Heptuna’s Contributions to Biosonar

The dolphin Heptuna participated in over 30 studies that helped define what is known about biosonar.

It is not often that it can be said that an animal has a research career that spans four decades or has been a major contributor (and subject) in more than 30 papers in peer-reviewed journals (including many in *The Journal of the Acoustical Society of America*). However, one animal that accomplished this was a remarkable bottlenose dolphin (*Tursiops truncatus*) by the name of Heptuna (Figure 1). Indeed, considering the quality of Heptuna’s “publications,” we contend that were he human and a faculty member at a university, he would easily have been promoted to full professor many years ago.

Heptuna passed away in August 2010 after a career of 40 years in the US Navy. Because Heptuna had such a long and fascinating career and contributed to so much of what we know about marine mammal biosonar, we thought it would be of considerable interest to show the range of studies in which he participated.

Both of the current authors, at one time or another, worked with Heptuna and, like everyone else who worked with the animal, found him to be a bright and effective research subject and, indeed, “collaborator.” At the same time, we want to point out that Heptuna, although an exceptional animal, was not unique in having a long and very productive research career; however, he is the focus of this article because both authors worked him and, in many ways, he was truly exceptional.

Early History

Heptuna was collected in midsummer 1970 off the west coast of Florida by US Navy personnel trained in dolphin collection. He was flown to the Marine Air Corps Station Kaneohe Bay in Hawaii that then housed a major US Navy dolphin research facility. At the time of collection, Heptuna was estimated to be about 6 years old, based on his length (close to 2.5 meters, 8 feet) and weight (102 kg, 225 lb). His name came from a multivitamin tablet that, at the time, was a supplement given to all the dolphins at the Naval Undersea Center (NUC).
**Heptuna’s Basic Training**

When Heptuna first joined the Navy, he went through the standard “basic training” procedures used for all Navy dolphins. Exceptionally skilled trainers provided conditioning and acclimation to the Hawaii environment. Heptuna was a fast learner and quickly picked up a fundamental understanding of visual (hand signals) and tonal stimuli needed for specific experiments.

One of the things that made Heptuna such a great experimental animal, leading to his involvement in so many experiments, was that he had a great memory of past experimental procedures and response paradigms. Heptuna also had a willingness to work with the experimenter to figure out what he was supposed to learn. Sometimes, for the less experienced investigator, Heptuna would teach the experimenter.

**Heptuna’s First Study**

After initial training, Heptuna’s first research project was a study of sound source localization by University of Hawaii zoology graduate student, Donna McDonald (later Donna McDonald Renaud; Figure 2). Donna’s mentor, Dr. Arthur Popper, had not worked with dolphins, but he knew a few people at the NUC. He reached out to that group, and they were intrigued by the idea of working with a doctoral student. Donna, Art, and the leadership at the NUC decided that a sound localization study would be of greatest interest because no one had asked if and how well dolphins could localize sound (though it was assumed that they could determine the location of the sound source).

Donna was trained by Ralph Penner, the extraordinary head trainer at the NUC and Heptuna’s first trainer. Donna and Ralph first trained Heptuna to swim to a bite bar (a task he would use in many subsequent studies; Figure 2), hold his head still, and listen for a sound that came from distant underwater speakers. Heptuna had to discriminate sounds coming from his right or left as the speakers were moved closer together. The goal was to determine the minimal angle between the speakers that could be discriminated (MAA). As soon as Heptuna determined the position of the source, he would swim to a response point on the left or right (Figure 3). If he was correct, Donna would reward him with food.

Heptuna quickly picked up the task and for more than two years gave Donna interesting data that examined sound localization abilities for different frequencies and sounds (Re-

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1 This article is dedicated to the memory of Dr. Donna McDonald Renaud (1944-1991), the first investigator to do research with Heptuna.

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**Figure 2.** Heptuna’s pen for training in Kaneohe Bay, Hawaii. The speakers for the sound localization are at the far bars and the bite bar to which Heptuna held on is in the center of the first cross bar. Equipment is in the shack, and Donna Renaud is seen preparing to throw food to Heptuna. **Inset:** picture of Donna from 1980, kindly provided by her husband Maurice. Donna passed away in 1991.

