1988

The Acoustical Function of the Lower Jaw of the Bottlenose Dolphin, Tursiops truncatus (Montagu), During Echolocation

Randall Louis Brill
Loyola University Chicago

Recommended Citation

Brill, Randall Louis, "The Acoustical Function of the Lower Jaw of the Bottlenose Dolphin, Tursiops truncatus (Montagu), During Echolocation" (1988). *Dissertations*. 2574.
https://ecommons.luc.edu/luc_diss/2574

THE ACOUSTICAL FUNCTION OF THE LOWER JAW OF THE BOTTLENOSE DOLPHIN, *TURSIOPS TRUNCATUS* (MONTAGU), DURING ECHOLOCATION

by

Randall Louis Brill

A Dissertation Submitted to the Faculty of the Graduate School
of Loyola University of Chicago in Partial Fulfillment
of the Requirements for the Degree of
Doctor of Philosophy

June

1988

ACKNOWLEDGMENTS

This research was funded by a grant from the Chicago Zoological Society and assisted by the Parmly Hearing Institute.

Additional assistance for which I am grateful was provided by staff members of the Naval Ocean Systems Center; Sam Ridgway made possible the loan of the Ampex recorder, Whitlow Au tested the neoprene materials, and Patrick Moore provided as much moral support as he did time and technical advice. I also wish to express my thanks to Earl Murchison and Norm Chun.

I am sincerely grateful to the trustees and staff members of the Chicago Zoological Society/Brookfield Zoo. I would particularly like to thank George Rabb, Penny Korhumel, Edith Duckworth, the members of SEACON, Ed Krajniak, Mary Rabb, Don Doubek, Joe Chabus, Rich Weissensel, John Buckley, Ed Hausknecht, Steve Stratakos, Pete Skach, Steve Piler, and Martha Bryant (who prepared this manuscript). I am especially grateful to the trainers who made this experiment happen; Martha "Marty" Sevenich, Tim Sullivan, Janet Sustman, Ron Witt, and Brenda Woodhouse.

The valuable assistance and support of the faculty and staff of the Parmly Hearing Institute is gratefully acknowledged with special thanks to Chuck Wheeles for building some of the audio components and Patrick Harder for providing the programming assistance necessary for signal analysis.

I would like to thank the members of my dissertation committee, Dick Fay, Toby Dye, Ken Norris, and Bill Yost, for their encouragement, support, and patience.

The influence and support of all of my friends and colleagues is gratefully acknowledged. I would especially like to thank my parents, my wife Sue, and my sons Dan and Jimmy for their love and understanding while this effort was in progress.

Finally, I would like to acknowledge the invaluable contribution of one very cooperative and patient dolphin, Nemo.

VITA

The author, Randall Louis Brill, is the son of Frederic Anton Brill and Mary Ann (Parizek) Brill. He was born on March 1, 1949, in Chicago, Illinois.

His elementary education was obtained at the Maternity of the Blessed Virgin Mary Catholic grammar school. His secondary education was initiated at Quigley Preparatory Seminary-North and completed at Weber High School in Chicago.

In September, 1967, Mr. Brill entered Northeastern Illinois University on an Illinois State Teacher's Scholarship and received a Bachelor of Arts degree in Secondary Education--Mathematics with a major in psychology in August 1971. In 1970, while attending Northeastern Illinois University, he was elected to membership in Psi Chi--The National Honor Society in Psychology.

Mr. Brill was a teacher of mathematics, science, and language arts at St. John Vianny School in Northlake, Illinois, from September 1971, to June 1975. In December 1974, he published an article entitled "A project for the low-budget mathematics laboratory: the game of Kalah" in the National Council of Teachers of Mathematics journal, Arithmetic Teacher.

In August 1975, Mr. Brill received a Master of Arts degree in Human Learning and Development--Interpersonal Psychology from Governors State University in Park Forest South, Illinois.

In August, 1975, he joined the staff of the Chicago Zoological Society--Brookfield Zoo to assume a position in the training and care of marine mammals including dolphins, seals, sea lions, and walrus and assumed the responsibility of head trainer in 1977. In August 1981, Mr. Brill was promoted to the senior staff position of Supervisor of Marine Mammal Training, the position he currently holds. During his career with the Chicago Zoological Society, Mr. Brill has been active in several professional organizations including the International Marine Animal Trainers Association, the Society for Marine Mammalogy, and the American Association of Zoological Parks and Aquariums. He is also a member of the Acoustical Society of America and the American Psychological Association.

