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Construction of spatial features in echolocating bottlenose dolphins (*Tursiops truncatus*)

A Dissertation submitted in partial satisfaction of the requirements
for the degree Doctor of Philosophy

in

Experimental Psychology

by

Katie Anna Christman

Committee in charge:

Timothy Gentner, Chair
Simone Baumann-Pickering
Timothy Brady
James Finneran
John Wixted

2024

The Dissertation of Katie Anna Christman is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

University of California San Diego

2024

DEDICATION

To Kyle, for never letting me settle.

EPIGRAPH

in omnia paratus

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ABSTRACT OF THE DISSERTATION

Construction of spatial features in echolocating bottlenose dolphins (*Tursiops truncatus*)

by

Katie Anna Christman

Doctor of Philosophy in Experimental Psychology

University of California San Diego, 2024

Professor Timothy Gentner, Chair

Dolphins use an advanced biosonar system to accurately navigate and forage in their environment. They have the unique capability to rapidly detect and classify underwater targets in a complex acoustic environment and do so more precisely than man-made underwater sonars. Dolphins use the fine-scale temporal and spectral features of the echo-waveforms to determine different attributes of the target and rely on echo-delay, the time between their emitted sound

pulse “click” and the return of the reflected echo to determine the range to a target. In this dissertation, phantom echoes are used to determine the effect that changes in mean echo-delay, i.e. range, have on echo-delay discrimination abilities and which fine-scale acoustic features dolphins use to create a coherent mental representation of a target.

In Chapter 1, the dolphin’s ability to detect changes in echo-delay as a function of range was determined. Chapter 2 then tested the dolphin’s ability to discriminate between the ranges of two targets at different mean ranges. In this experiment targets were presented successively, meaning, the dolphin had to hold the range of one target in memory while they compared it to the second target. Chapters 1 and 2 conclude that as mean range increases greater than 10 m the dolphin’s ability to discriminate between echo-delays degrades rapidly.

Chapter 3 explores the possibility of the dolphin using spectral cues to determine the difference in range between two targets that are presented simultaneously. First, the dolphin’s peripheral auditory system was modeled to determine available spectral cues. The dolphin’s ability to discriminate the difference in range between two targets was then tested and compared under successive and simultaneous conditions. Although spectral cues were available to the dolphin, the results from the simultaneous condition suggest limited improvement when compared to the successive condition. Lastly, Chapter 4 focuses on the auditory perceived cues the dolphin may use to convert fine-scale spectral and temporal information into a coherent mental representation. By manipulating echo-phase information the results suggest that for fine-scale echo-delays the dolphins may use a pitch cue to discriminate between complex targets.

INTRODUCTION

Dolphins have the unique capability to precisely navigate and forage in their environment through an advanced biosonar system. Dolphins emit high frequency (up to 130 kHz) short duration (~50-80 µs) pulses, known as “clicks”, that interact with their surroundings and return echoes (Au, 1993). Dolphins use a series of temporal, spectral, and amplitude cues from the return echoes to accurately construct a representation of their external world. By using these cues echolocating dolphins can quickly detect and classify objects in an acoustically complex environment at a performance rate higher than man-made sonar systems (Roitblat et al., 1995; Moore, 1997; Vishnu et al., 2022).

Many studies have determined that dolphins use echo-delay to determine the distance or range to a target (Murchison, 1980b; Au, 1993). Echo-delay is defined as the time it takes for the emitted signal to travel to the object and for the echo to return to the dolphin. The large differences in echo-delay that allow the dolphin to determine range are often referred to as “large spatial features”. Although echo-delay allows the dolphin to gauge the range to a target, this temporal cue carries little insight about the physical attributes of the target. The physical attributes of a target are thought to be decoded using the fine structure of the echo waveform which allows the dolphin to perceive “small spatial features”. Small spatial features of a target create unique spectral information that is produced by their acoustic reflection (Au and Pawloski, 1992; Branstetter et al., 2020). Several experiments have quantified the dolphin’s ability to detect and discriminate targets with differing fine scale temporal and spectral features (Au et al., 1980; Au and Turl, 1991; Au and Pawloski, 1992; Au and Nachtigall, 1995; Pack and Herman, 1995; Herman et al., 1998; Delong et al., 2008; Branstetter et al., 2020). However, little is known about the effects changes in range (i.e. echo-delay) have on the dolphin’s ability to accurately classify targets and the underlying mechanisms used by the dolphin to decode the fine scale temporal and spectral features into useable information (i.e. a coherent mental representation of the target).

Phantom echo generators (PEGs) have been used for over five decades to investigate animal biosonar. The first PEGs were used to study echolocating bats in the early 1970s (Simmons, 1973). A decade later, a PEG was designed to investigate dolphin biosonar (Au et al., 1987; Aubauer and Au, 1998; Finneran et al., 2016c). PEGs extract the amplitude and timing information of the animals emitted biosonar signal which is then used to generate a phantom echo that is delayed in time and projected back to the animal giving the appearance of an echo from a more distant target. PEGs are a useful tool to studying biosonar because acoustic features of the echo, such as amplitude and timing, can be manipulated independently.

Additionally, within the last two decades, studies have paired behavioral PEG tasks with the collection of auditory evoked potentials (AEPs). AEPs have become a common technique to non-invasively study the auditory system of echolocating dolphins (Supin et al., 2001; Houser and Finneran, 2006; Nachtigall et al., 2008; Pacini et al., 2011; Li et al., 2012). The auditory brainstem response (ABR), a specific AEP generated by structures ascending from the auditory nerve to the midbrain, can be recorded rapidly and non-invasively. The ABR comprises the first neural responses to an auditory stimulus and allows waveforms to be detected when using surface electrodes (Burkard and Don, 2007). Therefore, the ABR can be used to analyze how changes in amplitude and inter-click interval (ICI) can affect perceived signal-to-noise ratios (SNRs) during echolocation.

In this dissertation, a series of behavioral experiments were conducted to determine the effect changes in mean echo-delay have on the dolphin’s echo-delay discrimination abilities and to better understand how dolphins decode fine-scale acoustic features. In Chapter 1, the dolphin’s ability to detect a 20 μs “jitter” delay is tested at 17 different mean echo-delays simulating ranges from 2.5 – 20 m. Relative echo level (REL), defined as the level of the echo at the dolphin relative to the click source level in terms of dB, was held constant in order to equate performance differences to changes in echo-delay and not associated SNRs. Additionally, AEPs were collected to determine if changes in performance corresponded to lower perceptible SNRs due to forward masking from the dolphin’s emitted click on the return echo. Chapter 2 determines range discrimination thresholds at seven mean echo-delays simulating ranges from 1.75 – 20 m. In this chapter, dolphins were trained to inspect two simulated targets that are presented successively and report which target has the shorter echo-delay. Similar to Chapter 1, REL was held constant for all echo-delays. The successive presentation of targets requires the dolphin to hold the range information of one target in memory as they compare it to the second target. Chapters 1 and 2 emphasize the effects that manipulating large spatial features have on echo-delay discrimination abilities while chapters 3 and 4 focus on the dolphin’s ability to discriminate and decode small-scale echo-delays or small spatial features. Chapter 3 investigates the spectral cues available to the dolphin during a range discrimination task if the targets are presented simultaneously versus successively as they were in Chapter 2. A model of the dolphin peripheral auditory system was first built to determine available spectral cues and then dolphin’s range discrimination abilities were tested and compared between successive and simultaneous conditions.

Chapter 4 further examines the acoustic features the dolphin uses to determine small spatial features of a target. In this experiment dolphins are trained to identify when the time between echo-highlights, known as the inter-highlight interval (IHI), increases in duration. The experiment is conducted under a constant phase and a random phase condition. The random phase condition removes certain acoustic cues available to the dolphin to determine whether those cues are paramount in the dolphin’s ability to accurately discriminate between targets.

CHAPTER 1 The effects of range on a jitter discrimination task in echolocating bottlenose dolphins (*Tursiops truncatus)*

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ABSTRACT:

There are limited studies examining how changes in target range may affect dolphin biosonar discrimination. In the present study, the ability of bottlenose dolphins to detect changes in echo-delay was measured as a function of mean echo-delay (simulated target range). The dolphin's task was to produce a conditioned acoustic response when phantom echoes with a fixed echo-delay began to "jitter" by ±10 μs on successive presentations. Dolphins' detection abilities were tested at 17 different mean echo-delays, simulating target ranges from 2.5 – 20 m. Phantom echo level relative to the emitted click was held constant. Auditory evoked potentials to the self-heard click and returning echo were also collected. Results showed that jitter detection performance decreased as range decreased below ~5 m, as a result of reduced echo signal-to-noise ratio caused by increasing forward masking of the echo by the emitted click. Performance also decreased for ranges greater than 10 m, despite perceived echo amplitude increasing with range from progressive release from forward masking as echo-delay increased. This result suggests that increases in echo-delay interfere with the dolphin's echo-delay discrimination abilities.

Keywords: Dolphin, Echolocation, Biosonar, Target ranging

I. INTRODUCTION

Dolphins have evolved to accurately navigate and forage using an advanced biosonar system. Using spectral and temporal cues, dolphins can rapidly detect and classify underwater objects in complex acoustic environments more accurately than current man-made underwater sonars (Au, 1993; Branstetter et al., 2020; Finneran et al., 2020; Vishnu et al., 2022). Dolphins use echo-delay, the time between emission of each sound pulse (“click”) and the return of the corresponding echo, to determine the range of a target (Murchison, 1980b; Au, 1993). Fine-scale temporal and spectral features are used to determine physical attributes of the target (Au et al., 1980; Au and Turl, 1991; Au and Pawloski, 1992; Au and Nachtigall, 1995; Branstetter et al., 2020). Numerous studies have been conducted to quantify the dolphin’s capability to detect and discriminate underwater objects (Pack and Herman, 1995; Herman et al., 1998; Delong et al., 2008), or discriminate between echoes using fine-scale temporal or spectral features (Au and Pawloski, 1992; Branstetter et al., 2020). However, few studies have investigated how the distance to an object (target range, i.e., echo-delay) affects the dolphin’s ability to detect and classify objects.

Murchison (1980b) examined the effects of target range on a dolphin’s ability to detect an object and to determine the range resolution between two target ranges. In the maximum detection range experiment the dolphin detected targets with two differing target strengths (TSs), -28 and -42 dB. Detection hit rate began to decline at 66 m for the -42 dB target and 77 m for the -28 dB target, suggesting target detection declined as range increased due to the decrease in received echo level. In the range resolution experiment, a dolphin was trained to identify the closer of two spherical foam targets at slightly different ranges. The range of the closer target varied from 1 – 7 m, and target strengths were -34 dB, approximately 35 dB above a normal hearing dolphin's echo detection threshold when the target range is 20 m [see Christman et al. (2024)], meaning the returning echoes were audible at all ranges. However, the dolphin's performance decreased with an increase in range. Results from this experiment suggest that as range increases the increasing echo-delay causes a decrease in the dolphin's echo-delay discrimination abilities.

Penner (1988) trained dolphins to detect a target at five different ranges from 40 – 120 m. The primary finding was that expectation of target range could affect performance. However, the data also showed that, even when range was not varied across sessions or blocks, the dolphin's detection ability began to decline as the range increased towards 120 m, due to a decrease in received echo level primarily caused by geometric spreading loss.

Finneran et al. (2013) investigated the effects of range and relative echo level (REL) on the dolphin's ability to perform a change detection task using phantom echoes. REL can be defined as the level of the echo at the dolphin relative to the click source level in terms of dB. The change detection task was presented at different ranges spanning from 2.5 – 80 m. Five different RELs were tested for each range spanning from -50 dB to -90 dB. Additionally, a range-dependent REL condition was tested that simulated geometric spreading loss associated with range. During this condition as REL decreased at the longest ranges (56 and 80 m) performance decreased most likely due to the lower received echo levels at the longer ranges. Performance also decreased at the -90 dB REL condition when the range decreased below 10 m due to the effects of forward masking on the received echo from the dolphin's outgoing click.

Finneran (2013) discovered that during an echo change detection task for ranges greater than 75 m dolphins begin to use "packets", emitting a burst of clicks and waiting for the corresponding echoes to return before sending out the next burst or packets. The dolphins' change detection ability was tested at ranges from 25 – 300 m. When echo level was held constant between the different ranges tested a decrease in performance was observed for the shortest ranges (< 50 m) and for the longer ranges tested (>350 m). However, when echo level was manipulated to simulate geometric spreading loss echo change detection performance began to decrease at the longer ranges (>100 m) and varied depending on the simulated TS.

In summary, several past experiments indicate that the dolphin's ability to detect targets and identify changes in a target can be affected by the range (Murchison, 1980b; Penner, 1988; Finneran, 2013; Finneran et al., 2013). In most cases, the decrease in detection ability can be explained by the decrease in echo level with increasing range resulting from geometric spreading loss. However, some studies with fixed relative echo level still show a decrease in performance as range and echo-delay increase. Because dolphins operating at short ranges typically emit a single click and wait for the corresponding echo to return before emitting another click (Evans and Powell, 1966; Morozov et al., 1972; Au et al., 1974; Au, 1980; Au, 1993), increasing the echo-delay also increases the time interval between successive clicks or echoes (the inter-click interval, ICI). Previous studies have shown that dolphins can combine information across multiple echoes to improve detection performance (Altes et al., 2003). The extent to which increasing echo-delay or the time interval between successive echoes might interfere with this process and limit detection or discrimination performance is unknown.

The primary goal of the current experiment was to determine the effects of range when REL was held constant during an echo-delay discrimination task. Holding REL constant removes the confound of changes in echo level with range. Previous jitter-delay discrimination experiments report jitter-delay thresholds below 1 μs at a 10 m range and performance above ~95% correct detection for a jitter-delay at 20 µs (Finneran et al., 2023). The current experiment tested the dolphin's ability to detect a 20 µs jitter-delay at 17 different echo-delays, simulating ranges from 2.5 – 20 m. Additionally, auditory evoked potentials (AEPs) in response to the dolphin's emitted click and returning echo were recorded to see if changes in performance could be explained by effects of forward masking of the received echo by the emitted click.

II. METHODS

A. Subject and test environment

The subjects and test environment were identical to Finneran et al. (2023). The subjects were two male bottlenose dolphins, Comet (COM) and Spout (SPO) ages 7 and 6 respectively, at the time of the experiment. COM and SPO both had normal hearing with an upper frequency hearing limit greater than 120 kHz [see Strahan et al. (2020)]. Additionally, both dolphins had extensive experience participating in psychophysical experiments with phantom echoes [see Finneran et al., (2020) and Finneran et al. (2023)].

Testing occurred at the US Navy Marine Mammal Program in San Diego Bay. During each trial, dolphins positioned themselves on a "biteplate" that was ~1 m below the water's surface. The biteplate was supported by an aluminum frame that was constructed to ensure there were no obstructions surrounding the dolphin's melon or lower jaw. The biteplate was oriented so that the dolphin faced San Diego Bay looking through a clean netted panel. Two piezoelectric transducers (TC4013, Reson Inc., Slangerup, Denmark) were attached to the biteplate via polyvinyl chloride (PVC) posts. One transducer acted as the click receiver and was ~0.7 m from the dolphin and in line with the dolphin's melon. The second transducer, also ~0.7

m from the dolphin, was in line with the dolphin’s lower jaw and acted as the echo projector. Mean water depth in the area was ~10 m and ±10° azimuth of the dolphin’s biosonar transmission beam was free from obstructions for ~1 km of distance. Other dolphins, snapping shrimp, and boat traffic were the primary sources of ambient noise in the area. Median ambient noise pressure spectral density levels from 10 – 150 kHz were approximately ~70 dB re 1 $\mu Pa^2/Hz$ and decreased linearly with the logarithm of frequency to ~50 dB re 1 $\mu Pa^2/Hz$.

B. Task description

The subjects participated in a biosonar change detection task similar to Finneran et al., (2020, 2023 #33160). The dolphin’s task began with them stationing on the biteplate and emitting echolocation clicks while listening to returning echoes, then producing a conditioned acoustic response (COM burst pulse and SPO whistle) when the echoes changed from a fixed echo-delay echo (echo A) to a jittering echo-delay (alternating between echo B_1 and B_2 on each consecutive echo). Echo B_1 always had an echo-delay 10 µs greater than echo A, while echo B_2 always had an echo-delay 10 µs less than echo A, creating the 20 µs jitter between the B_1 and B_2 echoes. The dolphins’ ability to detect the 20 µs jitter in echo-delay was tested at 17 different mean echo-delays simulating ranges from 2.5 m to 20 m.

Dolphins participated in 80-100 trials each weekday. Echo change trials consisted of ~80% of the trials while control trials accounted for the remaining ~20%. During an echo change trial the dolphin was presented echo A for 3-8 s randomly at which point the echo would begin jittering between echo B_1 and echo B_2. The jittering echo was presented for 1.5-s. If the dolphin responded at any point during the 1.5-s interval the trial was classified as a *hit*. If the dolphin did not respond during this period the trial was classified as a *miss*. Control trials consisted of echo A being presented to the dolphin randomly between 4.5-9.5-s. The dolphin was required to withhold their response for the entire duration of the trial to be classified as a *correct rejection*. If the dolphin responded during a control trial or prior to the presentation of the jittering echo during a change trial the trial was classified as a *false alarm*. Hits and correct rejections were marked with an underwater acoustic bridge and followed with a fish reward, while misses and false alarms were marked with an underwater acoustic “delta” and followed by no fish reward.

A minimum of 60 trials were conducted for each subject and range combination. Each session began with a ten-trial “warm-up” at the 10 m range to gage motivation for the day; as previous research determined that the COM and SPO were consistently above ~90% correct under these conditions (see Finneran et al., 2020; Finneran et al., 2023). Following the warm-up, the mean echo-delay of the target was changed randomly in five trial blocks. After the completion of ~95 trials, five “cool-down” trials were conducted, under the same conditions as the warm-up trials, to ensure stimulus control and maintain motivation.

C. Echo generation

Phantom echoes were created using the same phantom echo generator (PEG) used for experiments 0-2 in Finneran et al. (2023). The dolphin’s clicks were captured by the click receiver, amplified and filtered (5-200 kHz bandwidth: VP-1000, Reson Inc. and 3C module, Krohn-Hite Corporation, Brockton, MA) then input to an NI PXIe-7852R device (National Instruments, Austin, TX) containing a Virtex-5 LX50 FPGA. The analog click signal was then digitized with 16-bit resolution at ~741 kHz. When the received digitized signal exceeded a pre-determined amplitude threshold, the click waveform was extracted and convolved with a target impulse response function to create the echo-waveform. The echo-waveform was then scaled in amplitude, delayed, and converted to an analog signal. The analog echo waveform was filtered and amplified (5-200 kHz, 3C module, M7600, Krohn-Hite Corps) and used to drive the echo-projector. REL was held constant for all echo-delays tested and was set to ~15 dB above the subjects' echo-detection threshold for a single-highlight echo.

D. AEP recording

AEPs were recorded using three non-invasive gold-plated surface electrodes embedded in suction cups. The non-inverting electrode was placed along the dorsal midline, ~3 cm from the posterior edge of the dolphin's blowhole, the inverting electrode was placed ~1 cm behind the left external auditory meatus, and the common electrode was placed in the water near the dolphin. The electrode signals were input to a biopotential amplifier (ICP511; Grass Technologies, West Warwick, RI), bandpass filtered (300 to 3000Hz), and the potential difference between the non-inverting and inverting electrodes was amplified by 100 dB. The differential electrode signal represented the instantaneous electroencephalogram (EEG). The EEG signal was digitized by the PXI 6368 at 2 MHz at 16 bit and later down-sampled to 100 kHz during analysis. To maintain motivation, the electrodes were worn for about half of the session in blocks of ten trials at varying simulated ranges each session, ensuring enough EEG time "epochs" per simulated range.

E. Analysis

Behavioral performance was quantified by calculating hit rate, false alarm rate, and sensitivity (d′) for each subject and range. Hit rate was calculated by dividing the number of hits by the total number of echo change trials, while false alarm rate was calculated by dividing the number of false alarms by the total number of control trials. To account for response bias for each subject, sensitivity was quantified by calculating d′. To calculate d′, hit rates of 1 were replaced with 1-0.5/N and false alarm rates of 0 were replaced with 0.5/N, where N is equal to the total number of echo-change or control trials for each subject and range (Stanislaw and Todorov, 1999).

ICI, peak-to-peak (p-p) sound pressure level (SPL), center frequency, and (centralized) root mean square (rms) bandwidth for received clicks for each subject and range were calculated with custom software. Clicks were only analyzed if they occurred prior to the dolphin's response for hit and false alarm trials, whereas for correct rejection and miss trials all clicks were included.

Evoked potentials were analyzed for each trial by first identifying 40 ms time epochs that began 2 ms prior to the dolphin's click arriving at the click receiver. For each time epoch, the instantaneous EEG signal was saved and coded with the subject, range, and click SPL. Similar to analysis for the acoustic properties, only epochs that occurred prior to the dolphin's response for hit and false alarm trials were included for EEG analysis, whereas for correct rejection and miss trials all clicks were included for EEG analysis. The EEG epochs were grouped by subject and range and were then binned to include only click SPLs between 217 – 219 dB re 1 μPa, as these click amplitudes were present the most across both subjects and ranges and allowed for the averaging of ~700 epochs or more. The resulting epochs for each subject, range, and click SPL bin were then synchronously averaged. The corresponding auditory brainstem response (ABR) for each click and echo were identified within the averaged EEG waveforms using the estimated time of click generation and echo reception based on the dolphin’s distance (~0.7 m) from the click receiver and echo projector. For each ABR, the P4 and N5 peaks were identified [see Popov and Supin (1990)]. ABR amplitudes and latencies were characterized using the P4-N5 p-p amplitude and N5 peak latency, respectively. Statistical analysis was conducted in R (R Core Team, 2019) using linear models to determine the significance of click and echo ABR amplitude and latencies as a function of range.

III. RESULTS

Figure 1 shows the hit rate, false alarm rate, and sensitivity as functions of range for each subject. Subjects had the highest sensitivity for ranges between 5 and 10 m. Sensitivity decreased quickly as the range increased past 10 m. Sensitivity also decreased when the range was less than 5 m. COM’s overall sensitivity was higher than SPO’s for the majority of ranges tested.

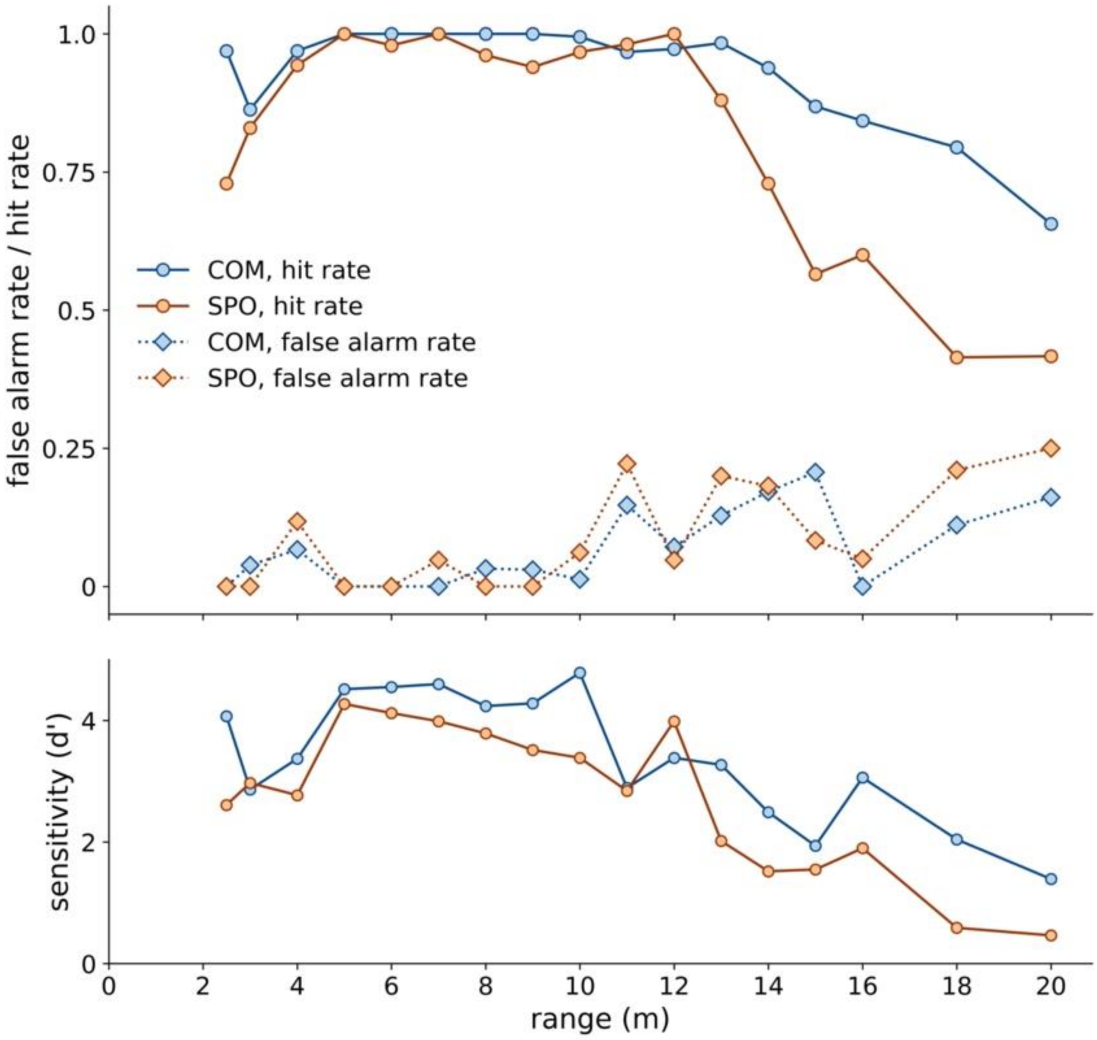

Figure 1.1: Behavioral performance for jitter discrimination as a function of range. Hit rate and false alarm rate (top plot), and corresponding d’ values (bottom plot) for COM (blue) and SPO (orange).Solid lines represent the hit rate while dotted lines represent the false alarm rate.