**Figure 3.** Heptuna hitting the response paddle, ca. 1972. These were the days before many electronics, so the trainer had to see what the animal did and then reward him immediately.
naud and Popper, 1975). The results showed that Heptuna (and other dolphins) could localize sounds in water almost as well as humans can in air.

Because dolphins live in a three-dimensional acoustic world, Donna decided to ask whether Heptuna could localize sound in the vertical plane. The problem was that the study site was quite shallow and there was no way to put sources above and below the animal. To resolve this, Donna decided that if she could not bring the vertical plane to Heptuna, she would bring Heptuna to the vertical plane. She switched the bite bar to a vertical position and trained Heptuna to do the whole study on his side. As a consequence, the same sound sources that were left and right in the earlier experiments were now above and below the animal’s head. Donna found that the MAA for vertical localization was as good as that for horizontal localization, suggesting a remarkably sophisticated localization ability in dolphins.

**An Overview of Heptuna’s Studies**

Shortly after completing the localization study, Heptuna started to “collaborate” with another well-known male dolphin, Sven. Heptuna and Sven began training to detect targets on a “Sky Hook” device, which moved and placed calibrated stainless steel spheres and cylinders underwater at various distances from the echolocating animals. The purpose of the Sky Hook was to determine the maximum distance at which dolphins could detect objects of different sizes and types (Au et al., 1978).

As training continued, Dr. Whitlow Au, a senior scientist at the NUC, attended the sessions conducted by Ralph Penner or Arthur (Earl) Murchison. Whit recorded the animals outgoing echolocation signals (see Au, 2015 for a general history of dolphin biosonar research). These signals were analyzed in an attempt to understand and quantify the echolocation abilities of dolphins. As Whit clearly stated, “In order to better understand the echolocation process and quantify the echolocation sensitivity of odontocetes, it is important to determine the signal-to-noise ratio (SNR) at detection threshold” (Au and Penner, 1981, p. 687). Whit wanted to refine his earlier estimates of the animal’s detection threshold based on the transient form of the sonar equation.

Because the earlier thresholds were done in Kaneohe Bay where the background noise was variable and not uniform with respect to frequency, a flat noise floor was needed. Thus, Heptuna was exposed to an added “nearly white-noise source” that was broadcast while he performed the target detection task. The results showed that at the 75% detection threshold, Heptuna’s threshold was at a level of 77.3 dB re 1 μPa/Hz, whereas it was 74.8 dB for a second dolphin, Ehiku. Whit went on to speculate that this difference may have been due to the abilities of the two animals to distinguish time separation pitch (TSP). In human hearing, TSP is the sensation of a perceived pitch due repetition rate. For dolphins, the concept suggests that the ripples in the frequency domain of echoes provides a cue, an idea that persists in modeling dolphin sonar today (Murchison, 1976; Au, 1988).

**Heptuna and Echolocation Studies**

Heptuna’s biosonar career continued under the tutelage of Earl and Ralph. Earl had begun a long series of experiments on echolocation range resolution of dolphins, and Heptuna was the animal of choice because of his experience. Heptuna faced a new experimental paradigm in this study, requiring him to place his rostrum in a “chin cup” stationing device and echolocate suspended polyurethane foam targets to his left and right (Figure 4). His task was to press a paddle on his right or left corresponding to the closer target. Earl would randomly adjust the targets to one of three preselected ranges (1, 3, or 7 meters). Heptuna was stationed behind an acoustically opaque visual screen so that he could not see or echolocate the targets, and Earl would move one target ever so slightly, moving it a set distance closer or further away in relation to the test range.

Heptuna was the subject for three of Earl’s studies of range resolution. Earl found that Heptuna’s performance indicated that his range resolution conformed closely to the Weber-Fechner function. In human psychophysics, the law relates to the perception of a stimulus; the magnitude of the stimulus when it is just noticeable is a constant ratio (K) of the original stimulus (ΔD/D = K) or conforms to Stevens power law. The results led Earl to speculate how Heptuna’s performance would compare with the results of other echolocation experiments. One important observation from Heptuna’s results
led Earl to suggest that Heptuna (and by extension other dolphins) had the ability to focus his echolocation attention on a segment of time that encompassed the returning target echo, allowing the dolphin to ignore sounds before and after the echo (Murchison, 1980).

