

Acoustic behaviour of bottlenose dolphins under human care while performing synchronous aerial jumps

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ABSTRACT

Synchronous behaviours occur when two or more animals display the same behaviour at the same time. However, the mechanisms underlying this synchrony are not well understood. In this study, we carried out an experiment to determine whether or not Bottlenose dolphins use acoustic cues when performing a known synchronised exercise. For this, we recorded three dolphins while they performed requested aerial jumps both individually or synchronously in pairs, with a hydrophone array and a 360° underwater video camera allowing the identification of the subject emitting vocalisations. Results indicated that in pairs, dolphins synchronised their jumps 100% of the time. Whether they jumped alone or in pairs, they produced click trains before and after 92% of jumps. No whistles or burst-pulsed sounds were emitted by the animals during the exercise. The acoustic localisation process allowed the successful identification of the vocalising subject in 19.8% of all cases ($N = 141$). Our study showed that in all ($n = 28$) but one successful localisations, the click trains were produced by the same individual. It is worth noting that this individual was the oldest female of the group. This paper provides evidence suggesting that during synchronous behaviours, dolphins use acoustic cues, and more particularly click trains, to coordinate their movements; possibly by eavesdropping on the clicks or echoes produced by one individual leading the navigation.

1. Introduction

Synchrony is defined as the precise coincidence of events in time (Ravignani, 2017). Thus, synchronous behaviours occur when two or more animals perform the same behaviour at the same time (Connor et al., 2006), and have been described for several animal species in different sensory modalities (e.g., visual, acoustic) (reviewed in Herzog, 2015). The degree of synchronisation varies from time intervals of less than one second, to several minutes (Sakai et al., 2010). For example, visual synchrony occurs between fireflies (*Pteroptyx* spp.) that synchronise their bioluminescent flashing at night (Buck, 1988), and between male fiddler crabs (*Uca annulipes*) that wave their major claws in synchrony in order to attract females (Backwell et al., 1999). Ex-

amples of acoustic synchrony have been described in the courtship vocalisations of male long-tailed manakins (*Chiroxiphia linearis*) (Trainer and McDonald, 1993) and male frogs (*Kassina kuvangensis*) (Grafe, 2003). Many synchronous animal displays, such as those mentioned above, are driven by competition (Ravignani et al., 2014). Some species, however, perform synchronous behaviours linked to cooperation. This is the case for humans during sports and musical activities (Launay et al., 2016), as it is for dolphins (*Tursiops truncatus*) when allied males synchronise their vocal behaviour to coerce females (Moore et al., 2020).

In dolphins, the term “synchrony” has been used in two different ways. First, to describe group members that perform non-random grouping behaviours, such as swimming and breathing in synchrony

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(Hastie et al., 2003; Fellner et al., 2013); and second, to describe behaviours that are performed ‘simultaneously’ or ‘in unison’ (Mann and Smuts, 1999; Connor et al., 2006). Simultaneous behaviour has been described in several dolphin species. Pantropical spotted dolphins (*Stenella attenuata*) synchronise their movements as a defensive response while being herded in tuna nets (Pryor and Kang-Shallenberger, 1991). Synchronous behaviour has been reported in Atlantic spotted dolphins (*Stenella frontalis*) as a means of dominating larger sized opponents (i.e., Bottlenose dolphins (*Tursiops truncatus*)) during aggressive interspecific interactions (Cusick and Herzing, 2014). Male Indo-Pacific Bottlenose dolphins (*Tursiops aduncus*) have been observed to synchronise their surfacing behaviour during social interactions with female consorts (Connor et al., 2006; Sakai et al., 2010) and whilst herding females (Connor et al., 1992; Connor and Smolker, 1996), but also as a signal of alliance unity and a means to maintain and strengthen social bonds (McCue et al., 2020).

Vocal synchrony has also been described in a number of species: Spinner dolphins (*Stenella longirostris*) synchronise their vocalisations when dispersing from bays (Brownlee and Norris, 1994) and during cooperative prey herding (Benoit-Bird and Au, 2009). Offshore populations of Bottlenose dolphins (*Tursiops truncatus*) have shown evidence of vocal synchrony in order to maintain contact in a large home range (Janik et al., 2011). Finally, simultaneous vocal and visual signals have been reported for this same species during intraspecific aggressions (Herzing, 2015).

Sounds emitted by dolphins are classified into three structural categories and two functional classes. Structurally, sound production is thus categorised into whistles or tonal sounds (reviewed in Janik, 2009), clicks or pulsed sounds (Au et al., 1974), and burst-pulsed sounds (Diaz-Lopez and Bernal-Shirai, 2009). Functionally, whistles and burst-pulsed sounds play a role in communication and social interactions (reviewed in Herzing, 2000). Clicks, however, are used for echolocation, which can be defined as the acoustic representation of one’s surroundings, obtained by the production and emission of clicks and the subsequent nervous integration of the perceived echoes (Au, 1993).