Mr. Brill has authored several publications on the training, husbandry, and research of marine mammals, a list of which follows.

1977 Naturalistic behavior display for the sea lions (Zalophus californianus) at the Chicago Zoological Park. Proceedings of the Second Conference on the Biology of Marine Mammals (Abstract).

1978 Bucket...action...whistle...bingo! a look at training dolphins. Brookfield Zoo Bison, April/May.

Brookfield's Seven Seas Panorama: the first inland dolphinarium. Proceedings of the Annual Conference of the International Marine Animal Trainers Association, 1978.

1979 Love is 1800 pounds of walrus. Brookfield Zoo Bison, Dec/Jan.

1980 Can you see with your ears? Brookfield Zoo Bison, June/July.

A survey of the status of marine animal trainers in the United States and Canada. Proceedings of the Annual Conference of the International Marine Animal Trainers Association, 1980.

1981 R.I.R. in use at the Brookfield Zoo's Seven Seas Panorama: random and interrupted reinforcement redefined in perspective. Proceedings of the Annual Conference of the International Marine Animal Trainers Association, 1981.

An alternative to the consistent use of food as a reinforcer in the training of marine mammals. Proceedings of the Fourth Biennial Conference on the Biology of Marine Mammals (Abstract).

Proceedings of the Annual Conference of the International Marine Animal Trainers Association, 1981. J. Barry and R. Brill, eds.

Dolphin training does a flip. Brookfield Zoo Bison, Oct/Nov.

1982 Dolphin training does a flip--part II. Brookfield Zoo Bison, Dec/Jan.

The trainer's role in the environment of the captive dolphin. Proceedings of the Annual Conference of the International Marine Animal Trainers Association, 1982.

1984 Dolphins do not live by fish alone. Brookfield Zoo Bison, Feb/March.

1985 The jaw-hearing dolphin: a study in progress. R. Brill and P.J. Harder. Proceedings of the Sixth Biennial Conference on the Biology of Marine Mammals (Abstract).

1987 Evidence for an acoustical pathway to the inner ear through the lower jaw for an echolocating dolphin (*Tursiops truncatus*). R. Brill, M. Sevenich, T. Sullivan, J. Sustman, and R. Witt. J. Acoust. Soc. Am., Suppl. 1, 82:S57 (Abstract).

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CONTENTS OF APPENDICES

INTRODUCTION

Dolphin Echolocation

Echolocation is the ability of an organism to listen to the echoes of its own emitted sounds and then use information extracted from those echoes to determine the location and other characteristics of the echoing object (Norris, 1969). In 1793, Spallanzani (as cited by Griffin, 1958) suspected that bats depended upon their hearing ability to navigate in flight through the dark. He conducted a series of experiments in which the ears of bats were plugged with wax causing disorientation. However, neither Spallanzani nor his contemporaries were able to determine the existence or source of any acoustical stimulus that the bats might have used. It was not until 1941 that Griffin and Galambos demonstrated that bats emitted high-frequency signals and determined that they did, in fact, echolocate.

With the advent and use of SONAR in World War II, interest in the acoustics of the underwater environment began to grow and along with it, an interest in the sound production and reception abilities of cetaceans. Fish (1949) described sounds produced by cetaceans and referred to a category that she labeled "echo-ranging pings." In the late 1940s, McBride (as noted by Schevill, 1956), the first curator of Marineland of Florida, speculated in his notes that the dolphin's ability to avoid fishing nets was reminiscent of the echolocating bat. Schevill and Lawrence (1956) reported hearing acoustical signals as a dolphin avoided a net in order to obtain fish in both turbid water and at night. Kellogg (1961) reported a series of experiments which required a dolphin, in turbidity or darkness, to avoid metal pole barriers, select preferred fish food as opposed to non-preferred fish, and to avoid clear plexiglass barriers.

