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Being "there" for surprises and delights in cetacean and pinniped biology

The Kenneth S. Norris Lifetime Achievement Award Lecture
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Sam Ridgway with a favorite species, *Tursiops truncatus* (Photo by Shawn Houllis, LifeShadows Photography).

When Society President, Andrew Read, told me of my Kenneth S. Norris Lifetime Achievement Award, I was surprised. Humbled, I recalled the generous support that Ken Norris had given my career. He was always a friend, often a mentor, and regularly in my thoughts, even today. I only regret that in our busy lives, I had not spent more time in the company of Ken and his dear mate Phyllis. The award is also significant because the two previous recipients, Gerald Kooyman and Toshio Kasuya, both are good friends and respected colleagues (see electronic supplement, p. 1).

Recently, when colleagues told me that my work would be honored with special sessions at the 156th meeting of the Acoustical Society of America in Miami, Florida, I tried to think of an apt metaphor. Forrest Gump came to mind. Gump was the character played so brilliantly by Tom Hanks in the Robert Zemeckis' movie based on Winston Groom's novel. In an airy connection with Gump-like surprises, in 1954, I had even received a letter from Coach Paul "Bear" Bryant inviting me to play gridiron football. Unlike Forrest, I did not excel on that field; however, like Gump, I flowed through the latter half of the 20th century bumping into one amazing challenge after another.

The Military Draft in 1960 Enabled My Career

Graduating in veterinary medicine from Texas A&M University in 1960, during the time of compulsory military service, I applied for an Air Force commission. I was deployed to California where my military assignment was to be a base veterinary officer caring for sentry dogs, monitoring research animals, and overseeing commissary food inspections. Almost immediately, however, I focused in on the developing Navy interest in dolphins. In the early 1960s, I became Animal Health Officer and a founder of the Navy Marine Mammal Program (NMMP) at Naval Missile Center, Point Mugu, California. William B. McLean and Thomas G. Lang, in particular, were interested in the mechanics of how dolphins swim so fast. These physicists reasoned that something might be learned from dolphin movement in the ocean to improve the mechanisms of torpedoes, submarines, and ships so they would move faster with less energy (see Wood 1973). As it turned out, the focus of the program was not as narrow. A brilliant and practical physicist, McLean was in charge of thousands of scientists and engineers. His philosophy was to collect a small, motivated group of scientists and engineers and let them figure out what really needed to be done. The scope of the program was expanded to "bionics" (the science of designing instruments or systems modeled after the capabilities of living organisms). Dolphin echolocation was a promising topic for investigations taken up by William (Bill) E. Evans and C. Scott Johnson. Diving capabilities were also promising. I pursued this work in addition to my animal medical duties. Forrest G. Wood left Marineland of Florida, where he had been curator, to become the chief biologist of our program. B. A. Powell came down from headquarters in China Lake, California to become our director and chief explainer of what we were doing with dolphins in the U.S. Navy.

Over the years, beginning in 1963, I attended many scientific conferences where I met leaders in marine research who transfused my career. I have included additional information and pictures in the electronic supplement, Figures S4–S6.

Focus on Medicine and Diving—Mostly

Until the spring of 1963, when our main dolphin-holding pool at Point Mugu was completed, we had to travel about 50 miles south to work with two dolphins kept at Pacific Ocean Park (POP) in Santa Monica. Robert M. Miller, a veterinarian in nearby Thousand Oaks, California handled veterinary care at POP. I was able to work with him on various cases (Miller and Ridgway 1963). With the help of a local pathologist, D. Gordon Johnston, we were able to diagnose some wild stranded dolphins (Ridgway and Johnston 1965). Later, parasitologist Murray Dailey contributed to these efforts (Ridgway and Dailey 1972).

We had access to Navy watercraft for exploring the local marine life. We plied waters of the California Channel Islands. Although many species were seen in these waters, depending on time of year, Pacific white-sided dolphins, *Lagenorhynchus obliquidens* and the Dall's porpoise, *Phocoenoides dalli*, most interested us because of their apparent swimming speed. We caught several for our studies using a hoop net deployed from the bow of the boat by my associate Morris Wintermantel (Ridgway 1966*a*). Deborah Duffield made progress training Dall's porpoises for handling (see electronic supplement, pp. 2–5, Fig. S1–S3).

With my colleague D. Gordon Johnston (an M.D. pathologist), we used radioiodine injections to assess the blood volumes of Dall's porpoise, Pacific white-sided dolphin, and bottlenose dolphin, *Tursiops truncatus*. The Dall's porpoise had a very high blood volume, a very large heart (Ridgway and Johnston 1966, Ridgway and Kohin 1995), and high blood hemoglobin levels. We concluded that the high oxygen transport ability afforded the Dall's porpoise the ability for faster swimming and deeper diving, perhaps to pursue swifter and deeper prey or to avoid predators (Ridgway and Johnston 1966, Ridgway 1966*a*).

Point Mugu is just 50 miles north of the University of California at Los Angeles. Not only was Ken Norris there but so was George A. Bartholomew (Bart to us). Bart had students interested in marine mammals. I was told that Bart had crawled across Channel Islands beach sand, rectal thermometer in hand, to take the temperature of a sleeping northern elephant seal bull (*Mirounga angustirostris*). He was our kind of teacher!

Somewhere I read that the blow of a dolphin or whale was a bit like steam escaping from a teakettle. If this were true, then the escaping air would be saturated with water vapor. My observations of swimming dolphins and porpoises at sea suggested that the blow consisted mainly of surface water thrown up by forceful exhalation. Harry N. Coulombe and Bill Evans were both students of Bart. They convinced me to stick a small temperature and humidity-measuring device through the blowhole and into the nasal cavity of some of our cooperating bottlenose dolphins and Pacific white-sided dolphins. The results were surprising, counterintuitive, and delightful. Rather than exhaling water-saturated air as terrestrial mammals do, our animals saved some water by exhaling air that was not saturated (Coulombe *et al.* 1965).

Dolphins Readily Learned to Cooperate in Experiments

At Point Mugu in the 1960s, we were all about operant conditioning. Operant conditioning is used to modify voluntary behavior. When an animal moves toward a desired behavior, a bridging stimulus provides immediate communication. The bridging stimulus was often followed by a food reward so that the animal was ready to repeat the behavior (Skinner 1951). Cetaceans and pinnipeds, active and alert, readily responded to operant conditioning. This allowed us to have animals working with us while swimming freely in the open sea.