When Earl finished his range resolution studies, Heptuna became available for other research. Whit Au wanted to continue to explore Heptuna’s hearing abilities. Because Whit and Patrick Moore had worked together on earlier experiments involving sea lion sound source localization (Moore and Au, 1975), they teamed with Heptuna to better understand his hearing using receiving models from classic sonar acoustics. This began a multiyear research effort to characterize Heptuna’s hearing (e.g., Moore and Au, 1983; Au and Moore, 1984; Branstetter et al., 2007).

The first task was to collect masked hearing thresholds at unexplored high frequencies and compute critical ratios and critical bands (Moore and Au, 1983). Armed with these data, it was possible to start a series of experiments to measure Heptuna’s horizontal- and vertical-receiving beam patterns (Au and Moore, 1984). This was the first attempt to quantify the receiving beam pattern for an echolocating marine mammal. The investigators used a special pen with a 3.5-meter arc that filled two sides of a 9-square-meter pen. Heptuna stationed at the origin of the arc on a bite plate and was required to remain steady during a trial. Having Heptuna grab the bite plate was easy as this was something he had done in earlier studies using a chin cup. Still, having Heptuna transition to the new 1.5-meter depth of the bite plate proved to be a challenge. Heptuna did not like the aluminum pole used to suspend the bite plate above his head to hold it in position for the horizontal measurements. Wild-born dolphins avoid things over their heads, which is why it is necessary to train them to swim through underwater gates with overhead supports.

Once Heptuna was satisfied that the horizontal pole was not going to attack him, the experiment began. The arc in the pen allowed positioning of the signal source about Heptuna’s location in 5° increments. For the horizontal beam measurements, two matched noise sources were placed at 20° to the animal’s left and right and the investigators could move the signal source. During all of the testing, Heptuna’s stationing was monitored by an overhead television camera to ensure he was correctly stationed and unmoving.

After data acquisition for the horizontal beam was finished, Heptuna moved to the vertical beam for measurements. Again, Heptuna proved to be a dolphin of habit. He tried every possible way to station on the vertical bite plate just as he had before on the horizontal bite plate except turning on his side. This was perplexing because this was a behavior that Donna McDonald had used in her study (it was found later that he twisted in the opposite direction for Donna). The issue was overcome by slowly rotating the bite plate from the horizontal position to the vertical position over several training sessions and then Heptuna started the vertical measurements. From these data, it was possible to compute Heptuna’s directivity index and model a matched pair of receiving transducers that had the same directivity as the animal. Two major observations of the beam patterns were that as the frequency increased, the receiving beam became more narrow (a similar result was found in the bat; Caspers and Müller, 2015) and that the receiving beam was much broader and overlapped with the transmit beam (Au and Moore, 1984).

**Heptuna and Controlled Echolocation**

Moore’s observations over several echolocation experiments found a wide variation in clicks, some with a high source level but with a lower frequency and vice versa. The question became, “does the dolphin have conscious control over click content?” Can he change both the level and frequency of the click as needed to solve an echolocation problem or is it a fixed system so that as the dolphin increases the level, the peak frequency also increases?

Again, Heptuna was chosen to help answer this question. This began a very difficult and long experiment involving echolocation. Heptuna took part in a series of experiments designed to tease out if the dolphin actually had cognitive control over the fine structure of the emitted click. Dr. Ronald Schusterman had already demonstrated tonal control over a dolphin’s echolocation click emission. Schusterman et al. (1980) trained a dolphin to echolocate on a target only when a tone stimulus was present and to remain silent when it was not. This experiment started with the attempt to place both Heptuna’s echolocation click source level and frequency content under stimulus control while he was actively detecting a target echo.