COM participated in 1,819 trials and SPO participated in 1,514 trials over the course of the experiment. This resulted in 4.0×10^5 clicks being analyzed for COM and 2.6×10^5 clicks being analyzed for SPO. Both subjects mean click waveforms and corresponding spectra were similar to those previously reported for dolphins (Finneran et al., 2020). Corresponding echo waveforms were longer in duration and corresponding spectra had a higher peak frequency as a result of the echo projector transmitting response (Fig. 2).

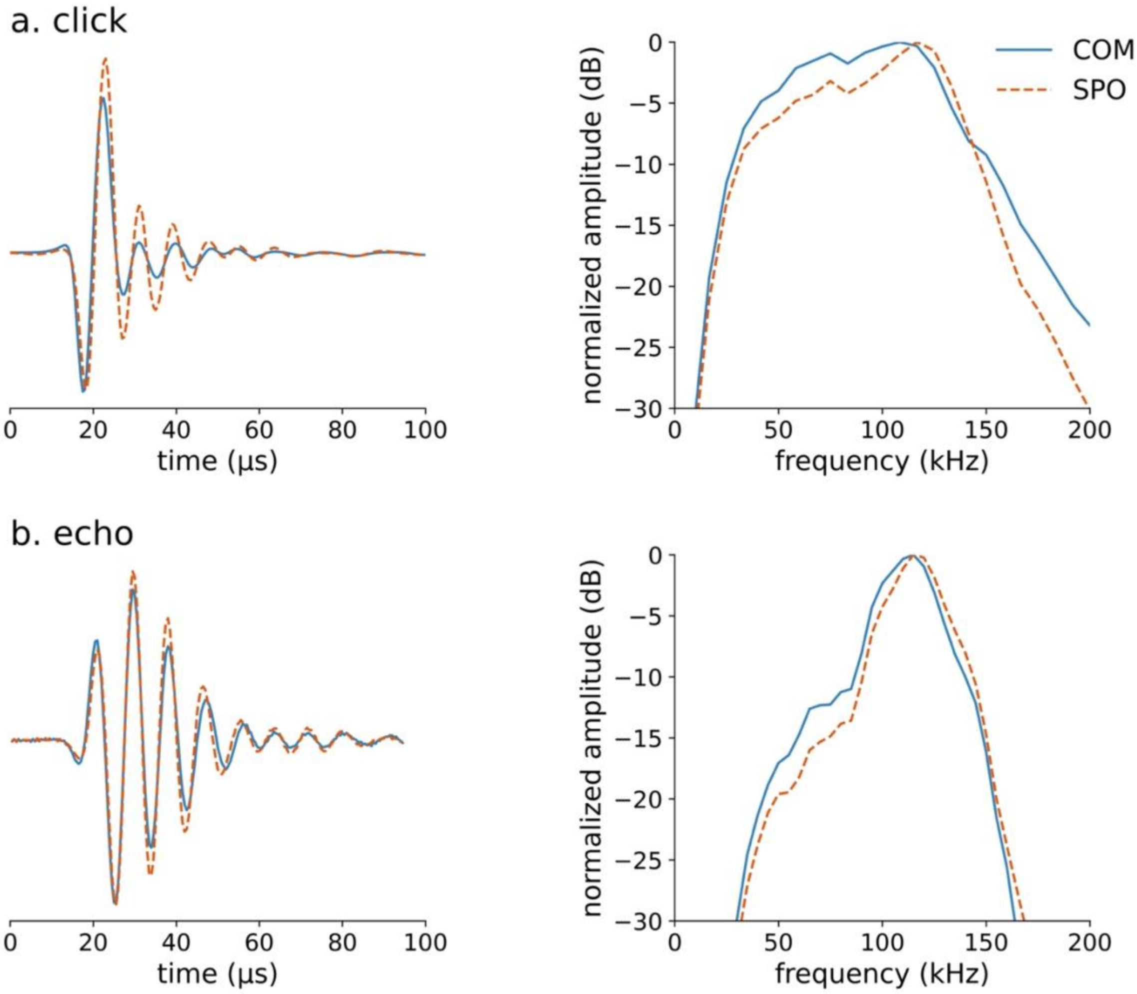

Figure 1.2: Acoustic click and echo waveforms and corresponding spectra. (a) Representative normalized mean click waveforms for COM (blue solid line) and SPO (orange dotted line) and corresponding spectra. (b) Normalized phantom echo waveforms and spectra for COM (blue solid line) and SPO (orange dotted line).

Click acoustic parameters are shown in Figure 3. COM’s ICIs increased with range to ~5 m and then remained steady from 6 – 20 m. In contrast, SPO’s ICIs showed a faster and more consistent increase with range, and were larger and more variable. Additionally, for ranges greater than 6 m for COM and 8 m for SPO, a subset of ICIs were less than the echo-delay for the simulated range being test. For both subjects, p-p SPL increased as range increased, however, this change was slight and only spanned ~3 dB from 2.5 – 20 m. For both subjects, the rate of change of p-p SPL was greater for ranges less than 10 m and began leveling out for ranges greater than 10 m. Additionally, the rate of change of p-p SPL for SPO was greater than for COM. For COM center frequency decreased with an increase in range to 13 m and then remained consistent to 20 m. For SPO center frequency decreased with an increase in range up to 6 m and remained rather consistent from 7 – 20 m. For COM rms bandwidth was consistent from 2.5 – 10 m; for ranges greater than 10 m it increased slightly and became more variable. For SPO rms bandwidth decreased from 2.5 – 4 m and then remained consistent from 5 – 20 m.

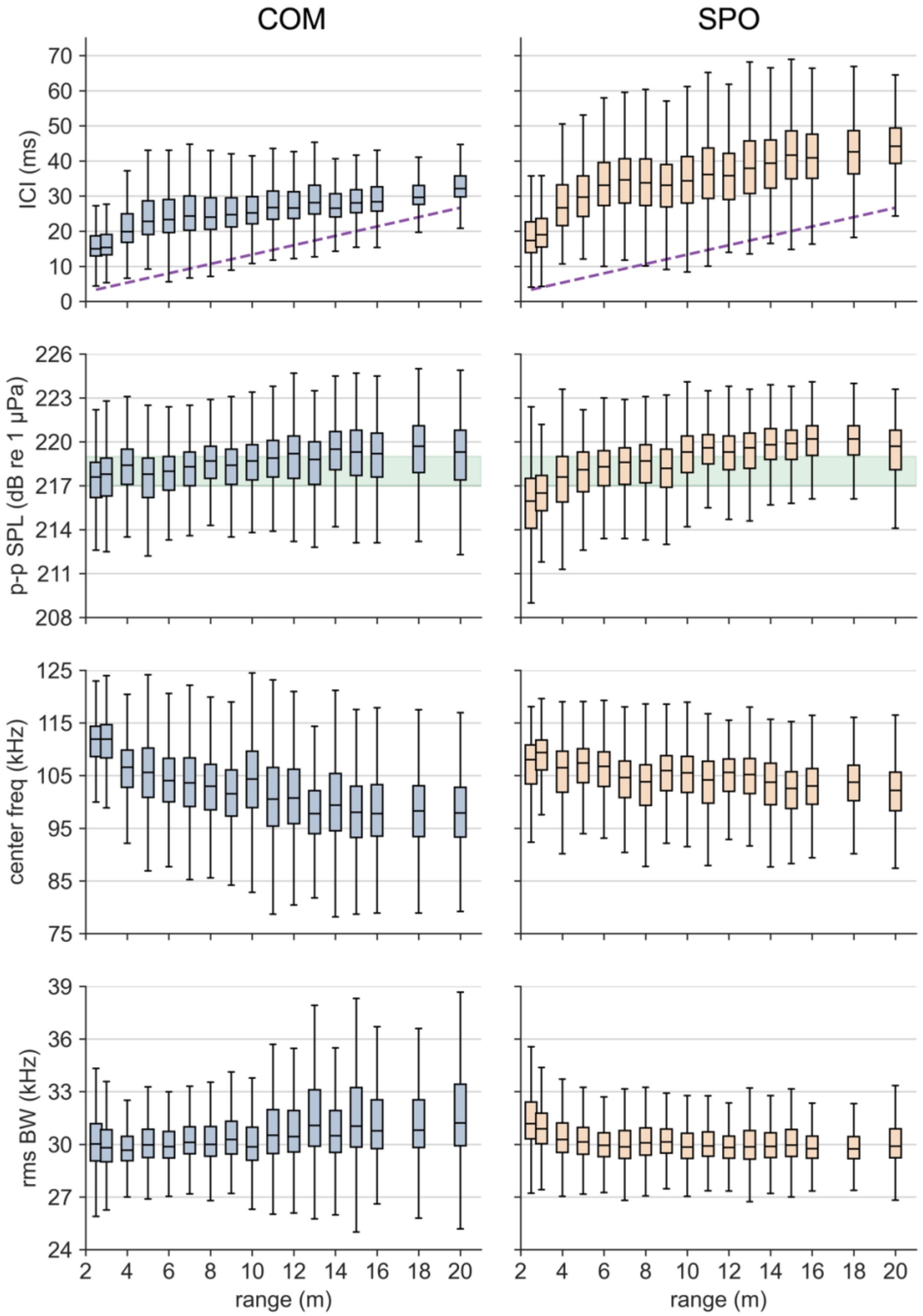

Figure 1.3: Boxplots illustrating subjects' click acoustic parameters. COM (left) is in blue and SPO (right) is in orange. From top to bottom are the two subjects ICIs, p-p SPLs, center frequencies, and rms bandwidths for each range tested. The center line in the box indicates the median and the upper and lower edges of the box represent the inner quartiles. The whiskers represent click parameters that fell within 1.5 times of the upper and lower quartiles (Waskom, 2021). The purple dotted line on the top ICI plot represents echo-delay for each range. The light green rectangle in the p-p SPL plot represents the bin of clicks, 217 – 219 dB re 1 μPa, used for EEG analysis.

Figure 4 shows the averaged click and echo ABRs at the 10-m range for SPO and Figure 5 shows all click and echo ABRs for SPO at all ranges. Click and echo ABRs matched the typical morphology of the dolphin's ABR (Popov and Supin, 1990). Additionally, the pre-auditory wave (PAW) described in Finneran (2018) was distinct for both subjects just prior to click emission. Due to the smaller amplitudes of echo ABRs, P4 and N5 peaks were chosen for analysis as other peaks were not identifiable at all ranges. Echo ABRs at ranges less than 5-m were not included in analysis due to overlap of the click ABR. However, this overlap did not affect the click P4 and N5 responses and therefore ABRs for all ranges were included in the click data analysis.

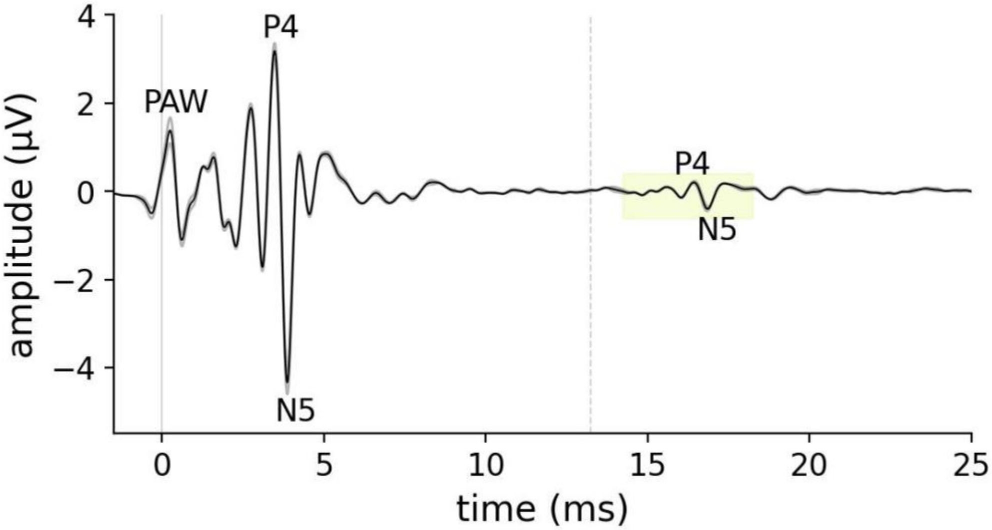

Figure 1.4: Averaged ABRs (black) and two sub-averages (gray) for the emitted click and received echo at a 10 m range for the dolphin SPO. The PAW, and P4 and N5 responses for both the click and echo ABR are annotated. The gray solid line at time zero marks the approximate time at which the dolphin emitted his click. The gray dotted line is the approximate time the echo was received by the dolphin. The yellow box identifies the time window of the echo ABR.

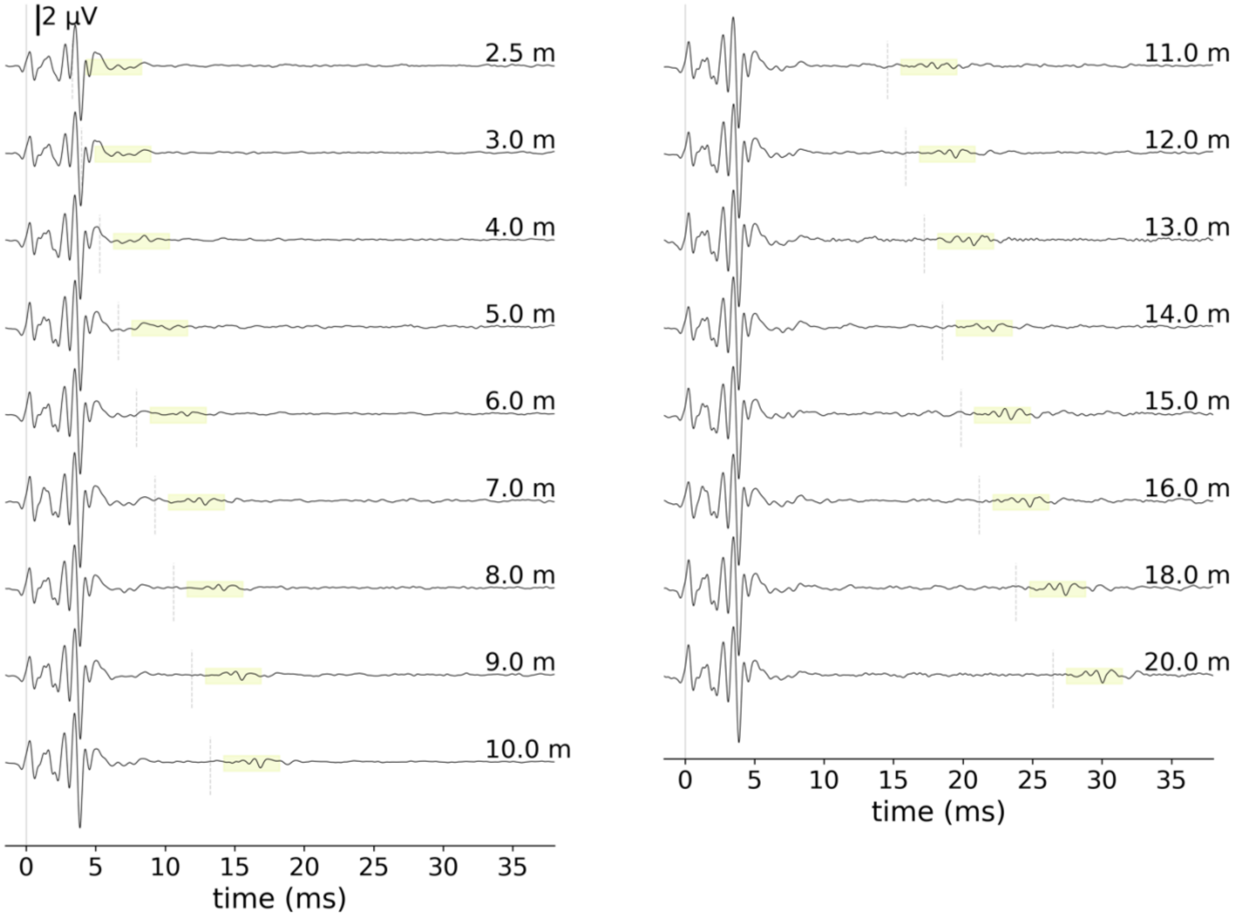

Figure 1.5: Measured ABRs for the self-heard click and received echo for the dolphin SPO at all ranges tested. The simulated target range is indicated with each trace. The gray solid line is the approximate time of click emission and the gray dotted line is the approximate time the return echo was received. The yellow box identifies time window of the received echo ABR. For ranges less than 5 m note the visible overlap in click and echo ABRs.

Click and echo ABR amplitudes and latencies as a function of range are displayed in Figure 6. Table 1 summarizes the results from linear models for click and echo ABR amplitudes and latencies as a function of range. Click ABR amplitudes increased significantly with range for both dolphins, however, SPO’s click ABRs were consistently higher, with a steeper slope resulting in greater statistical significance. Click ABR latencies decreased with range for both dolphins, though the rate of change was small (1-2 μs/m). Range was determined to be statistically significant in predicting click ABR latencies for both COM and SPO. Both subjects echo ABRs, as expected, were smaller in amplitude than their click ABRs. Similar to click ABR amplitude, range was determined to be a significant predictor of echo ABR amplitude for both subjects. Like SPO’s click ABRs, his echo ABR amplitudes were consistently higher than COM’s and the rate of change with range was larger. Range was a significant predictor for echo ABR latency for SPO and not for COM, however, the rate of change in echo ABR latency with range was small for both dolphins (3-6 μs/m).

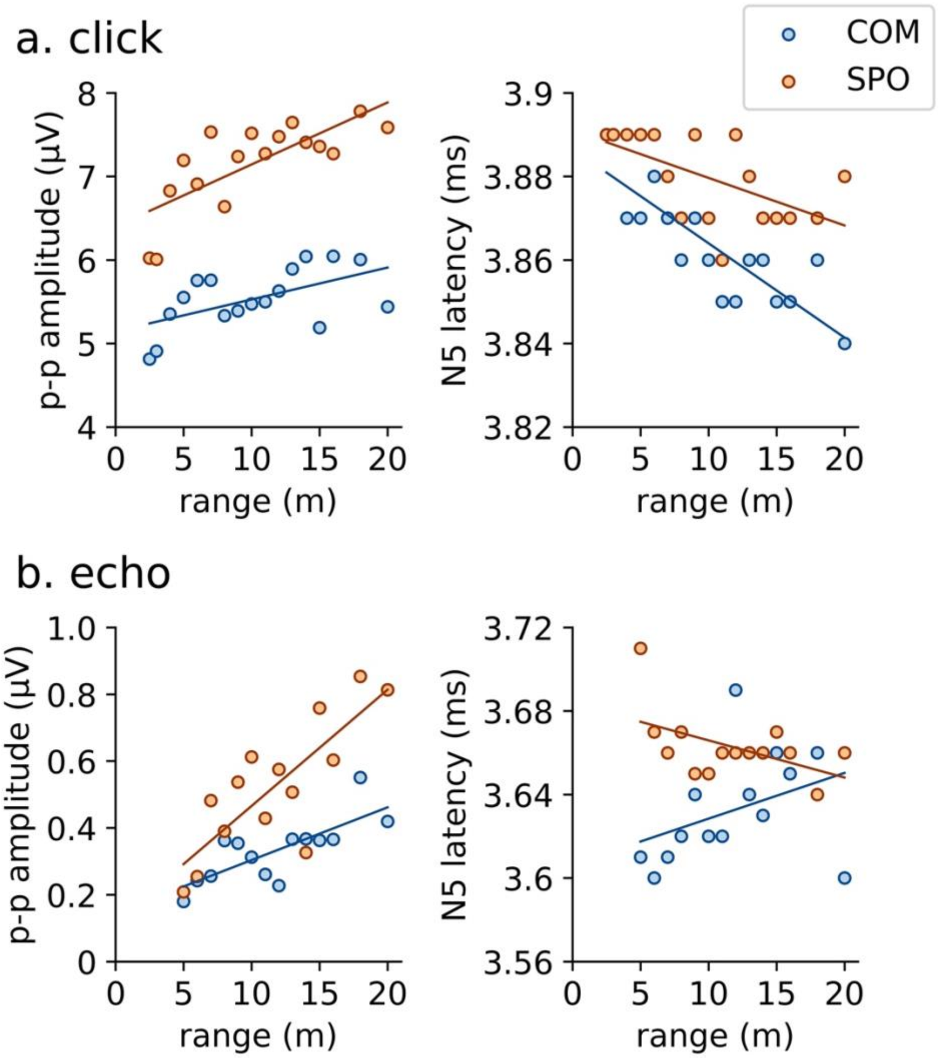

Figure 1.6: Click and echo ABR amplitudes and latencies as a function of range. (a) Click ABR P4-N5 p-p amplitudes and N5 peak latencies, and (b) echo ABR P4-N5 p-p amplitudes and N5 peak latencies for COM (blue) and SPO (orange) as a function of range. Note the different y-axis scale ranges for the click and echo ABR amplitudes and latencies.

Table 1.1: Results for linear models built to determine range as a significant predictor for click and echo ABR amplitudes and latencies for each subject. The associated F statistic, p-value, adjusted R^2, and slope are reported for each click and echo ABR amplitudes and latencies for each subject. Slopes are described in µV/m for amplitudes and µs/m for latencies. Significance is defined by $p \leq 0.001$***, $p \leq 0.01$**, $p \leq 0.05$*.

Subject	ABR	amplitude/latency	F Statistic (df 1; 15)	p-value	R^2	Slope
COM	click	amplitude	6.8	<0.05*	0.26	0.038
SPO	click	amplitude	19.6	<0.001***	0.54	0.074
COM	click	latency	38.7	<0.001***	0.70	-2
SPO	click	latency	7.9	<0.0*	0.30	-1
COM	echo	amplitude	15.1	<0.01**	0.47	0.016
SPO	echo	amplitude	31.0	<0.001***	0.65	0.035
COM	echo	latency	2.4	0.145	0.08	3
SPO	echo	latency	15.53	<0.01**	0.48	6

IV. DISCUSSION

The current experiment looked to determine the effects of changes in mean echo-delay (i.e. range) on an echo-delay discrimination task when REL was held constant. Additionally, AEP data was collected to determine the effects of forward masking from the emitted click on the received echo. Because the analysis used a limited range of click SPLs (3 dB) and the REL was constant, the acoustic echo SPLs were also constrained to 3 dB. Therefore, the decrease in ABR amplitude can be attributed to a decrease in echo-delay causing the emitted click to increasingly mask the returning echo. This is reflected in the ABR data, which show echo ABR amplitudes decline with decreasing echo-delay. Interestingly, click ABR amplitudes also increased and latencies decreased with an increase in range. This result suggests that not only was there an effect of forward masking on the received echo from the emitted click, but also an effect of forward masking on successive emitted clicks. Previous experiments suggest that the effects from forward masking from a dolphin's click could continue for up to 100 ms when click source levels were 204 – 209 dB re 1 µPa (Finneran et al., 2013; Finneran et al., 2016a). Click levels analyzed in the current experiment were ~10 dB higher than in previous experiments and ICIs were all below 70 ms, therefore it is not surprising that click ABRs were significantly affected by changes in echo-delay since ICI tended to increase with echo-delay.