In early 1964, Deborah Duffield came to work with me. We began training a bottlenose dolphin we called "Tuf-Guy" (later shortened to "Tuffy") for diving studies in the open ocean (for details see Ridgway 1966*b*, Ridgway *et al.* 1969, Ridgway 1987). We began the training gradually by releasing the animal in Mugu Lagoon (Fig. S7) calling him to and fro using a strobe (ACR Model 4 C pilot rescue beacon) that made a repeated high-frequency click (Ridgway 1966*a*, *b*). The animal would respond to the underwater strobe from distances as great as 500 m (Ridgway 1966*b*).

The dolphin obviously had great sensitivity to high-frequency clicks. We marveled at his ability to recognize small objects in the turbid, visually near-opaque waters of Mugu Lagoon. Debbie trained Tuffy to accept suction cup blindfolds, a method we copied from Ken Norris (see Norris *et al.* 1961). Blindfolded, Tuffy readily swam through a maze of hoops in our main pool at Point Mugu. Scott Johnson had an even more impressive echolocation demonstration. Blindfolded, his bottlenose dolphin "Salty" could find and retrieve an ordinary vitamin pill from the bottom of his tank.

Another great leap forward was produced by C. Scott Johnson (a Ph.D. in nuclear physics) who was training a Bottlenose dolphin for the first audiogram (Johnson 1966, 1968). As health officer I wanted to do periodic physical examinations on each animal. I checked the animal all over, looked in its mouth, listened to the chest with a stethoscope, and took a blood sample for analysis. At first we had to catch the animal and do the exam out of the water. In 1964, Scott Johnson had his dolphin trained to cooperate so the physical could be done in the water (Fig. 1). The training of these "medical behaviors" was very useful to me and, more importantly, it made the procedures much easier on the animals. A few years later our Navy program helped found the International Marine Mammal Trainers Association and through these member trainers Scott Johnson's example spread through the marine mammal community. Killer whales, *Orcinus orca,* white whales, *Delphinapterus leucas,* bottlenose dolphins*, Tursiops truncatus,* Pacific white-sided dolphins, *L. obliquidens,* and California sea lions, *Zalophus californianus*, readily cooperate in all sorts of exams including phlebotomy, endoscopy, ultrasound, milk collection (Ridgway *et al.* 1995), and many other procedures (Ridgway 2008). These trained behaviors make the exams easier and safer for animals and people. In recent years this methodology has even migrated to the zoo community for use with animals such as pandas and elephants.

We had only worked with Tuffy in Mugu Lagoon when Deborah Duffield left to start graduate school at Stanford University in the fall of 1964 (Duffield was the first of four trainers that were primary with Tuffy; she was followed by Wallace Ross, Blair Irvine, and Bill Scronce). The open ocean release of Tuffy was not accomplished until later in 1964. By February 1965 we had an ocean pen (netted enclosure anchored about 100 m off shore of Point Mugu).

We established a buoy in 600 m of water about five miles off Point Mugu. Daily the dolphin would follow our boat out to the buoy where we could tie up and put

Figure 1. In 1964, Physicist, C. Scott Johnson, had his auditory research dolphin "Salty" trained so that I could do a complete physical examination in the water with cooperation of the dolphin. The stethoscope is not in my right ear. The left one has always worked better (U.S. Navy photograph).

down a diving test switch. On our trips to sea, I was surprised to see that the dolphin immediately positioned on the stern wave of our boat, getting somewhat of a free ride by surfing most of the way out to the dive site (proof of this dolphin energy conservation was provided by Williams *et al.* 1992). Sometimes, when there were large waves at the dive site, we were delighted to watch Tuffy break off and entertain himself for a few minutes by riding these large waves. I wondered how this natural surfing ability had developed. Over the years, watching many dolphin mothers and calves, I realize that the dolphin starts to attain the surfing ability soon after birth as it positions to ride the pressure wave of the mother's larger body moving through the water.

Five days each week, Tuffy lived in a netted enclosure just off shore. Daily, we released him for open ocean diving tests and work with human divers. On Friday afternoon, he followed us back through the mouth of Mugu Lagoon to be lifted into our main concrete pool. There he spent the weekend socializing with other dolphins in the program until returning to work at sea on Monday morning.

The human diver work came first. One of the original seven Mercury astronauts, M. Scott Carpenter, transferred to underwater work. He joined Navy aquanauts in the Sea Lab II program. A habitat had been put on the ocean bottom at 63 m depth. Diver aquanauts would spend 45 d living in the habitat, equilibrated to the sea's pressure, and exploring the sea bottom off La Jolla California near Scripps Institution of Oceanography during the fall of 1965. I accompanied the dolphin as we flew down in a helicopter to work with the Aquanauts. A floating enclosure was built in the area to house Tuffy between jobs. After a brief period of adaptation, the dolphin worked well with the aquanauts. The dolphin made dives down to the area of the habitat to deliver tools, carry rescue lines, and provide communication (see Wood and Ridgway 1967, Ridgway 1987; Fig. S8). Thus, in the fall of 1965, we showed for the first time that a dolphin could work with humans while free and untethered in the open sea.

After Sea Lab, there were many requests for the services of our dolphins. Tuffy participated in the recovery of missile cradles, and drill mines, and other expensive objects from the ocean bottom (to see examples of what dolphins do in recent times visit the NMMP website at http://www.spawar.navy.mil/sandiego/technology/mammals/). In between these jobs, the dolphin was available for our research. He surfed beside our boat to the buoy tethered in deep water. We had the dolphin dive and press a switch at the end of a cable. On his return to the surface, the dolphin exhaled into an underwater funnel so that we could analyze his breath after dives and after similar periods of breath holding near the surface (see electronic supplement, pp. 13–15, Fig. S9).

John Kanwisher came out from Woods Hole to work with us, especially on breath analysis. We had several questions that the dolphin helped us answer. Seals, especially fat ones, tend to exhale before diving. This last exhalation has been considered as a protective mechanism for prevention of nitrogen supersaturation on deep dives. Although it had been considered that dolphins might exhale before diving to limit the amount of nitrogen absorbed in the tissues, two independent studies in the 1960s showed that dolphins take a deep breath before leaving the surface and dive with lungs full (Norris *et al.* 1965, Ridgway *et al.* 1969). Norris *et al.* also observed that the dolphin dived frequently without extended surface intervals. We (Ridgway *et al.* 1969) measured the amount of air in the dolphins lungs, showed that they dive with lungs full, and exhaled breath analysis revealed that the lungs are fully collapsed (no gas exchange in alveoli) below about 100 m. The dolphin dived at about 3 m/s to the end of our cable-suspended dive test switch at 300 m depth. We arranged a camera system that allowed the dolphin to take his own picture as he pushed a plunger on our diving test switch. Thus we got good photographs of the dolphin's thoracic collapse at a depth of 300 m (Fig. 2). Watching the dolphin diving in the open ocean gave John Kanwisher and me more perspective on the importance of cetaceans in the marine ecosystem. "One feature of gross nutrient dynamics is upwelling: the lifting of nutrients from deep waters such as that accomplished by rising currents off southern Africa in the Atlantic and off South America in the Pacific. Cetaceans play an analogous role on a surprisingly large scale.... Tied to the surface by their air breathing, marine mammals tend to move nutrients upward. Even the whale's fecal output does not move downward: because it is liquid, it tends to disperse rather than sink when it is released" (Kanwisher and Ridgway 1983).