Heptuna had to learn to station on a bite plate and then place his tail on a tail rest bar behind him, close to his fluke. This stationing procedure was necessary to ensure that Heptuna was stable and aligned with the click-receiving hydrophone, ensuring on-axis sampling of his clicks. Heptuna found this new positioning not at all to his liking. And much like the vertical bite plate with the beam pattern measurements issue mentioned in *Heptuna and Echolocation Studies*, Heptuna...
avoided that tail rest pole. He moved his tail up, down, right, and left, always trying to not have that “thing” touch his tail. By systematic and precise reinforcement of small tail movements, however, Heptuna finally touched the device with his tail.

With Heptuna finally positioned correctly, it was possible to start the detection training. Whereas the stationing training took weeks, Heptuna was 100% in detection performance in just one 100-trial session! To capture outgoing clicks, Marion Ceruti, a colleague, and Whit developed a computerized system that could analyze the echolocation click train that Heptuna emitted, computing both the overall peak level and peak frequency of the emitted clicks while doing a real target detection task (Ceruti and Au, 1983).

During a trial, a computer monitored Heptuna’s outgoing clicks and would alert the experimenter if Heptuna met the criterion of either high or low source level or high or low peak frequency and whether the signal was correct. When the computer sounded a high-frequency pure tone, Heptuna would emit loud clicks above the criterion, and when the computer sounded a lower frequency tone, he would keep his clicks below the level criterion. The experimenters also established a frequency criterion, and when the computer sounded a fast-pulsed tone, Heptuna was to keep his peak frequency above a fixed frequency, whereas when the pulses were slow, he kept his peak frequency below a fixed criterion. After intensive training, the experimenters managed to develop stimulus control over Heptuna’s click emissions. As a full demonstration that Heptuna had learned this complex behavior, mixed tones and pulse rates signaled him to produce high-level, low-frequency clicks and vice versa. Heptuna had learned to change his emitted level and peak frequency during an echolocation detection trial and demonstrated conscious control of his echolocation clicks (Figure 5; Moore and Pawloski, 1990).

Because Heptuna could produce high source level clicks, above 200 dB re 1 μPa (at 1 meter), Ken Norris, one of the great pioneers of dolphin echolocation studies, thought that Heptuna could test the prey-stunning theory that he and Bertel Møhl (see the article about Møhl in Acoustics Today by Wahlberg and Au, 2018) had been developing. The hypothesis was that with their very high intensity clicks, dolphins could stun potential prey, making capture much easier. Thus, began a truly exciting experiment involving Heptuna, fish in plastic bags, and suspension devices to hold the bags in front of the animal as he produced very high source level clicks. Bags burst because of bad suspension, sending fresh fish swimming away, with Heptuna giving chase. After many false starts, the bag size, suspension apparatus, and Heptuna were under control. The results did not, however, support the idea of prey stunning by dolphin clicks (Marten et al., 1988).

During this set of experiments, Heptuna had excellent control of his head placement, and Whit wanted to take advantage of the animal’s stationing to refine his vertical emission beam pattern measurements. Heptuna’s positioning was a level of improvement in accuracy over Whit’s first emitted-beam measurements. For this experiment, the control computer would signal Heptuna to echolocate the target (1.3-centimeter-diameter solid steel sphere located 6.4 meters in front of the bite plate) and report whether it was present or absent. Whit used six vertical hydrophones to measure Heptuna’s emitted beam for each click emitted. Whit computed Heptuna’s composite beam pattern over 2,111 beam measurements and showed that the vertical beam was elevated by 5° above the line of Heptuna’s teeth. Whit then calculated the vertical beam to be 15° different from his first measurements. He considered this difference to be attributable to both differences in head anatomy and better control over stationing by Heptuna (Au et al., 1986a).

Heptuna and “Jawphones”

William (Bill) Evans, a graduate student of Dr. Kenneth Norris, used contact hydrophones in suction cups to measure...
dolphin emitted signals. Bill’s work was groundbreaking echolocation research (Evans, 1967). Using Bill’s idea but in reverse, Moore developed the concept of “jawphones” to test dolphin interaural hearing by measuring interaural intensity and time differences. The first pair of jawphones used a Brüel & Kjær (B&K) 8103 miniature hydrophone positioned horizontally along the lower jaw of the animal for maximum efficiency (Figure 6). This position was used because the pathway of sound to the ear in dolphins is through the lower jaw (Brill and Harder, 1991).

