

Acoustic behavior in bottlenose dolphins (*Tursiops truncatus*) during a target discrimination task

Ariana Hernández Sánchez

Examiner, Urban Friberg
Supervisor, Jordi Altimiras



CONTENTS

Abstract	3
1.Introduction	4
1.1 A biological sonar system: Echolocation.....	4
1.2 Odontocetes and sound production system	4
1.3 Background research in echolocating bottlenose dolphins	7
1.4 Motivation and purpose of the study.....	7
2.Materials and methods	9
2.1 Study subjects and facility	9
2.2 Animal training	10
2.3 Experimental setup and procedure.....	10
2.4 Acoustic recordings	12
2.5 Data analysis	14
3.Results	14
3.1 Task performance and behaviour.....	15
3.2 Performance and target strength of the different materials.....	16
3.3 Scanning behaviour.....	19
4.Discussion	19
5. Conclusions	23
6.Societal and ethical considerations	24
7.Acknowledgements	24
8.References	24

ABSTRACT

Echolocation, is an active sensory system found in dolphins and bats. It gives an acoustic representation of the surroundings by the animal emitting clicks, detecting and analysing echoes. By adjusting the properties of the emitted sounds, the animal can alter the type of obtained information. Here we study how freely moving bottlenose dolphins may use their dynamic sound production and hearing abilities, along with head and body movements, to detect and classify objects. Studying how animals exploit and experiences the environment and soundscape while in motion with a simplified echolocation task, allow a full understanding of the processes behind target detection and discrimination capabilities during natural biosonar circumstances. Inspired by previous studies on harbour porpoises we compare the differences in performance between porpoises and dolphins. We show that dolphins perform similar scanning behaviours to porpoises during target inspection, and also a stereotyped switch from relatively long interclick intervals to very short ones in the so-called buzz phase approximately 1 m before interception with the target. Even though the dolphin's biosonar signals have a broader bandwidth than the porpoise's, the discrimination performance is not better in the former than the latter. The explanation for this surprising result is not clear but may indicate that porpoises are better in exploiting the bandwidth of their biosonar signals than previously have been thought.

Keywords: Buzzing, dolphins, discrimination, echolocation, scanning, toothed whales

1 INTRODUCTION

1.1.A biological sonar system: Echolocation

The sensory world of animals is acoustically dynamic and complex (Moss et al. 2014). Animals experience the challenge of analyzing biologically relevant signals to communicate with conspecifics, reproduce, find food, avoid predators and navigate (Moss et al. 2014). The aquatic environment does not always present the best visibility conditions. Aquatic animals that rely on echolocation, can hunt and orient themselves using sound rather than vision (Surlykke & Nachtigall, 2014).

Echolocation is a unique sensory process where an animal actively emits signals for detecting changes in its environment through the received echoes (Surlykke & Nachtigall, 2014). Echolocation abilities are found in some mammals, such as many bats as well as dolphins, porpoises and other toothed whales (i.e. Odontocetes) (Surlykke & Nachtigall, 2014), and in a few species of birds (Griffin, 1974). Most echolocating animals use high intensity, directional ultrasonic clicks to find and intercept prey and to navigate in their environment (Au, 1993, Surlykke & Nachtigall, 2014). Odontocete sonar is defined as a combinate highly dynamic transmission system, coordinated with a specialized hearing and signal detection system. Using the sound-production apparatus with highly specialized tissues, they emit high-power signals in a narrow acoustic beam (Cranford et al. 1996). The returning echoes are received by extremely sensitive ears, and transformed into neural signals that reach the brainstem and the cortex forming an acoustic representation of the animal's surroundings (Au, 1993).

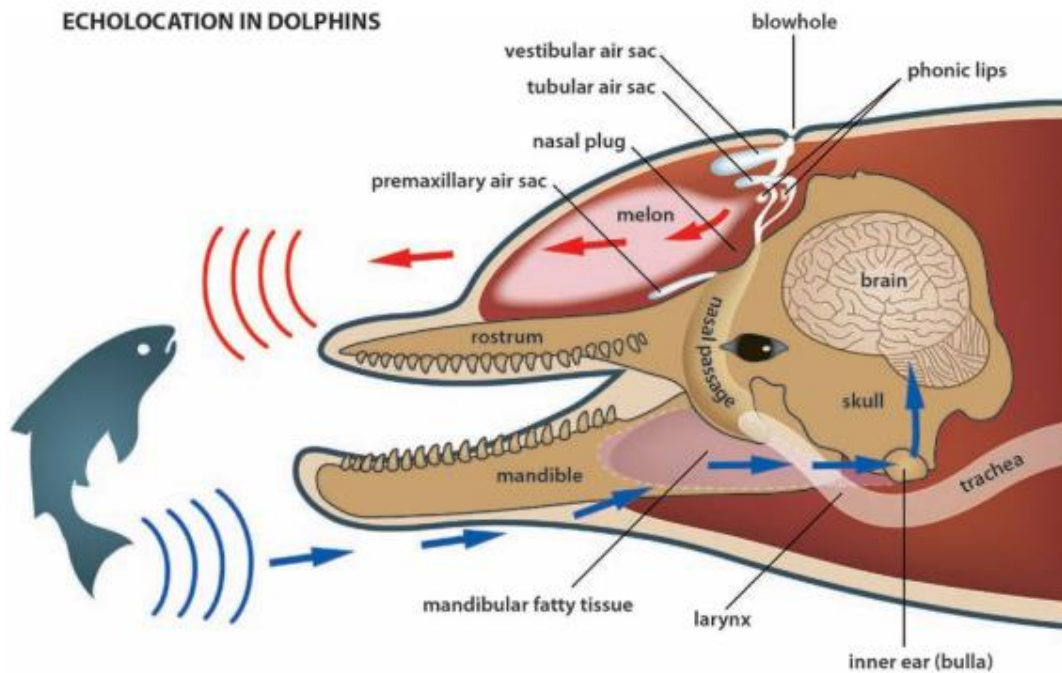
Toothed whales and bats have the most adaptable and developed biological sonar system of all animals (Brock et al. 2014). Toothed whales produce signals for echolocation similar to bats detecting insects in the dark, in the same frequency range, from 10 to 200 kHz (Madsen & Surlykke, 2013). Most bats echolocate with tonal signals of either constant or variable frequency, whereas most toothed whales use broadband clicks. Both bats and odontocetes changing the intervals between the signals in response to acoustic conditions and variation in target distance (Surlykke & Nachtigall, 2014).

1.2 Odontocetes and sound production system

In pursuit of prey, odontocetes and bats perform similar biosonar behaviours which can be classified into three stages: (1) search, (2) approach, and (3) terminal buzz (Johnson et al. 2006, Schnitzler and Kalko 2001). These three phases have been studied in quite some detail for many species of bats. For several species of odontocetes, there has been documented the existence of search, approach and terminal buzz phases even though the level of detail of our understanding of the function of each phase is poor, especially for the end of hunting chases (Wisniewska et al. 2014).

Toothed whales are present in many marine habitats, ranging from rivers and shallow coastal waters to deep pelagic zones (Brock et al. 2014). They are divided into ten families with 69 species, including dolphins (Delphinidae), porpoises (Phocoenidae), and beaked whales (Ziphiidae; Brock et al. 2014). Toothed whales have evolved a remarkably specialized nasal sound production system. The animals' nasal passages have migrated to a dorsal location, so that they are able to breath when at the surface through the blowhole. In most toothed whales the upper nasal passages contain a selection of diverticula along with a pair of fatty bursae placed in a pair of phonic lips, identified as the source of echolocation clicks (Cranford et al. 1996; Madsen et al. 2003) and also tonal sounds (Madsen et al. 2011). Echolocation signals are produced by forcing pressurized air through the phonic lips (Brock et al. 2014) and the sound energy propagates onwards through the animal's head, transferred from the nasal area to the forehead through fatty tissue called the melon (Figure 1).

One important key for the development of echolocation was the adaptation of the cetacean ear for sound reception in water (Brock et al. 2014). Besides toothed whales having some of the most sensitive ears in the animal kingdom, their auditory sensitivity, signal structure and source level is flexible, to improve target detection and classification in clutter as they approach a target (Brock et al. 2014).