The dolphins echo-delay discrimination sensitivity was highest for simulated ranges between 5 – 10 m, with a noticeable decrease in performance for ranges less than 5 m and ranges greater than 10 m. The ability to discriminate changes in echo-delay for ranges less than 5 m was likely a result of decreasing echo SNR at short ranges. ABR echo amplitudes continued to decrease with a decrease in range, suggesting that the decrease in performance resulted from the lower SNR caused by forward masking on the received echo from the emitted click. Finneran et al. (2013) reports similar results at the lowest REL (-90 dB) condition tested. When REL is decreased the dolphin must increase their click level to be able to detect the return echo. As the range decreases, the higher amplitude click level will have more of an effect on forward masking of the received echo. The present results differ from those of Murchison (1980b), which showed that range discrimination continues to improve as range decreases down to 1 m. However, Murchison (1980b) utilized physical targets with a TS of -34 dB (approximately 35 dB above the dolphin's threshold at 20 m), rather than phantom echoes with fixed REL. It is possible the dolphin in Murchison (1980b) was able to lower its click level to reduce the effects of forward masking while still maintaining sufficient echo SNR for discrimination. In the current experiment, having the REL only 15 dB above the dolphins' echo detection thresholds possibly did not afford them the same opportunity.

Echo-delay discrimination abilities also began to degrade as simulated target range increased greater than 10 m. Although this phenomenon had been seen in previous studies (Murchison, 1980b; Penner, 1988; Finneran, 2013; Finneran et al., 2013), in the current experiment a decrease in SNR with an increase in target range can be ruled out since REL was held constant at all ranges. Additionally, echo ABRs show that the perceived echo level likely increased as range increased due to release from forward masking. Therefore, some other factor associated with increasing echo-delay must be responsible. One hypothesis is that as echo-delay and/or ICI increases dolphins may have trouble combining multiple echoes into a coherent mental representation. This hypothesis is consistent with Finneran et al. (2013) which suggests the use of packets during long range echolocation tasks due to the inability to utilize multi-echo processing with large echo-delays. In the current study, the difference in acoustic parameters and performance between subjects also supports the hypothesis that as ICI increases with range, the increasing time between successive echoes may make building a coherent mental representation across multiple echoes more difficult. COM's ICIs were consistently shorter in duration than SPO's ICIs. COM's echo-delay discrimination performance was consistently better than SPO's performance. This result suggests that by using shorter duration ICIs, COM was able to better combine multiple echoes into a coherent mental representation more accurately than SPO. Interestingly, as range increased greater than 6 – 8 m the number of ICIs below the two-way travel time also increased, likely due to the unpredictability of the range as it changed randomly every five trials. Penner (1988) saw similar results in ICIs when range changed in blocks of ten trials or on a trial-to-trial basis. Additional research would need to be conducted to determine if all ICIs would increase above the two-way travel time if simulated range was consistent throughout each session.

V. CONCLUSIONS

Jitter delay acuity in bottlenose dolphins declines as echo-delay increases, likely due to the increasing time between when the dolphin emits their click and receives the corresponding echo. A hypothesis for this occurrence is that the increase in echo-delay, also results an increase in ICI that could potentially lead to the dolphin building a less coherent mental representation of the target. There was also a decline in performance at ranges less than 5 m, lower SNR due to the effects of forward masking can attribute to the decline in performance. Click ABR results also show effects of forward masking on subsequent clicks as well, not just the associated echoes.

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CHAPTER 2 The effects of range and echo-phase on range resolution in bottlenose dolphins (*Trusiops truncatus*) in a successive comparison task

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ABSTRACT:

Echolocating bats and dolphins use biosonar to determine target range, but differences in range discrimination thresholds have been reported for the two species. Whether these differences represent a true difference in their sensory system capability is unknown. Here the dolphin's range discrimination threshold as a function of absolute range and echo-phase was investigated. Using phantom echoes, the dolphins were trained to echo-inspect two simulated targets and indicate the closer target by pressing a paddle. One target was presented at a time, requiring the dolphin to hold the initial range in memory as they compared it to the second target. Range was simulated by manipulating echo-delay while the received echo levels, relative to the dolphins' clicks, were held constant. Range discrimination thresholds were determined at seven different ranges from 1.75 – 20 m. In contrast to bats, range discrimination thresholds increased from 4 to 75 cm, across the entire ranges tested. To investigate the acoustic features used more directly, discrimination thresholds were determined when the echo was given a random phase shift (±180°). Results for the constant-phase versus the random-phase echo were quantitatively similar, suggesting that dolphins used the envelope of the echo waveform to determine the difference in range.

Keywords: Dolphin, Echolocation, Biosonar, Target ranging

Preliminary data presented at the 184th Meeting of the Acoustical Society of America, Chicago, IL.

I. INTRODUCTION

Determining the distance (range) to objects in the environment is a critical feature of animal biosonar. The primary cue that echolocating animals use to resolve object range is the echo-delay, the time it takes for the emitted acoustic signal to travel to the target and its echo to return to the animal (Simmons and Vernon, 1971; Simmons, 1973; Murchison, 1980b; Au, 1993). The delay corresponding to the first echo from a target allows the animal to determine the range to the target, whereas echoes from multiple reflectors within a target and separated by small time scales (i.e., up to hundreds of microseconds) allow the animal to determine spatial features of the target (Simmons et al., 1990a; Au, 1993). By using large and small time-scale echo-delays, echolocating animals can quickly detect and classify objects within their environment at a performance rate higher than any man-made system (Roitblat et al., 1995; Moore, 1997; Vishnu et al., 2022).

Past studies of echo-delay resolution in microchiropteran bats required the bats to treat the task as either a successive or simultaneous comparison task (Simmons and Vernon, 1971; Simmons, 1973; Roverud and Grinnell, 1985; Simmons and Grinnell, 1988; Masters and Jacobs, 1989; Mogdans and Schnitzler, 1990). A successive task requires the animal to echo-inspect one target and store that information in memory and then compare it to a second target. In a simultaneous task, the animal is presented both targets simultaneously and can capitalize on cues created by the reflection of both targets from the same incidental echolocation pulse (Simmons, 1973; Roverud and Grinnell, 1985; Simmons and Grinnell, 1988; Masters and Jacobs, 1989). Simmons (1973) trained the big brown bat (*Eptesicus fuscus*) on a two-alternative forced choice (2AFC) task in which it inspected a target to the right, then compared it to a target to the left, and reported which target was closer. The angular separation between the two targets was 40°, which allowed the bat to ensonify both targets with a single pulse (Simmons, 1973; Simmons, 2014). Four different absolute ranges (30, 60, 120, and 240 cm) were tested. For the remainder of this publication absolute range of the targets relative to the echolocator will be referred to as "range", and difference in range between the two targets as "ΔR". During threshold testing the range of the farther (S-) target was held constant, while the S+ target was shifted closer to the bat (e.g., at a range of 30 cm, S+ would be shifted between 20 and 29 cm, while S- was always presented at 30 cm). Discrimination thresholds (75% correct) were ~1.2 - 1.4 cm (equivalent echo-delays of ~60 – 80 µs) and did not vary significantly across the four ranges tested (Simmons, 1973). The experiment was replicated with a phantom echo generator (PEG) at the 30 cm range to present different echo-delays while removing other range parameters (i.e., echo-amplitude and spectral parameters). Performance and thresholds for both physical objects and the PEG were similar, suggesting that the bats determined the range of the targets by the arrival time of the corresponding echoes (Simmons, 1973). Additional experiments where a single range was tested with different bat species produced similar discrimination thresholds of ~1 cm (Roverud and Grinnell, 1985; Surlykke and Miller, 1985; Masters and Jacobs, 1989).

Murchison (1980b) replicated the bat experiment conducted by Simmons (1973) with a bottlenose dolphin (*Tursiops truncatus*) but reached a different conclusion. Rather than finding discrimination thresholds constant at all ranges, thresholds increased with an increase in range. Like Simmons (1973), a 2AFC paradigm was used where the dolphin ensonified two, 7.62-cm diameter foam spheres with target strengths of -34 dB and reported which sphere was closer in range. The two spheres were arranged with 40° of angular separation relative to the dolphin at ranges of 1, 3, and 7 m. Differing from Simmons (1973), the closer target (S+) remained constant while the farther target (S-) changed in range (e.g., at a range of 1 m, S+ would always be presented at 1 m, while S- was presented between 1.01 and 1.1 m). Discrimination thresholds (∆R at 75% correct) were 0.9, 1.5, and 3 cm (12, 20, and 40 μs echo-delay) at ranges of 1, 3, and 7 m, respectively, indicating that as range increased the resulting ∆R at threshold also increased. Whether the dolphin completed the task using a simultaneous or successive process is unknown. Moore, et al. (2008) suggests that dolphins can detect the presence of a spherical target with a target strength (TS) of -27 dB and when azimuthal angles from the center of the dolphin's beam were greater than ± 20°. However, with the lower TS, -34 dB, of the targets used in Murchison (1980b), and the narrow beamwidth of high frequency content in the dolphin's echolocation beam, it is questionable if the dolphins could have extracted useable information from both targets with a single click (Au et al., 1986; Finneran et al., 2014; Finneran et al., 2016b). Therefore, whether differences in performance as a function of range in the bottlenose dolphin versus the bat represent a true difference in sensory system capabilities or simply differences in experimental design is unknown.

The current experiment tested dolphin range discrimination thresholds in a successive comparison task using a two channel PEG system. Testing was conducted in a 2AFC paradigm at seven different ranges from 1.75 – 20 m. Additionally, at an absolute range of 7 m, threshold testing was conducted using both constant echo-phase and a random phase shift (±180°) that was assigned to each echo. Previous research suggests that big brown bats and dolphins appear sensitive to changes in echo phase during jitter delay experiments (Simmons, 1979; Menne et al., 1989; Simmons et al., 1990b; Moss and Simmons, 1993; Finneran et al., 2019; Finneran et al., 2020; Finneran et al., 2023). However, studies with pale spear-nosed bats (*Phyllostomus discolor*) where echo phase was changed by manipulating the phantom target impulse response duration, rather than delay, suggests that these bats could not use the complete echo phase spectrum but only the portion that encodes echo-delay (Schörnich and Wiegrebe, 2008). Whether changes in echo-phase affect the dolphin’s ability to discriminate ranges between targets is unknown. The random phase shift had the effect of altering the fine structure of each echo waveform to shift the positions of the waveform peaks and valleys from echo-to-echo — without changing the waveform envelope. By removing consistent fine echo structure, only the envelope of the echo waveform could be used to determine range. These experiments determined discrimination thresholds as a function of range and echo phase that had not been previously identified.

II. METHODS

A. Subjects and test environment

Two bottlenose dolphins participated in the study: Eclipse (ECL) (male 7 years) and Lark (LRK) (female 17 years). Upper-frequency limits (UFL) for their hearing, defined as the frequency at which electrophysiological auditory steady-state response thresholds reached a sound pressure level (SPL) of 120 dB re 1 µPa, were ~56 kHz for ECL and ~136 kHz for LRK. ECL was considered to have high-frequency hearing loss and LRK was considered to have full-bandwidth hearing, which was defined as a hearing range with a UFL $\geq$ 120 kHz (Johnson, 1966; Houser and Finneran, 2006; Strahan et al., 2020).

Tests were conducted in a 9 × 9 m floating netted enclosure at the U. S. Navy Marine Mammal Program in San Diego Bay, CA, between September 2021 and July 2022. During each trial, the dolphin positioned itself in an underwater PVC “hoop station” located at ~1 m depth and supported by a single vertical post. Response paddles were located ~0.3 m to the dolphin’s left and right. The hoop station was oriented so that the dolphin faced San Diego Bay through a netted frame (Fig. 1). Beyond the frame, at 1.2 m distance and ± 20° azimuthal angle from the center-point of the hoop station, were two pairs of piezoelectric transducers (TC4013, Reson Inc., Slangerup, Denmark). Each transducer pair operated as one of two independent channels (left/right) in the PEG system. One transducer in each pair served as the dolphin’s biosonar click receiver and the other as the echo projector for the associated channel. An additional piezoelectric transducer was embedded in a silicone suction cup and placed in the center of the dolphin’s melon, approximately 3 cm above its rostrum. The hydrophone on the melon was used to estimate the time of click emission (see below). The nearest underwater structures within ±20° of the dolphin’s main biosonar transmission axis while in the hoop station were ~500 m in distance. The mean water depth was ~10 m. Ambient noise consisted of snapping shrimp, vessel traffic, and other dolphins. Median ambient noise pressure spectral density levels were approximately 69 dB re 1 $\mu Pa^2/Hz$ at 10 kHz and decreased linearly with the logarithm of frequency to 52 dB re 1 $\mu Pa^2/Hz$ at 150 kHz.

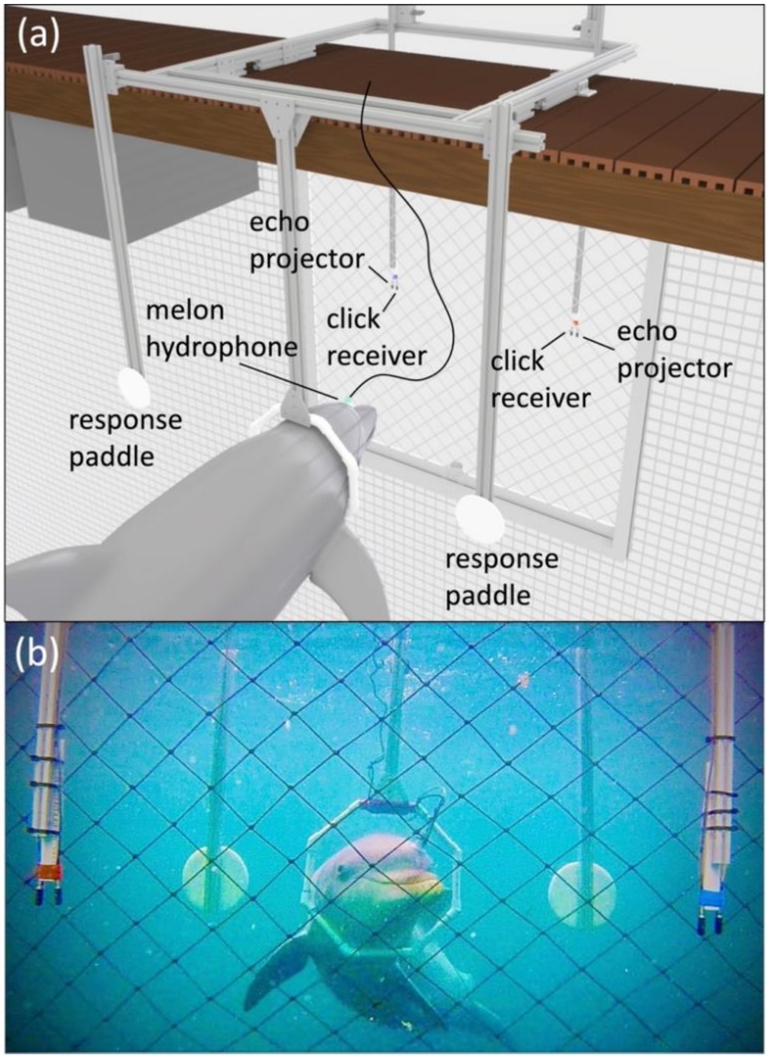

Figure 2.1: Illustration of the apparatus for the 2AFC range discrimination task. (a) The dolphin was positioned in the hoop facing out of the netted enclosure towards San Diego Bay. Two pairs of piezoelectric transducers were positioned 20° to the left and right of the dolphin and served as the click receivers and echo projectors for a two-channel PEG. (b) Image of the dolphin, ECL, participating in the biosonar task. The camera was positioned in San Diego Bay facing towards the enclosure.

B. Task Description

The dolphin’s task was to position itself in the hoop and produce echolocation clicks towards the left or right click receiver while listening to returning phantom echoes from the corresponding projector. After ensonifying both sides, the dolphin was required to leave the hoop and touch the response paddle corresponding to the side (left or right) that produced the phantom echoes with the shorter echo delay (S+). Each dolphin participated in one session per day and sessions were run daily, Monday-Friday. Sessions lasted ~25 min and consisted of ~60 individual trials. Each trial began with the PEG off and the dolphin directed to position itself in the hoop. Once positioned, the PEG was turned on for 4 s, with each PEG channel simulating a target at a different range. The dolphin could leave the hoop anytime during the 4-s trial to make its choice. Trials where the dolphin left the hoop prior to triggering echoes from both the left and right channels and trials where the dolphin did not touch a paddle were not included for analysis; these comprised 1.3% of the total trials.

Thresholds were measured at seven different simulated ranges with no phase shift and at the 7-m range with each echo given a random phase shift. Data collection for each range took ~3-5 weeks and occurred in the following order 10, 5, 7, 3, 1.75, 14, and 20 m, followed again by 7 m with random phase shifts. To ensure the dolphins were comparing the range of both simulated targets versus using a template of the S+ range stored in memory, the S+ and S- ranges roved around the ranges listed above from trial to trial. The specific range of the S+ on a trial-to-trial basis was selected from a distribution in which the mean was defined by the range being tested and with the standard deviation set to 15 cm. Random selection of the S+ range was limited to a normal distribution truncated at ± 3 standard deviations. At 1.75-m range, roving was limited to a minimum range of 1.4 m due to the physical distance to the transducers and the minimum time required by the PEG to generate an echo. This distribution still allowed for distinct separation of distributions between each range tested.

Seven or eight ΔRs were tested each session depending on range. Each session began with warm-up trials, where each unique value of ΔR was presented to the dolphin in descending order across trials. After the warm-up, ΔR was randomized from trial to trial, while ensuring an equal number of trials on the left and right for each ΔR. At least 36 trials were conducted at each range and ΔR combination, except for ECL at 20 m (28 trials at ΔR = 22 and 65 cm and 32 trials at ΔR =45 cm), where he demonstrated a decrease in motivation and willingness to participate when the range was set to 20 m.

Relative echo level (REL, the echo sound exposure level (SEL, in dB re 1 $\mu Pa^2 s$) at the listening position relative to the click SEL at the click receiver) was held constant as the range varied. REL was set to 15 dB above ECL's detection threshold, which was also the highest possible REL for the hardware. As REL was independent of simulated range, apparent target TS increased with increasing range (Table I). Due to his high-frequency hearing loss, ECL's effective TSs were estimated by applying a low-pass filter to the echo at his UFL of 56 kHz. REL was set to 35 dB above LRK's detection threshold, resulting in a REL 14 dB less than ECL's REL. These adjustments were applied between subjects to produce similar TSs for each dolphin (Table I).

Table 2.1: Simulated TS for ECL and LRK at each range. The effective TS for ECL was estimated by first low-pass filtering the echo at 56 kHz to simulate his high-frequency hearing loss.

Range (m)	**ECL TS / Effective TS (dB)**	**LRK TS (dB)**
1.75	-67 / -87	-81
3	-58 / -78	-71
5	-49 / -69	-63
7	-43 / -63	-57
10	-37 / -57	-51
14	-31 / -51	-45
20	-25 / -44	-39

C. Echo Generation

The PEG was implemented using an NI PXIe-7856R device containing a Kintex-7 160T FPGA. Clicks emitted by the dolphin were captured by the left, right, and melon click receivers, amplified, filtered (5–200 kHz, VP-1000 and 3C module, Krohn-Hite Corporation, Brockton, MA), then digitized by the PXIe-7856R with 1-MHz sampling rate and 16-bit resolution. If the digitized hydrophone signal exceeded an amplitude threshold, click waveforms were extracted from the left and right channels and times-of-arrival were obtained from all three channels. Three criteria were used to determine if the digitized click signal from the left or right channel “triggered” the PEG and resulted in echo generation from that side: (1) the digitized hydrophone signal on that channel exceeded the amplitude threshold, (2) the click p-p amplitude on that channel (left or right) was greater than the amplitude of the same click on the other channel, and (3) the time-of-arrival difference (TOAD) between the click received by the left/right hydrophone and the same click received by the melon hydrophone was less than the nominal acoustic travel time for that simulated target range. Criterion (2) ensured that echoes were only generated from a single channel, the side the dolphin's beam was primarily directed towards. Criterion (3) ensured that the dolphin remained in the hoop during the echo inspection. Click waveforms that triggered the PEG were convolved with a target impulse response function to create the echo waveform. The echo waveform was then scaled in amplitude, delayed, and converted to analog (PXIe-7856R, 1 MHz, 16 bit). To minimize effects of dolphin head movement within the hoop, the delay of each echo was corrected using the TOAD between the click received by the left/right hydrophone and the same click received by the melon hydrophone (an indication of the dolphin's instantaneous position relative to the click receiver). The analog echo waveform was then filtered (5–200 kHz, 3C module), amplified (M7600, Krohn-Hite Corp.), and used to drive the echo transmitter. The hydrophone signals and echo waveforms were also digitized at 2 MHz and 16-bit resolution by an NI PXIe-6368 multifunction data acquisition device (National Instruments, Austin, TX) and stored for later analysis (Figure 2).

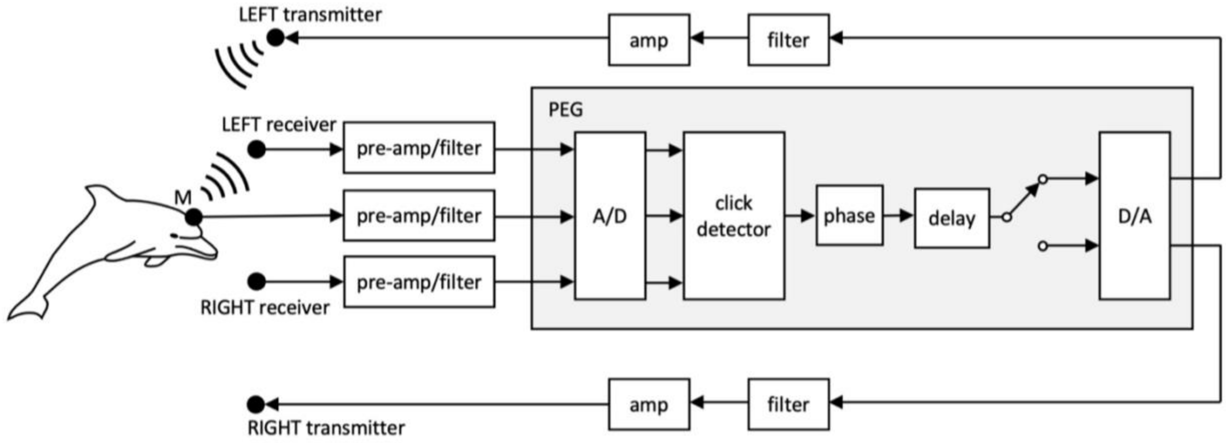

Figure 2.2: Block diagram of the PEG biosonar task. Clicks produce by the dolphin were received by the left, right and melon (M) hydrophones, amplified, filtered, and passed to the analog-to-digital converter. The click detector then determined if criteria were met for an echo to be generated and whether the echo was to be projected from the left or right PEG channel. The echo was then delayed to simulate the assigned range. Analog echoes that were produced by the PEG were then filtered, amplified, and projected by the left or right echo transmitter.

Convolution was performed in the frequency domain using a fractional delay technique (Välimäki and Laakso, 2000) to obtain echo-delay resolutions below the 1-µs sampling interval. Target transfer functions included only phase and delay elements. Larger-scale echo delay, in integral multiples of 1-µs, was achieved by changing the position of the echo waveform in the digital-to-analog converter output buffer. In this fashion, echo delays up to ~200 ms could be achieved with resolution < 0.001 µs. In practice, echo delay resolution was limited by the inherent “jitter” in the system, primarily arising from motion of the transducers relative to the hoop (e.g., caused by water motion). The inherent jitter, estimated by repeatedly triggering the PEG using a representative electronic click waveform and measuring the delay of the resulting acoustic echoes in the center of the hoop was ±0.4 µs.

Operation of the PEG was verified before each session by replacing the dolphin click signal input to the PEG analog-to-digital (A/D) converter with a representative recording of an on-axis dolphin click. Calibrations were performed prior to each session by broadcasting the analog echo waveforms from the left echo projector and recording the acoustic echoes (without the dolphin present) with the right click receiver, this method was then reversed (right projector to left click receiver). Calibrations over the course of the study varied by ±1 dB.

D. Analysis

Statistical analysis was conducted in R (R Core Team, 2019). The quickpsy package was used to build the psychometric functions using the cumulative normal distribution function to fit proportion correct versus ΔR for each range (Linares and López-Moliner, 2016). Model parameters were estimated using maximum likelihood. Threshold was calculated at the 75% correct rate from the psychometric function and the 95% confidence intervals were calculated by bootstrapping the data with 1000 iterations. A linear mixed model was built with absolute range and subject as main effects; however, subject was non-significant ($p = 0.609$) and therefore removed from the model. Data for the subjects were subsequently combined.