Heptuna had no issues with the jawphones because he was trained to wear them as eye cups to occlude his vision for past echolocation experiments. The jawphones were attached to Heptuna’s lower jaws, and subsequent thresholds for the pure-tone stimuli were determined. To assess Heptuna’s interaural intensity difference threshold, the level of the stimuli was set at a 30-40 dB sensation level (SL). The study used wideband clicks that were similar to dolphin echolocation clicks but that were more suited to the animal’s hearing and better represented signals that the animal would naturally encounter. Stimuli were set to a repetition rate corresponding to a target echolocated at 20 meters (40 ms). Using a modified method of constants and a two-alternative forced-choice response paradigm, data were collected for both interaural intensity and time difference thresholds. The results clearly indicated that the dolphin was a highly sophisticated listener and capable of using both time and intensity differences to localize direct and reflected sounds (Moore et al., 1995).

Heptuna Moves to San Diego

In 1992, the Hawaii laboratory was closed and the personnel and animals moved to what is now the Space and Naval Warfare Systems (SPAWAR) Center in San Diego, CA.

Randy Brill, who was then working at SPAWAR, wanted to try to see if there were specific areas of acoustic sensitivity along the lower jaw of the dolphin and other areas around the head. The first thing Randy wanted was to collect thresholds from Heptuna and a second younger animal named Cascade. Using the matched jawphones, it was possible to collect independent thresholds for both the right and left ears of both animals in the background noise of San Diego Bay.

The resulting audiograms for Cascade revealed well-matched hearing in both ears (Brill et al., 2001). However, the results for Heptuna were startling because they showed that Heptuna, now about 33 years old, had hearing loss in both ears, with a more substantial loss in his right ear. Furthermore, Heptuna now had a significant hearing loss above 55 kHz.

In contrast, when Heptuna was tested at age 26 with the jawphones, his hearing was considered unremarkable because independent thresholds for his ears were closely matched for test frequencies of 4-10 kHz (Moore and Brill, 2001). These data for Heptuna are consistent with the findings of Ridgway and Carder (1993, 1997) showing that dolphins experience age-related hearing loss. Heptuna was another example of a male dolphin losing high-frequency hearing with age, a condition that is similar to presbycusis in humans and that is now known to be common in older dolphins (see the article in Acoustics Today by Anderson et al., 2018 about age-related hearing loss in humans).

The results of the free-field thresholds for Cascade at 30, 60, and 90 kHz provided additional support for the use of jawphones as a means to place the sound source in closer proximity to the animal and concentrate the source in a small, localized area. Jawphones have become a tool in the exploration of hearing in dolphins and are used in many experiments conducted at the US Navy Marine Mammal Program and other facilities and in the assessment of hearing in stranded and rehabilitating odontocetes.

Heptuna and Beam Control

Heptuna’s hearing loss notwithstanding, the investigators forged ahead to explore the idea that dolphins may control their emitted echolocation beam, allowing them to better detect targets. This involved animals free swimming in the open ocean as they echolocated. Using a new research device that could be carried by the dolphin, the Biosonar Measurement Tool (Houser et al., 2005), it was found that a dolphin could detect echoes from a target before the target entered to animal’s main echolocation beam.

Figure 6. Heptuna wearing “jawphones” during one of Patrick Moore’s studies in the early 1990s.
This was a behavior that led to an experiment to identify if the dolphin could detect targets off the main beam axis and to quantify their capabilities. To that end, Heptuna was used to explore emitted-beam control. Investigators (Lois Dankiewicz, Dorian Houser, and Moore) devised an experiment to have Heptuna once again station on a bite plate and detect echoes from targets placed at various positions to his right and left. This time, he would be echolocating through a matrix of hydrophones so that the investigators could examine various parameters of each emitted click at each position in the matrix of hydrophones and determine the beam pattern for each click in his emitted click train (Figure 7).