Source: © Gorter (2012a, b)

Figure 1. Anatomy of a dolphin generating an acoustic signal. From Gorter 2012, in Klemas (2013). Echolocation signals are emitted by the phonic lips and propagate through the melon before entering the water.

Echolocating toothed whales and bats decrease their click intensity as well as increase their rate of calling with decreasing target range (Rasmussen et al, 2002; Au and Benoit-Bird, 2003, Surlykke et al., 2014). Their click rate is always adjusted to ensure that echoes from targets of interest arrive before a subsequent click is produced (Ladegaard et al. 2019). The echolocation signals of toothed whales can be classified into four basic categories: Broadband high-frequency (BBHF) clicks, narrowband high-frequency (NBHF) clicks, FM upsweeps, and intense broadband lower frequency clicks (Wahlberg et al. 2011). The most common type of biosonar signal for toothed whales is a short, broadband signal that puts out as much energy as its production mechanism allows (Brock et al. 2014). It is believed that the type of echolocation signal is adjusted to the ecological conditions of its environment and prey. This generates variations in signal parameters between species, and even within the same species solving different echolocation tasks (Brock et al. 2014).

In dolphins, differences in the source level and peak frequency of the buzzes are found within the same individual (Au, 1993). A common characteristic is their change in the acoustic gaze when approaching a target. In their study of harbour porpoise biosonar Wisniewska et al. (2012) stated that by adjusting the direction and depth of their gaze,

animals can select visual inputs for cognitive processing, allowing them to manage the sensory load from complex and noisy scenes. The acoustic gaze adjustments provide fast updates on the location of the target with high pulse rates during the buzz phase, and the low source level decreases the complexity of the auditory scene (Wisniewska et al. 2012).

In addition, echolocators decrease ICIs (inter-click intervals) in the final approach towards a target or prey item, producing a so-called *terminal buzz* (Doh et al., 2018, Simmons et al., 2014). When entering the buzz phase, they dramatically reduce the energy output as well as peak pressure per sonar pulse (Madsen and Surlykke, 2013). In porpoises, Wisniewska et al (2015), demonstrated the beam width increases during the final approach phase to allow an accurate judgment of range and heading towards the target. As the animal approximates the target, the temporal and spectral structure of the clicks are also modified (Wisniewska et al. 2012). Previous studies suggested dolphins probably use echo trains rather than individual echoes to discriminate between objects (DeLong et al., 2007, Helweg et al., 1996).

1.3 Background research in echolocating bottlenose dolphins

Bottlenose dolphins (*Tursiops truncatus*) are the most well-studied odontocete species concerning all aspects of sound production, reception, and biosonar performance in stationary setups. Many studies show bottlenose dolphins use broadband, ultrasonic signals to localize, classify, recognize and approach prey (Reviewed by Au 1993). However, little is known about dolphin biosonar in moving animals, as well as of the process of controlling click emissions (Liling et al. 2019). Dolphin biosonar has been demonstrated to be very adaptive, with the animal controlling different aspects of the signal, such as source level, peak frequency, bandwidth, and beam geometry. Other factors such as task difficulty, environmental conditions, animal age and experience also affect the animal's echolocation signals (Moss et al. 2014). Dolphin echolocation clicks can have an extensive frequency bandwidth (>85 kHz) with energy commonly between 20 and 130 kHz, but the dolphin can also control the spectral content of the click and benefit from signals of narrower band width (Houser et al. 1999, Muller et al. 2008).

1.4 Motivation and purpose of the study

Research efforts have tried to understand how animals select and organize auditory events from an acoustically complex environment (Moss et al. 2014). To investigate their full

dynamic capacity, animals should be tested in a more realistic task, with the dolphins swimming freely. Under controlled conditions, we can understand how auditory events are treated in trained animals and they can wear suction cups on their eyes (eyecups) to prevent the use of their vision. Previous experiments on bats have shown that specific aspects of the biosonar behaviour can be best determined if the animal is moving around freely and performing semi-natural target interceptions (Moss et al. 2011, Wohlgemuth et al. 2016). In the wild, dolphins are highly mobile during target detections and discriminations with their sonar, scanning the environment from different angles to obtain useful information.

In the dolphin discrimination task studied here, the animal is forced to use echolocation by being blindfolded, depending entirely on its hearing abilities, and more specifically, the spectral and temporal resolution of its auditory system (Branstetter et al. 2020). The ability to discriminate ensonified targets demands knowledge of the spatial relationships between an object's characteristics that are obtained by returning echoes sent back (Altes et al. 2003). To successfully locate the target, the animal must analyze the collected acoustic information from the returning echoes (Griffin et al. 1960). Perhaps the animals change their echolocating behavior to optimize the information return corresponding to the different phases of the hunt, since target detection, tracking and interception present different challenges (Beedholm et al. 2021). Further, it may receive echoes from multiple targets, as well as signals produced by other animals in the vicinity. For a simple detection task, the optimal echolocating behavior would be to center the beam as precisely on the target as possible (Beedholm et al. 2021). In contrast, for free-moving target approaches, other echolocation strategies may come into play, for example one that would optimize positional information, tracking, or classification (Beedholm et al. 2021).

Research with animals under human care have contributed with essential information about the biosonar systems, revealing the extraordinary sensitivity and accuracy of echolocating animals /in discrimination of targets (Johnson 2014) and object recognition (Harley 2008).

A great deal is known about how odontocetes emit and receive biosonar signals. However, we lack critical data to address important questions such as why their sonar excels over man-made sonars in terms of target detection and classification. To understand the physiological mechanisms behind odontocete sonar, we need to study their hearing, sound production and behavior during realistic target detection trials for potential applications.

Understanding links between the structure and pattern of biosonar signals emitted by dolphins and the accomplishment in behavioral tests of target localization and perception is needed to learn how echoes are processed (Simmons et al. 2014).

To overcome these limitations, we designed an experiment with bottlenose dolphins (*Tursiops truncatus*) swimming freely along the pool actively discriminating between two hydrophone-equipped targets with three different materials. Our approach is to study freely moving animals that can use their dynamic sound production and hearing abilities, along with head and body movements, to detect and classify objects. Inspired by Wisniewska et al. (2012) we compare the differences and similarities between porpoises and dolphins in their biosonar behaviour, showing that dolphins as broadband echolocators have an active and acute control over their sonar signals.

2 MATERIALS & METHODS

2.1. Study subjects and facility

Experiments were done with two bottlenose dolphins, a male (M1) and a female (F1). Both animals were born under human care and are housed at the dolphinarium in Loro Parque, Tenerife, Spain. M1 was born in 2002 and F1 in 1999. During the experiment they were 19 years old and 22 years old, respectively. Both dolphins had been trained for several years using operant conditioning, during 4 daily training sessions where they get their full diet irrespectively of performance. M1 had however never before been trained for echolocation tasks, when F1 was already trained to wear eyecups and a simple object detection task.

All dolphins were housed in an open-air enclosure consisting of five interconnected pools separated by net gates. Experimental training and testing were made in an irregular oval pool with dimensions of 25 x 15 m (maximum length and width), and a max depth of 3m. The experimental animal normally shared pools with other dolphins, but it was separated into the experimental pool prior to the start of a training or testing session. To avoid any anxiety from social separation, there were always an additional dolphin present in the pool during the experiment.

2.2 Animal Training

From September to November 2021 the dolphins were trained for the task of distinguishing between targets using echolocation. The targets were two spheres made of different materials, the standard one (S+) being aluminum. The two targets selected for the task had different echo characteristics but with identical visual appearance. First, we accustomed the dolphins to wear eyecups for longer periods of time. After that, we introduced the aluminum target and moved it around in their pool. The dolphin had to find it, touch it, and come back to the trainer to get rewarded. We then introduced the second target, made of PVC, in locations where it was unlikely that the dolphin would touch it. The goal was to have the PVC ball in the environment, so that the dolphin could locate it but learn to ignore it. When the dolphin got better in only responding to the aluminum sphere, we moved the plastic ball into positions that made the choice more difficult. We then desensitized the dolphins to the experimental equipment: pole, target balls, cables and hydrophones, and the underwater camera. Data collection was initiated after dolphins were able to discriminate the aluminum from the plastic target with a success rate of 80%.