Vocalisations associated with cooperative behaviours have been described in Bottlenose dolphins (Eskelinen et al., 2016) and killer whales (van Opzeeland et al., 2005). Such cooperative behaviours do not necessarily involve the expression of the same movement or behaviour in a fully synchronised manner. However, the fact that there is a communicative process during cooperation in these experiments, leads us to believe that when two or more dolphins engage in a synchronous behaviour, information may be flowing between them. This flow of information can involve a communication process (Johnson, 2015) and may occur by use of one of several sensory channels. Underwater, visibility can be limited (i.e., turbidity, depth, light), in contrast, sound travels well (Tyack and Clark, 2000). Therefore, the expression of acoustic cues to synchronise behaviours is a plausible assumption.

The use of acoustic cues to perform simultaneous movements is difficult to investigate in free-ranging dolphins for two main reasons: First, low visibility underwater in most of their habitats (Würsig and Pearson, 2015) (with the exception of a few locations such as the Bahamas (Herzing, 1996) or Fernando de Noronha in Brazil (Silva Jr. et al., 2005)) allow neither clear determination of the degree of synchronicity, nor the localisation of the individual emitting the sound. Second, even with good visibility, the occurrence of synchronous behaviours, the identification of the individuals performing them and the replication of tests cannot be controlled by the experimenter.

Management of dolphins under professional care provides a favourable opportunity to study the mechanisms underlying synchronisation due to the fact that a synchronous behaviour can be requested from the target animals and be replicated several times. The clarity of the water and the proximity for observations allows for direct recording

of behavioural sequences as well as the identification of the individual emitting a vocalisation by use of a hydrophone array.

Dolphins in human care facilities regularly engage in behaviours simultaneously (e.g., jumps) and, through positive reinforcement, can be trained to display these synchronous behaviours upon request (Brando, 2010). However, it is unknown how dolphins manage to synchronise their actions and whether or not they use acoustic cues to coordinate their simultaneous behaviours. The first aim of this study was to explore the potential involvement of acoustic cues during a simultaneous exercise requested by a caregiver (or trainer). Thus, if synchronisation relies on the emission of acoustic signals, one might assume that acoustic signals will be emitted during the exercise and that acoustic cues will be different depending on whether the individuals perform the exercise alone or in synchronisation with another individual. The second aim of the study was to identify the category of sounds emitted during such an exercise, as well as the identity of the emitters.

2. Methods

2.1. Study subjects and facility

The synchronisation experiment was conducted in February and March of 2017, at the Boudewijn Seapark (Bruges, Belgium). Overall, this facility consists of five connected pools that are not acoustically isolated: a main presentation pool, two holding pens, a medical pool and a quarantine pool. The depth of the pools is 3 m in the shallowest areas and 5.6 m at the deepest point of the main show pool (Fig. 1). The training sessions with caregivers take place in all pools, but the experiment was carried out in the main pool.

Of the 8 Bottlenose dolphins (*Tursiops truncatus*) present on site, three were selected for the experiment: two adult females, Puck and Linda, aged 51 and 41 years respectively (F51 and F41), and one sub-adult male, Kite, aged 12 years (M12). They have been living together in the facility since May 14th, 2014. Puck has always been the dominant female of the group. According to the caregivers, she displays a low compatibility to work with Kite (M12) but a high compatibility to work with Linda (F41) (i.e., they can perform exercises together without any conflict arising). The two females originate from the wild, while the male was born in another facility. The choice of these dolphins was based on two criteria: Firstly, the three animals had undergone several years of training to perform the same exercise both individually and collectively. Secondly, their training for performing this exercise began at the same period, meaning that no individual was more experienced than the others.

During the experiment, the other group members were kept in the two holding pens, and a trainer was responsible for maintaining their heads above water to avoid the propagation of their potential acoustic emissions through the pools. This procedure prevented erroneous localisation of the emitting individual, as vocalisations originating from outside the experimental pool could be detected and localised during acoustic processing.

2.2. Recording device

Simultaneous audio and video recordings were collected using a 360° audio-video system, BaBeL (BioAcoustique, Bien-Être et Langage) (López Marulanda et al., 2017). Underwater video data was collected using a GIROPTIC 360° video camera with three lenses covering 120° each, allowing a 360° view of the main pool. Audio recordings were conducted with four synchronised hydrophones at a sampling frequency of 96 kHz and coded in 24 bits. Details regarding the functioning of this hydrophone array are described in Lopez-Marulanda et al. (2017). The distance between the hydrophones varied from 2.4 m to 3 m. This system has been tested in a pool with artificial sounds and presents an accuracy of $\pm 10^\circ$ in localising the direction of the sound’s

