

# Dolphin (*Tursiops truncatus*) echoic angular discrimination: Effects of object separation and complexity

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A bottlenose dolphin was tested on its ability to echoically discriminate horizontal angular differences between arrays of vertically oriented air-filled PVC rods. The blindfolded dolphin was required to station in a submerged hoop 2 radial m from the stimuli and indicate if an array with two rods ( $S+$ ) was to the right or the left of a single rod ( $S-$ ). The angular separation between the two rods ( $\theta_w$ ) was held constant within each experiment while the angle between the  $S+$  and the  $S-$  stimuli ( $\theta_b$ ) varied to produce angular differences ( $\Delta\theta = \theta_b - \theta_w$ ) ranging from 0.25 to 4°. In experiment I,  $\theta_w$  was maintained at 2° and in experiment II,  $\theta_w$  was maintained at 4°. Resulting 75% correct thresholds (method of constant stimuli) were 1.5 and 0.7°, respectively. The two main findings of this study are: (1) decreasing the number of targets does not aid in localization, and (2) increasing the space between the rods enhances localization. Taken as a whole, the experiments suggest dolphins have a well-developed ability to resolve spatial information through sonar. © 2007 Acoustical Society of America. [DOI: 10.1121/1.2400664]

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## I. INTRODUCTION

The dolphin's ability to echoically resolve fine spatial details from an object will be dependent at least upon the physical characteristics of the object, the characteristics of the dolphin's sonar signal, the dolphin's auditory signal processing of the returned echoes, and the dolphin's ability to localize echoes from the various reflecting object features. The focus of the present study is to determine the limit of the dolphin's echolocation spatial acuity in the horizontal plane.

### A. Background

The incident sonar signal from a bottlenose dolphin<sup>1</sup> can be described as a broadband transient with peak frequencies between 40 and 140 kHz, durations as short as 40  $\mu$ s, and peak-to-peak sound pressure levels often exceeding 220 dB re: 1  $\mu$ Pa (Au, 1993). The concave shape of the dolphin's skull, coupled with the focusing properties of the lipid melon, focus the signal forward in a tight beam, elevated about 5° above the rostrum, with a 3 dB beam width of approximately 10° (Au, 1980). Consequently, targets directly forward of the melon will be highly ensonified, increasing the signal-to-noise ratio relative to peripheral targets. The high frequency, short duration properties of individual clicks

contribute to the dolphin's ability to resolve fine spatial details. Higher frequencies allow for echo returns from small targets, provided the target's spatial extent is greater than the wavelength of the incident signal. High frequency components also allow dolphins to detect small structural features within a target that may facilitate target identification. Short duration clicks can improve range resolution by limiting overlapping echoes from closely spaced objects in the same line of acoustic propagation. In addition, fine temporal resolution, demonstrated by an auditory critical interval of 264  $\mu$ s (Moore *et al.*, 1984) allows the dolphin to resolve echoes occurring in close temporal proximity.

Despite the challenges imposed by an aquatic environment (e.g., sound traveling approximately 4.5 times faster in water than in air), several of the standard terrestrial mammalian localization mechanisms also appear to be well developed in dolphins. When a sound source originates off the midsagittal plane, a differential distance from each ear to the sound source is produced. The differential distance results in arrival time differences between the two ears known as interaural temporal differences (ITDs). A differential distance between the ears, coupled with sound shadowing by the head, will also produce an intensity difference between the ears known as interaural intensity differences (IIDs). Moore *et al.* (1995) investigated the dolphin's ability to utilize ITDs and IIDs. Jaw phones (i.e., hydrophones embedded in rubber suction cups and attached to the right and left lower jaws)

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were used to provide precise control over binaural stimulus presentation to the dolphin. ITD thresholds were as small as  $7 \mu\text{s}$  for a 30 kHz pulse. For sonar-type pulses (with higher peak frequencies above 60 kHz) ITDs were between 17 and  $18 \mu\text{s}$ . IID thresholds were below 1.0 dB for all frequencies tested. Thus, both ITDs and IIDs appear to be very salient cues a dolphin could employ to localize sound sources.

Recently, Branstetter *et al.* (2003) investigated a dolphin's ability to echoically resolve angles between multiple targets in the horizontal plane. A blindfolded dolphin positioned its head within a stationary, vertically oriented hoop, 2 radial m from the stimuli, and then indicated whether an array with four rods ( $S+$ ) was to the left or the right of an array with two rods ( $S-$ ), by pressing a corresponding paddle. The angular separation between the rods within each array ( $\theta_w$ ) was maintained at  $2^\circ$  but the angular separation between the two arrays ( $\theta_b$ ) was varied to produce angular differences ( $\Delta\theta = \theta_b - \theta_w$ ) ranging between  $0.25^\circ$  and  $4^\circ$ . A modified method of constant stimuli, used to test for angular discrimination ability, yielded a psychometric function with a 75% correct threshold of  $1.6^\circ$  (see Fig. 8). The results were consistent with passive hearing studies that determined the smallest possible angle (minimum audible angle or MAA) between two sound sources that would allow the two sources to be perceived by the dolphin as discrete. Renaud and Popper (1975) reported the horizontal MAA for 30, 60, and 90 kHz pure tones as  $2.5^\circ$ ,  $3.0^\circ$ , and  $3.0^\circ$ , respectively. Horizontal and vertical MAAs for click stimuli ( $35 \mu\text{s}$  duration, 64.35 kHz peak frequency) were  $0.9^\circ$  and  $0.7^\circ$ , respectively.

The results from Branstetter *et al.* (2003), suggested that the dolphin's echoic spatial acuity was sufficient to support cross-modal matching of objects between vision and echolocation as shown by Pack and Herman (1995) and Herman *et al.* (1998). Because the dolphin in these studies interrogated relatively large objects (approximately  $43 \text{ cm}^2$ ) at relatively short distances ( $<1 \text{ m}$ ), the angle the objects subtended, and the angles between object components, were much greater than the angular differences threshold of  $1.6^\circ$ . Hence, the objects and object features used in the cross-modal studies should be resolvable through the dolphin's echolocation sense.