2.3 Experimental setup and procedure

The transparency of the water allowed us for direct visual observations of the swimming behavior and sound recording of the acoustic behavior of the animals during the discrimination task. Trials for each animal were run in sessions with a maximum of 5 trials per session and up to three sessions per day. We had four different target solid spheres of 50.8 mm diameter made of four different materials: Aluminum, PVC, brass and steel. Dolphins were first trained to identify the aluminum sphere as the standard target, and we thereafter started the experiment with the easier discrimination (PVC).

Target spheres were suspended by a 4 mm diameter polyester and 139 cm long rope hanging from a 4.5-m-long aluminum pole. Targets and hydrophone cables were hanging from a carabiner, to switch between targets. The targets were positioned at 4m and 3m from the pool wall to avoid acoustic reflections. On each trial the spheres were lowered into the water to a depth of 1 m to avoid acoustic interference from surface reflections (Figure 2). To keep distances consistent a mark was made in the pole and in the target strings.

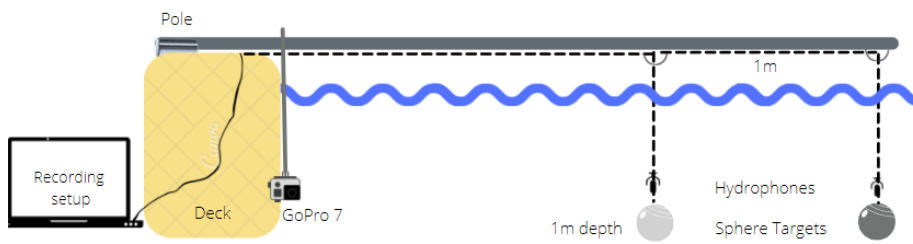


Figure 2. Experimental setup from the side view of the pool

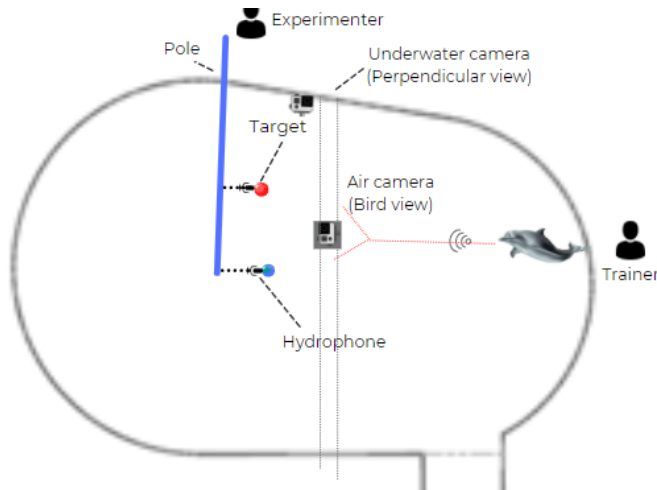


Figure 3. Experimental setup from an aerial view.

Following Wisniewska et al. (2012), we investigated the detailed swimming and biosonar behaviour in bottlenose dolphins while the animal actively moved towards and selected between two targets of different materials. We recorded the dolphins swimming across the pool and approaching the targets while performing a two-alternative forced choice task (Schusterman, 1980). We recorded the dolphin echolocation clicks by measuring the received signal at two hydrophones placed above each target, as well as by filming the animal's swimming movements during the trials (Figure 3 and 4), gaining valuable information on how the animal is 'allocating' its sonar clicks to inspect the two targets to make its decision.

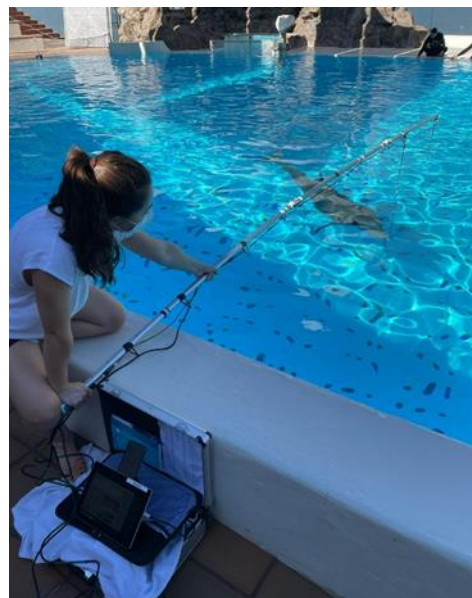


Figure 4. Experimental session. Experimenter holding pole with both targets hanging, attached to recording setup, and dolphin choosing which ball to swim up to. The animal is then called back to a trainer located outside the picture to the left.

Data collection started in November 2021 and was completed in January 2022 for both dolphins. The dolphins wore opaque gelatin eyecups to prevent their use of vision while solving the tasks. Both dolphin and trainer were 13 m away from the targets, waiting for the experimenter to be ready. The trial started when the trainer gave a hand touch signal to the dolphin to indicate it to swim and locate the targets. The trial ended when the dolphin touched one of the targets with its rostrum. If the target choice was correct the trainer blew the whistle to let the dolphin know return to the starting location and get rewarded with a fish. If the dolphin made an incorrect choice the pole with the targets was taken out of reach, and the dolphin would swim back to the starting location and without obtaining any reward. Each session started with one warm-up trial, presenting only the aluminum (S+) target. The warm-up trials were excluded from the analysis. There was a 30 seconds intertrial interval for changing the position of the standard and comparison targets and the order of the materials. Whether the standard target was to right or left was decided by a pseudo-random table (www.randomizer.org), same for both dolphins and different for each material. Every session consisted in five trials, and there was no time limit for completing the task. During each trial, an additional trainer kept the second dolphin present in the experimental pool with its head out of the water to avoid its sounds interfering with the recordings of the experimental dolphin.

2.4 Acoustic recordings

Two custom-built hydrophones (10x20mm prolate spheroid elements, flat frequency response ± 2 dB between 100 and 160 kHz courtesy D. Wisniewska) were attached 1 cm above each ball to receive the sonar clicks as the dolphins approached the targets. The same hydrophone was assigned to each target in every session. After completion of trials, the hydrophones were calibrated in a 3m deep 3 m diameter water tank using relative calibration with a Reason 4014 hydrophone as a standard, which sensitivity previously had been determined using reciprocity calibration. The experimental hydrophones all had a sensitivity of -210 dB re 1 μ Pa (± 2 dB). Hydrophone signals were amplified by either 20 dB (F1) or 40 dB (M1) and band-pass filtered (1-160 kHz) with a custom-made amplifier-filter unit before being digitized at a sampling rate of 500 kHz with 16 bits with a multifunction data acquisition board (National Instruments USB-6251, Austin, TX, USA) and saved on a computer. The lower amplification of data from F1 was done to avoid signal clipping due to generally higher click output levels from that individual.

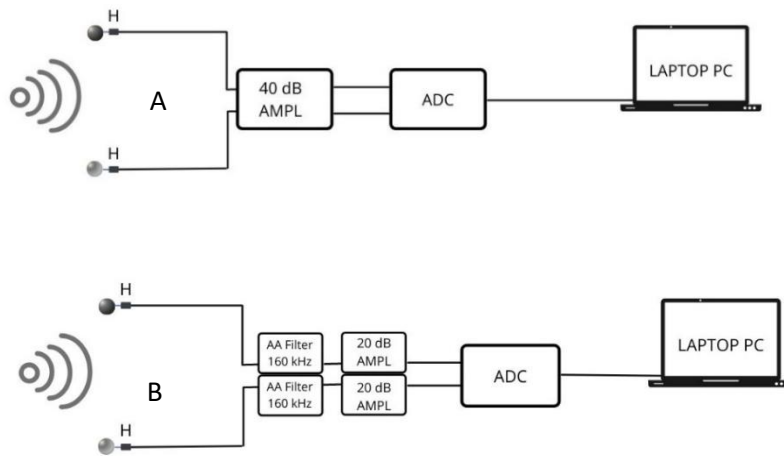


Figure 5a, b. A- Recording configuration for the male dolphin. Sonar clicks received by the hydrophones (H) at the targets were amplified, bandpass-filtered and digitized using an analog-to-digital converter (ADC). B- Recording configuration for female dolphin.