With breath analysis and photographs of thoracic collapse in a dolphin diving freely in the open ocean, we had confirmed the calculations of G. C. C. Damant (1934) who wrote "the air in the whale's lungs must stand at the same pressure as the water outside the thorax. At 100 m the total pressure is about 11 atmospheres

Figure 2. Dolphin presses the dive test switch at 300 m triggering a photograph showing thoracic collapse that is especially evident behind the flipper (U.S. Navy Photograph).

absolute, so at that depth, the whale's lung is compressed until an average alveolus has only one eleventh of the volume it had when the whale left the surface and began to dive. This shrinking of the alveoli must greatly decrease the surface available for diffusion and, in addition, the epithelium of the alveolus must become thicker, still further hindering diffusion. The effect of these changes is to obstruct the entrance of excess nitrogen into the blood when the whale is at considerable depth."

On single deep dives, alveolar collapse appeared to be a sufficient explanation of why dolphins have no problem with nitrogen bubbles or bends (Ridgway *et al.* 1969). Air exchange was prevented by alveolar collapse below a certain depth. However, published observations showed that, while feeding, dolphins might dive in bouts returning again and again to depth with very short surface intervals (Norris *et al.* 1965, Evans 1971). We were able to revisit this question about multiple dives with short surface intervals with two trained dolphins in the mid-1970s. First, our laboratory was moving to San Diego in 1970 to be near the submarine Navy. During this move, I had an opportunity to study at Cambridge University.

Discoveries on Seal Physiology

In 1970, to forward an interest in neurobiology, I was awarded a fellowship to study at Cambridge University in England from 1970 to 1972. We built seal pools atop Professor Harrison's Anatomy Department in Cambridge. Icelandic farmers donated gray seals for the studies. Icelandic Air flew the seals to England. After the seals were accustomed to living in our fourth floor pool (see electronic supplement, p. 20, Fig. S14), we anesthetized and surgically implanted the seals with transmitters to broadcast physiological data. The implants built by Peter Joyce in the Cambridge Physiology Department, had a magnetic locking reed switch. It could be turned on or off by passing a magnet over the skin. After the surgical incision had healed, the transmitter was activated. The transmitters remained in place for a year or more. During prolonged observation periods, electroencephalogram (EEG), electrooculogram (EOG), electrocardiogram (ECG), and eye movements could be recorded continuously. Using these transmissions, we studied seal response to sound, their control of heart function, and their sleep (Harrison *et al.* 1972, Ridgway *et al.* 1975*a*, Ridgway 1976).

Response to sound: Hearing in young gray seals—We presented tone pips of 100 ms to seals to assess their hearing both in water and out. The EEG was averaged for 500 ms after each of 100 tones using a computer of averaged transients (CAT). The CAT produced a record of the response evoked from the seal's nervous system. By reducing the amplitude of the tones in stepwise fashion, we could determine the seal's hearing threshold at different frequencies (Ridgway and Joyce 1975). Seals could hear better underwater than in air. Sensitivity was greater under water and the frequencies of best hearing sensitivity were roughly eight times higher (4 kHz in air and 32 kHz underwater). These results were similar to results of behavioral audiograms in air and in water of common seals *(Phoca vitulina)* recorded by Bertel Møhl (1967).

Gray seal heart function—Whenever a seal's transmitter was turned on the ECG was transmitted continuously. This allowed us to link heart action with seal behavior (Harrison *et al.* 1972, Ridgway and Joyce 1975). The bradycardia or heart rate slowing of aquatic animals has been studied for more than 100 yr. As a well known example, when Scholander (1940) submerged a seal strapped to a board, he observed in the ECG "an immediate decline from a frequency of about 150/min to 10/min, in other words, down to one-fifteenth. The sudden transition, as of an inhibitory shock, with a heart pause of 12 s . . . points distinctly to the reflex nature of the onset of the bradycardia . . .[and further on another occasion when the seal was restrained underwater but, unlike the previous experiment, could stick its nose up for breaths] We see that total submergence of the animal does not necessarily induce bradycardia. On the other hand a grip on the neck, indeed a mere threatening movement of the hand over its submerged head, was sufficient instantaneously to bring about the bradycardia."

I wanted to test the facultative component of bradycardia without any restraint or handling of the seal. We built a large glass observation tank where the seals were free to swim about. The tank was completely filled with water but with a small breathing hole that I could plug at will to eliminate the seal's access to air (see electronic supplement, p. 21, Fig. S15). A surprise awaited me the first time I plugged the seal's breathing hole. The seal appeared to inspect the plug for a minute or two, then it exhaled under water a large bubble of air (250–1,000 mL), which remained beneath the tank's glass ceiling. On exhaling, the seal's heart rate rose momentarily as during other exhalations under water. The seal then settled to the bottom of the tank. The heart rate was very slow, only 3 or 4 beats per minute (bpm). After a minute or two, it returned to the bubble it had exhaled, still beneath the glass, and, with an amazing deftness of one nostril, sucked it in almost entirely again with an increase in heart rate (Harrison *et al.* 1972, Ridgway 1976).

It was not until this behavior of exhaling under the glass ceiling and then re-breathing the exhaled air had been observed in three of the seals that the possible significance of this behavior came to mind. Such behavior might be of value to seals making prolonged shallow dives under ice, since carbon dioxide would rapidly diffuse from the exhaled air bubble into the seawater allowing the seal to unload some carbon dioxide. I dubbed this "gill" behavior since it might allow the animal to make some direct respiratory exchange with the seawater. Some populations of gray seals do spend time on and around ice. Although gray seal-under-ice-behavior has not been studied, it is known that Weddell seals (*Leptonychotes weddellii*) can swim long distances under ice from one breathing hole to the next (Kooyman 1968). Our seals were captured on Icelandic shoreline as pups only a few weeks of age. It is unlikely that they had under ice experience. For the "gill" behavior I observed to be innate suggests that the behavior must be important to the survival of the species.

I initiated a warning buzzer to signal the seal that the breathing hole would be blocked. The seal would rush to store air under the glass roof of the pool. Because the storing and re-breathing of air complicated the heart responses, I installed stopcock ports to release the stored air. I shall always remember the reproachful look of the seal as I stole his stored air!