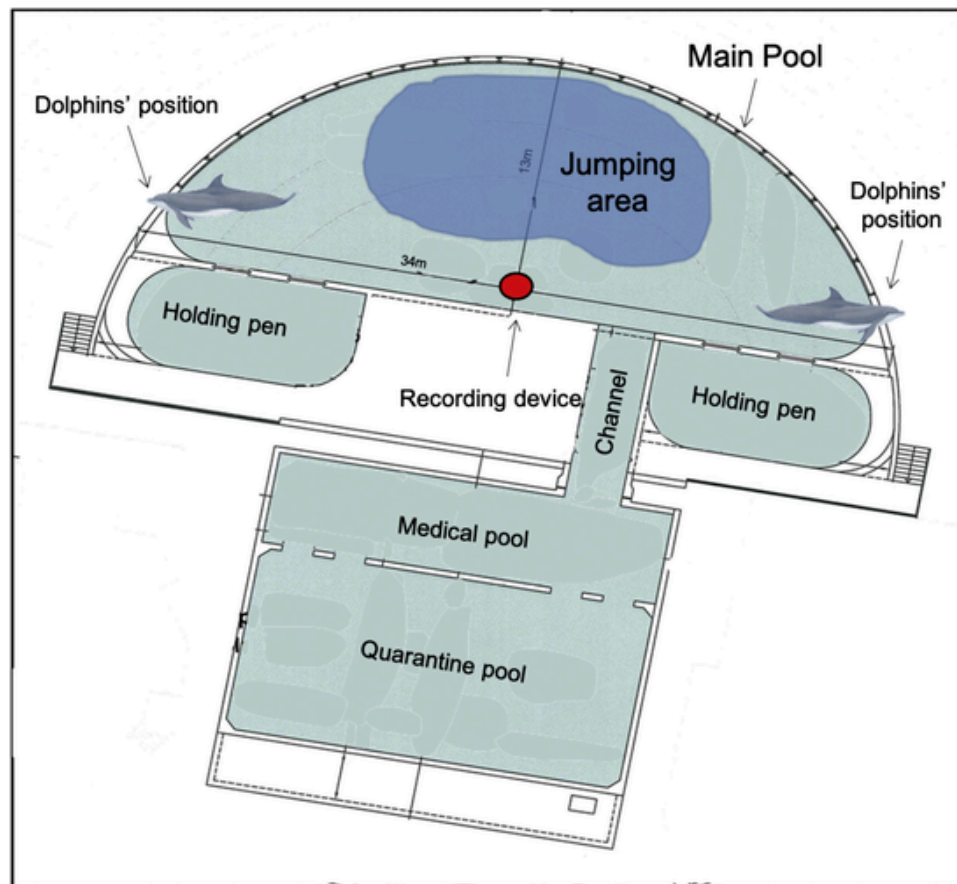


Fig. 1. Top view of the enclosure at the Boudewijn Seapark (Belgium). The location of the hydrophone array during the recordings is marked by a red dot. During the experiment, the tested animals were placed at opposite sides of the main pool. At each trial the dolphins moved to the centre of the main pool (jumping area) to perform the jumps.

source (Lopez-Marulanda et al., 2017). In addition, we used a GoPro hero 3+ to record a back-up video of the experiment as seen from the surface. Videos and audio recordings were synchronised. A single video file was created from the 360° video camera and was associated to the audio track obtained by BaBeL and its corresponding spectrogram (FFT size: 1024, overlap 50%, Hanning window) which was obtained using the software Audacity 2.0.6 (GNU General Public License).

Before the beginning of each experimental session, the BaBeL device was set up in the main pool, suspended from a buoy and held in place using two ropes fixed to the sides of the tank and a pole held by a motionless observer at the pool's edge (Fig. 1).

2.3. Habituation process

Before carrying out the experiment, the dolphins were gradually habituated to the presence of the BaBeL device in the water. The habituation process involved six one-week phases, which were gradually built-up over the period leading up to the recording sessions. The first phase consisted in positioning the device on the side of the main pool, out of the water, but within sight of the subjects. In the second phase, a caregiver held the device while standing on a raised, mobile, underwater platform located in the channel that connects the main pool to the quarantine pool. During this phase, the subjects could see the device in the water but their attention was controlled by other trainers (i.e., when necessary, they were distracted in order to avoid any contact with, and potential damage to the equipment). During the third phase, the subjects were allowed to swim freely for a limited time in presence of the device which was held by a trainer as described in phase 2. Exploration time was gradually prolonged, and subjects were rewarded

for ignoring the device. In the fourth phase, the device was suspended in the water while the subjects' attention was controlled by the trainers. In the fifth phase, the device was left alone in the pool while the subjects swam around freely. They were provided with enrichment items in order to distract them from the BaBeL equipment. In the final phase, the device was randomly placed in the water, with or without the presence of enrichment items.

2.4. Experiments

The "backflip" (i.e., jumping with the dorsal part of the dolphin facing the water's surface) was selected for use in the experiment, as this exercise, both individually and collectively, had been known to the study subjects for several years. In both cases, whether individually or collectively, the dolphins perform the backflip repetitively until the trainer blows a whistle to indicate that the task had been well performed and that they can be rewarded (fish). For the experimental sessions, and depending on the subjects' motivation, the trainers decided to let them jump between one and five times before blowing the whistle (i.e., to indicate the end of the requested exercise).