The current study builds on the findings of Branstetter *et al.* (2003). One goal of Branstetter *et al.* was to generalize the findings to the cross-modal paradigm (Pack *et al.*, 2002). If the dolphin can echoically resolve fine spatial details from multiple echoes in the angular discrimination experiment (Branstetter *et al.* (2003)), the dolphin can probably echoically resolve fine details in the cross-modal experiments. Because the objects in the cross-modal experiments (Pack *et al.*, 2004) were three dimensional with multiple features that produced multiple echoes, the stimuli in Branstetter *et al.* (2003) were composed of multiple targets (four rods vs two rods) thus producing multiple echoes as well. However, the resulting complex stimuli may not have been optimal to produce the smallest echoic angular discrimination threshold. In humans, reducing the number of distracting sound sources can aid in localization (Wightman and Kistler,

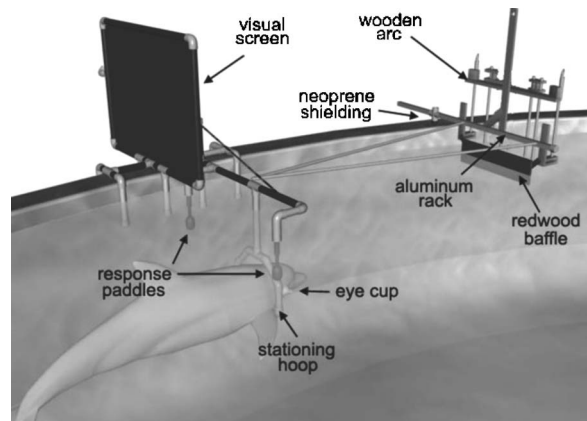


FIG. 1. Experimental apparatus with dolphin in underwater stationing hoop.

1997). We employed this tactic in Experiment 1 of the current study by reducing the  $S+$  and  $S-$  stimuli to two rods and one rod, respectively.

In the Branstetter *et al.* (2003), experiment, the angular difference between the rods within each array ( $\theta_w$ ) was always  $2^\circ$ . The proportion correct at an angular difference of  $2^\circ$  was 83% compared to 93% at  $4^\circ$ . This suggests when  $\theta_w = 2^\circ$ , the perceived positions of the rods were subject to spatial blurring. The echoes from each rod could have effectively masked each other. In humans, an improvement in the ability to localize sound sources occurs due to increased spatial separation (Langendijk *et al.*, 2001). We adopted this strategy in Experiment II by increasing  $\theta_w$  to  $4^\circ$ . If all the rods were more fully resolvable, perhaps the dolphin could make better decisions about the rod positions relative to one another.

## II. GENERAL METHODS

### A. Subject

The subject for the study was a 16-year-old, male, Atlantic bottlenose dolphin (*Tursiops truncatus*) named Hiapo. Hiapo was the same dolphin used in the Branstetter *et al.* (2003) study. Hiapo was housed in two interconnected seawater tanks (each circular tank was 1.8 m deep with a diameter of 15.2 m) with three female dolphins at the Kewalo Basin Marine Mammal Laboratory in Honolulu, Hawaii. During the experimental procedures, Hiapo was maintained alone or with one other dolphin. Approximately 11.8 kg of herring, capelin, smelt and squid were fed to Hiapo daily, a portion of which (2.9 kg) was fed during the experiment.

### B. Apparatus

The same experimental apparatus (see Fig. 1) employed from Branstetter *et al.* (2003) was employed in all of the experiments presented here. A complete description can be found in Branstetter *et al.* (2003). A detailed summary is presented here.

The dolphin was trained to wear latex rubber suction cups (eye cups), over its eyes to prevent the use of vision during the experiment. A submerged, vertically oriented, hollow, PVC stationing hoop was attached to the tank wall. The hoop was submerged approximately 55 cm below the sur-

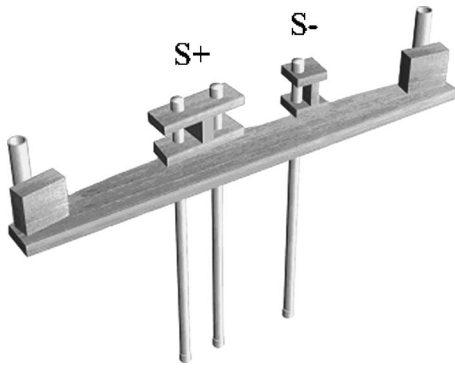


FIG. 2. PVC rods on wooden rack showing S+ and S- stimuli.

face. Two submerged response paddles were connected to the periphery of the stationing hoop allowing the dolphin to exit the hoop and respond to either the left or right paddle. The stimuli were presented using a customized aluminum rack, which was positioned 2 m from the tip of the dolphin's rostrum. A redwood baffle at the bottom of the rack occluded inspection (visually or echoically) of the tips of the stimuli when they were positioned on the rack prior to full immersion in the water.

The experimental stimuli consisted of vertically oriented, schedule 40, PVC rods (Fig. 2). Each rod was air filled to provide a high impedance mismatch to water making them highly reflective to dolphin sonar signals. In all experiments, the positive stimulus to respond to (S+ stimulus) consisted of two rods and the negative stimulus not to respond to (S- stimulus) consisted of one rod. Each PVC rod was 1.9 cm in outer diameter, 1.7 cm in inner diameter and 75 cm in length. PVC caps were placed on each end of each rod (2.7 cm outer diameter, 2.3 cm length) to ensure they were airtight. A total of 12 PVC rods with caps were used to construct three S+ stimuli and three S- stimuli. Each rod and cap was constructed from the same type of PVC with the same batch number ensuring the material composition was nearly identical. However, as a precaution, before each session, each rod and each cap were randomly assigned to an S+ or an S- array to control for the possibility that Hiapo could learn to identify a particular rod artifact associated with a particular array.