To record the trials, we used LabView 2019 (ver. 19.0.1f1) with Multi-Devices Bio-acoustic Recorder (custom-made program by A. Moriat, National instruments). Before or after the experimental sessions a Soundtrap v1.7 Ocean Instruments NZ was used for recordings of the ambient noise level in the pool during 30 sec to 1 minute.

Before and after the experiment, the hydrophones were synchronized with the air camera and the underwater camera by tapping gently on the hydrophones. The underwater camera, GoPro 7 was mounted on a PVC pole next to the wall of the pool, 157cm aside from the pole, at a depth of 50cm from deck, and 1 m above the balls, resulting in a perpendicular view of the field. The bird view camera, GoPro 9 was attached to a pulley system with a metal plate attaching the camera 3,4m above the water surface of the pool. The camera was filming in Max Lens Mode with a 155° angular horizontal field of view, centered over the targets and covering a horizontal range of 15,3m at the water surface. The cameras (GoPro9 and GoPro7) recorded continuously at a rate of 59 fps, 94 fps, and 30 fps respectively. Given the frame rate of the cameras and the sampling rate of the acoustic recording system, the synchronization was accurate to within less than 33ms.

2.5 Data analysis

MATLAB R2021a was used for various aspects of acoustic signal selection, and video analysis. Performance differences for different comparison materials for each animal were tested with ANOVA.

For the video analysis we used a Drone Video Measure program, developed by Prof. Henrik Midtiby, University of Southern Denmark, including a dolphin recognition algorithm to obtain its track and heading. For the tracking algorithm the following points were marked every second frame for each trial: Tip of beak, blowhole and targets. With this we were able to measure dolphin head orientation and position over time in the trials, and a determined distance from the blowhole to the target when the dolphin starts the terminal buzz during echolocation. We were able to determine which one of the targets the dolphin pointed its head at, and its swim path while approaching the target. A subset of trials was tracked at full frame rate, i.e. 25frames/s, using the in-air camera, to determine the minimum video tracking rate that allowed a faithful reconstruction of the animal's movements.

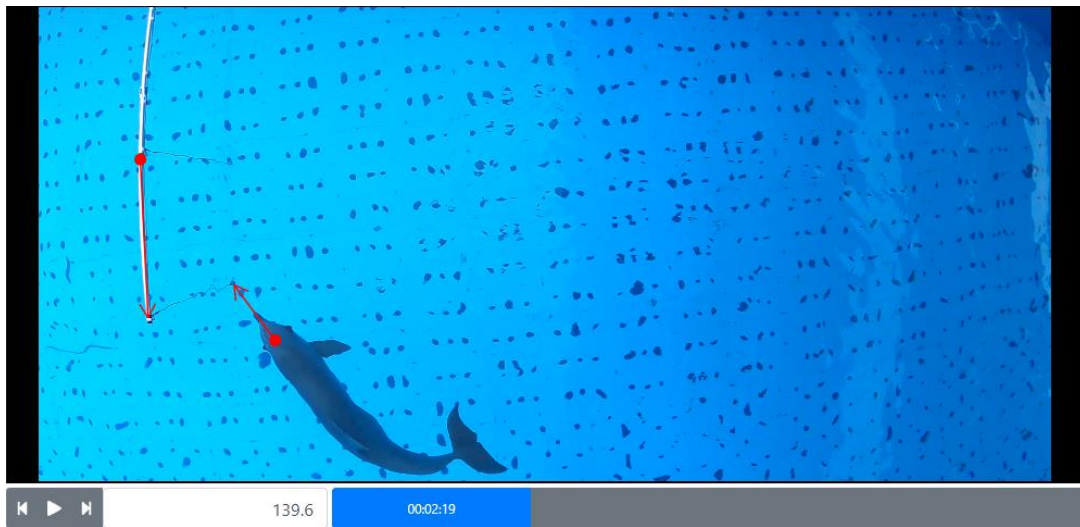


Figure 6. Screenshot of the video analysis program with a fixed known distance of 1m between each target, and head orientation from blowhole to beak indicated by an arrow. Red circle indicated the location of the blowhole.

3 RESULTS

A total of 320 trials were performed with the two study dolphins (Table 1), with a minimum of 30 trials per material and animal. Only a subset of these trials (30 per material, per animal) met the requirements to be analyzed, i.e., that the animals remained

in the camera's field of view throughout the approach, and that video and audio were obtained correctly.

Table 1. Summary of data collection. Left number of trials run in the experiment, and right number of trials used for the analysis. All columns are number of Corrects/Incorrects.

Animal	Number of trials run (C/I)			Overall success rate (C/I)	Number of trials used for analysis (C/I)		
	PVC	Brass	Steel		PVC	Brass	Steel
Aquiles (M1)	42/8	42/8	16/14	100/30	25/5	24/6	16/14
Clara (F1)	49/1	49/1	16/14	114/16	29/1	29/1	16/14

C: Correct response I:Incorrect response

3.1. Task performance and behavior

After the dolphin was sent by the trainer, it swam directly towards the targets in every trial. The male (M1) approached the targets with a curved swim path in all trials, keeping left away from the pool wall. The female (F1) used a frontal approach to the targets in 67.7% of the trials, and a slightly curved route in 33% of the trials (Figure 7).

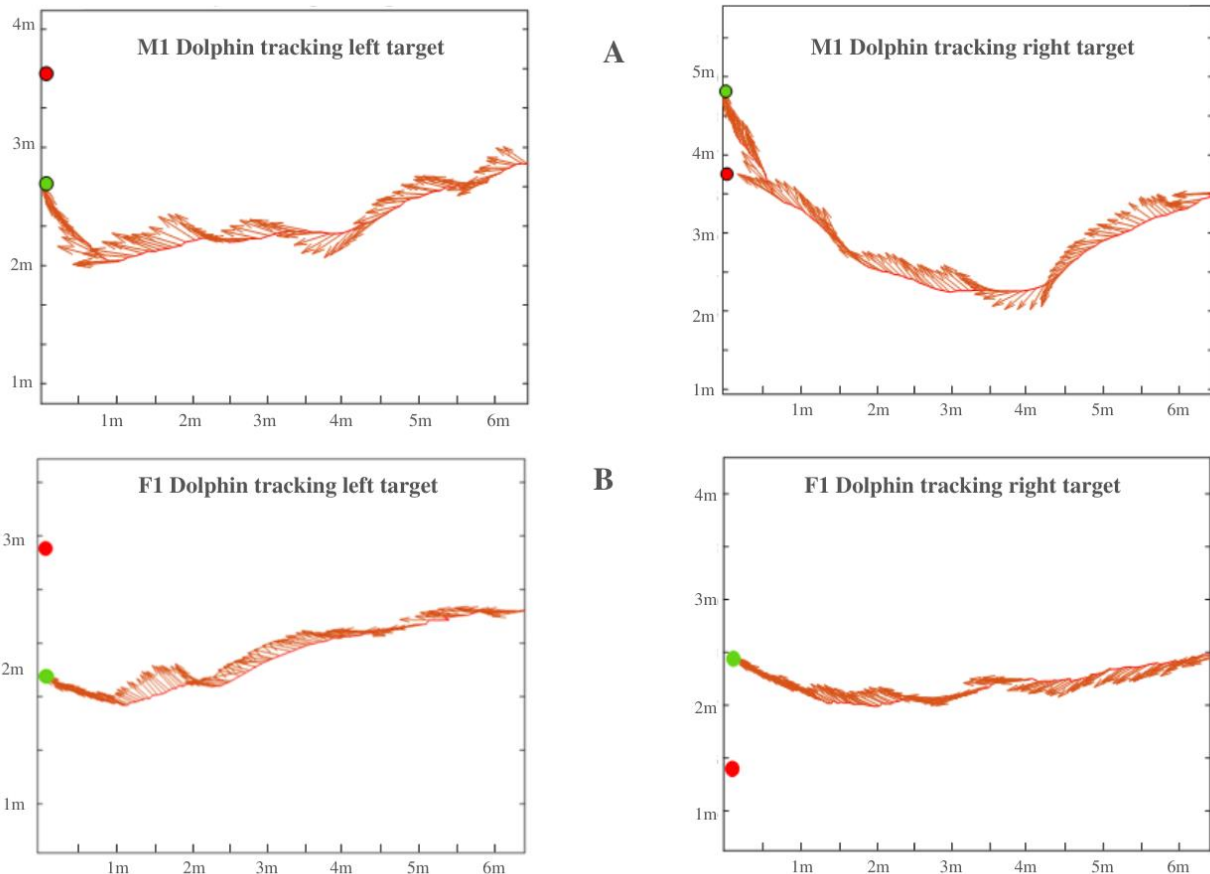


Figure 7a, b. Graph showing the tracking of the swimming path of each individual from head orientation measuring blowhole to snout every 3 ms during the same trial. Above, M1 swimming paths to left and right target showing a curved and side approach. Below, F1 swimming paths to left and right showing an approach to the targets from the front. Green circle shows the correct target (S+) and red circle is the incorrect one.