We carried out 30 experimental sessions (max. two per day) in which subjects were asked to perform the "backflip" exercise. During each experimental session, trainers asked subjects to perform the "backflip" exercise five non-consecutive times. Each "backflip" exercise requested by a gestural command was considered a trial. Each trial varied in duration, beginning when the trainer asked the subject to perform the "backflip" and ending when the trainer blew the whistle indicating that the behaviour could be stopped and that a reward was available. Between trials, other exercises were carried-out in order to

maintain the dolphins' motivation. The facility's schedule allowed us to carry out a total of 150 trials during the experiment. We aimed to get at least 30 repetitions of the exercise performed solo in order to carry out robust statistical analyses. Given that there were three subjects, we needed at least 90 trials in order to obtain these repetitions for each subject. We then decided to use the remaining 60 trials for two different pair combinations: 30 trials for Kite (M12) and Puck (F51) that had low compatibility for working together, and 30 trials for Linda (F41) and Puck (F51) that had high compatibility for working together. As a pair, Linda and Kite were not tested.

In order to facilitate the localisation process and to test the spontaneity of the synchronous behaviour for the trials performed collectively, the dolphins were positioned at opposite sides of the main pool (Fig. 1), each facing a trainer standing at the pool's edge. As such, each subject could see only the trainer's gestural commands directed at them and not those directed at the other subject. Once in position, the trainers produced the command to perform the backflip. These backflips were performed by the dolphins in the "jumping area", located in the centre of the main pool (Fig. 1).

2.5. Behavioural analysis

Underwater BaBeL videos and backup surface videos were analysed frame-by-frame in order to determine whether or not subjects jumped synchronously. A synchronous jump is achieved when the rostrums of both individuals break through the water's surface within 1/30 of a second of one another.

2.6. Localisation processing

Firstly, a visual inspection of the click trains allowed us to determine whether they were produced by the just one subject (i.e., a regular click train, with an increasing, decreasing or constant inter-click interval (ICI) or by more than one subject (i.e., irregular click train with no pattern of change in the ICI, a consequence of a presumable overlap of more than one click train). The localisation process was possible only when there was an absence of overlapping click trains.

Secondly, for the 60 trials carried out in pairs, localisation processing of the click trains was performed using a customised program created in MATLAB®, Version 2013a (Mathworks, Natick, MA, USA) (Blanchard, 2015) in order to identify which dolphin(s) emitted the vocalisations. This program uses a geometrical localisation method to estimate the positions of the acoustic sources. More specifically this method relies on the spatial distribution of the hydrophones and the measurement of the Time Delays Of Arrival (TDOA) of the acoustic wave from the sources, to the different hydrophones in order to calculate the positions of the sound source. The localisation was then displayed in the 360° video (see supplementary material) by a conversion position-pixel (Lopez-Marulanda et al., 2017).

2.7. Acoustic analysis

The acoustic analysis was based on click train production alone, as no whistles or burst-pulsed sounds were emitted by the subjects during the "backflip" exercise.

Click trains were defined as a series of four or more similar clicks with successively shorter ICIs (Roberts and Read, 2015). They were analysed using the pulse train analysis function of Avisoft-SASLab Pro version 5.2.07 (Raymond Specht, Berlin, Germany) in order to measure the click rate (number of individual clicks per second) for each trial. Click trains produced after the last jump of each trial (immediately after the trainer blew the whistle) were not taken into account for the pulse train analysis. This is due to the fact that click trains emitted after the trainer's whistle, for all subjects, had similar features to a "victory

squeal" or a "reward spectating buzz", a high-click-rate vocalisation that has been described previously by several authors (Ridgway et al., 2014; Dibble et al., 2016). If taken into account, this higher click rate could have been a source of bias for the statistical analyses.

2.8. Statistical analyses

Comparisons between the three individuals' click rates were performed using a Kruskal-Wallis test and post-hoc comparisons with Mann-Whitney tests. To assess whether the click rates differed between the exercises performed in solo or in pairs, we used a Wilcoxon signed rank test for each individual. All statistical tests were conducted using R statistical software version 3.02 (R Core Team, 2013).

3. Results

3.1. Synchronous behaviour

Video analyses showed that 100% of the "backflips" performed in pairs were synchronous. Inspection of the synchronised spectrogram indicated that for 92% of the jumps performed, dolphins produced a click train just before and after each backflip. In addition, the time elapsed between the signal given by the trainer and the backflip varied between 2.40 and 5.12 s (mean 3.8 s).

3.2. Localisation process

Visual inspection of audio recordings showed that 98% of the click trains emitted during collective jumps ($N = 141$) did not overlap. These vocalisations can therefore be considered to be produced by one individual only.

Localisation processing was carried out for the 141 click trains produced during collective exercises in order to assess the emitters' identity. In 103 cases (73.1%), the localisation was not achieved due to the reverberation of the sounds against the walls of the pool. In 10 cases (7.1%) the localisation was ambiguous because the two dolphins were placed one behind the other with respect to the camera. Finally, successful localisation was achieved for 28 (19.8%) click trains, 18 for the Linda/Puck (F41/F51) pair and 10 times for the Kite/Puck (M12/F51) pair. Puck (F51) was identified as the individual producing the clicks for all 18 trials (100% of the successfully localised trials) with Linda (F41) and for nine of the 10 trials (90%) with Kite (M12) (Fig. 2).