The rods in S+ stimulus were separated from each other by  $\theta_w^\circ$  from a 220 cm distance. This distance represented the radial distance from the arrays to the midpoint between Hiapo's mandibular windows on his lower jaw. An S+ and an S- stimulus were positioned on wooden arcs with the angular separation ( $\theta_b$ ) between the stimuli predetermined from a counterbalanced schedule. The angular difference can be defined as

$$\Delta_\theta = \theta_b - \theta_w,$$

where  $\Delta_\theta$  is the angular difference,  $\theta_b$  is the separation between the S+ and S- arrays (separation between the closest rods) and  $\theta_w$  is the angle between the rods within S+ array (Fig. 3). The dolphin can only identify the correct position of the S+ stimulus by comparing the angles between the rods of the S+ stimulus, and the angle between both stimuli. Thus,  $\Delta_\theta$  is a measure of the dolphin's angular discrimination abil-

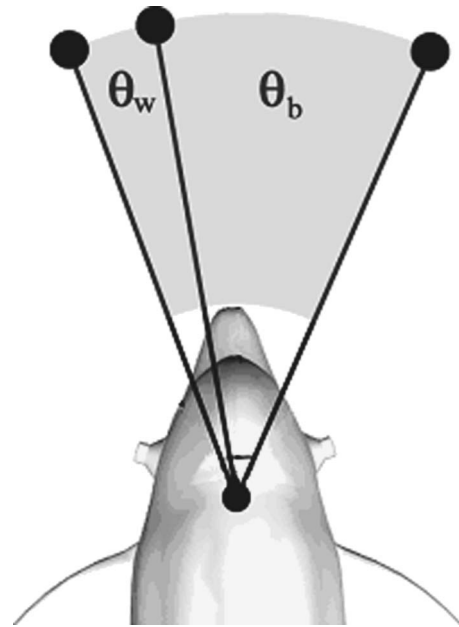


FIG. 3. Angular difference ( $\Delta_\theta$ ) between the rods relative to the dolphin is calculated by subtracting  $\theta_w$  from  $\theta_b$ .

ity. The arrays were centered on the wooden arc so the far end of the S+ array and the far end of the S- array were an equal distance to the center of the arc and, hence, the dolphin's median plane (see the Appendix).

When Hiapo was positioned inside the stationing hoop as far as his pectoral fins would allow, each rod was approximately 200 radial cm from the tip of his rostrum, 220 radial cm from his mandibular window and 245.7 radial cm from the center of the stationing hoop. This allowed Hiapo to pivot his head in the horizontal plane along a 45.7 cm radial arc (measured from the center of the stationing hoop to the tip of his rostrum) while the stimuli maintained a distance of 200 cm from his rostrum tip. The wooden arc was attached to a pulley system on the aluminum rack that was attached to both the tank wall and a wooden stand on the exterior of the tank (Fig. 1). The rack and the pulley system provided control over stimuli exposure time by allowing an assistant to lower the arrays when prompted. When lowered, the only part of the array submerged was the bottom 55 cm of the six rods. The rack was leveled using a standard bubble level. A visual screen (Fig. 1) prevented the trainer from seeing the stimuli and inadvertently cueing the dolphin towards the correct response.

Sonar emissions were recorded with a hydrophone (LAB-core systems, PZ-1A) placed approximately 15 cm in front of the stationing hoop at a depth of approximately 15 cm. When Hiapo was properly stationed in the hoop, the hydrophone was directly above his head and slightly behind his blow hole. The sounds were digitized at 44.1 kHz sampling rate and recorded with a Sony digital video recorder. Because the sonar emissions were already distorted by the low sampling rate, near field distortion was not considered an issue. Hiapo would emit sonar signals prior to array exposure and, after his response, only the clicks between the onset of array exposure to when he backed out of the hoop (monitored from recorded video) were considered for analy-

sis. Backing out of the hoop was operationally defined as when his eye cups crossed the hoop threshold on his way out of the hoop. Click trains for each trial were then manually counted by two independent observers from a hardcopy printout. Both observers were blind to which trial condition they were reviewing.

Response time (RT) for each trial was also recorded by an observer with a digital stopwatch. RT was defined as the time between the onset of stimulus exposure to when the dolphin pressed a paddle. The trainer (who, because of the visual screen had no knowledge of the stimulus array) vocally reported a paddle press.

### C. General procedure

At the beginning of each trial, the eye cups were placed on the dolphin. Hiapo remained at the trainer's station with his jaw held out of the water as an assistant then placed the stimuli on the rack and the tips of the PVC rods were gently submerged a few cm ( $<5$  cm) below the water surface to prevent a potential passive acoustic splash cue. This reduced the possibility of Hiapo passively listening to the stimuli tips while they were placed in the water. In addition, a water-soaked redwood baffle, attached to the aluminum rack was positioned about 5 cm beneath the surface in front of the tips of the rods (Fig. 1). Water-soaked redwood is known for its ability to absorb sound underwater (see Johnson, 1967). The baffle served to reduce any sound the stimuli may have made upon entering the water and prevented the dolphin from echolocating on the tips of the stimuli before they were fully lowered. Once the stimuli were in place, an experimenter in an elevated tower overlooking the tank instructed the trainer to signal the dolphin to enter the hoop. The trainer manually assisted the dolphin to insure that he was positioned in the hoop up to his pectoral fins. The experimenter then verbally instructed the assistant to lower the arrays into the water. The dolphin was required to echolocate and identify the location (left or right) of the  $S+$  array by backing out of the hoop and touching the corresponding left or right response paddle. The trainer verbally called out the dolphin's response, either "left" or "right," and an experimenter located on an elevated deck overlooking the pool, identified the choice as correct or incorrect, referring to the preplanned schedule. The trainer also functioned as a blind observer because the visual barrier prevented the trainer from seeing the stimuli and, thus, knowing the correct choice. Correct responses were rewarded with fish, and social reinforcement, followed by an inter-trial interval of approximately 35–40 s. The dolphin was called back to station for incorrect responses, did not receive a fish reward and proceeded directly into an inter-trial interval.

Two experiments were conducted.<sup>2</sup> Their presentation was counterbalanced (ABBA format) to control for any learning effects. Half of experiment I, experiment II were completed in consecutive order. Then, the remaining halves were conducted in reverse order (i.e., Exp. II, and then Exp. III). Prior to conducting these experiments, a Pilot study (Branstetter, 2005) was run to investigate how easily Hiapo would generalize from his initial arrays of four rods vs two

rods (Branstetter *et al.*, 2003) to two rods vs one rod, and to determine which angular separations would capture the full psychometric function.

## III. EXPERIMENT I

The goal of experiment I was to determine if echoically localizing targets is less difficult when the number of echoes received per incident signal is reduced. In humans, sound localizing performance progressively increases as the number of distracting sounds decreases (Wightman and Kistler, 1997; Langendijk *et al.*, 2001). In the current experiment, the number of potential echoes is reduced to three by decreasing the number of rods presented on each trial to three. If echo complexity, defined as the number of simultaneous echoes received, is a major factor influencing echoic angular discrimination, a threshold decrease is expected in the current experiment relative to the results of Branstetter *et al.* (2003).