Eventually seals gave up on storing air. One thing was clear after that, simply sounding the warning buzzer resulted in an immediate reduction of the heart rate to as low as 3 or 4 bpm.

Gray seal sleep—When we turned on the implanted telemetry, we could observe seal, EEG, ECG, and eye movements (EOG) over a 24 h period or more. During most of this time, observers were out of sight and the seals were left to their own devices. Twelve overnight 12 h observations were made on four different seals. These observations confirmed that seals can be fast asleep, with slow wave EEG, while resting on the bottom. Only slow wave sleep (SWS) occurred when the seal was resting on the bottom. The sleep of seals differed from the sleep of man and other terrestrial animals studied in several ways in that (1) sleep took place in water as well as out; (2) rapid eye movement sleep (REM) usually preceded SWS in the sleep cycle, whereas in terrestrial mammals REM usually follows a period of SWS; (3) REM sleep was accompanied by a rapid and steady heart rate, whereas in terrestrial mammals ECG is irregular during REM. REM sleep always occurred when the seal was resting at the surface or hauled out; never under water. We concluded that these seals may have evolved some modified sleep mechanisms for coping with their ocean environment while maintaining the need to sleep (Ridgway *et al.* 1975*a*).

Our work with seals at Cambridge got some unwanted attention when musical students in Downing College across the road learned to chorus with the seals at night. Horns would blow. Seals would respond "Woo" "Woo." These exchanges could go on for considerable periods. There were rumors that seals were being tortured late at night. I found no evidence that the seals regarded the student bugling as torture—my EEGs were proof that individual seals slept well. Probably both parties derived some amusement from the chorusing. Despite neighborhood noise complaints, we finished our seal studies in 1972. However, live seals were never again allowed in Cambridge.

Conditioned Bradycardia in Sea Lions

In San Diego, in 1973, I wanted to see if bradycardia could be trained. Don Carder, then a graduate student, built transmitters that we implanted in California sea lions to monitor their ECG. The sea lions were out of the water and dry. Carder gave a signal "down" and placed his hand on the floor. The sea lion placed its nose against his hand. By rewarding longer breath holds, periods of apnea were increased to 3 min or more. With simple apnea, the heart rate decreased from about 120 bpm to a range of 25–40 bpm.

Another sea lion, with no previous training, was conditioned to reduce its heart rate by gradually rewarding slower rates. Normally the sea lion's heart rate cycled between a high of 100–140 bpm during breathing and a low of 60–90 bpm during intervals between breaths. The animal's transmitted heartbeat was received on a radio broadcasting a "beep" with each beat to the trainer and to the animal. The trainer sounded a tone, and then, when the rate slowed, he sounded a police whistle as a bridge to alert the animal of the coming reward. Criteria for reward were gradually lowered until the sea lion reduced its heart rate to a range of 10–15 bpm for three beats (Ridgway *et al.* 1975*b*).

To compare conditioned bradycardia with immersion bradycardia, we repeated Robert Elsner's sea lion experiments in which he trained an animal to immerse its head in a pail of water. Our results were similar to those of Elsner *et al.* (1964). Head immersion was followed by reduction to 25–40 bpm within a few seconds.

Conditioned periods of apnea, nor head immersion in water, produce bradycardia as marked as that of the sea lion trained to reduce its heart rate. The marked reduction in heart rate that is often called diving bradycardia can be under voluntary control. It may be produced by various stimuli including fright. However, immersion in water is not necessary for the response. The physiological characteristics termed the "diving response" represent more global phenomena occurring in reptiles, birds, and fish (Gaunt and Gans 1969, Kanwisher *et al.* 1974, Gabrielsen *et al.* 1977) that in evolutionary terms long precede marine mammals. Of course aquatic mammals have perhaps made more use of this ancient physiological mechanism than any other group.

In the mid-1970s Alveolar Collapse and Nitrogen Uptake Revisited

We took advantage of an opportunity to have dolphins make frequent dives with a very short surface interval. These dive bouts emulated some observed in wild dolphins at sea (Evans 1971). Our two trained dolphins made 23 and 25 dives, respectively to 100 m in less than one hour at a dive site off San Clemente Island about 70 miles west of San Diego. Immediately on surfacing from the last dive in the series the dolphins beached onto a pad in our boat. I inserted a special Teflon membrane probe into the dorsal epaxial skeletal muscle for measuring nitrogen partial pressure in the muscle (see electronic supplement, Fig. S10). From the regression of the nitrogen values it was determined that on surfacing from the last dive the two dolphins had nitrogen supersaturation of 224% and 276%, respectively, of normal surface values (Ridgway and Howard 1979). These dolphin dive schedules are in excess of those known to produce decompression sickness in breath hold diving humans (Paulev 1965, Ferrigano and Lundgren 2003). However, our dolphins showed no signs of ill effects and no evidence of decompression sickness.

Anesthesia Research Led to Interest in Hearing

Keeping the animals healthy over many years required safe and effective anesthesia (see electronic supplement, pp. 17–18, Fig. S11). Anesthesia was also essential for some planned research. My anesthesia research (Ridgway 1965, Ridgway and McCormick 1967) enabled collaborations with pioneers in hearing and neurobiology. A dolphin pool was built at Princeton University. Surgery on the ear with James McCormick and Glenn Wever helped to elucidate dolphin sound conduction (McCormick *et al.* 1970).

At Point Mugu, I came to appreciate bioacoustics and psychophysics with mentors such as Bill Evans, C. Scott Johnson, and Ronald Schusterman (Ron often came down from SRI in the San Francisco Bay area of California). Robert L. Brownell, Jr. was a frequent visitor to Point Mugu in the 1960s. He often came along with David and Melba Caldwell from the Los Angeles County Museum. Already a circuit riding cetologist, Bob Brownell has to this day been a knowledge resource about worldwide cetology. In the late 1960s when I decided to edit a book, Bob was helpful (Ridgway 1972). Later, when Professor Harrison assigned me *Handbook of Marine Mammals* (Ridgway and Harrison 1981*a*, *b*, 1984, 1989, 1994, 1999), Bob was also very helpful along with Steven Leatherwood, G. Carleton Ray, William F. Perrin, Randall R. Reeves, and others.

The Dolphin Brain

No area of science is more challenging, and of greater significance, than trying to unravel the secrets of the brain and nervous system. With Professor Theodore Bullock, of the University of California in San Diego, we recorded from some auditory areas of the dolphin brain. We found separate brain centers. One for pulse sounds used primarily for sonar and another for whistle sounds used primarily for social communication (Bullock and Ridgway 1972). Sound from the ocean travels through the dolphin's lower jaw to the ear (McCormick *et al.* 1970). The large dolphin brain is the central processing computer. The auditory parts of this computer sort out signals from the ear. From observations of dolphin capability, we adduce that they must be turning neural impulses into picture-like images. To understand these brain processes is a great challenge of dolphin neurobiology.