Heptuna was asked to detect a water-filled stainless steel sphere and a hollow aluminum cylinder. Heptuna stationed on a bite plate that prevented his ability to move his head during echolocation. He was then asked to echolocate targets as they were placed at various angles to his left and right (Moore et al., 2008). Horizontal and vertical −3 dB beam widths were calculated for each click as well as correlations between click characteristics of peak frequency, center frequency, peak level, and root-mean-square (rms) bandwidth. Differences in the angular detection thresholds for both the sphere and the cylinder to the left and right were relatively equal, and Heptuna could detect the sphere when it was 21° to the right and 26° to the left. His detection threshold for the cylinder was not as good, being only 13° to the right and 19° to the left. The more interesting result became apparent when plotting his composite horizontal and vertical beam patterns. Both were broader than previously measured (Au et al., 1978, 1986b) and varied during target detection. The center part of the beam was also shifted to the right and left when Heptuna was asked to detect targets to the right and left. It was clear that Heptuna's echolocation clicks formed a dynamic forward-projected but movable beam with complex energy distributions over which the animal had some control.

**Heptuna and Contact Hydrophones**

Whit Au, pursuing his interest in dolphin echolocation clicks, traveled to San Diego to participate in our ongoing experiments. First, he wanted to determine the location where the echolocation beam axis emerges from the dolphin head and to examine how signals in the acoustic near field relate to signals in the far field. First, investigators (Brian Branstetter, Jim Finneran, and Moore) helped Whit as he placed various hydrophone arrays around the heads of Heptuna and a second dolphin, Bugs (Figure 8). Whit collected the clicks from the arrays and computed the position on the melon (a mass in the forehead of all toothed whales that acts as a lens to collimates emitted clicks) where the maximum amplitude of the signals occurred. Whit noted that each dolphin's amplitude gradient about the melon was different, suggesting anatomical differences in both the shape of the forehead and that the sound velocity profile of the animal's melon acted on the emitted signal. Heptuna typically emitted signals with amplitudes higher than those of Bugs by 11-15 dB (Au and Penner, 1981).

Whit also interpreted his results as demonstrating that the animal's emitted click was first shaped internally by the air sacs in its head and then refined by transmission through the melon. Whit suggested that his results supported Norris's
(1968) hypotheses that clicks produced by the phonic lips propagate through a low-velocity core in the melon that positions the emission path almost in the middle of the melon (Au et al., 2010).

An Appreciation

Heptuna’s studies described here are really only a “sample” of the work he was engaged in over his 40-year Navy career. The References include many of the research papers that involved Heptuna, and there were also studies that were never published. But the point of this article is that this one animal made substantial contributions to our basic understanding of hearing and echolocation in dolphins. Indeed, Heptuna has become a “legend” in dolphin research. This status likely arose because one of the unique things about Heptuna and, what made him such a valuable animal, was that he learned new tasks remarkably quickly and that he was not easily frustrated. Moreover, he had a really good memory for past training, and he quickly adapted to new tasks based on similar experiences in previous experiments, even many years earlier. And, although it is not quite “scientific” to say it, another thing that promoted Heptuna as an animal (and collaborator) of choice was that he was, from the very beginning in 1971, an easy and friendly animal to work with, something not true of many other dolphins!

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References


BioSketches

**Patrick W. Moore** retired from the US Navy Marine Mammal Program after 42 years of federal service. He was an active scientist as well as a senior manager of the program. Patrick received the Navy Meritorious Civilian Service Award in 1992 and again in 2000 for contributions and leadership in animal psychophysics and neural network models. He is a fellow of the Acoustical Society of America, a charter member of the Society for Marine Mammalogy, and a member of the American Behavior Society and coedited *Animal Sonar: Processes and Performance*. Patrick is currently a senior life scientist at the National Marine Mammal Foundation.

**Arthur N. Popper** is professor emeritus and research professor at the University of Maryland, College Park, MD. He is also editor of *Acoustics Today* and the Springer Handbook of Auditory Research series. His research focused on hearing by aquatic animals (mostly fishes) as well as on the evolution of vertebrate hearing. For the past 20 years, he has worked on issues related to the effects of anthropogenic sound marine life both in terms of his research and in dealing with policy issues (e.g., development of criteria).