The animals' performance in the target discrimination tasks is presented in Fig. 8. The dolphins made minor mistakes when discriminating the plastic (Figure 8a) or brass (Figure 8b) spheres from the aluminum sphere but the performance decreased when discriminating steel from aluminum sphere (Figure 8c). Even though the animals did not have a time limit for the discrimination task, they would usually take 9-10s to select a target from being sent from the trainer.

3.2 Performance and target strength of the different materials

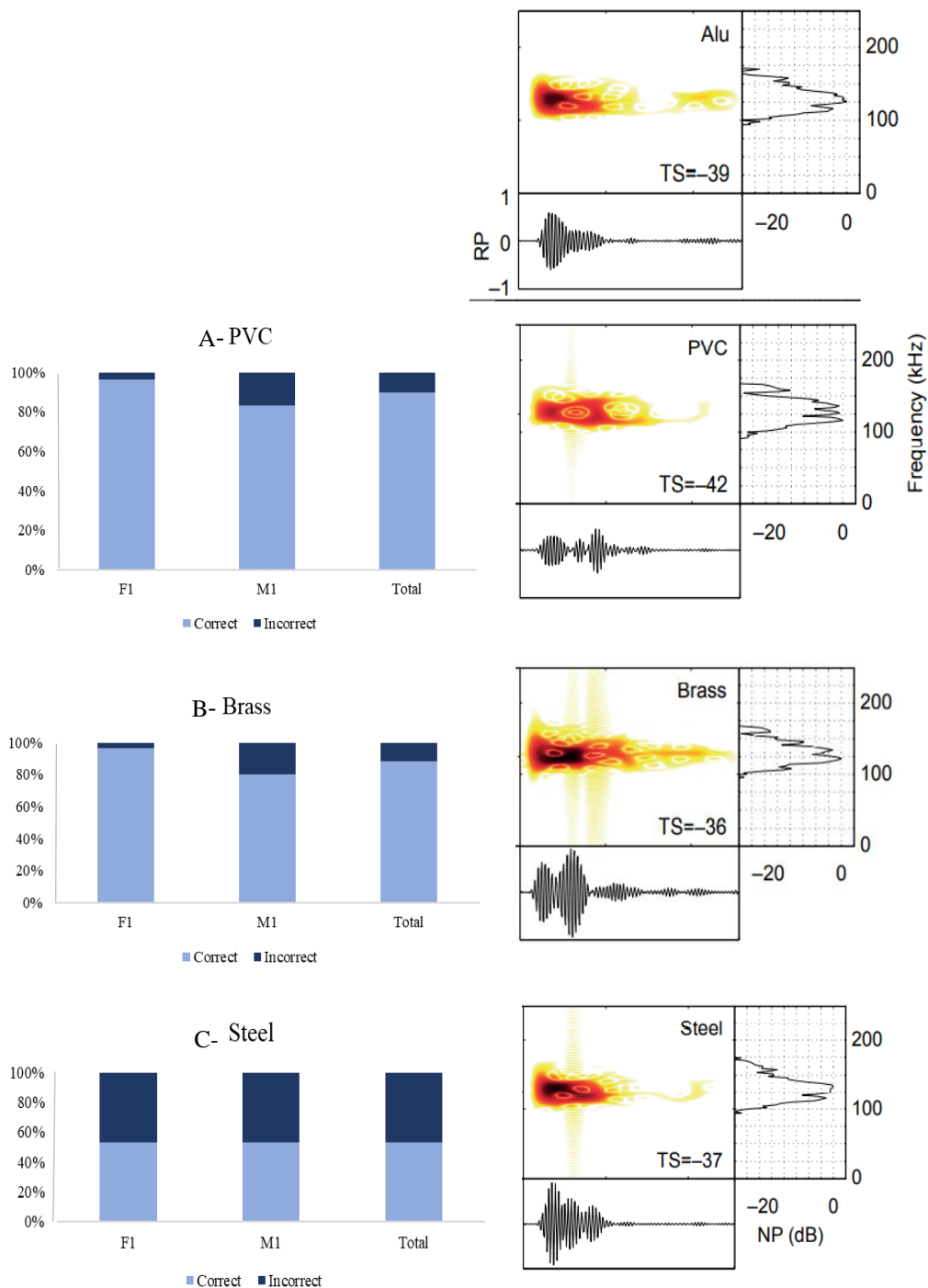


Figure 8. Relative pressure (RP), normalized power spectra (NP) and Wigner–Ville time–frequency distributions of the echo signatures returned by the ensonified standard (aluminum) and comparison (PVC, brass and steel) targets used in the present study with a porpoise-like sonar signal. In the left panels, an evaluation of the overall performance of the two animals on the discrimination tasks is shown in percentage, with the numbers in the bars indicating the sample sizes of trials.

Table 2. Overall performance of the two animals in the discrimination tasks shown in percentages.

PVC	Correct	Incorrect	Brass	Correct	Incorrect	Steel	Correct	Incorrect
Clara	96.6%	3.4%	Clara	96.6%	3.4%	Clara	53.3%	46.7%
Aquiles	83.3%	16.6%	Aquiles	80%	20%	Aquiles	53.3%	46.7%
Total	90%	10%	Total	88.3%	11.6%	Total	53.3%	46.7%

The dolphins made mistakes in 3.4-16.6% of trials with the PVC comparison target, 3.4–20% of trials with the brass target and 46.7% of trials with the steel target (Table 2). The reduction in performance was clearly related to the contrast in echoes between the standard (aluminum) and the material composition of the comparison target (Figure 8).

The performance of the two dolphins does not show any change over time (Figure 9), as would have been signs of learning. The dolphins were trained for the task beforehand, and the data collection did not start until they were able to discriminate with a success rate of 80% with the plastic comparison target, and this performance did not manifest any major changes during the experiment.

In the aluminum vs. plastic trials, M1 varied between three and five correct trials per session, and F1 was very consistent in the successes until Session 5 where she made one mistake (Figure 9a). In the discrimination of aluminum vs. brass, the performance of F1 improved slightly over time, as she made a mistake in the first session and never another one. For M1 with there were no failures in the last 3 sessions. In the aluminum vs. steel, there were mistakes in every session.