3.3. Comparison between click rates of localised click trains

As specified above, localisation processing allowed for the identification of Puck, almost exclusively, as the click train emitter. Comparisons between pair and solo conditions revealed that click rates produced by Puck were significantly higher when jumping with a partner (median: 20.77 clicks. sec⁻¹) than when jumping alone (median: 17.6 clicks. sec⁻¹) (Wilcoxon signed Rank Test: $W = 626$, $P = 0.043$) (Fig. 3).

To summarise, our results show that the dolphins always performed the exercise in synchrony, even if the gestural commands were given to each individual separately. We also demonstrate that subjects produced click trains when jumping both in solo and in pairs. Click trains produced when jumping in pairs were, for the large majority, produced by one individual only. Localisation processing was successful in 19.8% of all cases ($N = 141$). When successfully localised, results showed that, in 90% (Kite/Puck pair) and 100% (Linda/Puck pair) of cases, the individual producing the click trains was the older female, Puck (Fig. 2). Detailed analyses, based exclusively on Puck's click production, confirmed a significant increase of her click rate when performing the exercise in pairs.

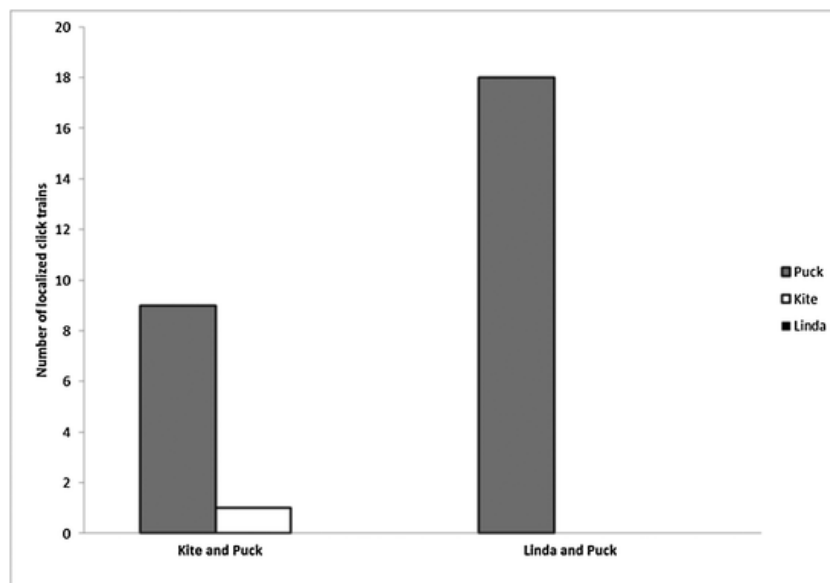


Fig. 2. Number of successfully localised click trains for each pair ($n = 28$): Puck (F51), Kite (M12) and Linda (F41).

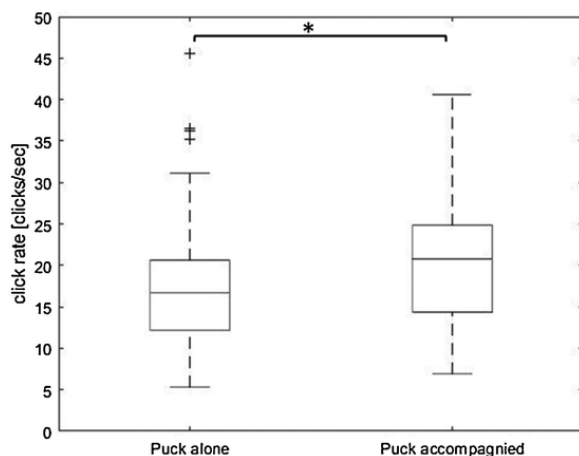


Fig. 3. Comparison between click rates of click trains produced by Puck (F51) when performing backflips alone and accompanied. Boxes represent 25th and 75th percentiles. Whiskers correspond to the 1st and 99th centiles. + represents the outliers. * indicates p values < 0.05 .

4. Discussion

In this experiment we studied the behaviour of three individuals, and two different pair combinations. Our results show that when dolphins are asked to perform synchronised jumps in pairs, only one of the two individuals involved emits vocalisations.

The low success rate for the localisation process can be explained by the fact that the dolphins carry out the exercise where they want in the pool. As a result, they are not necessarily placed in an optimal manner to allow for successful localisation. This limitation can be mitigated if we assume that every click train emitted in the pool had the same probability of being correctly localised. Indeed, localisation data collected during solo jumps (therefore, no ambiguity regarding the emitter) support this assumption, since the localisation was achieved for 20.1% of cases, a value close to the 19.8% achieved for the collective jumps.