### A. Stimuli

The  $S+$  stimulus was a two-rod array. The  $S-$  stimulus was a single rod (see Fig. 2). The angle between the rods within the  $S+$  array ( $\theta_w$ ) was held at a constant  $2^\circ$  and the angle between the  $S+$  and  $S-$  array ( $\theta_b$ ) varied to produce angular differences ( $\Delta_\theta$ ) of 4.00, 3.00, 2.50, 2.25, 2.00, 1.75, 1.50, 1.25, 1.00, and  $0.50^\circ$ . Ten angular differences were tested compared to only eight in Branstetter *et al.* (2003) to provide greater resolution estimating the psychometric function.

### B. Procedure

Each session began with six warm-up trials with an angular difference of  $4^\circ$ . The position of the  $S+$  array (left or right) was randomized with an equal number of left and right presentations within each session. An approximate 25 s inter-trial interval followed each trial to allow assistants to prepare the next set of stimuli. If the dolphin responded incorrectly on two or more warm-up trials, the testing session was aborted until the next day. If the dolphin responded correctly on five or more warm-up trials ( $p < 0.05$ , cumulative binomial), the test session began after a 1.5–2 min break. The modified method of constant stimuli was used for stimulus presentation. Angular differences were presented in descending order. Each of the ten angular differences was tested twice per session in two descending sweeps. The left or right position of the  $S+$  stimulus was randomized for the first ten trials. The position of the  $S+$  array in the second ten trials was the opposite of the first ten trials. For example, if the location of the  $S+$  array for an angular separation of  $2^\circ$  occurred on the left within the first ten trials, the position of the  $S+$  array for the same angular separation in the second ten trials would be to the right. This ensured that any potential right or left bias would affect angular differences equally. The last four trials were cooldown trials with an angular difference of  $4^\circ$ . Thus, a total of six warm-up trials, 20 test trials, and four cooldown trials were conducted each session. If the dolphin was incorrect on three or more of the warm-up and cooldown trials combined, the data from the session were eliminated from analysis.

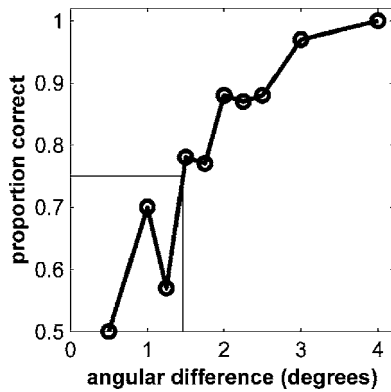


FIG. 4. Experiment I psychometric function with a 75% correct angular difference threshold of  $1.5^\circ$ .

### C. Results and discussion

A total of 35 sessions were conducted over the duration of experiment I. Two of the sessions were aborted because Hiapo failed to respond correctly to five or more of the warm-up trials. One session was aborted to repair the stationing hoop that Hiapo dismantled in mid-session. Two additional sessions were aborted because Hiapo would not respond to his trainer. Therefore, data from a total of 30 sessions were used for analysis. A psychometric function describing the dolphin's performance is plotted in Fig. 4. Each data point represents the percentage of correct responses for 60 trials. As the angular difference between the stimuli decreased, so did the dolphin's ability to discriminate the angular difference. Using a criterion of 75% correct responses, a threshold of  $1.5^\circ$  was obtained.

There was no significant linear trend effect of angular difference on the number of clicks (see Fig. 5) the dolphin emitted ( $F=0.97$ ,  $p>0.05$ ,  $y=-2.75x+195.45$ ). On average, the dolphin emitted 190.01 clicks per trial (SD=39.28). The maximum number of emitted clicks on a single trial was 287 while the smallest number was 97. There was a significant linear trend effect of angular difference on the dolphin's reaction time ( $F=14.42$ ,  $p<0.05$ ,  $y=-0.14x+4.79$ ). On average, the dolphin's response latency was 4.50 s (SD=0.81 s).

Maximum and minimum response latencies were 9.25 and 2.91 s, respectively. Although the dolphin appears to re-

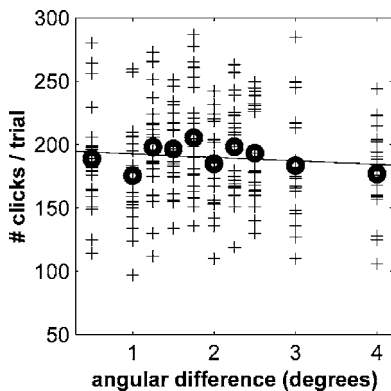


FIG. 5. Number of clicks/trial as a function of angular difference for experiment I. Pluses represent individual trials while bold circles are means for each angular difference.

quire significantly more time to respond as the angular separation decreases, the trend appears to be rather weak with a minor negative slope.

The current threshold compares very well with the threshold of  $1.6$  measured by Branstetter *et al.* (2003). These data suggest that the dolphin was able to simultaneously localize six sound sources (i.e., Branstetter *et al.*, 2003) approximately as well as it can simultaneously localize three sound sources (i.e., current study). Thus, within the limited stimuli used between Branstetter *et al.* and the current study, echo complexity does not appear to be a major factor governing echoic angular discrimination.

## IV. EXPERIMENT II

The goal of experiment II was to determine if the positions of the rods are less difficult to localize when each rod is more fully resolvable. The thresholds from experiment I and Branstetter *et al.* (2003) were  $1.6$  and  $1.5$  respectively. Because  $\theta_w$  was equal to  $2^\circ$  in both of these experiments, the rods may have been too close together to be fully resolvable. By increasing  $\theta_w$  to  $4^\circ$  each rod should be more fully resolvable, thus allowing the dolphin to make better judgments about the precise location of each rod relative to one another. If this assumption is true, the dolphin's angular discrimination threshold should be lower than those obtained by experiment I and Branstetter *et al.* (2003)

### A. Stimuli

For experiment II, the angle between the rods within the  $S+$  array ( $\theta_w$ ) was  $4^\circ$  and the angle between the  $S+$  and  $S-$  array ( $\theta_b$ ) varied to produce angular differences ( $\Delta_\theta$ ) of 4.00, 3.00, 2.50, 2.00, 1.50, 1.00, 0.50 and  $0.25^\circ$ .