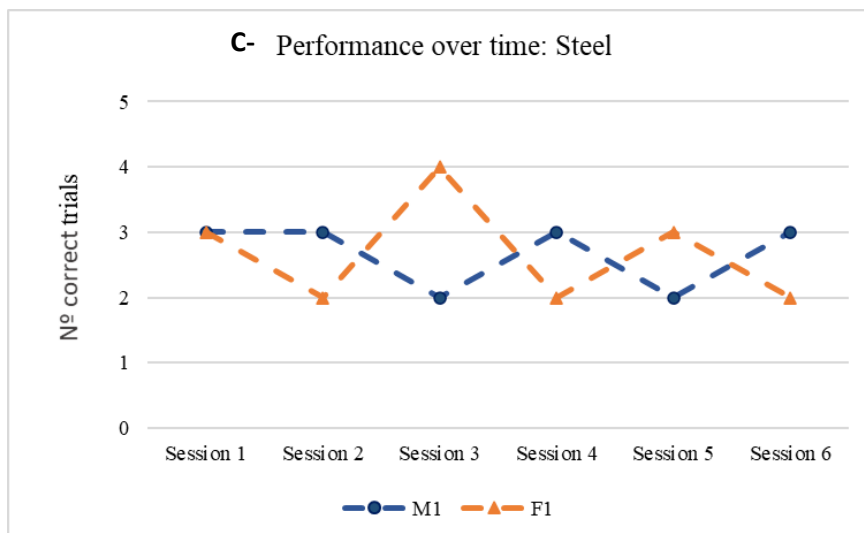
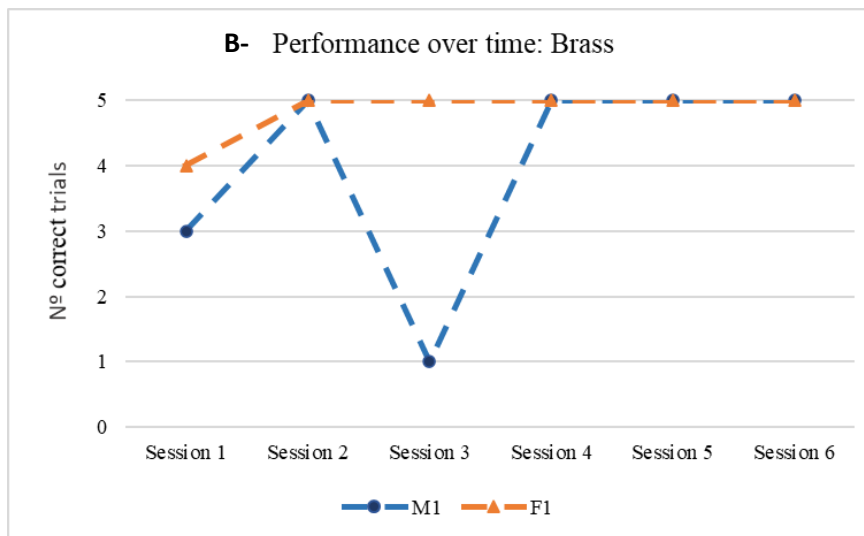
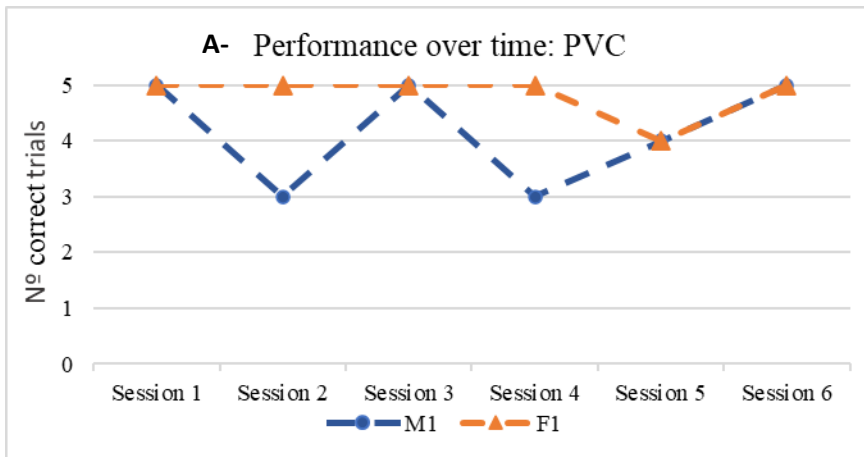


Figure 9 a, b, c: Performance of the two dolphins, M1 in blue and F1 in orange, over time during 6 consecutive sessions. In every session there were 5 trials. The performance does not show any learning trend over time.

3.3 Scanning behavior

While approaching the targets for making their choice the dolphin scanned the targets sequentially, taking between 2 to 8 scans during the last meters of approach in each trial before making a decision. To evaluate if the difficulty of the task influenced decision-making process, we compared the mean number of scans per material. M1 scanned each target target before deciding on an average of 4.4 times for plastic, 3.3 times for brass and 4.8 times for steel. F1 scanned 3.6 times for plastic, 3.9 times for brass and 5.9 times for steel, increasing proportionally with the difficulty. In both dolphins the highest number of scans corresponds to the most difficult task. There was a statistically significant difference in the number of scans per material, for each animal (ANOVA). $F= 4.8$; $df=2,3$ $p=.01$ for M1; and $F= 25.5$; $2,3$; $p < .00001$ for F1

Terminal buzzes were emitted in all target approaches for M1 and F1 and these were typically initiated at a distance of 0.4-0.8 m away from the target and continued until the animal turned the head away to return back to station. After the buzz was initiated, the animal did not change the decision but focused on same target until snout contact, also for the incorrect trials.

After regular clicking, the dolphins switched to rapid terminal buzzes while completing the approach to the target. During this phase, the animals continued to scan their beam over the selected target in both the horizontal and vertical planes, as indicated by the movements of the animals. In both dolphins, it was observed how they rotated their body to both sides during echolocation, so the head movement is not only in the horizontal axis, but also rotating from one side to another in their same axis of their bodies.

4 DISCUSSION

Studying how the dolphins solved a simplified echolocation task supplied us with a better understanding of the processes behind target detection and discrimination capabilities. The study of echolocation provides an interesting guideline to the evolution of sensory function and behavior (Surlykke & Nachtigall 2014). Often, the dolphin correctly reported whether or not the echoes matched those from the standard target (the aluminum sphere), indicating the presence of that target and no other (Harley 2008). In spite of the trials being made in a confined environment, the large size of the pool created an acoustic

environment approximating what wild bottlenose dolphins might encounter swimming freely when approaching prey in a shallow waters (Quintana-Rizzo et al. 2006). We therefore believe the conclusions drawn here has some bearing to how wild dolphins would behave.

In the following we discuss how bottlenose dolphins scan the environment to make a decision and thus which performance strategies they adopted to solve the discrimination task. We also compare the performance in an identical echolocation task for porpoises (Wisniewska et al. 2012). Just as porpoises, dolphins have an active and acute control over their sonar signals (Wisniewska et al. 2014), even though the signals are different in both temporal and frequency structure (Surlykke and Nacthigall 2014).

4.1. Task performance and behavior

Free-ranging echolocation toothed whales produce a sound, listens to it and analyze echoes that reflect from the surroundings (Maltby et al. 2010). In the present study the performance during the discrimination was generally high, but decreased when the dolphins were presented with targets giving similar echo spectra, as happened before with the harbor porpoises in Wisniewska et al. (2012). They suggested that spectral cues in particular were used by the porpoises to distinguish materials (Wisniewska et al. 2012) and our findings corroborate this for dolphins. As shown in the results one of the dolphins used the same strategy in all sessions, showing a curving approach for the decision making. This could be explained by some strategy adopted by other cetaceans swimming in circles to surround schools of fish or prey (Benoit-Bird, et al. 2009). This happened with one of the porpoises in Wisniewska et al. (2012) which frequently made curving approaches to the targets, covering larger distances and contributing to the longer trial durations. This indicates that in both species there are differences between each individual in the way of performing and approaching to the target. Auditory cues related to timing, direction, and spectral composition of the objects allows toothed whales to perceive, locate and recognize potential prey and obstacles (Pollak and Casseday, 1989; Thomas et al., 2004) and distinguish echoes from preferred prey (Au, 1993; Au et al., 2009).

In the case of the harbor porpoises, they made mistakes in 1.5–4% of trials with the PVC comparison target, 3–5% of trials with the brass target and 5–43% of trials with the steel target (Wisniewska et al. 2012). Thus, their errors percentages are lower than for both dolphins, and for all types of material. The better performance by the porpoises could be

explained by them having been trained in many previous echolocation tasks, whereas the dolphins used here had never been trained in such contexts. Or, our study may indicate that and maybe porpoises are better in solving echolocation tasks than what is usually assumed.

The difficulty for both animals increased when discriminating the steel and aluminum spheres, for which the echoes had similar spectra due to the smaller impedance differences between these materials (Au, 1993).

Due to the difficulty of the task each dolphin chose a side bias strategy (Kaplan et al. 2019) for the steel target, each of them with a different side. The dolphins would only pick the right ball when the aluminum one was randomly in the side that they were more likely to choose (Figure 9c). They decided to go for the same side in each of the trials, despite there was no reward. Regardless of the correct or incorrect ball. This may be due to the difficulty to differentiate the targets, understanding that at some point the aluminum target would be in that side and they would have a reward. Notably, many cetaceans demonstrate a significant right-side bias in foraging behaviours (Kaplan et al. 2019).