Custom software was used to calculate click acoustic parameters including inter-click-interval (ICI), peak-to-peak (p-p) SPL, center frequency, and (centralized) root-mean-square (rms) bandwidth. To restrict analysis to clicks near the main transmit axis, only clicks within ±3 dB of the maximum click p-p SPL for each individual trial were included in the analysis – these were considered on-axis clicks. Representative echoes were measured by inputting the mean on-axis click waveform of each subject into the PEG and then broadcasting the resulting echo and measuring the acoustic pressure at the center of the hoop. Measurements were repeated 1024 times and the acoustic pressure synchronously averaged to calculate the echo waveform. Effects of ECL’s high-frequency hearing loss on received echo levels were estimated by low-pass filtering the echo at 56 kHz (8th order Butterworth, zero phase) to obtain the “effective” echo waveform and spectrum.

III. RESULTS

A. Click acoustic parameters

Preliminary analysis displayed differences in LRK and ECL’s click production and therefore clicks were analyzed independently for each dolphin. This resulted in 1.2×10^4 clicks analyzed for ECL and 1.5×10^4 clicks analyzed for LRK. The mean click waveform and spectra for each dolphin showed characteristics of a normal dolphin click [Fig. 3(a)]. Projected echoes [Fig. 3(b)] were longer in duration and contained more high-frequency content than the dolphin’s clicks due to the characteristics of the projector transmitting response. Echo amplitudes for LRK were 14 dB lower than those for ECL; however, low-pass filtering using ECL’s upper hearing limit resulted in an effective echo with lower amplitude., see Fig. 3(b).

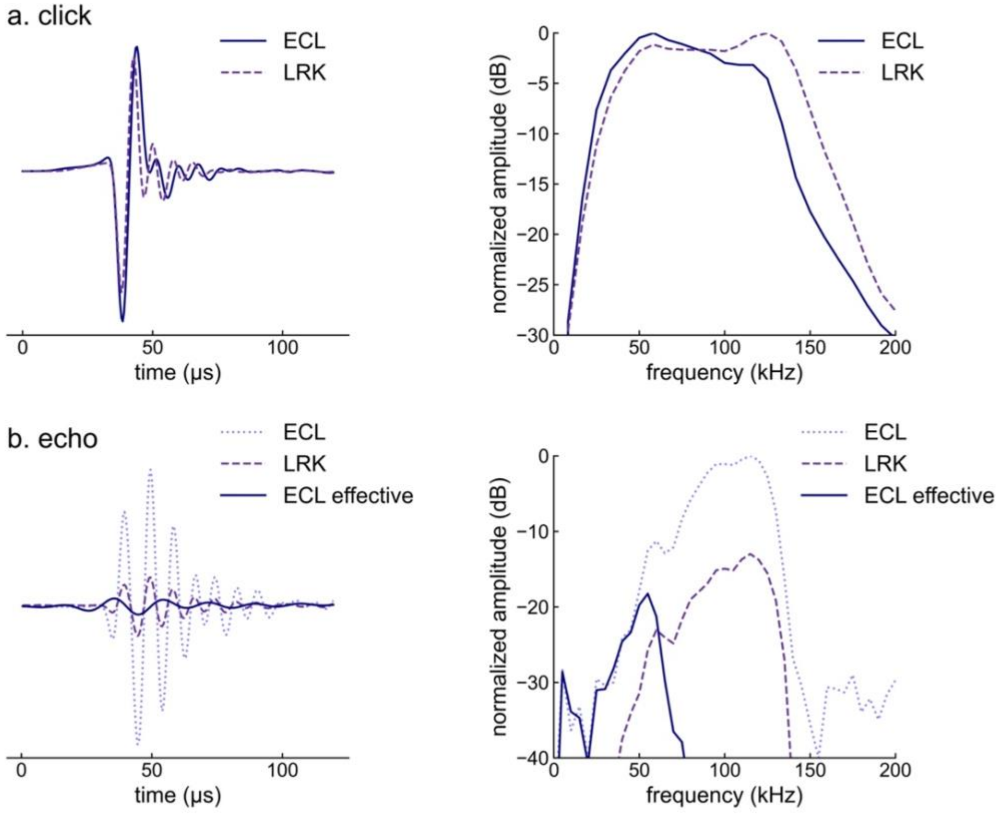

Figure 2.3: Averaged click and echo waveforms and corresponding spectra for the two subjects. (a) Normalized mean click waveforms (from both left and right click receivers) and corresponding spectra for each subject for trials conducted at the 7 m range. The mean amplitude of the waveform represents all clicks that were within ±3 dB of the maximum click amplitude for each trial. (b) Normalized phantom echo waveforms and spectra for each subject, and the effective echo waveform and spectrum when echoes were low-pass filtered to simulate ECL's high-frequency hearing loss.

Distributions of ICIs and p-p SPLs (dB re 1 μPa) for each dolphin were similar when inspecting the left and right PEGs. Therefore, clicks from the left and right PEGs were combined for analysis of ICIs and p-p SPLs (Fig. 4). ICI distributions were broad, especially at the longer ranges, due (in part) to roving the ranges of S+/S- and the multiple values of ΔR. ECL's ICIs varied from ~8 – 50 ms and generally increased with target range, except for the 5, 7, and 10 m ranges, where ICIs were similar. LRK's ICIs varied from ~3 – 40 ms and increased systematically with target range. ECL's click p-p SPLs varied from ~195 – 215 dB re 1 µPa and did not change systematically with a change in a range. LRK's click p-p SPLs varied from 190 – 215 dB re 1 µPa and tended to increase with target range.

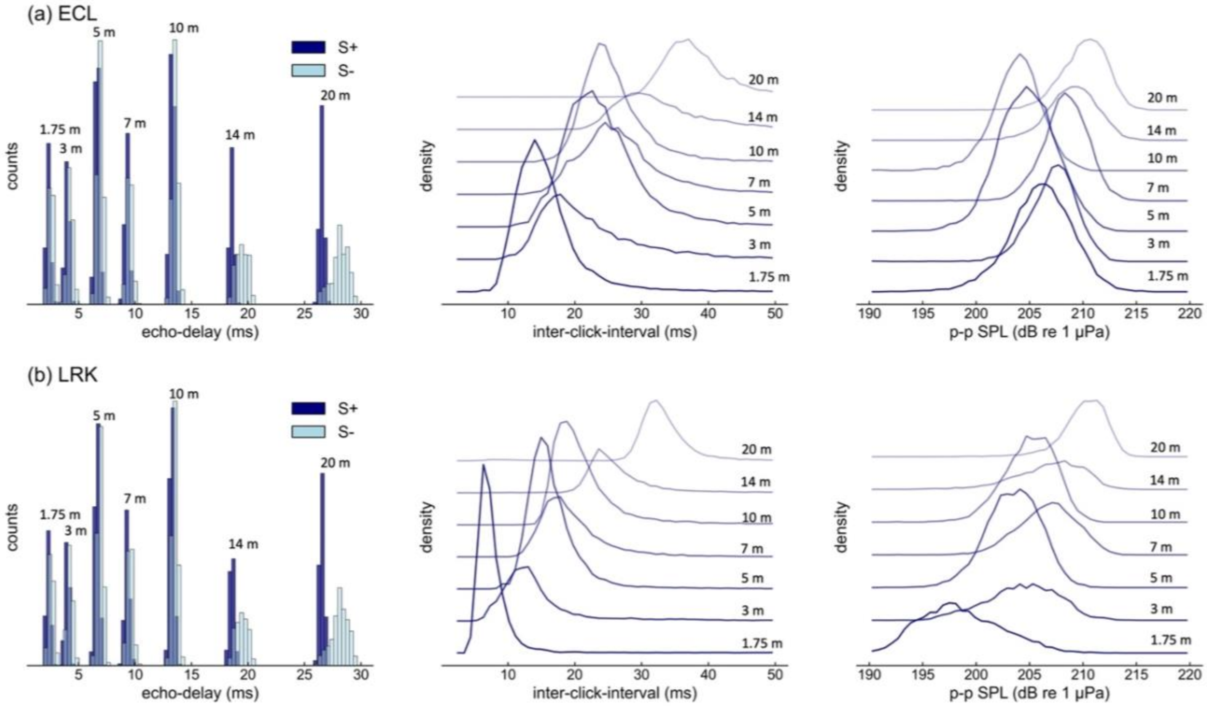

Figure 2.4: S+ and S- distribution, ICIs and p-p SPLs at each range for (a) ECL and (b) LRK. Histogram of S+ and S- echo-delay distributions (left), density of ICI distributions for each range (center), and density of p-p SPL distributions (right) capture characteristics of click production. Note that the distributions for S- include all the ΔRs for that range and therefore are naturally wider than the S+ distribution.

Distributions of center frequency and rms bandwidth for each dolphin differed between the right and left click receivers but remained consistent for different ranges. Therefore, clicks from the left and right PEGs were analyzed separately for the left and right receivers but absolute ranges were combined for each dolphin (Fig. 5). ECL and LRK both had fewer clicks analyzed on the right compared to the left because there were fewer on-axis clicks on the right. ECL's center frequencies were between 50 – 100 kHz for the left PEG and 55 – 90 kHz for the right PEG. While LRK's center frequencies were between 75 – 115 kHz for the left PEG and 65 – 105 kHz on the right PEG. ECL's rms bandwidths were between 25 – 40 kHz for the left PEG and 20 – 35 kHz on the right PEG. While LRK's rms bandwidths were between 25 – 40 kHz for the left and right PEGs (Figure 5).

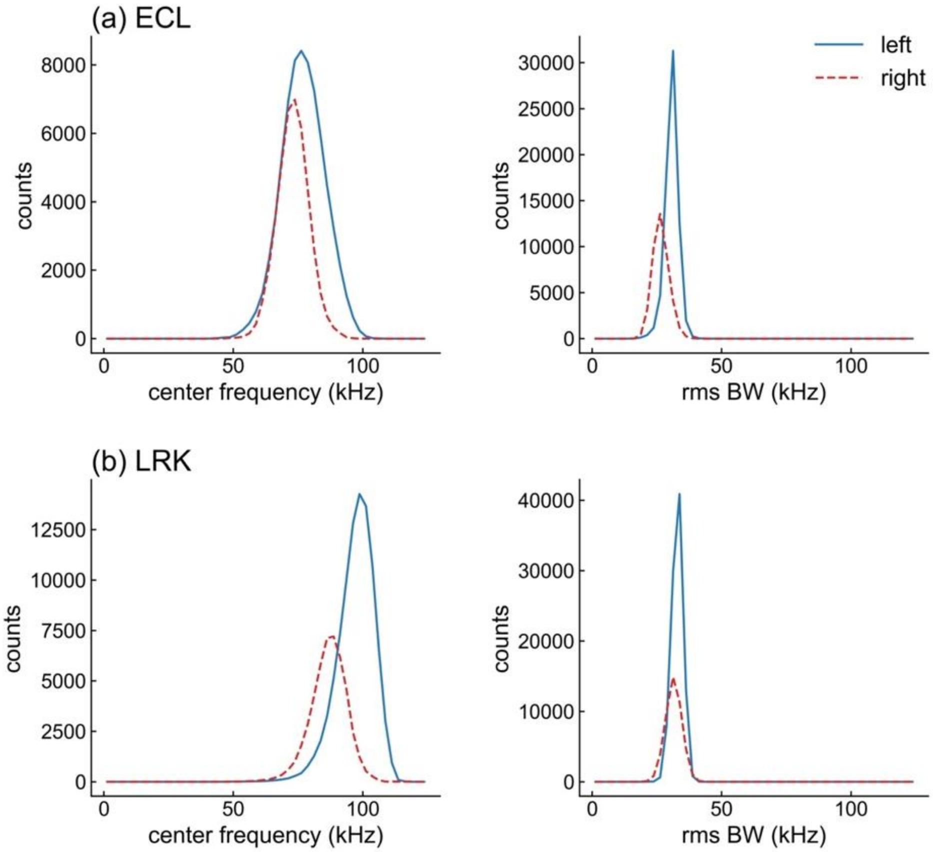

Figure 2.5: Histograms for (a) ECL and (b) LRK illustrating differences in center frequency and rms bandwidth. The plots on the right depict the center frequency for the left and right click receiver.

B. Behavioral performance for biosonar tasks

1. Performance as range changes

Figure 6 shows the performance of ECL and LRK at each range for the normal phase condition. Due to the lack of significant differences between subjects, data were combined to calculate psychometric functions. Thresholds were calculated by interpolating along the psychometric function to find the ΔR where the dolphins were 75% correct. Figure 7 shows the resulting thresholds as a function of range, with error bars representing the 95% bootstrapped confidence intervals. Data were fit well with a piece wise linear function, using the segmented package in R (Muggeo, 2003). The resulting slopes were 0.67 cm/m and 7.15 cm/m with a breakpoint of 11 m ($R^2 = 0.99$).

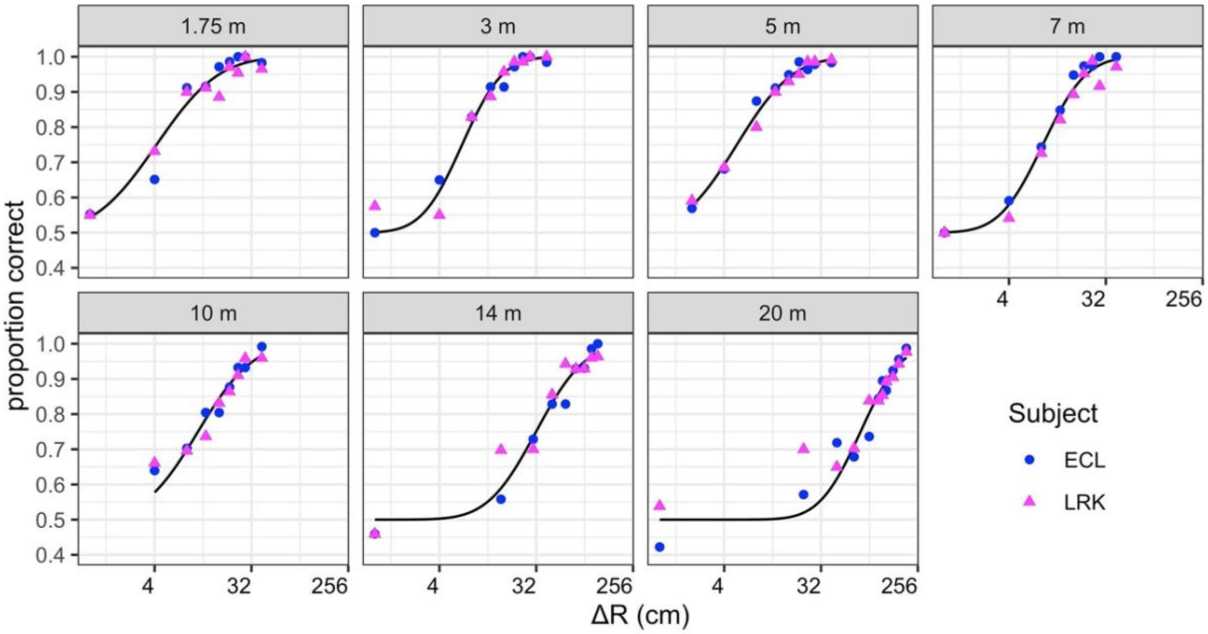

Figure 2.6: Performance for ECL and LRK for each absolute range tested as a function of ΔR. Data from both subjects were combined for calculation of the psychometric functions shown in black.

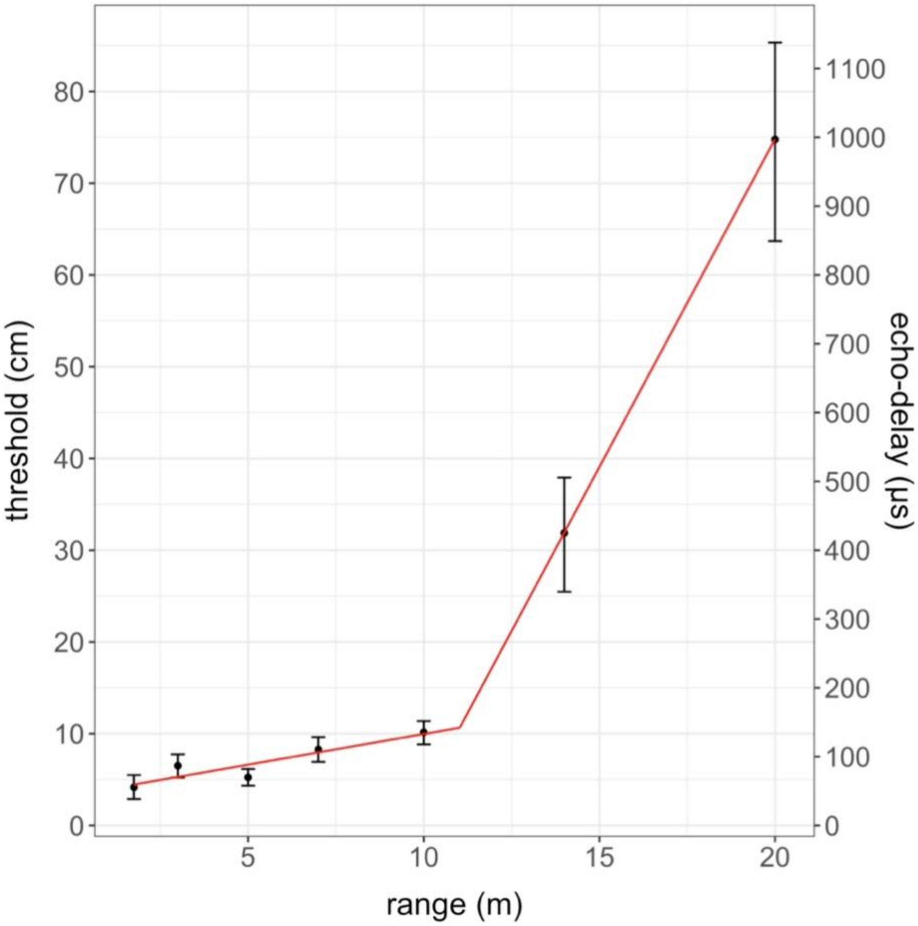

Figure 2.7: Threshold as a function of range for the two subjects combined. Error bars represent the 95% intervals confidence calculated by bootstrapping the data with 1000 iterations. The red line is the piece wise linear fit for all ranges with a break point at 11 m.

2. Performance with echo-phase randomized

Figure 8 compares performance at 7-m range between the normal phase condition (i.e., no echo phase shifts) and when each echo was given a random phase shift. Thresholds for the normal and random phase shift conditions were 8.27 and 8.73 cm, respectively. A linear mixed model was built to determine if the phase shift had a main effect, the model determined no significant differences between the normal phase and random phase shift condition ($p = 0.171$).

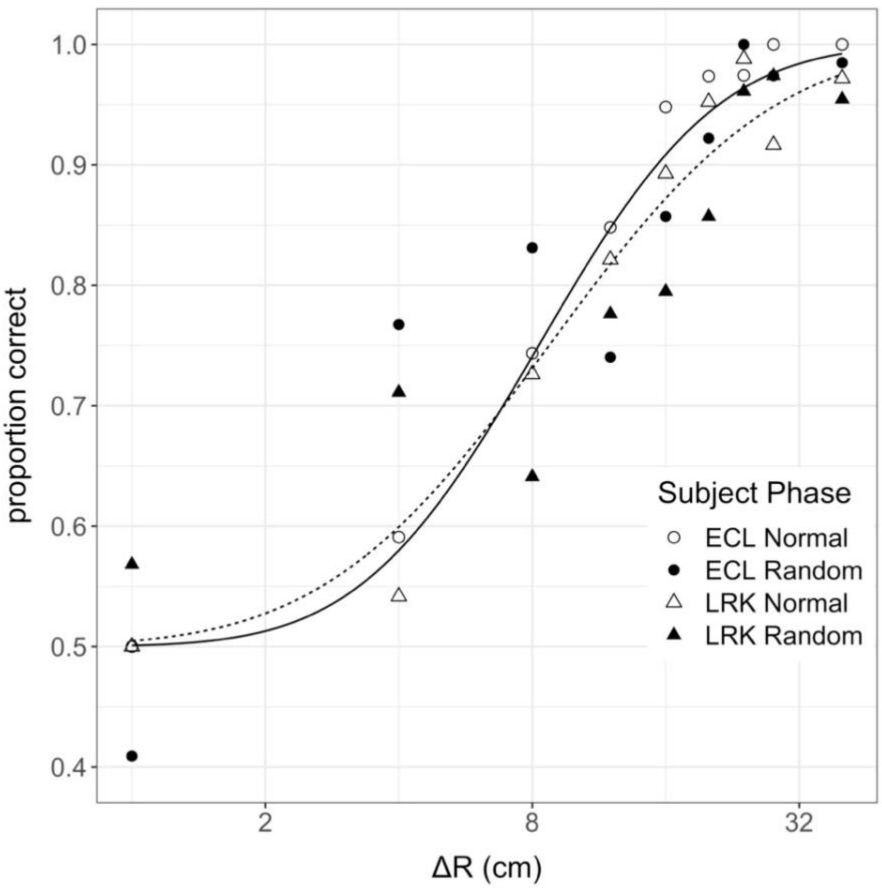

Figure 2.8: Performance for ECL and LRK when each echo was given a random phase shift (dotted line) and when the phase of each echo was consistent (solid line).

IV. DISCUSSION

A. Range resolution

The present experiment determined discrimination thresholds as a function of range, at farther ranges than previous dolphin and bat experiments, using phantom echoes rather than physical targets. Therefore, echo-delay could be precisely controlled and manipulated independently from echo amplitude. In the current study range discrimination thresholds were 4.1, 6.5, and 8.3 cm at 1.75, 3, and 7 m range, respectively, equating to echo-delay differences of 55, 87, and 110 µs. Thresholds were consistently higher than those reported by Murchison

(1980b): 0.9, 1.5, and 3 cm at 1, 3, and 7 m range (echo-delay differences of 12, 20, and 40 µs), respectively. Present results are also much larger than echo-delay thresholds obtained using a jittered-echo paradigm (Finneran, 2023). This suggests that a different mechanism is used for jitter detection than for successive ranging and that higher thresholds are not solely a result of the animal's head movement (Altes, 1989).

There could be several reasons for the high thresholds compared to Murchison (1980b). Murchison (1980b) used physical targets and therefore the target strength was constant with range, but echo-delay and relative echo level were coupled. In contrast in the present study relative echo level was held constant to decouple echo-delay and echo-level as much as possible. This results in the apparent TS decreasing as range decreases resulting in much lower TSs in the present study than in Murchison (1980b). The TS of the foam spheres in the previous study was -34 dB, where the simulated TS in the current study for ranges 1.75 to 7 m for LRK was -81 to -57 dB and the effective TS for ECL was -87 to -63 dB. Although these TSs resulted in echoes above each dolphin's echo detection threshold, the dolphin in the previous study could have benefitted from the higher echo SNR resulting from the higher TS. Additional research would need to be conducted to determine how differences in SNR affect range resolution in dolphins. The foam spheres used in Murchison (1980b) also would have reflected a complex echo, whereas in the current experiment the echoes were a replica of the dolphin's click representing a point target. The higher TS and simultaneous presentation of targets paired with the complex echo may have enabled the dolphin to utilize spectral interference patterns resulting from near-simultaneous reception of reflections of the same click from both targets as he scanned from one target to the other. Additional research is needed to determine whether the dolphin's performance would improve during a simultaneous process of range discrimination versus the successive process that was investigated in the current study.

Murchison (1980b) concluded that the range discrimination thresholds measured followed the Weber-Fechner function, defined as $\Delta R/R = K$, where R is the absolute range and K is a constant. In the current experiment the data fit this function up until the 10 m absolute range. Previous research suggests that different mechanisms are used for target identification at ranges greater than 14 m (Finneran et al., 2013). In the current experiment performance degrades rapidly at ranges of 14 m and greater. Given the limited data above 10 m it is not clear how thresholds continue to change as range continues to increase and if there is an upper limit beyond which they cannot discriminate between ranges. It has been reported at ranges greater than 75 m, that dolphins begin using click "packets", where the dolphin projects a burst of clicks and waits for the corresponding collection of echoes to return before sending out the next burst or set of packets (Ivanov and Popov, 1978; Ivanov, 2004; Finneran, 2013; Ladegaard et al., 2019). Thus, measuring range resolution at large ranges could be affected by an overall change in echolocation strategy beyond a certain target range.

