two or three individuals. Each sub-group remains with one trainer and performs different exercises during the session. This division is never forced and it is achieved by using positive reinforcement. The training session by itself can be considered as rewarding for the animals [Laule and Desmond, 1998], since they are positively reinforced when they perform exercises. A previous study conducted in this facility measured the breathing rate of animals before and after the training sessions [Jensen et al., 2013] as a possible indicator of stress [Broom and Johnson, 1993; Dierauf,

2001]. The results showed that the animals maintained the same breathing rate before and after the sessions [Jensen et al., 2013], indicating that the exercises they were asked to perform did not affect their level of stress. The increase in signature and non-signature whistle emission rates therefore is not likely to be explained by the animals being stressed during the training sessions. We suggest that the increase in non-signature and some signature whistle emission after training sessions is due to an augmentation of social behaviors. Before training sessions, dolphins can freely interact displaying affiliative, agonistic, and sexual behaviors [Herzing, 1996; Samuels and Gifford, 1997]. Since training sessions occur consistently approximately at the same hour, dolphins can perform anticipatory behaviors [Jensen et al., 2013] which could have an influence in their vocal production as has been found in captive false killer whales (*P. crassidens*) [Platto et al., 2015] and bottlenose dolphins in other facilities [Akiyama and Ohta, 2007]. Training sessions occur consistently approximately at the same hour and before these dolphins can perform anticipatory behaviors [Jensen et al., 2013] which could have an influence in their vocal production as has been found in captive false killer whales (*P. crassidens*) [Platto et al., 2015] and bottlenose dolphins in other facilities [Akiyama and Ohta, 2007]. During training sessions, the groups are subdivided and dolphins are asked to perform several exercises, where these activities modulate social interactions between animals. Finally, after the training sessions individuals are free to regroup as they want and the signature whistles might then be used as cohesion calls and copied as affiliative signals [King et al., 2014].

When comparing the emission rate of signature whistles before and after the training sessions we found that SW1, SW2, and SW3 emission rates increased after the training session and SW4 emission rate decreased after the training session. Signature whistles are individually specific [Caldwell et al., 1990], so it is highly probable that the four signature whistles identified were mostly emitted by four particular individuals with the exception of the cases where the signature whistles are copied [Janik, 2000; Tyack, 1986]. If this is the case, the signature whistles detected are not from the three males that were transferred between facilities because they are present before and after the transfer. One of the signature whistles (SW2) consists of several connected loops. Since the number of loops increases with the age of the individual [Caldwell et al., 1990], we suggest that SW2 probably belongs to one of the oldest animals in the group.

The differences found between the emission rates of each signature whistle type might be due to individual differences, meaning that the three individuals that emitted more signature whistles after the training sessions were probably seeking group cohesion or at least looking for social interactions. In contrast, one individual emitted more signature whistles before the training sessions probably looking for social interactions in a different moment.

These individual differences could be explained by the presence of different personalities in dolphins [Birgersson et al., 2014; Highfill and Kuczaj, 2007] that leads to individual variation in vocal activity. Since group composition and behavioral contexts influence dolphins' vocalization rate [Dos Santos et al., 1990; Jacobs et al., 1993; Cook et al., 2004; Hawkins and Gartside 2010], it would be necessary to identify the vocalizing dolphins and to observe the animals' behaviors during signature whistles emissions to explain the particular behavioral context that caused these individual differences. As a hypothesis, we suggest that non-signature whistles are intended to give information to listener dolphins, while signature whistles are used to give information about the emitter. The copy of signature whistles might play a role in spreading the information and letting the emitter know that the information has correctly been received. Vocal mimicry is an important part of communication in all species of mammals, but this is higher for cetacean species, in particular for toothed whales. These prolific vocal exchanges might probably be due to the development of their personalities, the features of their social structure and also the large diversity of their sound emissions.

In conclusion, our study shows that non-signature and particular signature whistle emission rate increases after scheduled training sessions in Parc Asterix dolphinarium. We suggest that animals might have been seeking social interactions after the sessions. We suppose that before the sessions, animals are free to interact, or not interact, with the partner(s) they choose, during the training sessions the group structure changes due to human intervention (trainers regroup particular dolphins into groups of 2–3 individuals), and after the training sessions dolphins freely regroup using signature whistles as cohesion calls. However, in order to validate this hypothesis, it is necessary to directly observe the animals' behaviors and to link the patterns of group association with whistle emissions. Moreover, during training sessions the trainers ask the dolphins to perform solitary and coordinated exercises, and their vocalization rate might also depend on the task the trainers ask them to perform. We can expect higher sound production rates during coordinated exercises and cooperative tasks [Eskelinen et al., 2016]. Linking whistle emissions to particular behaviors will be the next step to better understand how dolphins under human care communicate.

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