Although in both experiments the animals did not have a time limit for completing the discrimination, they would take 10–15s to complete it in the porpoises and 9-10s in the dolphins, in an approximate distance for both of 12m. The way an animal spends time examining targets in a discrimination task says something about the complexity of the task and the strategy adopted (Wisniewska et al. 2012).

Bottlenose dolphins as broadband echolocators were expected to perform better as a result of having more spectral information to work on, in comparison with the harbor porpoises which are narrow-band high-frequency echolocators. These results show that there are clear differences between individuals of the same species in terms of their ability to discriminate and use echolocation. Thus, as the results vary interspecifically too in the porpoises, differences might not be so wide but could be attributed to the actions of each individual.

Dolphins and harbor porpoises in detection and discrimination experiments demonstrated that they both increase the number of clicks and therefore the sampling effort when the task becomes more difficult (Au et al., 1982, Kastelein et al., 2008). As shown in bats accuracy of target localization increases with the number of “pulses” per group (Sändig et al. 2014). We only found a link between sampling effort, regarding scanning and target

material in one of the dolphins, but our sample size was too low to detect this, and get significant results as happened previously with the porpoises in Wisniewska et al. 2012.

4.2 Performance and target strength of the different materials

The aluminum sphere (the standard one), gives a rather even temporal signature, whilst the plastic gives a more complicated echo and lot of notches in the spectrum (Figure 8). This supplies many spectral and temporal cues for the animals to distinguish between them. For the brass vs. aluminum, the difference is less subtle both in time and frequency domain, making the task harder for one of the dolphins (M1), even though the other animal (F1) performed the same as with the plastic sphere. For steel sphere, the signatures of both materials were very similar and therefore the animals had a really hard time to decide which was the correct answer, reducing their success to chance level (50%) in both animals.

4.3 Scanning behaviour

Our dolphins combined buzzes with horizontal (Schevill and Lawrence, 1956) and rotational head movements. These movements became pronounced when the dolphin was within the last meters from the target, as has also been previously observed in fish reward trials (Norris et al., 1961). The same scanning was repeated with our dolphins when closing in on the targets. Dolphins when searching for prey and orienting themselves in space, like the bats in Seibert et al. (2013), move their sonar beam in all directions, often alternately back and forth as bottlenose dolphins did in this study. They also produced sequences without or irregular scanning motions. When approaching the array, the scanning movements amplitude decreased (Seibert et al. 2013).

An average of eight scans (i.e. four scans per target) was made during one trial for the porpoises (Wisniewska et al. 2012). This is twice as many scans made by the dolphins, which on average have four scans per trial. This average is the number of scans before the dolphins start buzzing, and the animal focus on a same target until snout is in contact, even if is not the correct one, assuming that is the moment they take the decision. This anticipatory behavior is surprising, as the animal has plenty of time to change target to the correct one. The animals are not performing any extra scans during incorrect trials, even though they would seemingly have time for it. We hypothesize that dolphins as broadband echolocators, decrease the number of scans back and forth to the targets, reducing the inspection with the sonar beam to collect all information required to build

their spatial image of the surroundings. In bats, differences in the scanning pattern showed that the scanning behavior depended on the echolocation task that was performed (Seibert et al. 2013).

How an echolocator animal makes decisions in a free-moving environment is a subject of much interest. The process involves weighing the sources of information, including not only the current context (Prat & Yovel 2020) but also previous experiences. Poor performance could be in view of the fact that subjects were not used to perform in discrimination tasks, and had never before participated in an echolocating experiment under blinded conditions. We do not have data on echolocation rates before and after the experiment with what is normal or not to assume is because they were not used to echolocate.

Nevertheless, laboratory experiments are limited to very specific situations, and it could be a simple difference in animals that are under human care and animals with previous experience echolocating in wild.

5 CONCLUSIONS

We observed clear differences between individuals of the same species in terms of ability to discriminate and use echolocation, but similar interspecies performance in relation to the materials chosen with the difficulty of the task.

Surprisingly dolphins performed poorer than harbour porpoises. It is not known if this is because the dolphins had no history of echolocation training like the porpoises did, or if porpoise sonar is better than assumed. Maybe we are exaggerating a bit the biosonar virtues of dolphins compared to porpoises. Even though dolphin clicks have a larger bandwidth, the bandwidth of porpoise clicks is still 30-40 kHz, which may give them sufficient information about subtle differences in target composition.

Distance of start buzzing is surprisingly close to the target if you compare to other echolocators. Harbour porpoises start buzzing around a meter from the target, whereas the dolphins started buzzing at 40-80 cm range. As the dolphin keep swimming towards the target it is buzzing at, we can use the buzz as a proxy for the distance at which the animal has decided which target to choose.

6 SOCIETAL AND ETHICAL CONSIDERATIONS

All applicable international, national and institutional guidelines for the care and use of animals were followed. Experiments were made under a permit from Fundación Oceanográfica, Valencia, permit nr. OCE-1-22. This experiment was carried out with permission from the Loro Parque and Loro Parque Foundation, owners of the dolphins used in this study.

7 ACKNOWLEDGEMENTS

I am very grateful to S.T. Ortiz, A.B. Smith, M. Wahlberg, A. von Bayern for helpful comments on an early draft of the manuscript and supervision during the whole project and the staff at Loro Parque, Tenerife for help with the training and data collection. I thank H. Skov Professor, University of Southern Denmark for developing the video analysis drone program and F. Jakobsen for assisting with it. Also, thanks to C. Moss and M. Amundin for their valuable inputs.

8 REFERENCES

- Altes, R.A., Dankiewicz, L.A., Moore, P.W., & Helweg, D.A. (2003). Multiecho processing by an echolocating dolphin. *Journal of the Acoustical Society of America*, 114, 1155–1166.
- Au, W.W.L. (1993). The sonar of dolphins. *Springer-Verlag*, New York.
- Au, W.W.L., & Benoit-Bird, K.J. (2003). Automatic gain control in the echolocation system of dolphins. *Nature*, 423, 861–863.
- Au, W.W., Penner, R.H., & Kadane, J. (1982). Acoustic behavior of echolocating Atlantic bottlenose dolphins. *The Journal of the Acoustical Society of America*, 71, 1269-1275.
- Beedholm, K., Malinka, C., Ladegaard, M., & Madsen, P.T. (2021). Do echolocating toothed whales direct their acoustic gaze on-or off-target in a static detection task? *The Journal of the Acoustical Society of America*, 149, 581-590.
- Benoit-Bird, K.J., & Au, W.W. (2009). Cooperative prey herding by the pelagic dolphin, *Stenella longirostris*. *The Journal of the Acoustical Society of America*, 125, 125-137.

- Branstetter, B. K., Van Alstyne, K. R., Strahan, M. G., Tormey, M. N., Wu, T., Breitenstein, R. A., ... & Xitco Jr, M. J. (2020). Spectral cues and temporal integration during cylinder echo discrimination by bottlenose dolphins (*Tursiops truncatus*). *The Journal of the Acoustical Society of America*, 148, 614-626.
- Breitenstein, R. A., ... & Xitco Jr, M. J. (2020). Spectral cues and temporal integration during cylinder echo discrimination by bottlenose dolphins (*Tursiops truncatus*). *The Journal of the Acoustical Society of America*, 148, 614-626.
- Cranford, T. W., Amundin, M., & Norris, K. S. (1996). Functional morphology and homology in the odontocete nasal complex: Implications for sound generation. *Journal of Morphology*, 228, 223–285.
- DeLong, C. M., Au, W. W. L., Harley, H. E., Roitblat, H. L., & Pytka, L. (2007). Human listeners provide insights into echo features used by dolphins (*Tursiops truncatus*) to discriminate among objects. *Journal of Comparative Psychology*, 121, 306–319.
- Doh, Y., Delfour, F., Augier, E., Glotin, H., Graff, C., & Adam, O. (2018). Bottlenose dolphin (*Tursiops truncatus*) sonar slacks off before touching a non-alimentary target. *Behavioural processes*, 157, 337-345.
- Fenton, B., Jensen, F.H., Kalko, E. K. V. , & Tyack, P.L. (2014). Chapter 2: Sonar Signals of Bats and Toothed Whales. A. Surlykke et al. (eds.), *Biosonar, Springer Handbook of Auditory Research* 51, 231, Springer-Verlag, New York.
- Gannon, D. P., Barros, N. B., Nowacek, D. P., Read, A. J., Waples, D. M., & Wells, R. S. (2005). Prey detection by bottlenose dolphins, *Tursiops truncatus*: an experimental test of the passive listening hypothesis. *Animal Behaviour*, 69, 709-720.
- Griffin, D. R., Webster, F. A., & Michael, C. R. (1960). The echolocation of flying insects by bats. *Animal behaviour*, 8, 141-154.
- Griffin, D. R. (1974). *Listening in the Dark: The Acoustic Orientation of Bats and Men*. *Dover Publications*, NY.
- Harley, H. E., & DeLong, C. M. (2008). Echoic object recognition by the bottlenose dolphin. *Comparative Cognition & Behavior Reviews*, 3.