### B. Procedure

Experiment II employed the identical procedure to experiment I, however, there were eight angular differences tested. A subjective decision was made to decrease the number of presented angular differences from ten (in experiment I) to eight to shorten the experimental sessions. The longer sessions appeared to result in a decrease of motivation by the dolphin. Thus, a total of six warm-up trials, 16 test trials, and four cooldown trials were conducted each session.

### C. Results and discussion

A total of 38 sessions were conducted. A three month hiatus resulted between the dates of January 8th and March 26th (2001) due to the death of a companion dolphin. The hiatus took place between sessions 18 and 19. During this time, a total of nine practice sessions (half the number of trials/session) were conducted to maintain the behaviors required for the experiment. An *a priori* decision was made to exclude all practice data from analysis. Experiment II resumed after the remaining companion dolphins were trained to facilitate (not interfere with) data collection. Six sessions were aborted because Hiapo failed to respond correctly to five or more of the warm-up trials. An additional two sessions were aborted because Hiapo chose to socialize with the

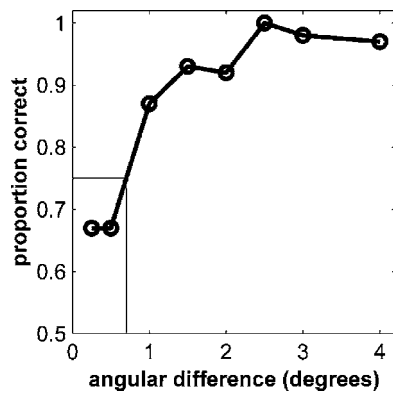


FIG. 6. Experiment II psychometric function with a 75% correct angular difference threshold of 0.7°.

other dolphins rather than respond to his trainer. Therefore, data from a total of 30 sessions were used for analysis. A psychometric function describing the dolphin's performance is plotted in Fig. 6. Each data point represents the percentage of correct responses for 60 trials. Using a criterion of 75% correct responses, a threshold of 0.7 degrees was obtained.

There was no significant linear trend effect of angular difference on the number of clicks the dolphin emitted ( $F=0.40, p>0.05, y=-1.16x+168.19$ ), nor was there a significant linear trend effect of angular difference on the dolphin's reaction time ( $F=3.98, p>0.05, y=-0.05x+3.91$ ). On average, the dolphin emitted 166.06 clicks per trial (SD=38.57). The maximum number of emitted clicks on a single trial (see Fig. 7) was 260 while the smallest number was 90. On average, the dolphin's response latency was 3.83 s (SD=0.67 s). Maximum and minimum response latencies were 8.70 and 2.17 s, respectively.

A point-by-point comparison between proportions correct from experiments I and II was done for each angular separation. The angular separations that experiment II did not have in common with experiment I were interpolated by averaging adjacent points and are denoted with an asterisk in Table I. Differences between points on the psychometric function were large enough to produce significant one-tailed  $z$  scores (indicated by bold  $p$  values) for all angular separation except for  $\Delta\theta=2.00, 3.00$  and 4.00. The proportions associated with the last two angular separations are similar due to a ceiling effect. The angular separations surrounding the 75% correct level are all significantly different, thus we conclude the threshold differences are real. A statistical comparison to Branstetter *et al.* (2003) was not conducted because the results in this study are not counterbalanced with the former study. However, a large leap of faith is not re-

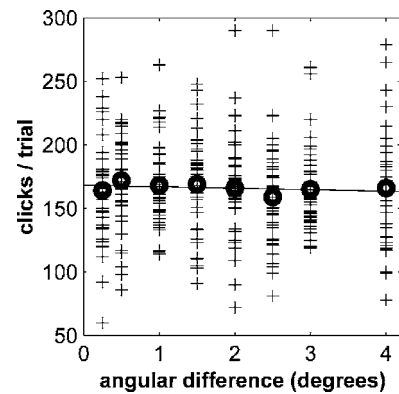


FIG. 7. Number of clicks/trial as a function of angular difference for experiment II. Pluses represent individual trials while bold circles are means for each angular difference.

quired to notice the similarity between the psychometric function of Exp I. and Branstetter *et al.* (2003), (see Fig. 8).

The number of clicks from experiment I and experiment II were also compared. To prevent any potential biases, only the angular separations the two experiments had in common were chosen for comparison ( $\Delta\theta=0.5, 1, 1.5, 2, 2.5, 3,$  and 4). Because there was no significant linear trend in either experiment, a grand mean was calculated for each experiment by pooling the data from the angular separation above. The resulting mean clicks per trial for experiments I and II were 186.52 and 166.35, respectively. There was no significant difference between these means,  $t(291)=1.47, p>0.05$  (two tailed).

Response time was also compared between experiments I and II with only the angular separation in common used for analysis. Despite the fact that there was a significant linear trend for reaction time in Exp. I, a grand mean was calculated for each experiment by pooling the data from the angular separation. There was a significant difference,  $t(739)=12.54, p<0.01$  (two-tailed) between the means of 4.5 and 3.8 s for experiments I and II, respectively. Because simply pooling data results in the most parsimonious comparison with the least amount of variance accounted for (compared to a linear model with more than a single parameter), the significant result is considered conservative.

The correlation between response time and number of clicks was examined for a random subset of trials within each experiment. A moderate low correlation resulted in Exp. I ( $R^2=0.24, n=99$ ) and a weak correlation resulted from Exp. II ( $R^2=0.07, n=92$ ).

TABLE I. A point-by-point comparison between proportions correct from experiments I and II was compared for each angular separation. The angular separations that experiment II did not have in common with experiment I were interpolated by averaging adjacent points and are denoted by an asterisk. Differences between points on the psychometric function were large enough to produce significant one-tailed  $z$  scores (indicated by bold  $p$  values) for all angular separation except for  $\Delta\theta=2.00, 3.00$  and 4.00.

Comparison Between Psychometric Functions from Exp. I and Exp. II										
$\Delta\theta$	0.50	1.00	1.25*	1.50	1.75*	2.00	2.25*	2.50	3.00	4.00
$z$	-1.85	-2.22	-4.13	-2.36	-2.40	-0.61	-1.78	-2.73	-0.58	...
$p$	<b>0.032</b>	<b>0.014</b>	<b>&lt;0.001</b>	<b>0.009</b>	<b>0.008</b>	<b>0.248</b>	<b>0.038</b>	<b>0.003</b>	<b>0.281</b>	...