Dolphin pairs were requested to synchronise their backflip even if the signal was given by two different trainers positioned on two opposite sides of the pool. The time elapsed between the signal from the trainers and the backflip varied between 2.4 and 5.12 s. This supports

the fact that this behaviour is not a stereotypical jump that would be carried-out automatically and invariably, after a precise delay following the gestural command. It seems there is a temporal adjustment between the dolphins that allows the observed synchrony. Synchronisation has been observed in the wild, where free-ranging dolphins spontaneously synchronise their movements and postures (Pryor and Kang-Shallenberger, 1991; Cusick and Herzing, 2014; Connor et al., 2006; Sakai et al., 2010; Connor et al., 1992; Connor and Smolker, 1996). An obvious question requires the identification of the cues used by these animals to synchronise their behaviour. The aim of this study was to test whether the acoustic modality plays a role in the performance of a synchronous action. Although we do not exclude the possibility that visual cues were used to produce simultaneous movements in the clear waters of this facility, our results suggest that acoustic cues might also be relevant to a certain extent. It is in fact reasonable to think, according to the parsimony principle, that if click trains, which have an energetic cost of production, are systematically emitted at each trial, they might play a role in the performance of the requested exercise. In addition, we demonstrated that the modality of click emission during solo trials (i.e., click trains produced by each dolphin jumping) differed from those observed during the collective synchronised trials (i.e., click trains produced by one dolphin only while the other remained quiet). Together, our results suggest that the acoustic channel might be used during the performance of synchronous jumps.

No whistles or burst pulsed sounds were produced during the jump exercise, whether performed alone or in pairs. These sounds have been reported to play a role in communication and social interactions (Herzing, 2000) and studies on Bottlenose dolphins under human care (Eskelinen et al., 2016) and on wild killer whales (van Opzeeland et al., 2005) have shown that clicks are not the primary vocalisation emitted during a cooperative task. In our study we did not investigate cooperation in problem solving (i.e., hunting for fish or obtaining fish from a container), but synchrony in movement, a task that might require acoustic cues that serve mainly to navigate, as clicks do. Furthermore, during the exercise, subjects performed an assigned and known behaviour when they were the only two individuals in the pool, meaning that they knew both what to do and who to do it with. Under these conditions, dolphins are probably not required to produce “communication vocalisations” to interact socially or to recruit a particular partner among a group of conspecifics.

Our results reveal that while performing a synchronous behaviour, a single individual emitted the click trains. There are two possible explanations for this behaviour: First, the dolphin that produces the click trains during the synchronised jumps, is using its sonar to echolocate its partner's movements. This, however, seems unlikely, as it does not explain why dolphins that produced clicks during solo jumps remained silent during collective jumps. The second possible explanation for this behaviour is that one of the dolphins remains quiet in order to eavesdrop on the clicks produced by its partner and that it uses this acoustic information (likely in combination with visual cues) to navigate and perform the jump as efficiently as it does when jumping alone. Dolphins can perform object recognition through echoic eavesdropping (Xitco and Roitblat, 1996; Götz et al., 2006; Gregg et al., 2007), we suggest here that echoic eavesdropping might also be used for navigation. The key question that may be raised is whether this potential role allocation is done randomly or depends on the dolphin's identity and status in the group.

We showed that in all ($n = 28$) but one successful localisations, the click trains were produced by the same individual, suggesting that one dolphin might acoustically lead the other during the exercise in pairs. It is worth noting that this individual was the oldest of the group (Puck). However, this subject did not have more training or perform the exercise better than the other two. Puck is likely to be the leading female of the group, as it has been described that in Bottlenose dolphins, under human care, the oldest females are often group leaders (Samuels and Gifford, 1997). In our study, Puck's leadership may be expressed through her predominant acoustic activity when paired with another individual. Also, when accompanied, Puck showed an increased click rate when performing the exercise, which might serve to facilitate coordinated movements. Our results suggest that Puck led the acoustic activity during the performance of synchronised jumps. Leadership has been defined as a situation where an individual steers the behaviour of others (King et al., 2009), and it has been reported in highly dynamic fission-fusion species, such as free-ranging Bottlenose dolphins, when they travel (Lewis et al., 2011). Our experiment supports this hypothesis and gives a possible explanation for a mechanism used to synchronise movements. This pilot study, therefore, lays the first foundations of these crucial and exciting questions. However, further investigation is needed to reveal which factors influence this leadership.

We cannot exclude the possibility that dolphins have learned to produce click trains while performing the "backflip" exercise by auto-shaping. This is defined as a form of conditioning in which a subject that has been given reinforcement following a stimulus, regardless of its response to that stimulus, consistently performs an irrelevant behaviour (Brown and Jenkins, 1968). If so, the dolphins would systematically produce click trains while performing the "backflip" exercise, which is not the case. Auto-shaping may also have led the dolphins to learn to remain quiet while another dolphin produces click trains. However, this alternative still implies that the behaviour (silence) appeared spontaneously, at least at the beginning of the learning process.

In conclusion, this study provides evidence that dolphins emit acoustic cues, and more particularly click trains, when performing known synchronised movements. Furthermore, when carrying out these synchronised movements, one individual possibly eavesdrops on the echoes produced by its partner and this probably helps them to navigate their own jump.

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Summary Statement

Bottlenose dolphins under human care emit click trains when synchronising requested aerial jumps. During these jumps, only one indi-

vidual produces the click trains while its partner eavesdrops on this acoustic leader.