To understand the living dolphin brain, I often worked with postmortem brains. These brains were not only from natural mortality in our own herd. Many brains were shared from my colleagues such as Lanny Cornell, Thomas Reidarson, Judy St. Leger, Les Dalton, Michael Walsh, and James McBain. This gave me the opportunity to examine massive brains from killer whales and false killer whales (*Pseudorca crassidens*). I received many brains of many different species from stranding networks through the good graces of NOAA Fisheries colleagues such as Al Myrick and William Perrin in California and from Forrest Townsend, Scott Wright, and Daniel O'Dell in Florida. James Mead and Charles Potter of the Smithsonian, always helpful with all kinds of pieces and parts, contributed to my brain collection. Thomas Albert and North Slope colleagues sent me brains from some bowhead whales. I regret that many results from these valuable specimens are still unpublished. However, a good deal of information has been published (*cf*. Ridgway and Brownson 1979, 1984; Ridgway 1986*a*; Ridgway *et al*. 1987; Demski *et al*. 1990; Tarpley and Ridgway 1994; Tarpley *et al*. 1994; Ridgway and Tarpley 1999; Manger *et al*. 1998, 2003, 2004; Marino and Ridgway 1999; Marino *et al*. 2000, 2001; Ridgway *et al*. 2002; Poth *et al*. 2005; Oelschläger *et al*. 2008, 2010).

Dolphin brains are large and more highly convoluted than other mammals including humans. The surface area of the cerebral cortex is large but the cortex is thin. The total volume of dolphin cortex is larger than that of chimpanzees and other higher primates, but only about 80% of that of humans. Compared to the human brain the dolphin brain has more white matter with larger conductive axons. Larger axons conduct nerve impulses faster. Brainstem transmission time is faster in dolphins than in humans (Ridgway *et al*. 1981). This is probably very important for a fast swimming animal finding prey by echolocation in water.

Anatomical and physiological findings have given me an impression of why the dolphin brain is so large. Detailed echolocation discrimination over long distances in the ocean required expansion of the cerebral cortex, cerebellum, and midbrain auditory centers. Detailed organization of auditory cortex described for owls (Knudsen and Konishi 1978) and bats (Suga 1984) may be even more complex in dolphins. For fine echolocation discrimination at meaningful range in water, the dolphin brain must map an extensive surrounding area of the environment with specific acoustic parameters. According to Suga (1984), mustached bats map an area of only about three meters. Target distances of 50–140 cm are best represented in bats. Dolphins with echolocation ranges of hundreds of meters must have a relatively huge brain map of their surroundings. Compared to the air environment of the bat, the water environment of the dolphin conducts sound more than four times as fast. Neurons performing equal echo delays of X ms will represent Y m in a bat in air but 4.5 Y m in a dolphin under water. Dolphins perform distance and azimuth discriminations even finer than bats (Bullock and Gurevich 1979). Specific neurons forming axes or coordinate arrangements may take up considerable space in the cortex and could be a major reason for the great expansion of the auditory areas of the dolphin brain (Ridgway 1986*b*) and the larger connecting axons. The dolphin brain is specialized for rapid, precise processing of auditory information and correlation of this information within its group and the ocean environment.

Compared to the human, the dolphin brain has more white matter relative to gray matter. The dolphin cerebellum is a larger portion of the brain. The corpus callosum connecting the two brain hemispheres is quite small. Blood supply to the two dolphin hemispheres is separate. This separate blood supply facilitates sleep with one hemisphere while the other hemisphere is awake. Auditory areas of the dolphin brain are massive compared to similar sized human brains. The dolphin brain is the central processing computer for a phenomenal echolocation ability that depends on the auditory sense. Their cooperation in complex tasks in tanks and in the open ocean has revealed that dolphins are quick animals. Understanding how the dolphin brain coordinates these typically mammalian, yet uniquely sized and arranged components is one of the great challenges of neurobiology.

Dolphin Far Field Brain Responses

With Professor Bullock, David Woods, and Robert Galambos (Ridgway *et al.* 1981, Ridgway and Carder 1983), we studied dolphin far field auditory brainstem responses (ABRs). These ABRs correlated well with the direct brain responses we observed several years before (Bullock and Ridgway 1972). ABRs might offer a way to test hearing in large whales. David Woods helped us find another very interesting brain response (Woods *et al.* 1986) Sometimes called the "ah ha" response in human studies, dolphins also showed an event-related brain potential. We thought the "ah ha" response might offer a "window on the dolphin mind." With the technology and non-invasive methods available today these event-related brain potentials offer fertile areas for scientific discovery.

Raymond Tarpley, who was a key person in founding the Texas Marine Mammal Stranding Network, accompanied Don Carder and me to Sea-Arama Marine World in Galveston, Texas. A sperm whale neonate (*Physeter macrocephalus*) stranded at Sabine Pass in September of 1989 and was moved to a concrete tank in Galveston for rehabilitation. During the middle of several nights, we were allowed to spend some time in the water with this neonate to record sounds and to test his hearing. We divided sounds produced by the sperm whale neonate into two categories. Clicks had peak frequencies of 500 Hz to 12 kHz (two classes, low and high) and grunts had energy below 3 kHz. ABR assessment of hearing abilities indicated that the neonate was most sensitive to sounds between 5 kHz and 20 kHz, but surprisingly, the calf could hear sound to at least 60 kHz (Ridgway and Carder 2001; see electronic supplement, Fig. S12–S13.).

I got a chance to explore the auditory capacity of another deep diver when my friend and colleague, Joseph Geraci, called one day. There was a young *Kogia* at the National Aquarium in Baltimore, Maryland. The animal had stranded a few months before. Plastic bags and other debris impacted his stomach. Treated at the Aquarium and now rehabilitated, there were plans to release the animal, "Inky," back into the Gulf Stream. "Inky" (see electronic supplement) had never produced any audible sound. Could he be deaf? Joseph suggested we test. Don Carder flew out with me and our considerable baggage of equipment for testing hearing and sound production. We were surprised and delighted when we put our broadband hydrophone in the pool with "Inky." We detected rapid, narrow band, high frequency pulses around 125 kHz. The animal was producing volumes of sound but at frequencies well above the human hearing range. We found the animal's hearing matched his pulses with best sensitivity from 90 to 150 kHz (Carder *et al.* 1995, Ridgway and Carder 2001). A healthy "Inky" was placed back into his natural environment (Scott *et al.* 2001).