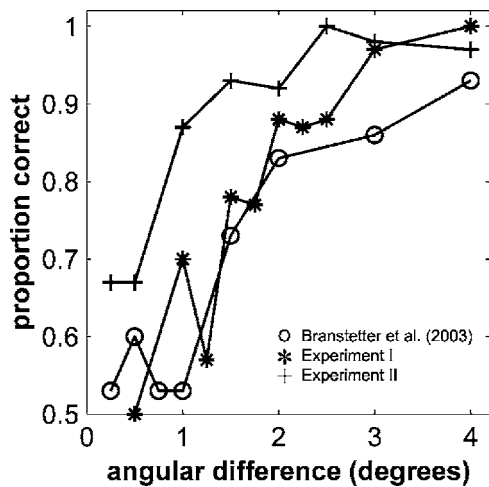


FIG. 8. Psychometric functions from Branstetter *et al.* (2003) and experiments I and II.

## V. GENERAL DISCUSSION

The two main findings of this study are: (1) decreasing the number of targets from six to three does not aid in localization, and (2), increasing the space between the rods enhances localization. Although the finding from experiment I (that decreasing the number of targets does not aid in localization), departs from human results (Wightman and Kistler, 1997; Langendijk *et al.*, 2001), this may be a selective adaptation for dolphins. During foraging, dolphins are required to echoically detect, track, and capture multiple fish, often schooling in close spatial proximity. Having the ability to localize multiple targets simultaneously would no doubt be advantageous, if not a basic requirement for this type of auditory predation.

The results were consistent with a passive hearing study that determined the smallest possible angle (minimum audible angle or MAA) between two sound sources that would allow the two sources to be perceived as discrete. Renaud and Popper (1975) reported the horizontal MAA for 30, 60, and 90 kHz pure tones as 2.5, 3.0, and 3.0°, respectively. Horizontal and vertical MAAs for click stimuli (35  $\mu$ s duration, 64.35 kHz peak frequency) were 0.9 and 0.7°, respectively.

The results from the current study, along with Branstetter *et al.* (2003), suggest that the dolphin's echoic spatial acuity is sufficient to support cross-modal matching of objects between vision and echolocation as shown by Pack and Herman (1995) and Herman *et al.* (1998). Because the dolphin in these studies interrogated relatively large objects (approximately 43 cm<sup>2</sup>) at relatively short distances (<1 m), the angle the objects subtended was much greater than the angular differences threshold reported here (For a more extensive discussion on this topic, see Branstetter *et al.*, 2003).

The question remains, how do dolphins segregate individual echoes among several closely spaced echoes? One possible explanation for these findings may be related to the phenomenon of "summing-localization blur" caused by simultaneous sound sources. For human listeners, if two *coherent* sound sources are presented simultaneously at an equal distance from the midsagittal plane, a single "phantom"

sound is perceived half the distance between the sound sources. Coherence can be defined as two signals that are identical and the degree of coherence can be calculated by the normalized cross correlation function. As the degree of coherence decreases, summing-localization blur decreases (Jeffress *et al.*, 1962). Although the PVC rods in the experiment were identical, during ensonification, adjacent rods are unlikely to produce coherent echoes. The incident signal of the bottlenose dolphin is not only directional with respect to amplitude, but also highly directional and asymmetric in the frequency domain. Au (1980) demonstrated that peak frequency of the incident signal was 122 kHz directly in front of the dolphin but was 38 kHz only 10° to the right and 115 kHz, 10° to the left of the dolphin. Thus, targets separated in space will produce echoes with different peak frequencies and, thus, varying degrees of coherence. Although Au (1980) did not measure peak frequencies for small angles off the median, we fit a fourth order polynomial to the data suggesting that at 2 and 4°, the peak frequencies of the echoes would be 109 and 94 kHz, respectively. Thus, echoes off the median plane would have spectral differences of 13 and 28 kHz for 2 and 4°, respectively. Although a polynomial is overly simplistic, spectral differences are nevertheless likely to be larger for rods separated by 4° compared to 2°. These spectral differences decrease signal coherence of adjacent rod echoes, and may aid the dolphin in degrading summing-localization blur for closely spaced objects. Even when the dolphin is pivoting its head, the target directly in front of the dolphin is likely to have a different frequency and amplitude signature than peripheral targets.

In addition, lower frequencies will not reflect well off of a small object compared to higher frequencies due to their relatively large wavelengths. For example, two incident signals with a 38 and a 122 kHz peak frequencies will have 4.0 and 1.2 cm wavelengths, respectively. Because the PVC rods have a 1.9 cm outer diameter, the 38 kHz signal will produce a much more attenuated echo than the 122 kHz signal. Thus only a small portion of the array will probably produce salient echoes per each individual outgoing click. During echoic interrogation, Hiapo would pivot his head in the horizontal plane, suggesting the dolphin was ensonifying only a portion of the stimuli at a time. Adding multiple targets (e.g., four vs two rods from Branstetter *et al.*, 2003) may not affect his localization ability through interference because peripheral targets will produce increasingly attenuated echoes.

Another mechanism that may aid in producing noncoherent echoes will be the dolphin head related transfer function (HRTF). The dolphin's head behaves as a position dependent spectral filter (Branstetter and Mercado, 2006; Aroyan, 2001; Supin and Popov, 1993; Ketten, 2000) as well as a shaded receiver (Mohl *et al.* 1999). Echoes from one position in auditory space (relative to the head) will be spectrally different in another position. Unlike the pinna which is responsible for HRTF in mammals, the most likely candidates for dolphin HRTFs are internal anatomical structures such as the lipid jaw channels (Ketten, 2000; Aroyan, 2001).