Uncited references

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CRedit authorship contribution statement

Juliana Lopez Marulanda: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing. **Olivier Adam:** Conceptualization, Methodology, Supervision, Project administration, Funding acquisition. **Chloé Huetz:** Formal analysis, Writing - review & editing. **Fabienne Delfour:** Conceptualization, Writing - review & editing. **Sander Vanderheul:** Investigation, Resources. **Torea Blanchard:** Conceptualization, Methodology. **Aurélié Célérier:** Conceptualization, Methodology, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.beproc.2021.104357>.

References

- Au, W.W.L., 1993. *The Sonar of Dolphins*. Springer-Verlag, New York, NY.
- Au, W.W., Floyd, R.W., Penner, R.H., Murchison, A.E., 1974. Measurement of echolocation signals of the Atlantic bottlenose dolphin, *Tursiops truncatus* Montagu, in open waters. *J. Acoust. Soc. Am.* 56 (4), 1280–1290.
- Backwell, P.R.Y., Christy, J.H., Passmore, N.I., 1999. Female choice in the synchronously waving fiddler crab *Uca annulipes*. *Ethology* 105 (5), 415–421.
- Benoit-Bird, K.J., Au, W.W., 2009. Cooperative prey herding by the pelagic dolphin, *Stenella longirostris*. *J. Acoust. Soc. Am.* 125 (1), 125–137.
- Blanchard, T., 2015. Innovation Audio-visuel Pour Le Sent an Improved Tool for Ethologists to Record and Suivi Des Grands Dauphins [Audio-visual Innovation for Collect Data on All Dolphins Present in a 360° Space Monitoring Bottlenose Dolphins] (Master's Thesis). Ecole Nationale Supérieure d'Ingenieurs du Mans, Le Mans. France.
- Brando, S.I., 2010. Advances in husbandry training in marine mammal care programs. *Int. J. Comp. Psychol.* 23, 777–791.
- Brown, P.L., Jenkins, H.M., 1968. Auto-shaping of the pigeon's KEY-pECK 1. *J. Exp. Anal. Behav.* 11 (1), 1–8.
- Brownlee, S.M., Norris, K.S., 1994. The acoustic domain. In: Norris, K.S., Würsig, B., Wells, R.S., Würsig, M. (Eds.), *The Hawaiian SpinnerDolphin*. University of California Press, Berkeley, CA, pp. 161–185.
- Buck, J., 1988. Synchronous rhythmic flashing of fireflies. II. In: *The Quarterly Review of Biology*, 63. pp. 265–289 3.
- Connor, R.C., Smolker, R.A., 1996. 'Pop' goes the dolphins: a vocalization male bottlenose dolphins produce during consortships. *Behaviour* 133, 643–662.
- Connor, R.C., Smolker, R.A., Richards, A.F., 1992. Two levels of alliance formation among male bottlenose dolphins (*Tursiops sp.*). *Proc. Natl. Acad. Sci. U.S.A.* 89, 987–990.
- Connor, R.C., Smolker, R., Bejder, L., 2006. Synchrony, social behaviour and alliance affiliation in Indian Ocean bottlenose dolphins, *Tursiops aduncus*. *Anim. Behav.* 72 (6), 1371–1378.
- Cusick, J.A., Herzog, D.L., 2014. The dynamic of aggression: how individual and group factors affect the long-term interspecific aggression between two sympatric species of dolphin. *Ethology* 120, 287–303.
- Dibble, D.S., Van Alstyne, K.R., Ridgway, S., 2016. Dolphins signal success by producing a victory squeal. *Int. J. Comp. Psychol.* 29 (1).