We have continued to use far field responses recorded from the dolphin head to assess animal hearing. This has greatly improved the diagnosis of hearing impairment. Prototype field methods (Ridgway and Carder 1983, 1997, 2001) were large and cumbersome; however, my colleague, James Finneran, developed a rugged, portable system to replace the considerable baggage we had previously carried. His portable system can be used to rapidly test hearing in marine mammals. Finneran's system, called EVREST, is based on a laptop computer. The computer runs software that Dr. Finneran developed. A trained operator with this system can rapidly do audiograms at distant marine parks or on beaches where whales or dolphins have stranded (Finneran 2009, Finneran *et al.* 2009).

Marine Mammal Hearing and the Effects of Human Generated Sound

Because hearing is crucial for echolocation and communication, the problem of deafness is a special concern for dolphins. Our colleague, Darlene Ketten at Harvard University and Woods Hole Oceanographic Laboratory examines marine mammal ears to pin down the anatomical signs of hearing loss and deafness. After Don Carder and I found a dolphin that was deaf and mute, we also found several older animals, mainly old males that had lost high-frequency hearing (Ridgway and Carder 1997). We sent the ears to Ketten. She has found numerous potential causes for ear damage including severe infections such as meningitis that can cause deafness even before birth. Parasites, especially flukes, and certain medications can also cause hearing loss (Finneran *et al.* 2005).

Deafness or high-frequency hearing loss can result from exposure to loud sound. In recent years, concerns have arisen about human-generated sound in the ocean—especially high-powered sonar. National Research Council committees were convened to assess this issue. Colleagues on the earliest of these committees, especially Dennis McFadden, urged collection of marine mammal data on temporary threshold shift (TTS) (Green *et al.* 1994). With my associates Don Carder, Wesley Elsberry, and Carolyn Schlundt, among others, we set out to collect such data to establish acoustic safety criteria. We reasoned that animals exposed to sound levels at or below the TTS level could not be injured by sound. Soon we were joined by James Finneran who has greatly expanded this work (see Ridgway *et al.* 1997, Schlundt *et al.* 2000, Finneran *et al.* 2000).

Dolphin Half-Brain Sleep and Vigilance

When I arrived in San Diego from Cambridge in October of 1972, I immediately began plans to study dolphin sleep with the transmitters we had used with the gray seals (Ridgway and Joyce 1975, Ridgway *et al.* 1975*a*). James McCormick (1969) observed dolphins at Point Mugu sleeping quietly at the surface with both eyes closed. John Lilly (1964) had proposed that dolphins sleep with one eye closed at a time, a monocular strategy in order to "assure that the animal is always scanning his environment with at least half of its afferent inputs." Further, Serafetinides *et al.* (1972) working in Robert Elsner's laboratory at nearby Scripps Institution of Oceanography in La Jolla, California had discovered some interesting EEG asymmetries in a brief study of a pilot whale. Behavioral and physiological observations including EEG were needed.

We had made some progress on such comprehensive dolphin sleep studies by June of 1974 when Bill Evans and I traveled to Moscow for the 1st International Theriological Congress. There we were treated to delightful intellectual exchanges in addition to the hospitality of Alexei Yablokov and many other Russian scientists. Senior Russian scientist, A. G. Tomilin, shook Bill Evans' hand declaring "It is a privilege to meet a classic in his own time!"

A surprise awaited us with a visit to Lev Mukhametov in Moscow. He was well ahead in dolphin sleep studies. He showed EEG data on multiple Black Sea bottlenose dolphins, clearly showing that the animals could alternate sleep from right hemisphere to left and *vice versa* (see the review of cetacean sleep by Lyamin *et al.* 2008). In San Diego, I had similar data but in only one dolphin. I did not publish a complete paper on my dolphin sleep studies until much later (Ridgway 2002).

So if a dolphin (or whale) can sleep with half a brain, what is the waking half doing? Can half-brain sleep allow dolphins to remain continuously vigilant? I got an opportunity to delve into some of these questions when Allen Goldblatt came to do a sabbatical with me. In the first study, we learned that dolphins could maintain a very high level of auditory vigilance for five continuous days (Ridgway *et al.* 2006*a*). In a second study, we found that dolphins could perform very well on a nighttime visual cognitive task during the five days of continuous vigilance (Ridgway *et al.* 2009).

Dolphin Reproduction

A major advance was achieved in 1975 with the Dolphin Breeding Workshop, supported by the Marine Mammal Commission and the Zoological Society of San Diego (Ridgway and Benirschke 1977). This workshop set the course for a self-sustaining population of bottlenose dolphins in North American facilities (see Ridgway 2008 for a picture of the attendees). This was followed by another productive workshop that solidified progress (Duffield and Robeck 2000).

For reproduction to take place, animals must be healthy. In order to diagnose disease, dolphins are trained to volunteer to cooperate in collection of blood samples, urine samples, fecal samples, milk samples, semen samples (Schroeder and Keller 1989), and skin scrapings from our marine mammals. One of our trainers, Tricia Kamolnick, made an important advance developing a milking device for use with dolphins. She trained female dolphins to accept milking (see Ridgway 2008). Trained lactating dolphins present ventrally at the side of the pen. One trainer supports her to keep the mammary slits out of the water. Meanwhile, the other trainer rinses the skin and mammary slit area with distilled water and applies a specially constructed suction cup pump; then the trainer collects 3–25 mL of milk rapidly. Freezing milk at −70°C allows for future analysis. We can determine nutritional value, secretion of medications, and evaluate health.

Female dolphins, even those that had never had an offspring, will sometimes lactate to nurse an orphan calf (Ridgway *et al.* 1995). Both of these advances were helpful because at times a female will not nurse her own calf. Milking can obtain the early colostrum (first milk or immune milk) that contains the protective immunoglobulins, rich nutrients, and other substances essential for protecting the offspring in early life. Feeding this essential milk supports the orphan until another female begins lactating to nurse the calf (Ridgway 2008).

Two older female bottlenose dolphins in their 30s, not lactating and reproductively senescent at the time, re-lactated within one week of their introduction to orphan calves. It is interesting to consider a possible role for induced lactation in free-ranging cetaceans. Old short-finned pilot whale females (*Globicephala macrorhynchus*) have been observed lactating even 10 yr after their last parturition (Kasuya and Marsh 1984, Marsh and Kasuya 1986). These observations have been interpreted as an extension of lactation from the last parturition in these reproductively senescent females. Our observations on bottlenose dolphins suggest another possibility—these older short-finned pilot whales may have re-lactated in response to suckling from calves produced by younger females. Rapid re-lactation to assist in rearing offspring within the herd may be a major benefit provided by these postreproductive females.