Of note are the apparent differences among the current study, Murchison (1980b) and the experiment conducted in bats by Simmons (1973). Simmons (1973) reported discrimination thresholds for ranges from 30 to 240 cm (echo-delays of 1.8 to 14.1 ms), to be ~1.2 - 1.4 cm (~60 – 80 μs) and reported little change in threshold with a change in range. However, Simmons (1973) did not correct for head movement. (Simmons and Grinnell, 1988) suggested that results from the 1973 experiment could be better characterized as measurement of the bat's head movement versus the ability to resolve range. If this were the case, the error from head movement would be similar as range increased, leading to similar thresholds at each range. In the current study, head movement was accounted for with a melon hydrophone while in Murchison(1980b) head movement was controlled by the dolphin placing its rostrum in a “chin cup” that allowed its head to scan right to left but controlled the range to each target. The restriction of head movement could therefore account for the threshold differences as a function of range among the bat and dolphin studies.

In the current study, there were no significant differences between the psychometric functions for normal and random phase conditions at 7-m range. This result is perhaps not surprising given the relatively large threshold at 7 m (i.e. larger than the echo envelope). Since randomizing the phase disrupts the fine structure, the random phase data further highlights that the echo envelope is utilized for determining range in a successive task.

B. Click emissions

A unique opportunity of the present study was to compare click emissions from LRK, with full hearing bandwidth, and ECL, who had high-frequency hearing loss with an upper frequency hearing limit of 56 kHz. Although there were no significant differences between their behavioral data, there were apparent differences between click emissions. The average center-frequency for ECL’s click was ~20 kHz less than LRK’s (although clicks for ECL still contained frequencies above the subject’s hearing range). There was a systematic increase in ICI with an increase in range for both subjects. However, at the closest range of 1.75 m LRK’s ICIs were ~ 4 ms where ECL’s are much higher at ~14 ms. LRK also decreased click p-p SPL at 1.75 m, and the p-p SPL continued to increase with range, even though relative amplitude remained constant for all ranges. Finneran (2013) reports similar results during an echolocation change detection task where REL was held constant at different simulated ranges. It is uncertain whether this is a natural response of the dolphin to increase click amplitude as range increases (Au and Benoit-Bird, 2003; Jensen et al., 2009) even in cases where REL is artificially held constant (Finneran et al., 2013). Interestingly, the p-p SPL of ECL's click varied slightly at the different ranges but did not change steadily with range. There is potential that this subject's high-frequency hearing loss was a contributor to this difference, as he could not decrease the p-p SPL of his clicks to the same level as LRK and still audibly hear the return echo. Additionally, ECL (age 7) is less experienced dolphin than LRK, age 17, and their strategies to complete the task could have been affected by their prior experience.

V. CONCLUSIONS

As target range increases, range discrimination thresholds in dolphins increase exponentially. In contrast to "jittered" delay resolution tasks, range discrimination in a successive comparison does not depend on echo fine structure, but rather on the echo envelope.

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CHAPTER 3 Differences between a successive versus simultaneous range discrimination task in an echolocating bottlenose dolphin (*Tursiops truncatus*)

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ABSTRACT:

A primary feature of bat and dolphin biosonar is the ability to measure echo-delay, both to determine absolute target range and to resolve range differences between targets. Measurements of range (i.e., echo-delay) discrimination thresholds in echolocating animals, however, vary across studies. This variance may reflect different test methods, such as whether the animal could simultaneously receive echoes from two compared targets (simultaneous condition), or only one target at a time (successive condition). The present study compares these test conditions directly in dolphins. First spectral cues available to the dolphin at various range differences under a simultaneous condition were determined by modeling the dolphin peripheral auditory system. Then dolphin echo-delay discrimination thresholds were measured under both simultaneous and successive conditions at simulated mean ranges of 3, 10, and 14 m to assess potential interactions across target range. Results indicate that the availability of spectral cues during the simultaneous condition imparted limited improvement relative to the successive condition where spectral cues were unavailable. Echo-delay discrimination thresholds showed an overall increase with an increase in range in both the simultaneous and successive conditions.

Keywords: Dolphin, Echolocation, Biosonar, Target ranging

I. INTRODUCTION

An important feature of dolphin and bat biosonar is the ability to determine the distance (range) to a target, as well as differences in range between targets. Previous research determined that large-scale echo-delay is the primary means used to determine target range (Simmons, 1973; Murchison, 1980b; Masters and Jacobs, 1989; Moss and Schnitzler, 1989; Au, 1993; Simmons, 2014; Christman et al., 2024), while small-scale echo-delays between multiple echoes from complex objects are used to resolve finer spatial features (Simmons et al., 1990a; Au and Pawloski, 1992). Small-scale echo-delays occur when more than a single echo falls within the temporal window. When echoes appear within this window research suggests spectral information is converted into spatial information (Simmons et al., 1990a; Branstetter et al., 2007). For echolocating bats and bottlenose dolphins, the temporal window durations are similar: ~350 µs in bats and ~260 µs in bottlenose dolphins (Moore et al., 1984; Au, 1988; Simmons et al., 1989). In dolphins, the ability to resolve echo features within the temporal window enables identification and discrimination of targets with greater accuracy than man-made underwater sonar systems (Roitblat et al., 1995; Moore, 1997; Vishnu et al., 2022).

Range resolution has been measured in bats and dolphins by training subjects to discriminate between two identical objects positioned at different azimuthal angles and slightly different ranges (Simmons, 1973; Murchison, 1980b; Christman et al., 2024). In these studies, it is not always clear if the animals were completing the task via a *simultaneous* ranging process or a *successive* ranging process. During successive ranging, the animal accesses information from a single target at a time and must hold the range information in memory while comparing to another target. For simultaneous ranging, both targets are presented concurrently and positioned such that the animal can ensonify both with a single echolocation emission. Echoes from the two targets arriving at the animal with echo-delay differences shorter than the temporal window create the potential for spectral cues that could be utilized during the discrimination process (Simmons, 1973; Simmons and Grinnell, 1988; Masters and Jacobs, 1989). Previous range discrimination experiments conducted with different methods are equivocal on whether animals in those studies used a simultaneous or successive ranging process, and whether performance would be enhanced by using a simultaneous process (Simmons, 1973; Troest and Mohl, 1986; Masters and Jacobs, 1989; Simmons, 2014).

In Simmons (1973), big brown bats (*Eptesicus fuscus*) were trained to discriminate between two targets with an angular separation of 40°. This separation allowed the big brown bat to ensonify both targets with a single biosonar pulse, which could have allowed the bat to utilize a simultaneous process (Simmons, 1973; Simmons, 2014). The big brown bat's range resolution was determined to be ~1-2 cm, equivalent to an echo-delay difference of ~60 – 120 μs, and remained consistent with changes in mean ranges of 30, 60, 120, and 240 cm (Simmons, 1973). Simmons (2014) suggested that the ranging process reported by Simmons (1973) was simultaneous, and that failure occurred at ~1-2 cm of range difference due to clutter masking of the closer target by the farther target. The clutter masking impacted the determination of whether echoes from the right or the left were received first. Additionally, Simmons (2014) proposed that if range discrimination thresholds are determined at the point where clutter masking occurs, thresholds will remain constant as mean range changes, consistent with the results of Simmons (1973). This hypothesis suggests that bats use a simultaneous ranging process, but whether spectral cues were used by the bat during the ranging process is unknown.

Troest and Mohl (1986) conducted an experiment where serotine bats (*Eptesicus serotinus*) had to detect whether a target was present or absent. Echo detection thresholds were determined with and without the presence of clutter (white noise). On trials where clutter was presented the clutter was delayed by 2 ms after the target. Troest and Mohl (1986) determined that target detection thresholds increased with the presence of the clutter. The results of this experiment question Simmons's (2014) hypothesis that failure occurs due to clutter masking; this experiment suggests that bats ability to detect the target decreased when the clutter was within 2 ms of the target echo-delay, which is an order of magnitude greater than the range resolution findings of Simmons (1973). The results of Troest and Mohl (1986) suggest that the bats in Simmons (1973) were not using a simultaneous process as the clutter from the farther target would have disrupted the bats' performance at echo-delays much higher than the ~60-120 µs threshold that was measured. On the contrary, Masters and Jacobs (1989) conducted a range discrimination experiment with a phantom echo generator (PEG) where the echoes possessed an inherent jitter in echo-delay causing the range to the targets to change from 2-4 cm between each emitted pulse. Range resolution thresholds from this experiment were ~1 cm, similar to Simmons (1973). With the inherent jitter in echo-delay introduced, range resolution results of ~1 cm were only possible if the bat completed the task via simultaneous ranging.

Murchison (1980b) conducted a range discrimination experiment with a single Atlantic bottlenose dolphin (*Tursiops truncatus*). Like Simmons (1973), a dolphin was trained to identify which of two foam spheres located at different azimuthal angles was closer. The two spheres had an angular separation of 40° and threshold testing was conducted at three different mean ranges (1, 3, and 7 m). The study concluded that as mean range decreased thresholds also decreased (Murchison, 1980b). This differed from the results of Simmons (1973), where range discrimination thresholds did not change with mean range. Christman et al. (2024) conducted an experiment similar to Murchison (1980b) with a two-channel PEG system. In this experiment, the dolphin was restricted to a successive ranging process by limiting received echoes from one simulated target at a time, based on whether the right or left PEG channel received the higher amplitude click emitted by the dolphin. Seven different mean ranges were tested and, like Murchison (1980b), thresholds increased with an increase in mean range. However, thresholds in Christman et al. (2024) were higher than those in Murchison (1980b); Christman et al. (2024) found thresholds of 6.5 and 8.3 cm (equivalent echo-delay 87 and 110 µs) at mean target ranges of 3 and 7 m, respectively, whereas Murchison (1980b) reported thresholds at 3 and 7 m to be 1.5 and 3 cm (20 and 40 µs). Interestingly, the delay corresponding to the lowest threshold (4.1 cm) reported by Christman et al. (2024) was 55 µs at a mean range of 1.75 m, similar to the ~60 µs value reported by Simmons (1973). Whether the dolphin in Murchison (1980b) used a successive or simultaneous ranging process is unknown, but the use of simultaneous ranging could explain the differences in thresholds from Christman et al. (2024).

The primary aim of the current study was to determine differences between a simultaneous and successive range discrimination task in a bottlenose dolphin. First a model of the dolphin peripheral auditory system was built to visualize spectral cues that would be available to the dolphin at three different range differences during simultaneous testing. Then behavioral experiments tested dolphin range discrimination thresholds in both a simultaneous and a successive comparison task using a two-channel PEG system. The goal was to determine if the differences in range discrimination thresholds reported by Murchison (1980b) and Christman et al. (2024) were related to the dolphin in Murchison (1980b) using a simultaneous ranging process. Testing was conducted using a two-alternative forced choice (2AFC) task at mean simulated target ranges of 3, 10 and 14 m.

II. METHODS

A. Peripheral auditory system modeling

A model of the dolphin peripheral auditory system (Branstetter et al., 2007; Branstetter et al.) was used to visualize potential spectral cues as the dolphin scanned across the left/right simulated targets during a simultaneous ranging process. The simulation included PEG transducers that were located at -10° (left simulated target) and +10° (right simulated target) azimuth. Five different dolphin beam azimuthal angles (θ = -10, -5, 0, 5, 10°) were simulated (Fig. 1). The model input consisted of two echo “highlights”, each based on the same representative dolphin on-axis click. Each highlight was delayed appropriately for the simulated echo-delay for the left/right PEG channels and scaled in amplitude according to the dolphin’s simulated azimuth relative to PEG transducer positions, using prior measurements of the dolphin transmitting and receiving beam patterns (Au and Moore, 1984; Au et al., 1986; Finneran et al., 2014). The difference in amplitude between the two echo-highlights was estimated to be ~34, 17, and 0 dB for q = ±10° (i.e., the opposite target is 20°off-axis), ±5°, and 0°, respectively. Whether the first or second echo-highlight was higher in amplitude depended on the dolphin’s beam angle and the side of the closer target. The model was built with the left PEG channel simulating the closer target and generalized the two-highlight echo being received at the center of the dolphin’s head.

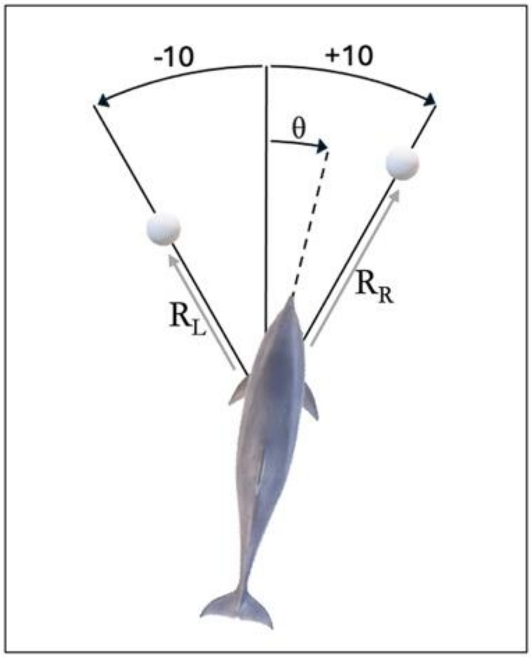


Figure 3.1: Design of the peripheral auditory model simulation. Spheres represent the simulated targets separated by ±10° in azimuth, with the left simulated target being closer than the right simulated target ($R_L<R_R$). The variable orientation of the dolphin in the azimuthal plane relative to the midpoint of the left and right targets is denoted by θ.

The model was built based on results from Christman et al. (2024). Modeling was done using performance at the mean range of 3 m for three different range differences (ΔRs): (1) 1 cm (equivalent echo-delay difference 13 μs, close to chance performance), (2) 6.5 cm (87 μs, near threshold), and (3) 20 cm (267 μs, above 90% correct). Due to differences in hearing capabilities between subjects reported by Christman et al. (2024) modeling was done to represent a dolphin with normal hearing as well as to represent a dolphin with significant hearing loss (upper frequency hearing limit of ~60 kHz) by applying a low-pass filter at 60 kHz (8th order Butterworth, zero-phase).

B. Subject and test environment

Apollo (APO), a seven-year-old, male bottlenose dolphin participated in the study. APO's upper-frequency hearing limit was determined via auditory evoked potential measurements to be ~70 kHz (see Strahan et al., 2020), which indicates substantial high-frequency hearing loss (Johnson, 1966; Houser and Finneran, 2006). Testing occurred in a 9 × 9 m floating netted enclosure at the U. S. Navy Marine Mammal Program in San Diego Bay, CA. The test environment was similar to that described in Christman et al. (2024): a hoop station was located at ~1 m depth, oriented so that the dolphin was echolocating into San Diego Bay through a netted frame, and flanked by response paddles on the left and right (Fig. 2). Two pairs of piezoelectric transducers (TC4013, Reson Inc., Slangerup, Denmark) were positioned on the other side of the netted frame at 1.2 m distance and ± 10 ° azimuthal angle from the midpoint of the hoop station. The transducer pairs operated as two (left/right) channels in a PEG system. One transducer in each pair received the dolphin's biosonar click and the other projected the electronic echo for the associated channel. The 20° angular separation between the left/right simulated targets was smaller than the 40° separation used by Murchison (1980b) and Christman et al. (2024). The angle was decreased in the present study to increase the opportunity for simultaneous reception of echoes from the left/right during simultaneous testing. The dolphin additionally wore on the center of his melon and approximately 3 cm above his rostrum another TC4013 that was embedded in a silicone suction cup. This hydrophone was used to estimate the time of the dolphin's click emission (see echo generation below). The area within ±10° of the dolphin's main biosonar transmission beam while in the hoop station was clear of obstructions for ~500 m in distance. The average water depth was ~10 m. Median ambient noise pressure spectral density levels over the duration of the experiment were approximately 69 dB re 1 µPa^2/Hz at 10 kHz, decreased linearly with the logarithm of frequency to 52 dB re 1 µPa^2/Hz at 150 kHz and consisted mostly of vessel traffic, snapping shrimp, and other dolphins.

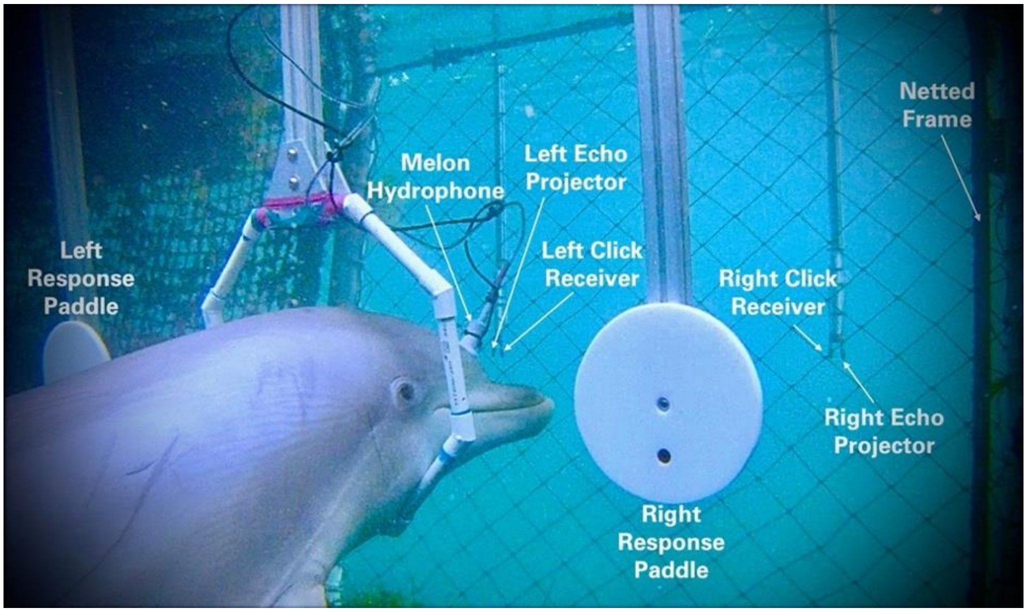


Figure 3.2: Experimental setup with the dolphin positioned in the hoop station, oriented toward San Diego Bay through a netted enclosure, and facing the left and right transducer pairs. A hydrophone embedded in a silicone suction cup was also placed on the center of the dolphin's melon to record the timing of each emitted click.

C. Task Description

The dolphin's task was to echolocate towards two simulated targets at different azimuthal angles and indicate the closer target. APO participated in one to two sessions per weekday. Sessions lasted ~25 min and consisted of ~60 – 80 trials. Each trial consisted of APO positioning himself in the hoop station and emitting clicks towards the left and right receivers while listening to the corresponding phantom echoes from the left and right projectors. During each trial, the left and right PEG channels were set to different echo-delays, simulating targets at different ranges. After inspecting the left and right simulated targets, APO was trained to leave the hoop and choose the paddle of the side that produced phantom echoes with the shorter echo-delay, simulating the closer (S+) target. Each trial began with the PEG turned off (received clicks would not generate echoes). Once APO was positioned properly in the hoop station, the trial started and the PEG was turned on for 4 s. During the 4-s trial APO could leave at any time to make his choice.

Range discrimination thresholds were measured at three different simulated mean target ranges: 3, 10, and 14 m and under both simultaneous and successive conditions. Simultaneous testing was conducted first, in the order 10, 3, 14 m, to expose APO to potential spectral information created by echoes from the left and right PEG channels arriving within the ~260-μs auditory temporal window (Vel'min and Dubrovskii, 1976; Moore et al., 1984; Au, 1988). During this condition APO was able to trigger both PEG channels with a single click, which allowed him to simultaneously receive echoes from both the right and left PEG channels as he scanned. Successive testing was done after simultaneous testing, in the order 14, 10, and 3 m. During this condition the dolphin could only trigger one PEG channel at a time, restricting him to using the echo-delay stored in his memory to compare the left and right simulated targets. The successive condition was tested last to avoid APO learning the task with only echo-delay information and subsequently ignoring potential spectral cues created by the simultaneous presentation of the simulated targets. Data collection for each range and condition took ~2-5 weeks. To prevent APO from using a template of each S+ target range stored in his memory versus comparing the left/right simulated ranges, the S+ and S- ranges roved from trial-to-trial around the mean range being tested. The amount of roving was selected from a normal distribution with standard deviation of 15 cm and limited to ±3 standard deviations.

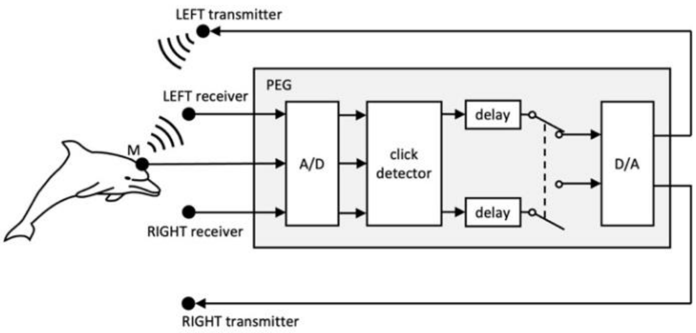
Nine ΔRs were tested during each session and differed with mean target range. Sessions began with a series of warm-up trials, where the values of ΔR being tested were presented to APO in descending order. After the warm-up, ΔRs were presented randomly from trial-to-trial. Each ΔR was presented on the left and right equally during each session. Data were collected across multiple sessions until at least 40 trials for each ΔR, range, and condition combination were obtained. Trials where APO only triggered echo playbacks from one PEG channel were not included in the analysis and therefore, a minimum of 30 trials per ΔR, range combination, and condition were analyzed.

Relative echo level [REL, the echo sound exposure level (SEL, in dB re 1 $\mu Pa^2 s$) at the listening position relative to the click SEL at the click receiver] was held constant as ΔR and mean range changed. Therefore, the simulated target strength (TS) increased with an increase in range. REL was set to the highest level possible for the hardware, which was ~20 dB above APO's echo detection threshold. Estimated TSs (based on SEL) were: -58, -37, and -31 dB at 3, 10, and 14 m, respectively. Due to APO's high-frequency hearing loss, effective TSs were estimated to be ~20 dB lower than calculated TSs (see Christman et al., 2024).

D. Echo generation

Biosonar echoes were generated using the same PEG described by Christman et al. (2024). If a click received at the right or left receiving hydrophone exceeded an amplitude threshold, click waveforms were extracted and times-of-arrival were obtained from the left, right, and melon hydrophone channels. Different criteria were used for the simultaneous condition versus the successive condition to determine if the digitized click signal from the left or right channel "triggered" the PEG and resulted in echo generation (Fig. 3). For the simultaneous condition two criteria had to be met: (1) the digitized hydrophone signal on the left or right channel exceeded the amplitude threshold, and (2) the time-of-arrival difference (TOAD) between the click received by the left/right hydrophone and the same click received by the melon hydrophone was less than the nominal acoustic travel time for that simulated target range. This ensured the PEG would only trigger an echo when the dolphin was stationed in the hoop. For the successive condition the same criteria as the simultaneous condition had to be met in addition to the click peak-to-peak (p-p) amplitude on that channel (left or right) was greater than the amplitude of the same click on the other channel; this ensured that echoes were only generated from the channel the dolphin's beam was primarily directed towards. The delay of each echo was corrected using the TOAD between the click received by the left/right hydrophone and the same click received by the melon hydrophone. This was done to account for the dolphin's head movement during the trial. The analog echo waveform, which was a replica of the dolphin's emitted click, was filtered (5–200 kHz, 3C module), amplified (7600M, Krohn-Hite Corp.), and projected through the echo transmitter. Received echolocation clicks and projected echo waveforms were digitized at 2 MHz and 16-bit resolution by an NI PXIe-6368 multifunction data acquisition device (National Instruments, Austin, TX) and stored for analysis.

(a) Successive



(b) Simultaneous

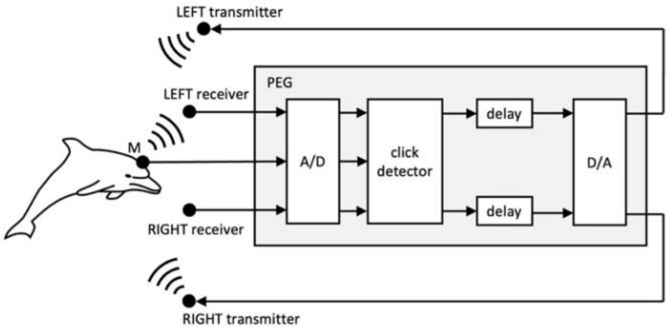


Figure 3.3: Block diagram indicates the procedures during the successive condition versus simultaneous conditions. (a) Block diagram shows the procedure for the successive condition. The click detector determined if criteria were met for an echo to be generated. The echo was then delayed to simulate the assigned range of the left or right transmitter (based on which receiver received the higher amplitude click), and projected the echo through the corresponding transmitter. (b) Block diagram illustrates the procedure for the simultaneous condition. The click detector determined if criteria were met for an echo to be generated. If so, echoes were then delayed to simulate the assigned ranges for the left and right transmitters, and projected through the corresponding transmitters.