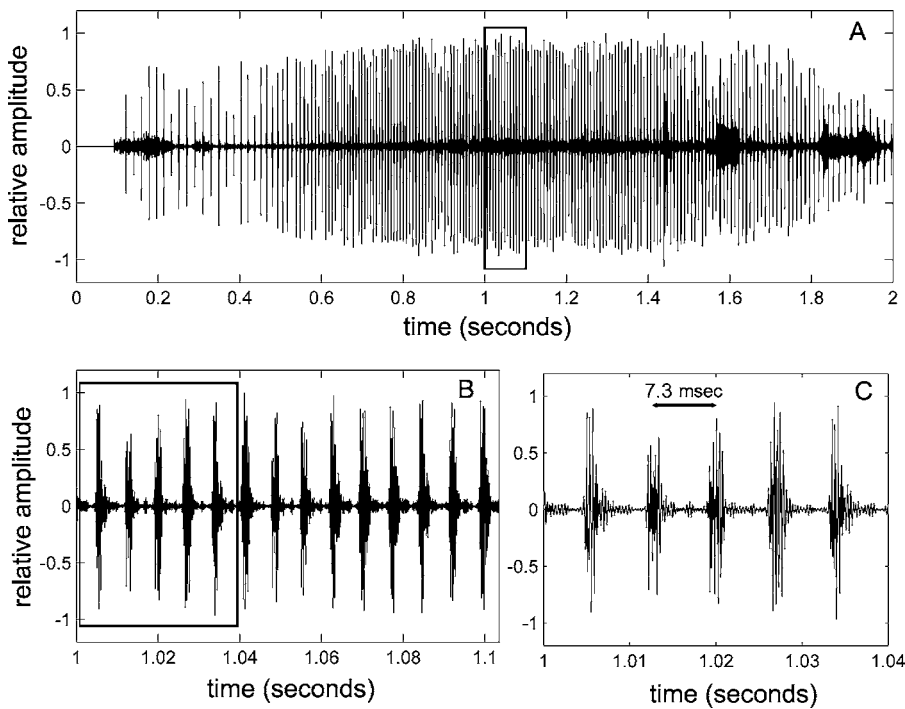


FIG. 9. An example of a standard click train from a trial in experiment I. (A) represents an entire click train from a single trial. (B) is a time expanded section from the rectangle in (A). (C) is a time expanded section from the rectangle in (B). Sampling rate was 44.1 kHz.

### A. Click trains

Figure 9 is a plot of a typical click train from the current study. The number of clicks a dolphin emits during a sonar task is highly variable but typically related to how much effort is used to interrogate an object (Roitblat *et al.*, 1990). For example, a dolphin's click quantity has been positively correlated to level of masking noise (Au and Penner, 1981) and target range (Thompson and Turl, 1990) during detection tasks. In addition, dolphins emit more clicks for objects that are harder to identify in delayed matching-to-sample tasks (Roitblat *et al.*, 1990). The dolphin in the current study displayed similar (but weak) trends in adaptive acoustic behavior (Figs. 5 and 7); however, none of the trends were above statistical chance.

Inter-click intervals (ICIs) from wild dolphins have been reported to fit a bimodal distribution (Lammers *et al.*, 2003). Echolocation signals typically have ICIs greater than 15 ms while burst-pulse signals (observed in social contexts) have ICIs that begin, persist and end below 10 ms (Lammers *et al.*, 2003). Laboratory studies suggest dolphins require a finite amount of time (lag time) to process each incoming click before generating another click. Lag times between 19 and 45 ms typically are added to the sound speed, two-way travel time for a number of experiments (see Au, 1993; p. 115–117). Although foraging dolphins sometime produce ICIs below the apparent minimum lag time (immediately before a prey capture), how these clicks are processed (or if they were processed at all) was a topic of speculation (Lammers *et al.*, 2003). Figure 10 displays ICIs from ten randomly sampled click trains from experiments I and II. Because of the large variability in the number of clicks between trials, only the first 20 clicks, the middle 20 clicks, and the last 20 clicks were used for analysis. All click trains had these three segments despite the overall number of clicks. The click trains in all of the experiments reported here typi-

cally start and end with longer and more variable inter-click intervals (Figs. 9 and 10) and lower amplitude clicks (Fig. 9). The stereotyped decrease and increase of the ICIs during the first 20 clicks and the last 20 clicks, respectively, may reflect the dolphin “focusing” the range of its sonar signal by dynamically adjusting the ICI to account for the delay of the object echo. The most stereotyped ICIs have an average interval of about 7.3 ms and occur during the vast majority of all click trains (Figs. 9 and 10). The two-way sound speed travel time for a target at a 200 cm distance is 1.3 ms. This suggests a lag time of 6.0 ms, considerably lower than previously reported (Au *et al.*, 1974; Au, 1980). Another possibility is that dolphins do not process echoes individually at short ranges, but perceive rapid echo returns as an auditory stream. ICIs would then be adjusted or “tuned” to decrease interference with the incident signal.

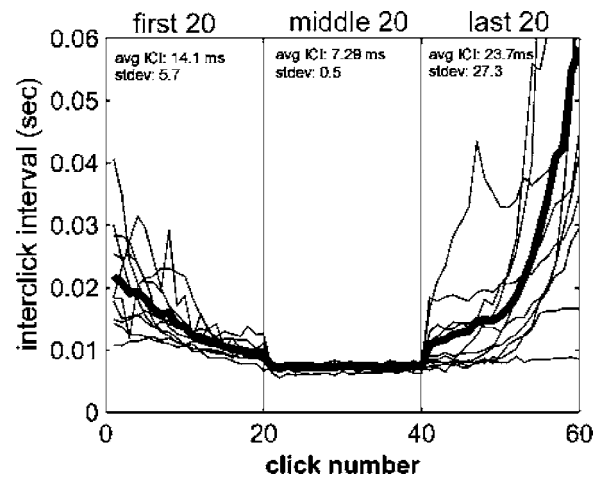


FIG. 10. Inter-click intervals sampled from ten randomly selected trials. Due to variable click train lengths, only the first, middle, and last 20 clicks in every train are compared. The bold line represents the average of the ten trials. The click trains in all trains start and end with longer and more variable ICIs. ICIs toward the center of the clicks trains are very stable.

One shortcoming of the current study is the absence of broadband acquisition of the dolphin's sonar signals. Dolphins are known to alter their sonar signals in the amplitude and frequency domain in response to environmental (Au *et al.*, 1985) and sonar task conditions (Au and Penner, 1981; Au, 1980). Because high frequency signals reflect better off of smaller object, the dolphin may selectively increase the higher frequency components of its sonar signal when attempting to resolve fine spatial details. This possibility remains untested.