Can the Dolphin Tell Us Where It Hurts?

The famous American actor, writer, commentator, and philosopher of the 1920s and 1930s, Will Rogers, once said, "The best doctor in the world is the veterinarian. He can't ask his patients what is the matter—he's got to just know." I have indeed wondered if we could improve on that situation by just listening to the dolphins for a long time through hydrophones mounted in their pools with the sound piped into my lab/office. Serious people often remarked, "What is that racket!" Bioacoustician Don Carder, and Sue Moore, then a student at San Diego State University, helped me to record and analyze many 24 h recordings of "that racket." We have made some progress. We found that female dolphins keep relatively quiet during their period of ovulation (Moore and Ridgway 1996). Because females are more receptive to the male during the period of ovulation, perhaps a quiet female dolphin can be more alert and selective of males!

Presenting Questions to the Animals

From our earliest work at Point Mugu we were always asking questions of our animals. We got their cooperation in asking: How deep can you dive? (Ridgway 1966*b*, Ridgway *et al.* 1969, 1984, Ridgway 1986*c*). How fast can you swim (Lang and Pryor 1966)? How fine a discrimination can you make with your echolocation? (Evans and Powell 1966). One of the great "operant conditioners" who, from the

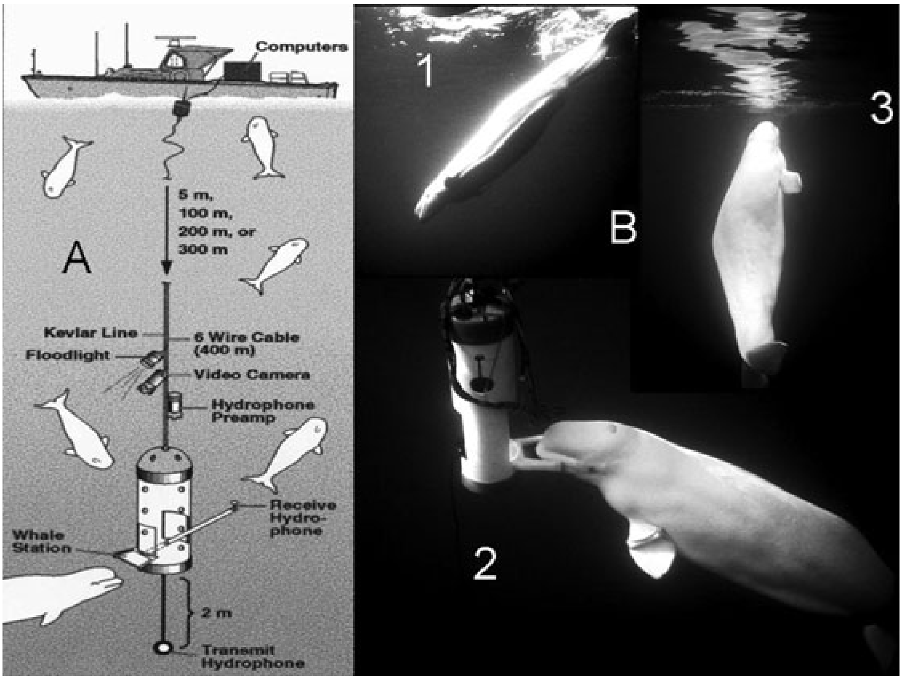

Figure 3. A. Schematic drawing of apparatus and procedure for testing white whale hearing in the open sea and at depth. Trained whales followed our boat a few miles offshore of San Clemente Island, California. A test platform with lights, video, sound projector, and hydrophones were lowered to a predetermined depth of 5, 100, 200, or 300 m. On a signal from the trainer in a boat at the surface, a whale dived down (B1) and stationed on the test platform (B2), a random set of hearing test sounds were initiated from a computer on the surface boat (A) and projected 2 m below the whale's ears. Each time the whale heard the sound it whistled and another lower level sound followed. In step-wise fashion sound was presented. Lower until the whale no longer responded, then higher until the whale whistled in response within 2 s. After a series of these steps in sound intensity, the trainer sounded a bridging stimulus and the whale returned to the surface for food reward (B3). Note that the whale approaches its own reflection as it returns to the surface. Depth did not influence hearing threshold (Ridgway *et al.* 2001) (U.S. Navy photograph).

earliest days at Point Mugu, was clever in getting animals to "enjoy" cooperating with us was Bill Scronce (see electronic supplement, p. 23, Fig. S17).

With the availability of faster computers in the 1980s, it became possible to interact with the animals on a more reasonable time scale of milliseconds rather than seconds. We trained dolphins and white whales to respond by whistling or burst pulsing to different computer generated sounds so that acoustic response times could be measured and behavioral audiograms could be collected more rapidly (Ridgway and Carder 1988, Ridgway *et al.* 1991, Ridgway and Carder 1997). This methodology allowed for the first audiograms collected in the open ocean at depths up to 300 m (Ridgway *et al.* 2001, Fig. 3). It also allowed us to chart the time course between echolocation and response to a target that the animal recognized (Ridgway and Carder

1988). This ability to have dolphins rapidly interacting with computer programs to carry out response paradigms has greatly facilitated behavioral audiometry and TTS measurement (Ridgway *et al.* 1997, Finneran *et al.* 2000, Schlundt *et al.* 2000). Additionally, the dolphin's response time gives a good idea of the animal's perception of stimulus strength allowing a better comparison of different acoustic or visual stimuli (Ridgway and Carder 1997, 2000; Ridgway *et al.* 2009).

Studying the Dolphin Brain with PET, SPECT, CT, and MRI

Another potential "window on the dolphin mind" appears with the use of modern scanning technology. With the help of collaborators, especially Dorian Houser and Carl Hoh we initiated the study of dolphin brain physiology with positron emission tomography (PET) and single-photon emission tomography (SPECT). These functional scans were augmented with computed tomography (CT) and magnetic resonance imaging (MRI). CT and MRI reveal more detail in hard tissue and soft tissue anatomy. Often used in studies of human physiology and medicine, PET and SPECT are noninvasive technologies that permit direct assessment of regional glucose metabolism and blood flow. In human subjects, functional imaging has been used in diagnosis of disease, in studies of complex cognitive tasks, and in localizing areas of sensory activation, initiation of motor movement, and visual attention.