The PEG was calibrated before each session by inputting a representative recording of an on-axis dolphin click to the PEG analog-to-digital (A/D) converter. The subsequent analog echo waveform was broadcast from the left echo projector and recorded with the right click receiver. The procedure was then reversed (right projector to left click receiver). Over the course of the study calibrations varied by ±1 dB.

E. Analysis

Statistical analysis of dolphin discrimination performance was conducted in R (R Core Team, 2019). Psychometric functions were created for each range and condition by fitting the cumulative normal distribution function to proportion correct versus ΔR. Fitting was done using the *quickpsy* package (Linares and López-Moliner, 2016), with maximum likelihood used to fit model parameters. The 75% correct discrimination rate from the psychometric function was used to calculate thresholds at each range and condition. The data were bootstrapped with 1000 iterations to calculate the 95% confidence intervals. A general linear model (glm) was built to test for main effects and interactions for mean range and condition. Follow on post-hoc tests using Tukey's method were conducted from the results of the glm model to test for significance between each mean range within each condition and between conditions.

Acoustic parameters including inter-click-interval (ICI), p-p sound pressure level (SPL), center frequency, and (centralized) root-mean-square (rms) bandwidth (BW) were analyzed using custom software. Clicks within ±3 dB of the maximum click p-p SPL for each trial, compared amongst the right and left click receivers, were included in the analysis – these were considered the on-axis clicks within the trial.

III. RESULTS

A. Simultaneous condition peripheral auditory modeling

Figure 4 illustrates the echo-waveforms, spectra, model output spectrograms, and echo-envelopes for the low-pass filtered model based on the dolphin's frequency and temporal resolution for a simultaneous condition. For ΔRs that were modeled at threshold and performance > 90%, there is a visible difference in the spectra and corresponding spectrogram when the dolphin scans from -5° past the midpoint to +5° [Fig. 4(b) versus Fig. 4(d) and Fig. 4(g) versus Fig. 4(i)]. Additionally, the echo-envelope for the ΔR when performance > 90% is visibly different when the dolphin scans from -5° past the midpoint to +5°. When the dolphin is at chance performance, there are no obvious differences between the model outputs when comparing -10 and -5° azimuthal angles to +5 and +10° azimuthal angles. Model results predict performance during a simultaneous condition to improve in comparison to a successive condition as there are visible spectral cues at a range difference where dolphin performance was reported to be at threshold by Christman et al. (2024) during a successive condition.

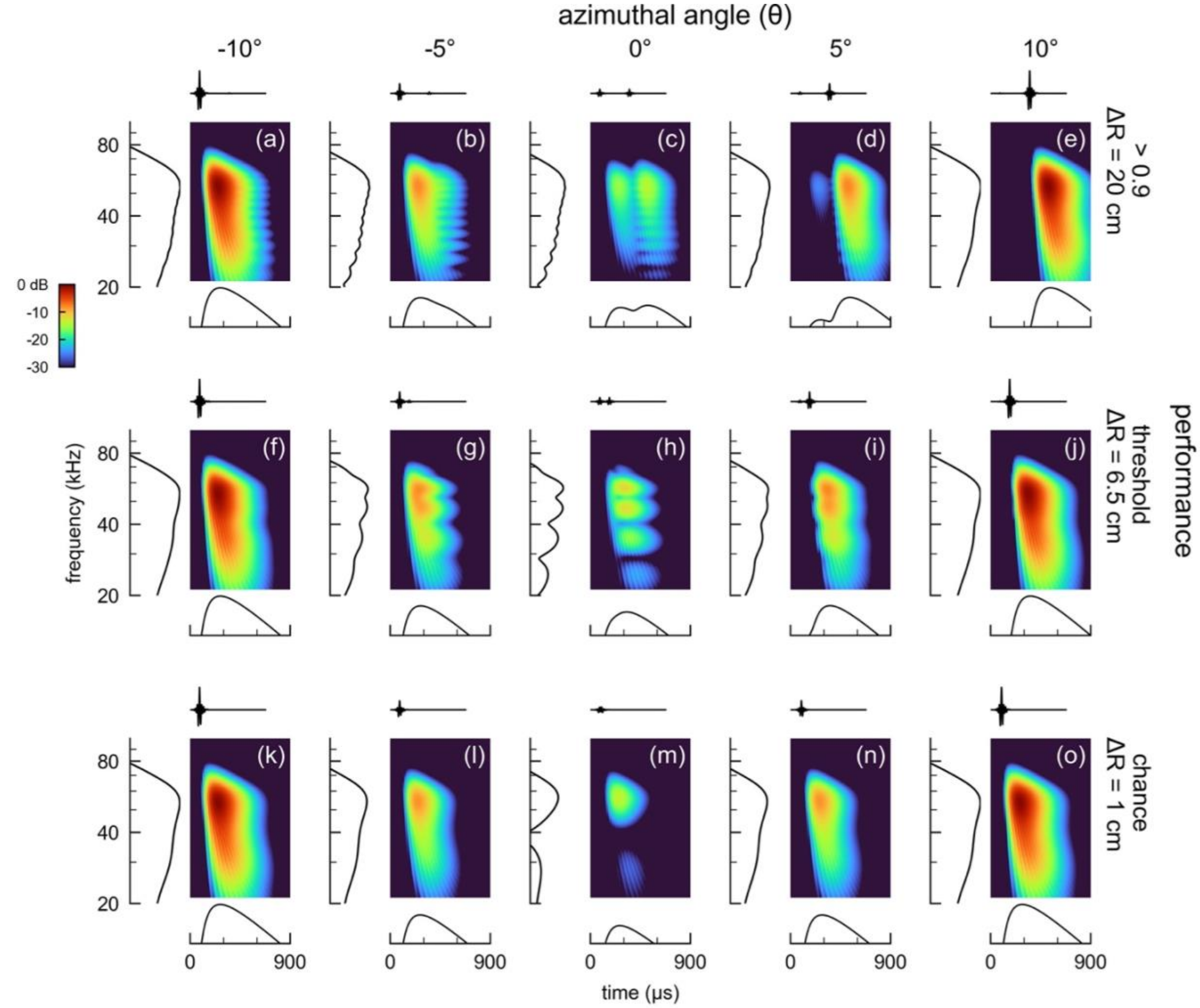


Figure 3.4: Dolphin peripheral auditory system model outputs at three different range differences (rows) and five different azimuthal angles (columns). The top row illustrates a ΔR of 20 cm, the middle row a ΔR of 6.5 cm, and the bottom row a ΔR of 1 cm. Each column illustrates one of the five θs modeled; -10° represents the dolphin's beam centered on the left simulated target, 0° the dolphin's beam centered at the midpoint between the left and right simulated targets, and +10° the dolphin's beam centered on the right simulated target. For each subplot [(a) – (o)], the top trace shows the echo waveform, the leftmost plot gives the frequency spectrum (collapsed across time), the rightmost plot shows the time-frequency spectrogram, and the bottom plot gives the echo temporal amplitude envelope.

B. Behavioral performance for biosonar tasks

Figure 5 shows the psychometric functions for each range and condition tested. Figure 6 shows thresholds as a function of range and condition, with the error bars representing the 95%

bootstrapped confidence intervals, and statistically significant results from the post-hoc tests determining individual contrasts between each mean range between conditions and within conditions. Thresholds for the simultaneous condition at 3, 10, and 14 m were 6.4, 6.6 and 21.6 cm (85, 88, and 288 μs of equivalent echo-delay) respectively. Thresholds for the successive condition were: 4.3, 9.6 and 25.7 cm (57, 128, and 343 μs of equivalent echo-delay) respectively. There were no significant differences between the simultaneous condition and successive condition at all three mean ranges [3 m ($z = -0.6$, $p = 0.99$), 10 m ($z = 1.9$, $p = 0.41$), and 14 m ($z = 2.2$, $p = 0.20$)]. For the simultaneous condition there was no significant difference between 3 and 10 m ($z = 1.5$, $p = 0.69$), but there were significant differences between 3 m and 14 m ($z = 6.9$, $p < 0.0001$) as well as 10 m and 14 m ($z = 8.2$, $p < 0.0001$). For the successive condition there were significant differences between all ranges tested: 3 and 10 m ($z = 3.2$, $p = 0.02$), 3 and 14 m ($z = 8.8$, $p < 0.0001$), and 10 and 14 m ($z = 9.7$, $p < 0.0001$). Additionally, there was no significant interaction between mean range and condition ($z = -1.7$, $p = 0.10$).

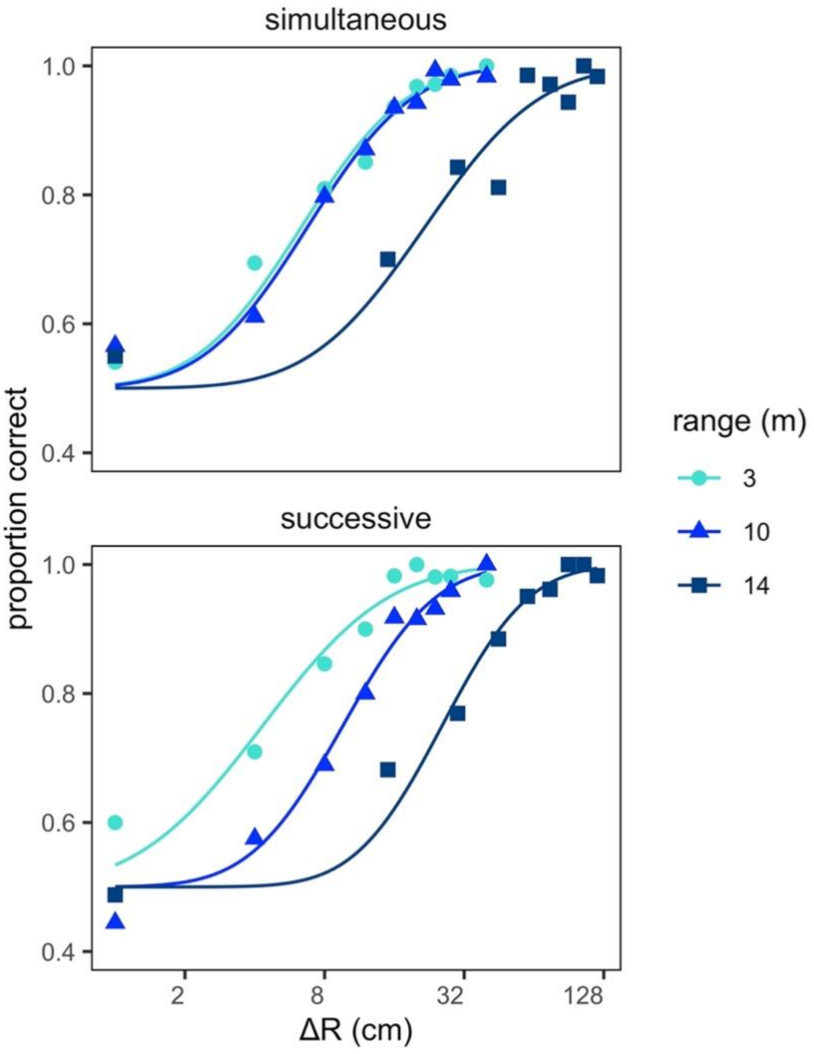


Figure 3.5: Proportion of successful discriminations as a function of ΔR for the simultaneous and successive conditions. Each absolute range tested is denoted by a different shape and color.

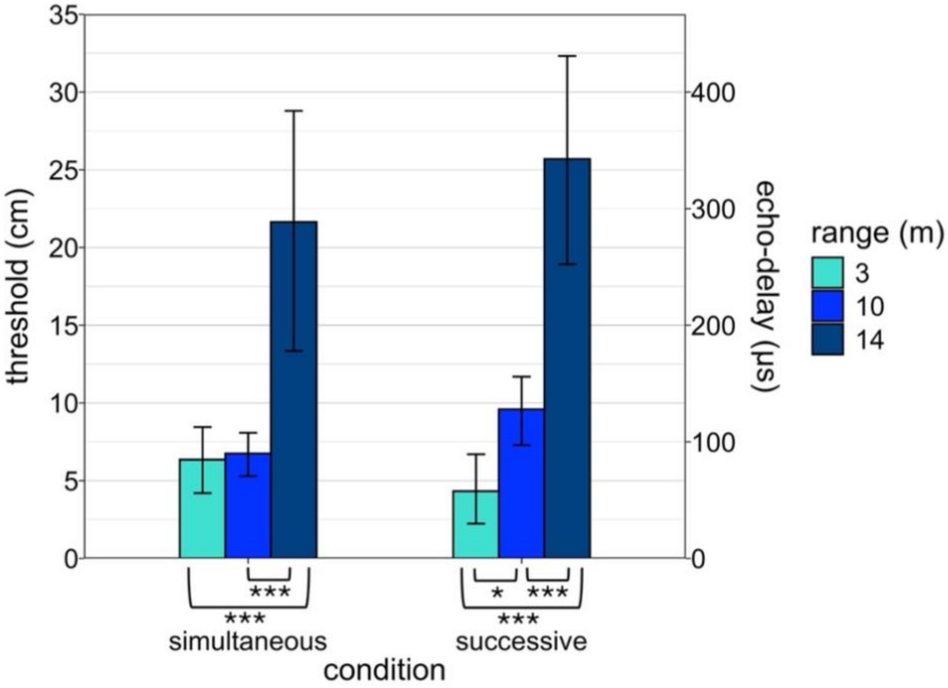


Figure 3.6: Range discrimination thresholds as a function of mean target range for the simultaneous and successive conditions. Error bars represent the 95% intervals confidence calculated by bootstrapping the data with 1000 iterations. Statistical significance defined as * $p < 0.05$, and *** $p < 0.001$.

C. Click acoustic parameters

Figure 7 shows distributions of center frequency, p-p SPL, rms BW, and ICI for each range, condition, and click receiver position (left/right). Only clicks with p-p SPL within ±3 dB of the maximum p-p SPL for that trial were included in the analysis (to limit the analysis to presumably on-axis clicks). This resulted in 3.8×10^4 total clicks being analyzed. For 93% of the trials, APO clicked towards the right receiver first and then scanned towards the left receiver. Across all three ranges and the two conditions, rms BW and center frequency were lower when he inspected the right simulated target versus the left simulated target. Additionally, on the left side at 3 m, on both sides at 10 m, and the right side at 14 m, the center frequency was lower for the simultaneous condition versus the successive condition. Overall center frequencies were lower for the right side than the left side. The distribution of ICIs increased as expected with range and p-p SPL increased with range, but there were no obvious differences for the ICIs or p-p SPL between the simultaneous and successive conditions.

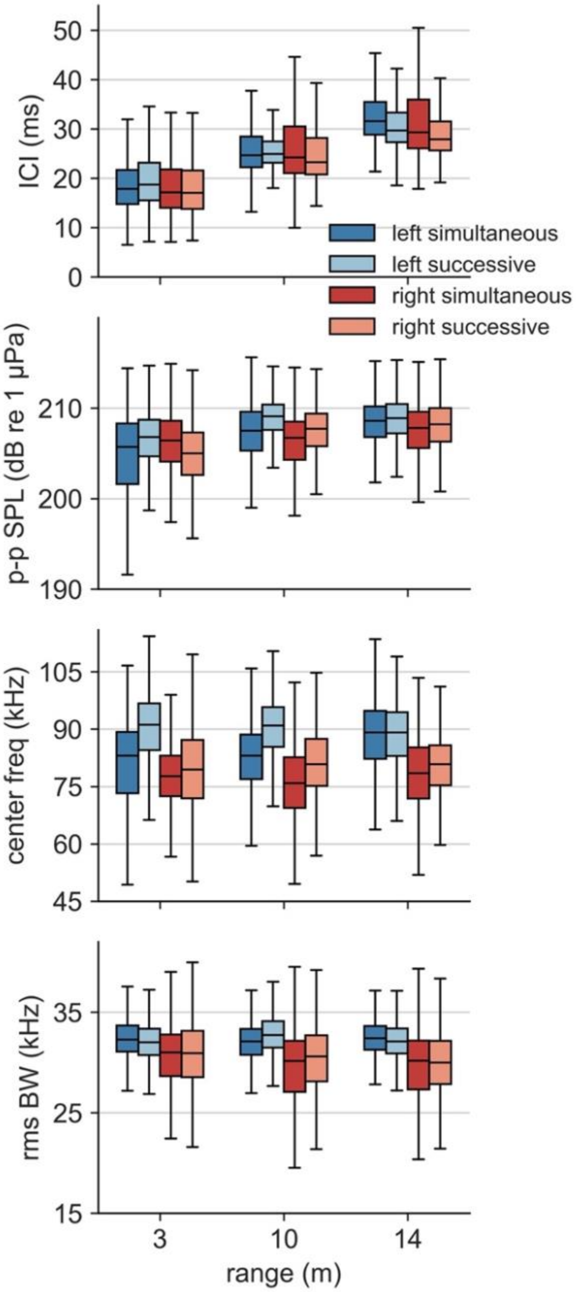


Figure 3.7: Boxplots showing the acoustic analysis for clicks received during the experiment. From top to bottom the ICI, p-p SPL, center frequency, and rms bandwidth are plotted. The center line represents the median and the box represents data within the inner quartiles. The whiskers represent data within 1.5 × the upper and lower quartiles (Waskom, 2021). Clicks received by the left click receivers are annotated in dark blue for the simultaneous condition and light blue for the successive condition. Clicks received by the right click receivers are annotated in dark red for the simultaneous condition and light red for the successive condition.

IV. DISCUSSION

A. Behavioral performance for biosonar tasks

The current experiment tested range discrimination thresholds at 3, 10 and 14 m under simultaneous and successive conditions. A primary goal of this study was to determine whether thresholds would decrease (and thus be more similar to Murchison (1980b)) when targets were presented simultaneously; i.e., when the animal had access to spectral cues created by echoes from the left and right simulated targets arriving within the temporal window. Thresholds from the current experiment for the simultaneous and successive conditions were greater than those reported by Murchison (1980b): for example, at 3 m range, simultaneous thresholds for the present experiment were 6.4 cm (85 µs), compared to 1.5 cm (20 µs) reported by Murchison (1980b). Access to spectral cues created by the two targets therefore cannot explain the discrepancy between the successive results from Christman et al. (2024) and Murchison (1980b). The specific reason for the discrepancy between thresholds remains unknown but could be a product of differences in methodology related to stimulus presentation order and/or the use of physical vs. phantom targets. Murchison (1980b) used a modified method of constants that aimed at pushing thresholds as low as possible. The current experiment, and Christman et al. (2024), presented the different ΔRs to the dolphin in a randomized sequence. Murchison (1980a) states that when presented with a ΔR of 2 cm at a range of 1 m without using a modified method of constants, performance was 53%. When using the modified method of constants established to "work" the dolphin down to lower ΔRs, the dolphin was 94% correct at the 2-cm ΔR. Additionally, the targets used in Murchison (1980b) had TSs of -34 dB. With APOs high-frequency hearing loss, effective TSs at all three ranges were at least 15 dB lower than reported by Murchison (1980b). The higher TS target used by Murchison (1980b) could have improved the dolphin’s ability to complete the task. In the current experiment, the target was also a point target, whereas in Murchison (1980b) the targets were 7.62 cm foam spheres with a lead core that hung 0.4 cm below the water surface. The targets had an additional weight suspended 0.9 m below them via monofilament line for additional stability. The complexity of the target set up, proximity of the targets to the water’s surface, and the higher TS of the targets in Murchison (1980b) could have produced more robust spectral/temporal cues relative to those of the current experiment.

When comparing the simultaneous condition to the successive condition, there was no clear trend between the conditions for the ranges tested. Simultaneous condition thresholds were nearly identical at 3 and 10 m range (6.4 and 6.6 cm, respectively). This result fits Simmons (2014) hypothesis that if a simultaneous process is being used, the spacing between the two echo-highlights created by the ∆R remains the same independent of mean range, and therefore thresholds will remain constant when range increases. In the current experiment and in Christman et al. (2024) range discrimination thresholds continue to decrease with a decrease in mean range when testing occurred in a successive condition. Simmons (2014) suggests that failure occurs during the simultaneous ranging process due to the farther target cluttering the closer target. This cluttering would not be present during the successive condition and could be a potential cause of APO’s improved performance during the successive condition at 3 m (though the differences were not statistically significant). It is possible that during a simultaneous ranging process the farther target cluttering the closer target will cause range discrimination thresholds to plateau and not decrease at the mean ranges less than 10 m, as seen during the successive ranging process.

Results of the current study for ranges greater than 10 m are similar to those found in Christman et al. (2024); i.e., thresholds under both conditions dramatically increased at 14-m range. This suggests that dolphins experience increasing difficulty discriminating range once the mean target range reaches ~14 m (~19 ms echo-delay), even when relative echo level is held constant. Previous range discrimination experiments conducted in bats and with physical targets in dolphins, i.e., Murchison (1980a), did not test ranges with echo-delays greater than ~13-14 ms. Therefore, for larger ranges there are no relevant results with which to compare the current data. A study of receiver-based automatic gain control in dolphins showed that beyond a 10–14 m range, release from forward masking could no longer compensate for the increasing echo attenuation with range (Finneran et al., 2013). Together with the present data, this suggests that the dolphin's biosonar system may be optimized for operation at ranges < ~14 m.

B. Click acoustic parameters

Click parameters during the simultaneous and successive sessions were generally similar, except the center frequency tended to be ~10 kHz lower during simultaneous testing at 3 m (left only) and 10 m. Corresponding changes in SPL did not always occur; when they did (e.g., 10 m, left side), the change in SPL was smaller than predicted from previous measurements of the relationship between click SPL and center frequency in *Tursiops* (~1 kHz/dB) (Finneran et al., 2014). Previous research suggests that dolphins can control the frequency content and amplitude of their clicks independently (Moore and Pawloski, 1990). Whether APO was manipulating his clicks as a strategy to perform better on the task is unknown. Notably, the majority of the clicks emitted by APO had center frequencies above his upper frequency limit of hearing of ~70 kHz for all ranges and both test conditions.

Click center frequency and bandwidth tended to be lower on the right side compared to the left, regardless of range or condition; a similar trend was observed by Christman et al. (2024). During the experiment APO inspected the right simulated target first on 93% of the trials. Murchison (1980a) also reported that the dolphin inspected the right target first on 90% of the trials. It seems likely that the observed differences in click center frequency and bandwidth are related to changes in click parameters over the course of the trial, i.e., bandwidth and center frequency likely increased during the trial, so clicks on the right tended to have lower center frequency and bandwidth.

C. Peripheral auditory model results versus behavioral results

The peripheral model results can give insight into spectral cues that the dolphin could potentially use when scanning between two targets at different ranges. The current model was built using a replicate of a dolphin click, and therefore does not represent the actual echo that would be received by the dolphin. Additionally, the model does not account for the "coloring" of the echo due to the transducer voltage response, the dissipation of higher frequencies for the off-axis target, and potential binaural cues available to the dolphin based on their head movement. However, the simple model gives insight on how spectral cues can change as the dolphin scans from the closer to the farther target, and how these cues change as the range difference between the two targets decreases. Of note is the visible difference in the model output spectrogram as the dolphin scans from left to right at range differences above threshold. No differences in the model output spectrogram were visible when the animal was at chance performance of range difference discrimination. Results from the behavioral experiment suggest that the dolphin's ability during the successive condition when relying on memory is very similar to that when additional access to spectral cues is provided during the simultaneous condition. Therefore, if the dolphin uses the spectral cues during the simultaneous condition, it does not result in significantly better task performance.

CONCLUSIONS

Peripheral auditory model outputs suggest that spectral cues could be available to the dolphin when determining small differences in range between targets. However, results from the behavioral experiments suggest that the availability of spectral cues imparts limited improvement during a simultaneous ranging task relative to a successive ranging task where spectral cues are unavailable. Both successive and simultaneous testing reveal increasing difficulty for dolphins to discriminate target ranges when the mean range exceeds 10 m, perhaps revealing the upper range within which dolphin biosonar is optimized.

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CHAPTER 4 The effects of inter-highlight interval and phase on echolocating bottlenose dolphins performing a two-highlight echo discrimination task

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ABSTRACT:

The dolphin's ability to discriminate and classify targets in their environment is a critical feature of their biosonar system. This requires the dolphin to convert echo-highlights with differing inter-highlight intervals (IHIs) reflected by complex targets into useful information. The current experiment tested the dolphin's ability to discriminate between simulated biosonar echoes with a standard IHI and a target echo that had a slightly increased IHI. Seven standard IHIs were tested from 50 – 750 μs. Threshold testing occurred under two conditions: a constant phase condition, where the two echo-highlights were in-phase, and a random phase condition, where the second highlight was given a random phase shift designed to disrupt cues based on changes in absolute positions of spectral peaks or notches. For standard IHIs within the temporal window (<300 μs), thresholds were an order of magnitude less for the constant versus random phase condition, suggesting the use of a pitch cue that is “blurred” for the random-phase condition resulting in elevated thresholds. For standard IHIs outside the temporal window (>300 μs) thresholds were higher than those for standard IHIs within the temporal window and similar between the constant and random phase conditions, suggesting the use of difference in timing of the highlight envelopes.