- Helweg, D.A., Au, W.W.L., Roitblat, H.L., & Nachtigall, P.E. (1996). Acoustic basis for recognition of aspect-dependent three-dimensional targets by an echolocating bottlenose dolphin. *Journal of the Acoustical Society of America*, 99, 2409-2420.
- Houser, D.S., Helweg, D.A., & Moore, P.W.B. (1999). Classification of dolphin echolocation clicks by energy and frequency distributions. *Journal of the Acoustical Society of America*, 106, 1579–1585.
- Johnson, M. (2014) Chapter 7: On-Animal Methods for Studying Echolocation in Free-Ranging Animals. *Biosonar, Springer Handbook of Auditory Research* 51, 231 , Springer-Verlag New York
- Kaplan, J. D., Goodrich, S. Y., Melillo-Sweeting, K., & Reiss, D. (2019). *Behavioural laterality in foraging bottlenose dolphins (Tursiops truncatus)*. *Royal Society Open Science*, 6, 190929.
- Kastelein, R.A., Verlaan, M., & Jennings, N. (2008). Number and duration of echolocation click trains produced by a harbor porpoise (*Phocoena phocoena*) in relation to target and performance. *The Journal of the Acoustical Society of America*, 124, 40-43.
- Klemas, V.V. (2013). Remote sensing and navigation in the animal world: an overview. *Sensor Review* 33, 3-13.
- Ladegaard, M., Mulsow, J., Houser, D. S., Jensen, F.H., Johnson, M., Madsen, P.T., & Finneran, J. J. (2019). Dolphin echolocation behaviour during active long-range target approaches. *Journal of Experimental Biology*, 222, jeb189217.
- Liling, Dupeng, & Zhangzhaohui (2019). Bottlenose dolphin echolocation clicks characteristics acquisition and analysis. *2019 IEEE International Conference on Signal Processing, Communications and Computing (ICSPCC)*, 1-4.
- Madsen, P.T., & Surlykke, A. (2013). Functional convergence in bat and toothed whale biosonars. *Physiology*, 28, 276–283.
- Madsen, P.T., & Wahlberg, M. (2007). Recording and quantification of ultrasonic echolocation clicks from free-ranging toothed whales. *Deep-Sea Research Part I: Oceanographic Research Papers*, 54, 1421–1444

- Madsen, P.T., Carder, D.A., Au, W.W.L., Nachtigall, P.E., Møhl, B., & Ridgway, S.H. (2003). Sound production in neonate sperm whales. *Journal of the Acoustical Society of America*, 113, 2988–2991
- Madsen, P.T., Jensen, F.H., Carder, D., & Ridgway, S. (2011). Dolphin whistles: A functional misnomer revealed by heliox breathing. *Biology Letters*, 8, 211–213.
- Maltby, A., Jones, K.E., & Jones, G. (2010). Understanding the evolutionary origin and diversification of bat echolocation calls. In *Handbook of Behavioral Neuroscience* (Vol. 19, pp. 37-47). Elsevier, New York.
- Møhl, B., Wahlberg, M., Madsen, P.T., Heerfordt, A., & Lund, A. (2000). Sperm whale clicks: Directionality and source level revisited. *Journal of the Acoustical Society of America*, 107, 638–648.
- Moore, P.W.B., Hall, R.W., Friedl, W.A., & Nachtigall, P.E. (1984). The critical interval in dolphin echolocation: What is it? *Journal of the Acoustical Society of America*, 76, 314–317.
- Moss, C.F., Chiu, C., & Surlykke, A. (2011). Adaptive vocal behavior drives perception by echolocation in bats. *Current Opinion in Neurobiology*, 21, 645–652.
- Moss, C.F., Chiu, C., & Moore, P.W. (2014) Chapter 8: Analysis of Natural Scenes by Echolocation in Bats and Dolphins.- A. Surlykke et al. (eds.), *Biosonar, Springer Handbook of Auditory Research* 51, 231, Springer-Verlag, New York.
- Muller, M.W., Allen, J.S., Au, W.W.L., & Nachtigall, P. E. (2008). Time-frequency analysis and modeling of the backscatter of categorized dolphin echolocation clicks for target discrimination. *Journal of the Acoustical Society of America* , 124, 657–666.
- Pack, A.A., & Herman, L.M. (1995). Sensory integration in the bottlenosed dolphin: Immediate recognition of complex shapes across the senses of echolocation and vision. *The Journal of the Acoustical Society of America*, 98, 722-733.
- Pollak, G.D., & Casseday, J.H. (1989). Tonotopic organization. In *The Neural Basis of Echolocation in Bats*. Springer Verlag, New York. 25-39
- Prat, Y., & Yovel, Y. (2020). Decision making in foraging bats. *Current Opinion in Neurobiology*, 60, 169-175.

- Quintana-Rizzo, E., Mann, D.A., & Wells, R.S. (2006). Estimated communication range of social sounds used by bottlenose dolphins (*Tursiops truncatus*). *The Journal of the Acoustical Society of America*, 120, 1671-1683.
- Rasmussen, M.H., Miller, L.A., & Au, W.W. L. (2002). Source levels of clicks from free-ranging white beaked dolphins (*Lagenorhynchus albirostris* Gray 1846) recorded in Icelandic waters. *Journal of the Acoustical Society of America*, 111, 1122–1125.
- Sändig, S., Schnitzler, H.U., & Denzinger, A. (2014). Echolocation behaviour of the big brown bat (*Eptesicus fuscus*) in an obstacle avoidance task of increasing difficulty. *Journal of Experimental Biology*, 217, 2876-2884.
- Seibert, A.M., Koblitz, J.C., Denzinger, A., & Schnitzler, H.U. (2013). Scanning behavior in echolocating common pipistrelle bats (*Pipistrellus pipistrellus*). *PLoS one*, 8, e60752.
- Simmons, J.A., Houser, D., & Kloepper, L. (2014) Chapter 6: Localization and Classification of Targets by Echolocating Bats and Dolphins. Surlykke et al. (eds.), *Biosonar, Springer Handbook of Auditory Research* 51, 231, Springer-Verlag New York
- Surlykke, A.M. & Nachtigall, P.E. (2014) Chapter 1: Biosonar of Bats and Toothed Whales: An Overview Annemarie- A. Surlykke et al. (eds.), *Biosonar, Springer Handbook of Auditory Research* 51, 231, Springer-Verlag New York
- Thomas, J.A., Moss, C.F., & Vater, M. (Eds.). (2004). Echolocation in bats and dolphins. *University of Chicago Press*, Chicago.
- Wisniewska, D.M., Johnson, M., Beedholm, K., Wahlberg, M., & Madsen, P.T. (2012). Acoustic gaze adjustments during active target selection in echolocating porpoises. *Journal of Experimental Biology*, 215, 4358-4373.
- Wisniewska, D.M., Ratcliffe, J.M., Beedholm, K., Christensen, C.B., Johnson, M., Koblitz, J.C., ... & Madsen, P.T. (2015). Range-dependent flexibility in the acoustic field of view of echolocating porpoises (*Phocoena phocoena*). *Elife*, 4, e05651.
- Wohlgemuth, M.J., Kothari, N.B., & Moss, C.F. (2016). Action enhances acoustic cues for 3-D target localization by echolocating bats. *PLoS biology*, 14, e1002544.