The dolphin brain is in the human size range but is more highly convoluted. Compared to human brains, the cortex is thinner, has less total cortical volume, and has more white matter to accommodate greater axon diameters. The dolphin cerebellum is 50% larger than the human cerebellum. Dolphins have a multi-tiered cerebral cortex with an extensive extra lobe, the paralimbic lobe. This lobe does not occur in mammals other than cetaceans. Because of its inaccessible location, there are no functional studies of the paralimbic cortex. Functional imaging offers an opportunity to study activity in this unique part of the dolphin brain during various stimulus conditions. Such studies might help reveal functional aspects of the paralimbic cortex, insular cortex, basal ganglia, cerebellum and other areas that have never been studied in the living animal (Houser *et al.* 2004, Ridgway *et al.* 2006*b*; see electronic supplement, p. 22, Fig. S16).

Being "There"

The fictional Forrest Gump often happened to be "there" for momentous events in the last half of the twentieth century. In my smaller, more specialized world of marine mammal science, events have often worked a little like that. The U.S. Air Force assigned me to California so I was "there" in 1961 to start work with Navy dolphins. I could mention many examples in the interim 48 yr, but a recent example stands out. I happened to attend a meeting in Hawaii with several experts on cetacean sonar and hearing. "There" on Oahu, with a group that included Bertel Møhl, Peter Madsen, Whitlow Au, Paul Nachtigall, and Alexander Supin, when a baby sperm whale stranded on Maui, we had an opportunity for testing hearing and the sound transmission path (Møhl *et al.* 2002). This again illustrated the Gump Effect: "Life was like a box of chocolates. You never know what you're gonna get."

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Rooster tails of two Dall's porpoises just off the bow of our boat near the Channel Islands, California in 1964. Dall's porpoises are fun to watch at sea. More than any other cetaceans, they seem to relish playing about the bow.

Figure S2. Debbie Duffield training a male Dall's porpoise at Point Mugu.

Figure S3. Dall's porpoise rests quietly while I inject in the central vessel of the tail fluke. I was surprised to find that Dall's porpoise, so energetic and active in the water, would lie quietly when out of the water on a soft pad.

Figure S4. from left to right, William E. Schevill, Kenneth S. Norris, and G. Carleton Ray, three of the key participants in the First International Symposium on Cetacean Research in 1963. The proceedings were edited by Norris (1966). Photo courtesy of G. Carleton Ray.

Figure S5. Organized mainly by Joseph Geraci a memorable tribute to William Schevill and Barbara Lawrence was held at Amelia Island Plantation, Florida, April 5–6, 1983. Back row, left to right: Carleton Ray, Al Vine, William Evans, Joseph Geraci, Sam Ridgway, Clayton Ray, Richard Backus, John Twiss, F. G. Wood. Seated: Mrs Vine, Mrs. Carr, Bill Schevill, Barbara Lawrence, Archie Carr, William Watkins.

Figure S6. A memorable meeting on physiology and bioenergetics in 1992 was sponsored by the Office of Naval Research and organized by Terrie Williams and Dan Costa. From left to right: Fish, Worthy, Williams, Davis, Ridgway, Ponganis, Gentry, Oliver, Taylor, Pabst, Friedl, Heath, Kooyman, Costa. Most of these "fools" have been stellar contributors to various aspects of marine mammal research."

Figure S7. Point Mugu Lagoon where our ocean training began. Arrow indicates Bioscience Facility with concrete dolphin and sea lion tanks. L = Point Mugu Lagoon proper. PO = Pacific Ocean.

Figure S8. Dolphin helper Tuffy with diver at SEALAB habitat at 63 m depth, September, 1965 off Scripps Pier, La Jolla, California.

Figure S9. Diagram of how dolphin Tuffy would dive on command to a test switch located at up to 300 m depth. After pressing the switch, the dolphin would exhale his breath into a water-filled funnel before surfacing to collect a fish reward.

Figure S10. Schematic of procedure from the study of Ridgway and Howard (1979). A. Dolphin dives to 100 m to press a test switch that has been lowered to depth. The process is repeated 23 to 25 times in 1 h. After the last dive, the animal slides onto a beaching pad (BP) on the boat at the surface. B. A probe is inserted into the dorsal epaxial muscle and connected to the mass spectrograph (MS) to measure nitrogen. On single deep dives, the alveolar collapse demonstrated in the Ridgway *et al*. (1969) study appeared to be sufficient explanation of why dolphins have no problem with nitrogen bubbles or bends since air exchange was prevented by alveolar collapse below a certain depth. However, published observations showed that feeding dolphins might dive in bouts returning frequently to depth with very short surface intervals (Evans 1971).

Figure S11. In this picture, the dolphin is anesthetized with a short-acting barbiturate that has been injected into the fluke vessels. I was not aware that my scowl was alarming my colleague (F). I (R) grimace as I insert an endotracheal tube so the dolphin could be maintained on gas anesthesia for a longer period. Norbert Flanigan (F), holding the dolphin mouth open with soft towels, appears alarmed by my grimace. James McCormick (M arrow), a graduate student of Professor E. G. Wever at Princeton came to work with me at Point Mugu in 1966. He was interested in the sound transmission path to the dolphin ear. We worked together on improving dolphin anesthesia and understanding the sound path. For modern cetacean anesthesia, see Dold and Ridgway (2007).

Figure S12. The author (with bald spot) assisted by stranding network volunteers and sperm whale neonate "Odie" during hearing testing with auditory brainstem responses (ABRs). A sensor in a suction cup is in the author's left hand. Attached to the whale's head, the sensor records the far field ABR responses from the whale's brain. The whale's ABRs at different frequencies are shown in the lower right. Although the largest responses were in the 10 to 20 kHz range, we were surprised that ample responses were present at 60 kHz.

Figure S13. A young *Kogia* dubbed "Inky" stranded and was rehabilitated by stranding network personnel after medical treatment by Brent Whitaker and Joseph Geraci. When Don Carder, Steven Murphy and I arrived at the aquarium in Baltimore and put in our high-frequency gear, we were surprised and delighted. The whale made numerous narrow-band high-frequency pulses in the 130 kHz range (panel upper right). Hearing sensitivity was best in the 90 to 150 kHz range. Later, the healthy whale was released back into the Gulf Stream.

Figure S14. A seal pool was constructed on the fourth floor of the anatomy building on Downing Site in Cambridge.

Figure S15. A large glass tank with a breathing hole was built for my experiments. A plug allowed me to block the seal's access to air. Plugging the breathing hole led to surprising results.

Figure S16. Two sides of the dolphin and the dolphin brain physiology may be viewed by functional scanning. MRI scans reveal anatomy. Different views of brain surface extracted from MRI are shown on the lower left. On the right a typical PET scan registered to an MRI shows areas of increased metabolism in the brain.

Figure S17. Bill Scronce is shown here at depth with dolphin Tuffy. Bill became an expert at applying operant conditioning techniques when our dolphins were in a concrete pool, in the open ocean at the surface, and even out at sea at depth as shown here.