Keywords: Dolphin, Echolocation, Biosonar, Target discrimination

I. INTRODUCTION

Dolphins and microchiropteran bats navigate their environment using advanced biosonar. The dolphin's ability determine target distance and small-spatial features of complex targets allows them to detect and classify targets in cluttered environments at a more rapid rate than man-made sonar systems (Roitblat et al., 1995; Moore, 1997; Vishnu et al., 2022).While it is known that these animals use large-scale echo-delays, i.e., the time between their emitted signal and the return echo, to determine distance to a target (Simmons, 1973; Murchison, 1980b; Au, 1993; Simmons, 2014; Christman et al., 2024), less is understood about the mechanisms used to resolve small-scale echo delays. Small-scale echo delays consist of echo-highlights that fall within the ~300-μs auditory temporal window and are thought to be temporally unresolvable by the auditory system (Vel'min and Dubrovskii, 1976; Au et al., 1988; Supin and Popov, 1995; Branstetter et al., 2020). The dolphin must convert these echo-highlights into useable information to discriminate between complex targets.

Previous research suggests that when echo-highlights fall within the temporal window, spectral information may be used to determine small-spatial features of targets based on the time separation of the echo-highlights (Au and Pawloski, 1992; Branstetter et al., 2020; Mulsow et al., 2023). The time separation between echo highlights (inter-highlight interval, IHI) directly corresponds to the spacing of peaks and notches within the frequency spectrum, where $\Delta f = 1/\Delta t$ (Δf is defined as the frequency spacing between the peaks and notches, and Δt is the IHI). Because of the reciprocal relationship, small changes in IHI can lead to large — and easily discriminated — changes in echo frequency spectrum. Echoes with multiple, correlated highlights could also give rise to a sensation of pitch — called time separation pitch (TSP) or repetition pitch (Thurlow and Small Jr, 1955; Thurlow, 1957; Mcclellan and Small Jr, 1965;

Bilsen, 1966; Bilsen and Ritsma, 1969). The difference in IHI between the two correlated signals "colors" the spectrum and could offer a perceptual cue that is created by the change in the peak-notch pattern.

Several previous experiments have tested the dolphin's ability to discriminate between echoes with different IHIs (Au and Pawloski, 1992; Branstetter et al., 2020). Au and Pawloski (1992) tested dolphins' ability to discriminate between physical cylinders with different wall thicknesses. Branstetter et al. (2020) conducted a similar experiment using electronic (phantom) echoes. In both of these studies, the phase relationship between the two echo highlights was constant. Results from the two studies were similar: discrimination thresholds for IHIs < 300 μs were < 1.5 μs, and for IHIs <120 μs thresholds were ~0.5 μs for the normal hearing dolphin tested.

Using a different approach, Mulsow (2023) tested the dolphin's ability to passively listen and discriminate between simulated echoes with two highlights under two different "phase conditions". In the first condition, the two echo-highlights were in phase, while in the second condition a random phase shift (see e.g., Finneran et al., 2023) was applied to each echo-highlight. The applied random phase shift results in Δf being held constant while the locations of the peaks and notches along the frequency axis occur at random for each echo. Therefore, the random phase condition would preserve perceptual cues based on Δf, but remove those based solely on spectral locations of peaks or notches. Mulsow (2023) determined that for IHIs < 300 μs the dolphin's IHI discrimination thresholds were significantly less for the constant phase versus the random phase condition. Whereas for IHIs > 300 μs thresholds were similar between the two conditions. The dolphins' ability to perform the task under the random phase condition means they could not solely rely on perceptual cues based on changes in frequency locations of spectral peaks or notches. These results therefore suggest that dolphins could be using a pitch cue that is reliant on the fine structure of the two highlights to discriminate between small differences in IHI. Results from Mulsow (2023) suggest that the random phase condition “blurs” this coloring resulting in higher IHI discrimination thresholds for IHIs within the temporal window. However, actual discrimination thresholds reported by Mulsow (2023) were higher than those previously reported for active biosonar tasks: ~6-11 s µs for IHIs of 250 µs and down to ~2 µs for IHIs < 120 µs. Higher thresholds for Mulsow (2023) can most likely be attributed to the task being conducted via passive listening versus the dolphin echolocating. How the random phase condition would affect the dolphin’s ability to discriminate between IHIs during active echolocation is unknown.

The primary objective of the current experiment was to test the differences between constant-phase conditions and random-phase conditions during an echolocation task using a phantom target, versus a passive listening task. The current experiment addresses potential causes for the higher thresholds for the constant-phase reported by Mulsow (2023) in comparison to Branstetter et al. (2020). While using echolocation, the dolphin can manipulate the amplitude, frequency, and timing of their outgoing clicks, resulting in a change of received echo content, potentially improving the dolphin’s performance. Similar to Branstetter et al. (2020) and Finneran et al. (2023), a fractional delay technique was used in the current experiment to test IHI discrimination thresholds not used in Mulsow (2023), which allowed for Δt below 0.5 µs to be tested. In the current experiment, random phase shifts were applied on an echo-to-echo basis versus the phase-shift being applied in 1-s blocks as in Mulsow (2023). Applying the random phase shift on an echo-to-echo basis versus in 1-s blocks should result in the potential “blur” of the pitch cue to be constant for the duration of each trial.

Discrimination thresholds were determined at seven different standard IHIs from 50 – 750 µs. Three standard IHIs (50 – 250 µs) within the temporal window were tested as a comparison to the active echolocation experiment conducted at a constant-phase condition by Branstetter et al. (2020) and the passive listening experiment at constant-phase and random-phase conditions conducted by Mulsow (2023). Four standard IHIs outside the temporal window (375 – 750 µs) were tested; these standard IHIs had yet to be tested in an echolocation experiment. The highest standard IHI tested by Branstetter et al. (2020) was on the edge of the temporal window (300 µs). An additional aim of the current experiment was to identify if IHI discrimination performance differs as the standard IHI outside the temporal window increases and if this change is consistent for the constant-phase and random-phase conditions. Additionally, as an "extreme" scenario, discrimination thresholds were tested when a single-highlight increased in echo-delay, essentially removing the first highlight from the two-highlight echo. The single highlight parameter was tested to determine whether the dolphins relied on the spacing between the two-highlights during an IHI discrimination task when the standard IHI is outside the temporal window, or if the dolphin was isolating the change in echo-delay of the second highlight.

II. METHODS

A. Subject and test environment

Two male bottlenose dolphins, Comet (COM) and Spout (SPO) (ages 7-8 during the period of testing) participated in the study. COM and SPO both had previous experience with cooperative psychophysical testing with "phantom" echoes (see Finneran et al., 2023). Both animals had normal hearing for a bottlenose dolphin with upper frequency hearing limits greater than 120 kHz [see Strahan et al. (2020)].

The test environment was similar to that described in Finneran et al. (2023). Testing took place in a 9 × 9 m floating netted enclosure at the U.S. Navy Marine Mammal Program in San Diego Bay, CA. During each trial the dolphins positioned themselves on an underwater "biteplate" ~1 m below the surface and supported by an aluminum frame. The frame was constructed to ensure the areas around the dolphin's melon and jaw area were free from obstructions. The biteplate was oriented so that the dolphin looked through a clean netted panel facing San Diego Bay. A pair of piezoelectric transducers (TC4013, Reson Inc., Slangerup, Denmark) was attached to the biteplate via polyvinyl chloride (PVC) posts. One transducer was positioned in line with the dolphin's melon and acted as a hydrophone (biosonar click receiver). The other transducer was positioned in line with the dolphin's lower jaw and acted as the echo projector. The nearest underwater structures within ±10° azimuth of the dolphin's biosonar transmission beam were ~1 km in distance and the mean water depth in the area near the dolphin was ~10 m. Ambient noise sources consisted of other dolphins, snapping shrimp, and boat traffic. Median ambient noise pressure spectral density levels were approximately ~70 dB re 1 $\mu Pa^2/Hz$ at 10 kHz and decreased linearly with the logarithm of frequency to ~50 dB re 1 $\mu Pa^2/Hz$ at 150 kHz.

B. Task description

The dolphin's task was to station on the biteplate, produce echolocation clicks towards the click receiver and listen to phantom echoes from the echo projector. Each trial started with the PEG producing a "standard" two-highlight echo with a specific IHI. Each echo highlight consisted of a replica of the received click. The dolphin was trained to produce a conditioned acoustic response (COM: burst pulse, SPO: whistle) if the echoes changed to a “target echo” with a larger IHI [Fig. 1(a)]. Threshold testing was conducted at seven different standard IHIs (50, 120, 250, 375, 500, 625, and 750 µs). Standard IHIs were chosen to include values within and outside the dolphin’s auditory temporal window [~250 - 300 µs, (Vel'min and Dubrovskii, 1976; Au et al., 1988)]. Each standard IHI was tested under two phase conditions: (1) constant phase, where the two echo highlights were in-phase (2) random phase, where the second highlight was given a random phase shift (range = ±180°) on an echo-to-echo basis for all standard and target echoes. The constant phase held the location and spacing of spectral notches constant for each IHI, while the randomized phase shift changed the location of the spectral notches while holding the spacing between the notches constant [Fig. 1(b)]. For all standard IHIs threshold testing was first completed for the constant phase condition prior to threshold testing for the random phase condition. Once testing was completed at all standard IHIs under both conditions, testing was conducted with a single-highlight echo, where the dolphin was presented a single-highlight echo at a constant echo-delay and produced the conditioned acoustic response to an increase in echo-delay. Threshold testing for the single-highlight echo was only conducted under the constant phase condition.

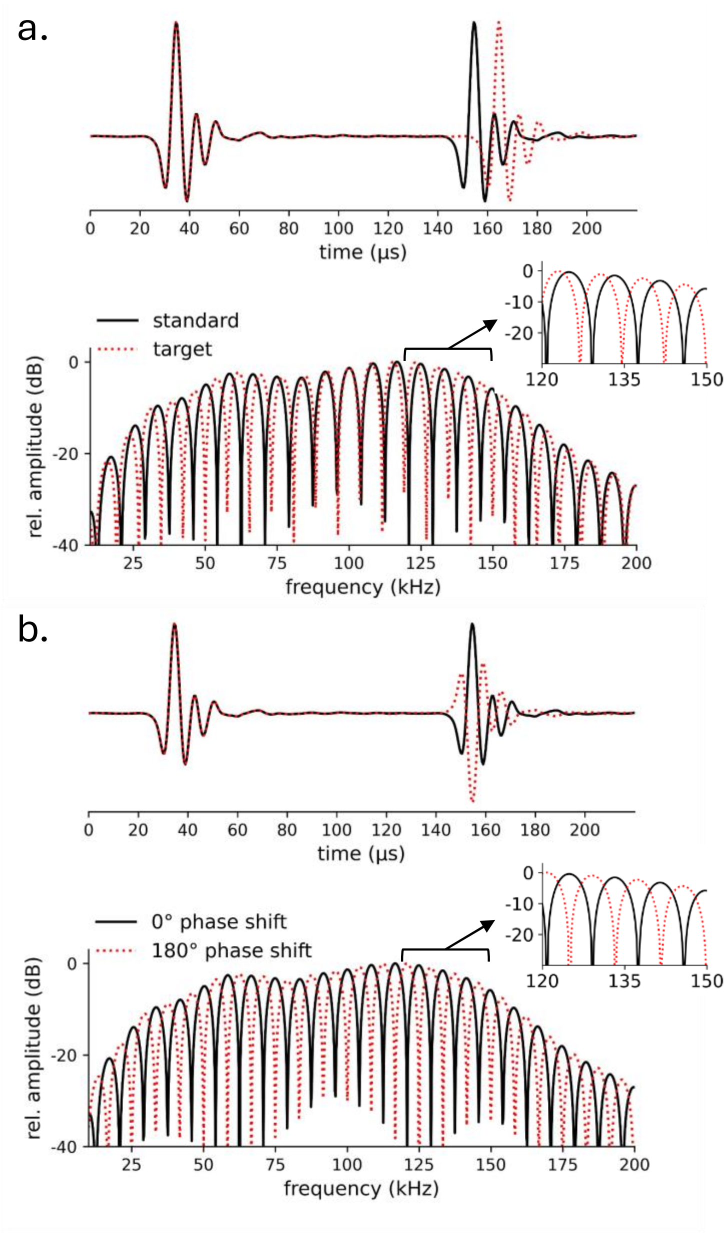

Figure 4.1: Effects changes in IHI and phase have one the frequency spectrum. (a) Effect of IHI change on two-highlight echo waveforms (upper) and spectra (lower). The solid black lines illustrate the waveform and spectrum for a standard echo with 120-µs IHI. The dotted red lines show the waveform and spectrum for a target echo where the IHI has increased by 10 µs. The IHI increase results in changes to both the echo spectral notch positions and spacings. (b) Effect of phase shift on two-highlight echo waveforms (upper) and spectra (lower). The solid black lines illustrate the waveform and spectrum for a standard echo with 120-µs IHI and no phase shift. The dotted red lines show the waveform and spectrum for an echo with the same IHI but a 180° phase shift applied to the second highlight. The phase shift causes the positions of the spectral notches to change, but does not affect the frequency spacing between the notches.

Dolphins participated in 1-2 sessions each weekday and each session consisted of 70-80 trials. Trials began once the dolphin was positioned on the biteplate. Sessions consisted of ~70% echo-change trials and control trials made up for the other ~30% of trials. For echo-change trials the standard echo was presented for 3 – 6 s followed by a 1-s presentation of the target echo. The dolphin was required to respond during the 1-s presentation of the target echo for the response to be considered a “hit”. For control trials the standard echo was presented randomly for 4 – 7 s; the dolphin was required to withhold response for the entire duration for the trial to be deemed a “correct rejection”. Hits and correct rejections were followed by an underwater acoustic bridge and a fish reward. “False alarms” were defined as trials where the dolphin responded during a control trial or during an echo-change trial prior the target echo being presented. “Misses” were defined as trials where the dolphin did not produce an acoustic response during the 1-s presentation of the target echo. False alarms and misses were indicated by a preconditioned incorrect sound and a 3-5 second delay prior to the dolphin being asked to participate in the next trial.

A modified method of constants was used to determine the smallest increase in IHI (or echo-delay for single-highlight) the dolphin could detect. Each session began with ten “warm-up” trials with a target echo condition where the dolphin consistently performed above 90% correct. Each target echo was presented to the dolphin in blocks of ten. For every block the dolphin’s performance was above 50% correct, the target echo (IHI or echo-delay) would decrease (i.e., become closer to the standard echo). After a block where performance was ≤ 50% correct, threshold testing would end and a “cool-down” block would be presented to the dolphin with the same target echo as the warm-up block. The “cool-down” block ensured stimulus control was maintained and preserved the dolphin’s motivation. At least 50 trials were conducted for each test condition.

C. Echo generation

The phantom echo generator (PEG) was a single-channel version of the device described in Christman et al. (2024). The signal from the click receiver was filtered and amplified (5-200 kHz, VP-1000, and 3C module, Krohn-Hite Corp., Brockton, MA), then digitized (1-MHz rate, 16-bit resolution, National Instruments PXIe-7856R). If the digitized signal amplitude exceeded a pre-defined threshold, click waveforms were extracted and convolved with a target impulse response function to create the echo waveform. The echo waveform was then scaled in amplitude, delayed in time, and converted to analog (1-MHz, 16-bit, PXIe7856R). The analog echo-waveform was then filtered, amplified (5-200 kHz, 3C module, M7600, Krohn-Hite Corps), and used to drive the echo-projector. Echo-delays for the S- and S+ echoes were fixed at 13.3 ms simulating a target range of 10 m. Relative echo level [REL, the echo sound exposure level (SEL, in dB re 1 $\mu Pa^2 s$) relative to the received click SEL] was set to ~30 dB above the subjects’ detection thresholds for a single-highlight echo. The amplitudes of the standard and target echoes roved ±3 dB on an echo-to-echo basis to eliminate any perceptual loudness cues that could potentially exist between the standard and target echoes.

D. Analysis

Hit rates were calculated by dividing the number of correct responses by the number of echo-change trials and false alarms were calculated by dividing the number of responses by the total number of control trials. Echo-change trials where the dolphin responded prior to the target echo were reclassified as control trials. To account for individual response biases, performance was quantified in terms of the sensitivity d’ (Stanislaw and Todorov, 1999). To calculate d’, hit rates of 1 were replaced with 1-0.5/N and false alarm rates of 0 were replaced with 0.5/N, where N is equal to the number of echo-change or control trials (Stanislaw and Todorov, 1999). A second order polynomial was fit to the d’ values vs. IHI functions and interpolation was used to determine a threshold of d’ = 1. The 95% confidence intervals at threshold were calculated by randomly selecting a subset of trials and bootstrapping the data without replacements for 1,000 iterations.

Biosonar behavior was quantified by calculating inter-click interval (ICI), peak to peak (p-p) sound pressure level (SPL in dB re 1 μPa), center frequency, and (centralized) root mean square (rms) bandwidth for received clicks for each combination of subject, standard IHI, and test condition. Clicks were only included for hit and false alarm trials prior to the dolphin’s acoustic response, while all clicks were included for correct rejection and miss trials.

III. RESULTS

A. Click and echo acoustic parameters

Over the course of the study COM and SPO participated in a combined ~19,000 trials resulting in the analysis of 7.7×10^6 clicks for COM and 5.3×10^6 clicks for SPO. Mean click waveforms and spectra for both subjects were similar to a typical dolphin click [Fig. 2(a)]. The spectra of projected echoes were colored by the echo projector transmitting response, resulting in echoes with longer duration and higher peak frequency compared to clicks [Fig. 2(b)]. To visualize changes in the frequency domain as the standard IHI increased, representative echoes were input into a model of the dolphin peripheral auditory system, providing an “auditory spectrogram" of the echoes accounting for the effects of the dolphin's peripheral frequency and temporal processing characteristics (Branstetter et al., 2007; Branstetter et al., 2020). Figure 3 illustrates the change in spectral and temporal representations as the standard IHI increases from within the temporal window (50 µs), to the edge of the temporal window (250 µs), and outside the temporal window (500 µs).

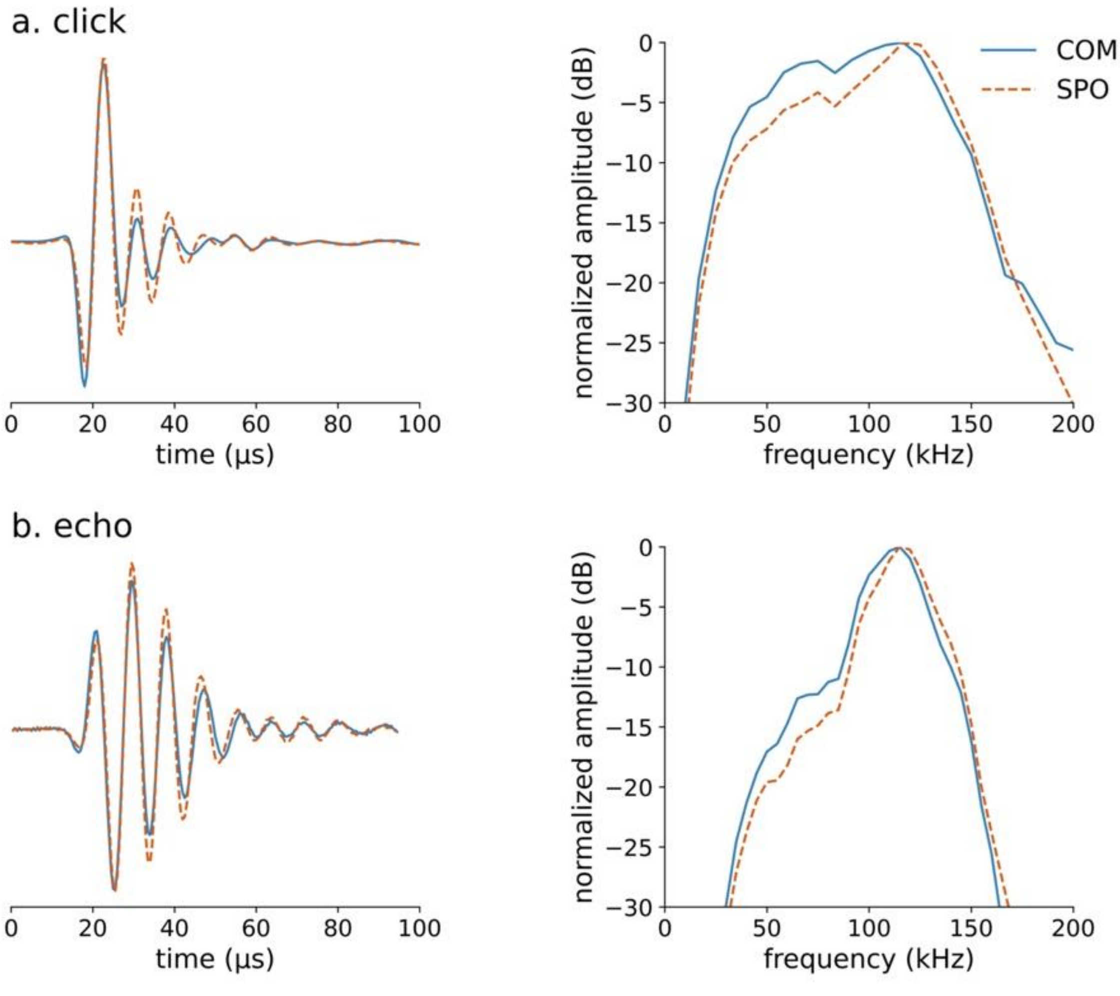

Figure 4.2: Dolphins' averaged click and echo waveform and corresponding spectrum. (a) Each dolphin's normalized mean click waveform and spectrum for clicks emitted during testing for the standard IHI of 50 µs under the constant phase condition. (b) Normalized mean phantom echo waveform and spectrum for each subject generated by the click waveforms in (a).

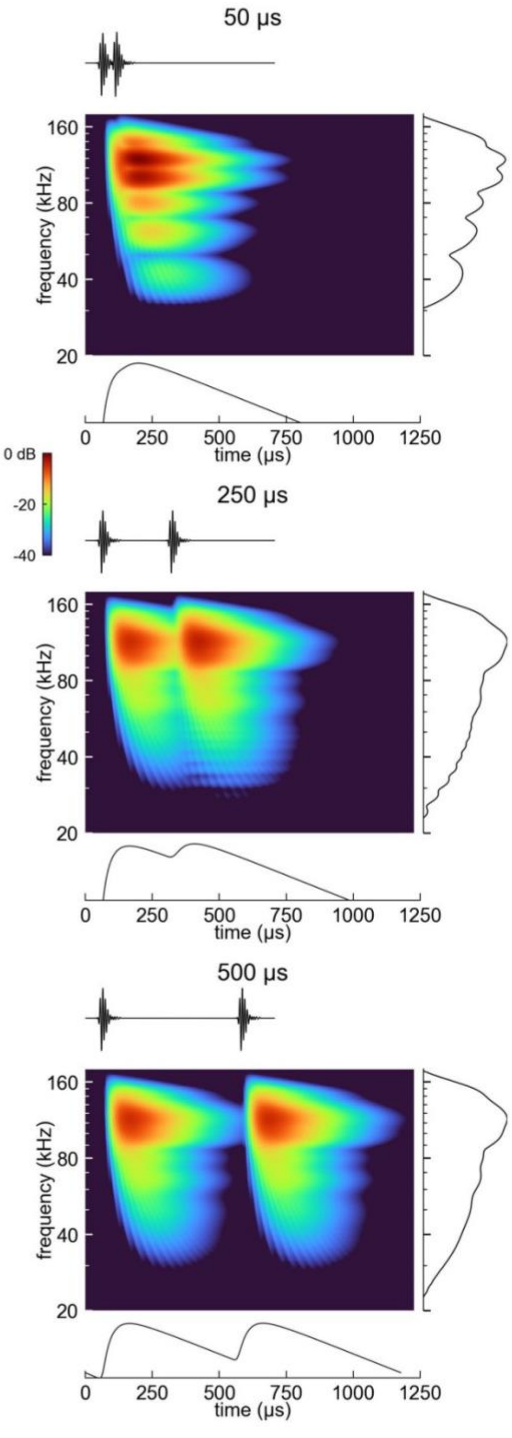

Figure 4.3: Dolphin peripheral auditory system representations for echoes with IHIs of 50 µs (top), 250 µs (middle), and 500 µs (bottom). For each standard IHI the center image shows the auditory spectrogram. The echo waveform is shown above the auditory spectrum. To the right is the time-independent spectral envelope, and below is the frequency-independent temporal envelope. As IHI increases beyond the dolphin temporal window duration (~250 µs), spectral cues dissipate, and temporal cues as seen in the echo envelope begin to become more distinct.