## B. Response time

Pooling the results from the above studies (significant trend in experiment I and significant difference between experiments I and II) suggests there is a subtle relationship between task difficulty and the amount of time the dolphin uses to make a response. Spending more time on a more difficult task makes intuitive sense. Because there was no significant difference in the number of clicks within on between the experiments, the difference in response time may reflect decision making time rather than observation time.

## C. Auditory mechanisms

Of the auditory mechanisms used for sound source localization, the easiest to evaluate are ITDs. Using a simple two-receiver model (see Branstetter *et al.*, 2003), ITDs were calculated from the obtained angular discrimination thresholds. ITDs for thresholds of 1.6 (Branstetter *et al.*, 2003), 1.5 (Experiment I) and 0.7 (Experiment II) resulted in ITDs of 2.6, 2.4, and 1.1  $\mu$ s, respectively. The smallest dolphin ITD threshold measured by Moore *et al.* (1995) was 7  $\mu$ s for click stimuli with a peak frequency of 30 kHz. For click stimuli with peak frequencies between 60 and 90 kHz, ITD thresholds were between 17 and 18  $\mu$ s. The ITD thresholds from the angular discrimination studies are several times smaller than those reported by Moore *et al.* (1995). In addition, Moore *et al.* (1995) calculated an ITD, for the dolphin MAA of 1° (Renaud and Popper, 1975), would be about 1.3  $\mu$ s. Again, the MAA ITD was several times smaller than those reported by Moore *et al.* (1995). There are at least two possibilities for the resulting discrepancies. First, the model used for calculating ITD in the current study was overly simplistic. The model did not take into account reflective or refractive properties of the dolphin's head such as those produced by the skull or the lipid channels in the lower jaw. The internal structures of the dolphin head could possibly increase the ITD threshold. However, it is unlikely that the ITD threshold could be increased by several factors to be consistent with ITDs measured by Moore *et al.* (1995). Second, the dolphin may not have used ITDs for fine angular discrimination. IIDs, binaural spectral differences or monaural spectral cues may have been used instead. IIDs are more salient at higher frequencies for terrestrial mammals and dolphins (Supin and Popov, 1993). The high degree of sound shadowing produced by the dolphin head (>20 dB; Supin and Popov, 1993) and the high level of IID sensitivity (<1 dB) measured by Moore *et al.* (1995) suggests IIDs may play a significant and possibly dominant role in sound

source localization for fine horizontal angular discrimination. The anatomical structures responsible for producing IIDs and binaural spectral differences remain speculative.

Although IIDs and ITDs can provide the horizontal position of a sound source, these cues typically provide little if any information about source elevation. For terrestrial mammals, vertical and monaural localization are due to the spectral filtering properties of the pinna. The pinna behaves as a position-dependent spectral filter that produces subtle differences in the received sound depending on the location of the sound source. The direction dependent transfer function created by the pinna (and to a lesser degree, the head and torso) is known as the head related transfer function (HRTF). Interestingly, auditory predators often display elaborately convoluted pinnae (e.g., members of the order *Chiroptera*) and asymmetry in external auditory apparatus (e.g., skull asymmetry in the barn owl, *Tyto alba*). Human studies suggests HRTF generated cues are greatest for higher frequencies (Kisler and Wightman, 1992; Middlebrooks and Green, 1992) and broadband sounds. Because dolphin hearing is both broadband with good sensitivity at higher frequencies, HRTFs may be a likely candidate for vertical and perhaps horizontal sound localization (for a more detailed discussion see Branstetter and Mercado, 2006).

## VI. CONCLUSION

The ability to localize fine spatial details through sonar no doubt has several advantages for wild dolphins living in visually restricted environments. For example, the Amazon River dolphin (*Inia geoffrensis*) feeds in shallow murky waters with very limited visibility. Still others such as the Hawaiian Spinner dolphin (*Stenella longirostris*) are nocturnal feeders (Perrin and Gilpatrick, 1994). Most dolphins typically prey on small fish and squid and are restricted to capturing prey in a serial fashion. Thus, a dolphin may be required to echoically isolate and capture prey tens to hundreds of times within a 24 h period. This taxing requirement demands a sonar system well adapted for precise target localization through echolocation. Echoic localization may also be important for protection from potential predators such as sharks or other marine mammals. Echoically locating and identifying predators at a distance may provide a dolphin with enough time to evade predation.

The results reported here demonstrate one of many methods of measuring spatial acuity through echolocation. Because we wanted these data to generalize well to the cross-modal data, we constructed the stimuli out of similar materials (PVS) with similar target complexity (multiple targets). A simpler test would require the dolphin to discriminate between two objects (example: large sphere vs small sphere). The angle between the objects could be adjusted in a similar manner as the studies presented here, perhaps yielding a finer estimate of the dolphin's angular resolution.

Although horizontal echoic angular resolution has been measured for a handful of conditions, only a single passive listening study has measured sound source localization in the vertical plane (Renaud and Popper, 1975). Despite the lack of binaural stimulus differences, the animal's MAA was

slightly smaller in the vertical plane. If this result can be corroborated, an even stronger case that dolphins employ HRTFs for fine sound source localization and echoic imaging can be made.

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## APPENDIX

The arrays were centered on the wooden arc so the far end of the  $S+$  array and the  $S-$  array were an equal distance to the center of the arc and, hence, the dolphin’s median plane. The center of the stimuli can be calculated by

$$\frac{\theta_w + \theta_b}{2}$$

As  $\theta_b$  was varied, the distance from the center of the rack to the furthest ends of the stimuli also varied. The position of the center of  $\theta_b$  relative to the center of the arc can be calculated by

$$D = \left( \theta_w + \frac{\theta_b}{2} \right) - \left( \frac{\theta_w + \theta_b}{2} \right),$$

where  $D$  is the distance from the center of the arc to the center of  $\theta_b$ . The solution for  $D$  is the constant  $\theta_w/2$ .

<sup>1</sup>Henceforth, the word “dolphin” will be used to refer to the bottlenose dolphin (*Tursiops truncatus*).

<sup>2</sup>Although only two experiments are reported here, a pilot study and a control study were also conducted, and counterbalanced (Branstetter, 2005). The control study demonstrated the dolphin was not using a potential time-delay confound from echoes reflecting off the tank wall.

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