- Eskelinen, H.C., Winship, K.A., Jones, B.L., Ames, A.E., Kuczaj, S.A., 2016. Acoustic behavior associated with cooperative task success in bottlenose dolphins (*Tursiops truncatus*). *Anim. Cogn.* 19 (4), 789–797.
- Fellner, W., Bauer, G.B., Stamper, S.A., Losch, B.A., Dahood, A., 2013. The development of synchronous movement by bottlenose dolphins (*Tursiops truncatus*). *Mar. Mamm. Sci.* 29 (3).
- Götz, T., Verfuß, U.K., Schnitzler, H.U., 2006. 'Eavesdropping' in wild rough-toothed dolphins (*Steno bredanensis*)? *Biol. Lett.* 2 (1), 5–7.
- Grafe, T.U., 2003. Synchronized interdigitated calling in the Kuvangu running frog, *Kassina kuvangensis*. *Anim. Behav.* 66 (1), 127–136.
- Gregg, J.D., Dudzinski, K.M., Smith, H.V., 2007. Do dolphins eavesdrop on the echolocation signals of conspecifics? *Int. J. Comp. Psychol.* 20 (1).
- Hastie, G.D., Wilson, B., Tufft, L.H., Thompson, P.M., 2003. Bottlenose dolphins increase breathing synchrony in response to boat traffic. *Mar. Mamm. Sci.* 19 (1), 74.
- Herzing, Denise, L., 1996. Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*. *Aquatic Mammals* 22, 61–80.
- Herzing, D.L., 2000. Acoustics and social behavior of wild dolphins: implications for a sound society. *Hearing by Whales and Dolphins*. Springer, New York, pp. 225–272.
- Herzing, D.L., 2015. Synchronous and rhythmic vocalizations and correlated underwater behavior of free-ranging Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in the Bahamas. *Anim. Behav. Cogn.* 2 (1), 14–29.
- Janik, V.M., 2009. Acoustic communication in delphinids. *Adv. Study Behav.* 40, 123–157.
- Janik, V.M., Simard, P., Sayigh, L.S., Mann, D., Frankel, A., 2011. Chorusing in delphinids. *J. Acoust. Soc. Am.* 130, 2322.
- Johnson, C.M., 2015. The cognitive ecology of dolphin social engagement. *Dolphin communication and cognition* 229–256.
- King, A.J., Johnson, D.D., Van Vugt, M., 2009. The origins and evolution of leadership. *Curr. Biol.* 19 (19), R911–R916.
- Launay, J., Tarr, B., Dunbar, R.L., 2016. Synchrony as an adaptive mechanism for large-scale human social bonding. *Ethology* 122 (10), 779–789.
- Lewis, J.S., Wartzok, D., Heithaus, M.R., 2011. Highly dynamic fission–fusion species can exhibit leadership when traveling. *Behav. Ecol. Sociobiol.* (Print) 65 (5), 1061–1069.
- Lopez-Marulanda, J., Adam, O., Blanchard, T., Vallée, M., Cazau, D., Delfour, F., 2017. First results of an underwater 360° HD audio-video device for etho-acoustical studies on bottlenose dolphins (*Tursiops truncatus*). *Aquat. Mamm.* 43 (2), 162.
- Mann, J., Smuts, B., 1999. Behavioral development in wild bottlenose dolphin newborns (*Tursiops sp.*). *Behaviour* 136 529e566.
- McCue, L.M., Cioffi, W.R., Heithaus, M.R., Barrè, L., Connor, R.C., 2020. Synchrony, leadership, and association in male Indo-pacific bottlenose dolphins (*Tursiops aduncus*). *Ethology*.
- Moore, Bronte, L., Connor, Richard, C., Allen, Simon, J., Krützen, Michael, King, Stephanie, L., 2020. Acoustic coordination by allied male dolphins in a cooperative context. *Proceedings of the Royal Society B* 287 (1924). doi:https://doi.org/10.1098/rspb.2019.2944.
- Pryor, Kang-Shallenberger, 1991. Social structure in spotted dolphins (*Stenella attenuata*) in the tuna purse seine fishery in the Eastern Tropical Pacific Ocean. *Dolphins Societies: Discoveries and Puzzles*. University of California Press, Los Angeles, California.
- Ravignani, A., 2017. Interdisciplinary debate: agree on definitions of synchrony [Correspondence]. *Nature* 545, 158.
- Ravignani, A., Bowling, D.L., Fitch, W., 2014. Chorusing, synchrony, and the evolutionary functions of rhythm. *Front. Psychol.* 5, 1118.
- Ridgway, S.H., Moore, P.W., Carder, D.A., Romano, T.A., 2014. Forward shift of feeding buzz components of dolphins and belugas during associative learning reveals a likely connection to reward expectation, pleasure and brain dopamine activation. *J. Exp. Biol.* 217 (16), 2910–2919.
- Roberts, B.L., Read, A.J., 2015. Field assessment of C-POD performance in detecting echolocation click trains of bottlenose dolphins (*Tursiops truncatus*). *Mar. Mamm. Sci.* 31 (1), 169–190.
- Sakai, M., Morisaka, T., Kogi, K., Hishii, T., Kohshima, S., 2010. Fine-scale analysis of synchronous breathing in wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *Behav. Processes* 83 (1), 48–53.
- Samuels, A., Gifford, T., 1997. A quantitative assessment of dominance relations among bottlenose dolphins. *Mar. Mamm. Sci.* 13 (1), 70–99.
- Trainer, J.M., McDonald, D.B., 1993. Vocal repertoire of the Long-tailed Manakin and its relation to male-male cooperation. *Condor* 769–781.
- Tyack, P.L., Clark, C.W., 2000. Communication and acoustic behavior of dolphins and whales. *Hearing by Whales and Dolphins*. Springer, New York, NY, pp. 156–224.
- van Opzeeland, I., Corkeron, P.J., Leysen, T., Simila, T., Van Parijs, S.M., 2005. Vocal behaviour of Norwegian killer whales, *Orcinus orca*, during carousel and seiner foraging on spring-spawning herring. *Aquat. Mamm.* 31, 110–119.
- Würsig, Pearson, 2015. *Dolphin societies: structure and function*. Dolphin Communication and Cognition: Past, Present, and Future. MIT Press.
- Xitco, M.J., Roitblat, H.L., 1996. Object recognition through eavesdropping: passive echolocation in bottlenose dolphins. *Learn. Behav.* 24 (4), 355–365.