Click acoustic parameters varied between the subjects and standard IHI (Fig. 4). For COM, ICI and p-p SPL decreased, while center frequency increased with increasing standard IHI, with the lowest ICI and p-p SPL and highest center frequency reported for the single-highlight condition. In comparison, SPO's ICI, p-p SPL, and center frequency remained consistent for all conditions. The rms bandwidth for SPO remained consistent for all standard IHI and single-highlight, however, for COM rms bandwidth became less variable as the standard IHI increased and for the single highlight. There are no notable trends for the acoustic parameters between the constant-phase versus random phase-conditions.

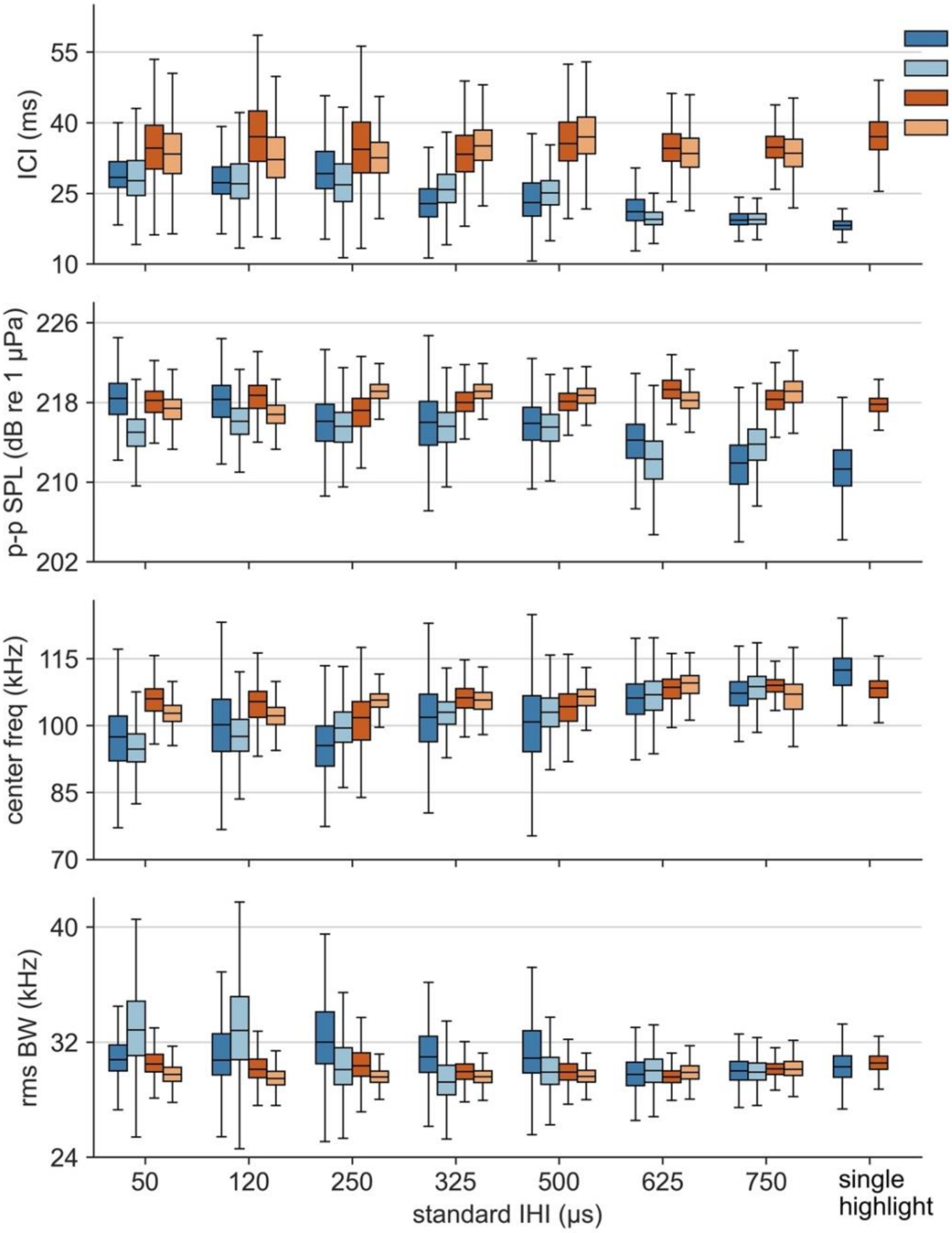

Figure 4.4: Boxplots (Waskom, 2021) showing COM and SPO's click acoustic parameters. From top to bottom the ICI, p-p SPL, center frequency, and rms bandwidth. The center line represents the median and the box represents data within the inner quartiles. The whiskers represent data within 1.5 × the upper and lower quartiles. COM's data is shown in blue and SPO's data in red. Values for the constant phase condition are depicted by the darker colors while values for the random phase condition are depicted by the lighter colors.

B. Behavioral performance for biosonar tasks

Figures 5 shows the hit rate, false alarm rate, and sensitivity (d’) as functions of the increase in IHI (two-highlight) or echo-delay (single-highlight). Figure 6 illustrates the detection thresholds (i.e., d′=1) obtained from the sensitivity data in Fig. 5. Overall, thresholds tended to increase with increasing standard IHI. For standard IHIs < 300 µs the constant phase condition thresholds were between ~0.4 – 0.9 µs. For the randomized phase condition, thresholds were an order of magnitude larger (~3 – 8 µs). For standard IHIs > 300 µs, thresholds for both conditions were similar (~15 – 40 µs). Thresholds initially decreased between the 375 and 500 µs standard IHIs then continued to increase as the standard IHI increased to 750 µs. Performance when discriminating an increase in the delay of a single-highlight was more variable for both subjects than testing for the two-highlight echo conditions. Thresholds were 76 µs for COM and 70 µs for SPO for the single-highlight delay change.

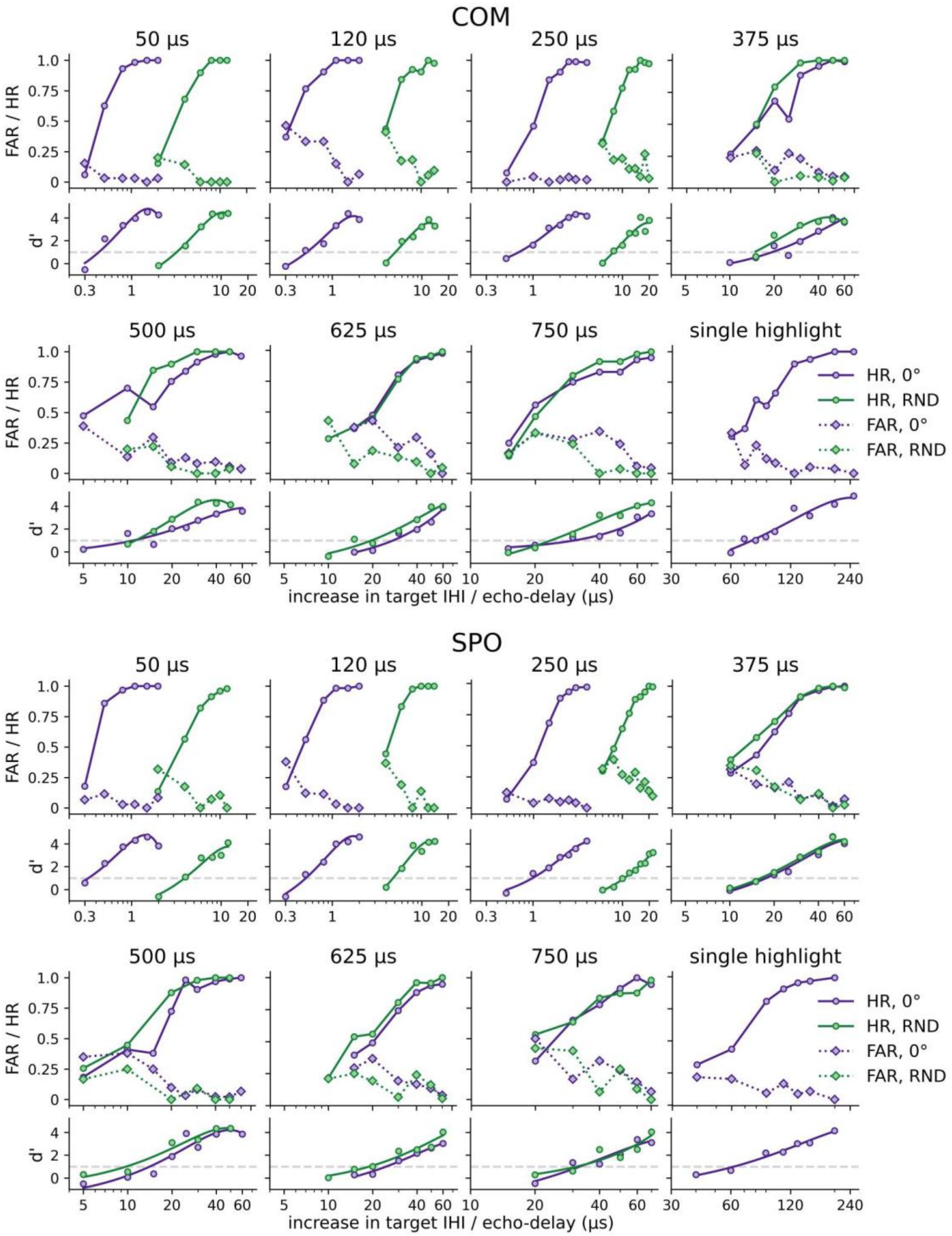

Figure 4.5: Behavioral performance for all IHIs tested. Hit rate (HR), false alarm rate (FAR) and corresponding d′ values for COM (top plots) and SPO (bottom plots) for each standard IHI, condition tested, and single-highlight paradigm. Constant phase is depicted in purple while random phase is depicted in green. The gray dotted line illustrates the point at which d′ = 1. Note that x-scale values change with an increase in standard IHI.

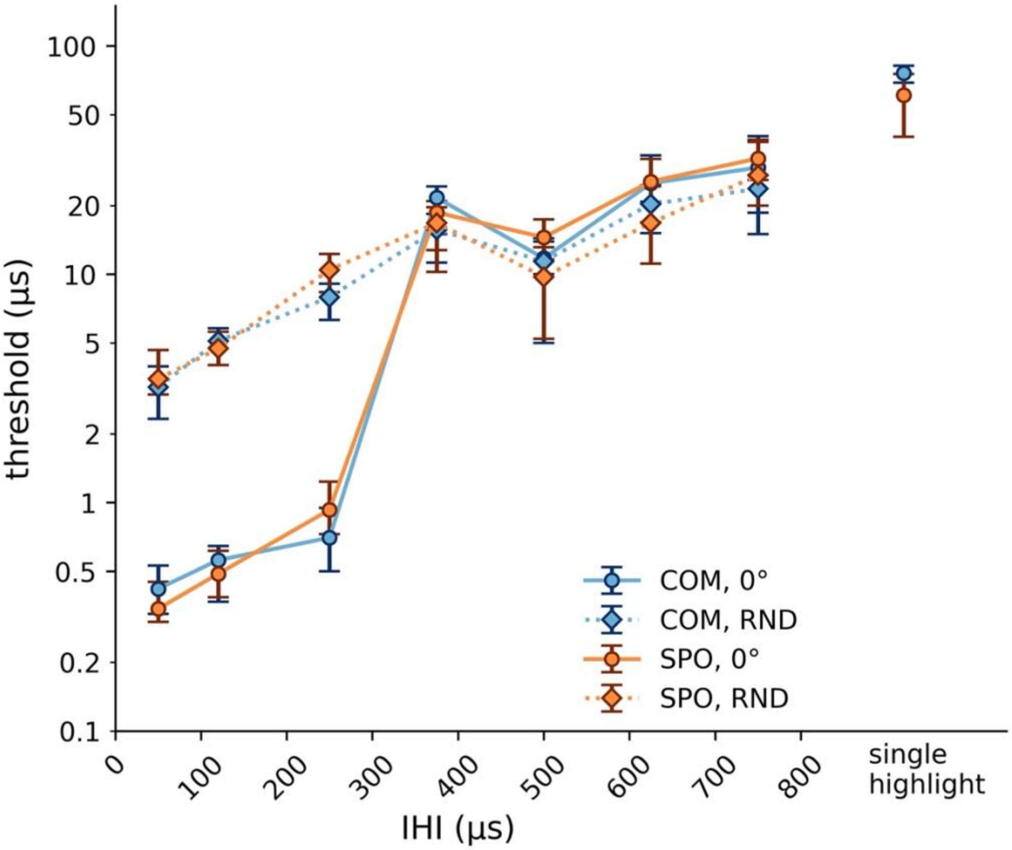

Figure 4.6: Thresholds for each subject and condition tested as a function of standard IHI tested, and threshold for an increase in echo-delay for the single-highlight (far right). COM is depicted in blue and SPO in orange. Constant phase is the solid line and random phase is the dotted line.

IV. DISCUSSION

A primary goal of the current study was to compare the dolphin's ability to detect changes in IHI for the constant-phase and random-phase conditions during an active echolocation task, as the previous study conducted by Mulsow (2023) was done via passive listening. Overall trends between the passive listening experiment and current experiment are similar, suggesting a general understanding of sound perception can be predicted by passive listening experiments. However, it is worth noting that although the trends were similar, all discrimination thresholds in the current experiment were lower than those reported by Mulsow

(2023). The fractional delay technique used in the current experiment [not used in Mulsow (2023)] may explain lower thresholds for the constant-phase condition at 50 and 120 μs standard IHIs than in the previous passive listening study. The primary difference in performance can most likely be attributed to a difference between a passive listening task versus an echolocation task. Mulsow (2023) used an inter-stimulus interval (ISI) of 50 ms, while in the current experiment with the simulated range being 10-m (echo-delay of ~13.33 ms) subjects' ICIs were mostly between 20-40 ms, resulting in a lower inter-echo interval (i.e. ISI). Christman et al. (2024) determined that as range increased during an echo-delay discrimination task, ICIs increased and resulted in an increase in discrimination threshold. This suggests that as the ICI and/or ISI increases the dolphin's resolution of the target may decrease. With the ISI in Mulsow (2023) being 10 ms longer than the dolphin's longest ICIs/ISIs in the current experiment, it is possible the dolphins were able to obtain a clearer resolution of the target in the current experiment. Additionally, the dolphin's ability in the present study to manipulate their click — and thus the returning echo — level and click frequency content could have also aided performance. While the acoustic click parameters between SPO and COM differed (COM changed ICI, p-p SPL, and center frequency with change in standard IHI and SPO did not), discrimination thresholds for each standard IHI and condition are similar between subjects. Therefore, it seems the individual differences in click manipulation for echolocation can vary between subjects, but this variation does not necessarily impact their overall performance.

For standard IHIs within the temporal window (<300 μs), discrimination thresholds were lower for the constant-phase than the random-phase condition. This trend was also noted by Mulsow (2023). However, results for the current experiment demonstrated that thresholds increased for both phase conditions with an increase in standard IHI, which was not seen at standard IHIs < 200 µs in Branstetter et al. (2020) or Mulsow (2023). This discrepancy could be due to differences in methodology. Mulsow (2023) did not use a fractional delay technique and therefore was unable to test IHI differences below 0.5 µs, consequently these sub-microsecond thresholds at 50 and 120 µs may have gone undetectable. When comparing the current experiment to Branstetter et al. (2020), it is possible the difference in outcome between 50 and 120 µs was due to a difference in stimuli. The current experiment presented echo-highlights that were a replicate of the dolphin's click and of equal amplitude, while Branstetter et al. (2020) used echo-highlights that were simulating a cylinder, resulting in the second highlight being lower in amplitude than the first highlight. This difference in amplitude between the first and second highlight reduces the perceptibility of the pitch cue and could have made the small differences in thresholds detected for standard IHIs < 200 µs differ from the current experiment.

Results from the current experiment follow the same trends as Mulsow (2023) and suggest that dolphins may use a pitch cue to discriminate between different IHIs within the temporal window. Bilsen (1966) determined that in humans perceived repetition pitch (TSP) can vary with a change in phase. Therefore, the introduction of the random-phase condition could have caused a "blurring" of the perceived pitch, resulting in higher thresholds; the change in IHI must be large enough to produce a salient change in pitch beyond the changes associated with the random phase. Although thresholds were higher for the random-phase condition, they follow the same trend as the constant-phase condition: an increase in threshold with an increase in standard IHI. This suggests that the "blurring" of perceived pitch elevated the threshold for each standard IHI in a similar manner.

For standard IHIs outside the temporal window (>300 µs) discrimination thresholds were greater (and phase-independent) when compared to those within the temporal window.

Interestingly, when shifting to a different standard IHI within the temporal window (e.g., testing 50 µs then testing 120 µs) the dolphins were able to adjust to the new standard IHI within 1-2 days. When shifting from 250 µs (inside the temporal window) to 375 µs (outside the temporal window), the dolphins took ~4 weeks to make the adjustment, almost as if a new experimental task was being trained. The increase in thresholds and training time when moving outside the temporal window suggests a shift in perceptual cue, most likely from pitched-based cue to a timing-based cue. Thresholds for standard IHIs outside the temporal window were similar between the constant-phase and random-phase conditions. If the dolphin’s shifted to using an envelope timing cue for IHIs outside the temporal window, it would be expected that performance would not be affected between the constant-phase and random-phase conditions, as the disruption of the fine structure of the two highlights would not disrupt the detection of IHI changes.

There was a noticeable decrease in threshold for both conditions between standard IHIs of 375 and 500 µs. After 500 µs thresholds began to increase with an increase in standard IHIs. The reasons for the dip in IHI discrimination threshold at 500 µs is unknown. Previous IHI discrimination research for passive listening and active echolocation did not test standard IHIs above 500 µs (Vel'min and Dubrovskii, 1976; Au and Pawloski, 1992; Branstetter et al., 2020; Mulsow et al., 2023). One hypothesis for this dip in performance could be that there is a “transitional period” as the time separation between echo highlights increase in duration from inside to outside the auditory temporal window. The dip in performance could be caused by the dolphin being in this transition state at the 375 µs standard IHI, still shifting from a pitch versus temporal cue which could result in confusion and lead to elevated thresholds. Previous research suggests the temporal window duration is between 200-300 µs (Vel'min and Dubrovskii, 1976;

Au et al., 1988; Au and Pawloski, 1992; Branstetter et al., 2020). However, Branstetter et al (2020) reports IHI discrimination thresholds at 300 µs to be < 4 µs for all three subjects tested, which is significantly lower than the thresholds (> 16 µs) in the current experiment and Mulsow (2023) for 375 µs. Suggesting that at 300 µs the dolphins are most likely using a pitch-based cue for the IHI discrimination. Follow on research would need to be conducted to understand the perceptual cues used by the dolphin as the standard IHIs transition from inside to outside the temporal window.

IHI discrimination thresholds for the single-highlight echo, where the dolphin reported an increase in echo-delay after removing the first highlight from the stimulus, were higher and more variable than when two-highlights were present (~32 µs at 750 µs standard IHI versus ~73 µs for a single-highlight). This result suggests that the dolphins continue to rely on the first highlight as a timing reference up to at least a standard IHI 750 µs. Additional research with higher standard IHIs would need to be conducted to determine when the first highlight becomes irrelevant in the IHI discrimination task. The single-highlight echo-delay discrimination experiment simulated a single change in range for the dolphins to detect. This detection essentially collapses the experiment conducted by Christman et al. (2024), where range discrimination thresholds were determined in a two-alternative forced choice task, from two range axes onto a single axis. Therefore, the lower thresholds in the current experiment (~73 µs versus ~135 µs) are to be expected because the change in range is immediate, whereas in Christman et al. (2024) the dolphin had to hold the range of one simulated target in memory for a longer time period while comparing to the other simulated target. Additionally, the threshold for the single highlight echo-delay discrimination in the current experiment is significantly higher than previous echo-delay "jitter" studies that determine jitter detection thresholds to be < 1 µs (Finneran et al., 2019;

Finneran et al., 2020; Finneran et al., 2023). The results of the current experiment are consistent with the idea that jitter-delay experiments reveal a hyper-acuity in dolphin range resolution versus the ability to discriminate ranges of two objects at different azimuthal angles (Altes, 1989).

CONCLUSIONS

Differences in IHI discrimination thresholds for constant-phase versus random-phase conditions are substantial for standard IHIs within the temporal window and equivalent for standard IHIs outside the temporal window. The lower thresholds for the constant-phase versus the random phase condition for IHIs within the temporal window suggests the use of a pitch cue, perhaps TSP, that is dependent on the relationship of the fine structure of the two highlights, to determine differences in IHI. When such a cue is “blurred” by applying a random phase-shift to the second highlight of the two-highlight echo the IHI discrimination becomes more difficult for the dolphins. For standard IHIs outside the temporal window, the similar thresholds between the constant-phase and random-phase conditions coupled with higher thresholds suggest the use of highlight envelope timing for discrimination of IHIs. Once standard IHIs are outside the temporal window, dolphins continue to use temporal differences between highlights to at least the standard IHI of 750 μs, as echo-delay discrimination thresholds for a single-highlight echo are higher than when the first highlight is available to the dolphin for reference.

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effects of inter-highlight interval and phase on echolocating bottlenose dolphins performing a two-highlight echo discrimination task," J. Acoust. Soc. Am. (in prep). The dissertation author was the primary investigator and author of this paper. This study was supported by the Office of Naval Research Code 322.

CONCLUSION

A primary goal of this dissertation was to determine the effects mean echo-delay (i.e. range) has on the dolphin's echo-delay discrimination abilities when REL is held constant. Chapter 1 determined that echo-delay discrimination abilities for a 20 µs jittering echo decreased for mean echo-delays that simulated ranges less than 5 m. Lower SNR due to the effects of forward masking explain the decrease in performance. However, in Chapter 2, unlike Chapter 1, the dolphin's range discrimination abilities continued to improve for simulated ranges less than 5 m. In Chapter 2 REL was set to 20-35 dB, depending on hearing capabilities of the subjects, above echo-detection thresholds while in Chapter 1 REL was set to only 15 dB above the subjects' thresholds. It is possible that in Chapter 2 the dolphins were able to lower their click levels to reduce the effects of forward masking while still sustaining necessary echo SNR for discrimination resulting in the continued increase in performance with a decrease in range.

The primary contribution of Chapters 1 - 3 was determining that there is a decrease in echo-delay discrimination abilities as target range becomes greater than 10 m. Although previous studies looked at the effects of target range, in these experiments REL was held constant to unconfound changes in SNR associated with a change in range. Therefore, differences in performance are attributed to only changes in echo-delay. Results from Chapter 1 determined the ranges tested in Chapter 2 as well as the decision to choose a REL that was farther above thresholds than in Chapter 1 to mitigate the effects of forward masking. Chapter 3 then modeled the spectral cues available to the dolphin while discriminating differences in range between two targets when presented simultaneously. The comparison of range discrimination performance between successively and simultaneously presented targets had never been previously tested. Although results from Chapter 3 suggest little to no improvement when the dolphin has access to spectral cues, the overall results from Chapters 1 - 3 suggest that as mean echo-delay increases the dolphin's echo-delay discrimination abilities degrade. A resulting hypothesis from Chapters 1 - 3 is that as echo-delay increases, dolphins struggle to combine multiple echoes into a coherent mental representation causing echo-delay discriminability to decrease.

An additional goal of this dissertation was to determine auditory cues used by the dolphin to decode fine scale temporal and spectral features into useable information. Chapter 4 determined that when echo-highlights fall within the temporal window, the dolphin's IHI discrimination threshold is more accurate for a constant-phase versus a random-phase condition during an echolocation task. A hypothesis for this result is that the dolphin is using a pitch cue that is dependent on the fine structure of the echo highlights to discriminate between small changes in IHIs. The difference in IHI for the random-phase condition must be larger than for the constant-phase condition for the pitch cue to be salient. Additionally, once IHIs are outside the temporal window, envelope timing differences are likely used to discriminate changes in IHI as the constant and random conditions yield similar results. Outside the temporal window thresholds continue to increase with increasing standard IHIs and are highest when there is only a single highlight that increases in echo-delay. This suggests the dolphin is still reliant on the time spacing between echo-highlights outside the temporal window rather than isolating the change in echo-delay of a single highlight. Through these experiments a better understanding was gained on how dolphins build a coherent mental representation of a target, and how the range to a target can affect the resolution of this mental representation.

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