While the behavioral data and tape recordings of signals emitted by dolphins reported by Schevill and Lawrence (1956) and Kellogg (1961) were supportive of dolphin echolocation, the possibility that the animals involved used visual cues to accomplish their tasks was not eliminated. Norris, Prescott, Asa-Dorian, and Perkins (1961) trained a dolphin to accept opaque rubber suction cups over its eyes and demonstrated that the animal was still capable of avoiding a maze of metal poles and discriminating between a gelatin capsule and a piece of mackerel cut to the same size and shape. Additionally, their evidence indicated that the echolocation signals being used by their dolphin were directional and were being emitted from the region of the forehead.

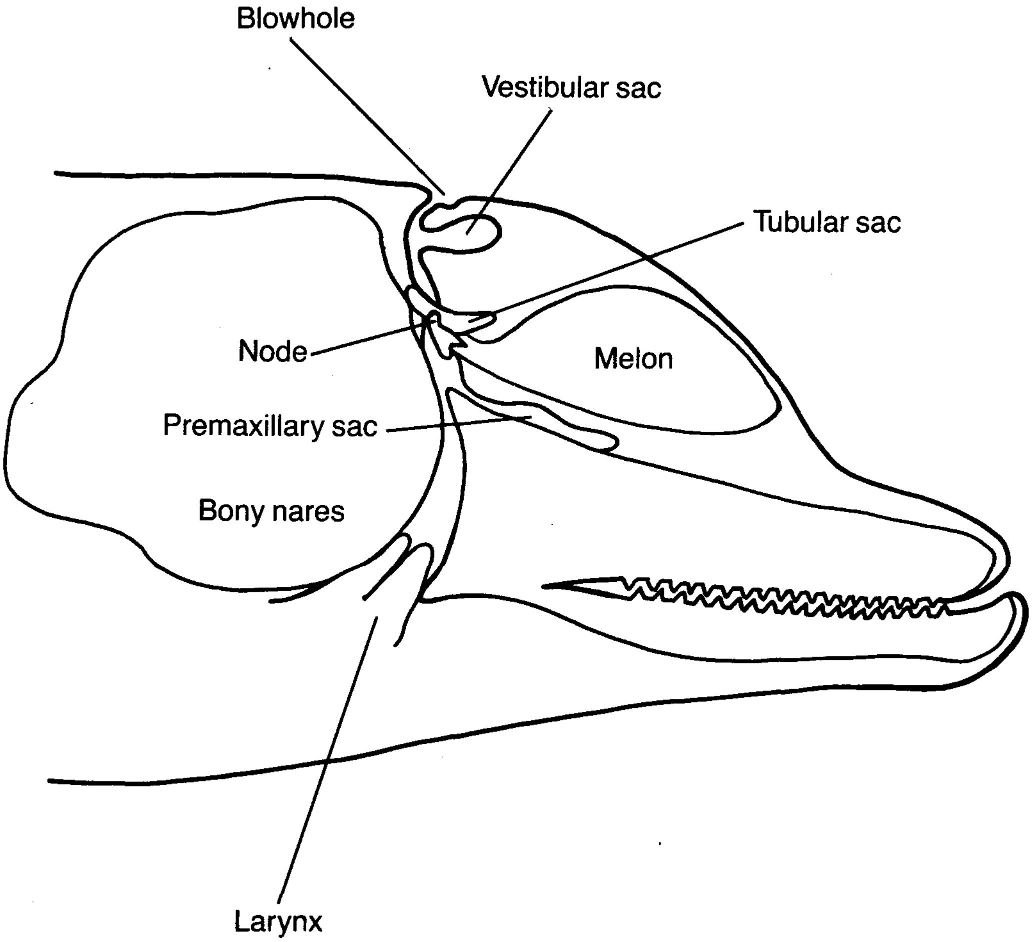
The work accomplished by Norris et al. (1961) ushered in an era of productive research on echolocation which has provided an abundance of information regarding the capabilities and sophistication of the odontocete biosonar system (see Nachtigall, 1980). Not adequately addressed, however, are the mechanics of the system; how echolocation signals are produced, emitted into the environment, and received by the inner ear (Popper, 1980a). Controversy over the sites of sound production and reception relative to echolocation in odontocete cetaceans has been evident in the literature over the last two decades. The theories that have been proposed can be summarized in two models. One suggests that acoustical signals used in echolocation originate in the larynx, are emitted in an omnidirectional field with some signals being channeled through the rostrum, and that the primary site of sound reception is the external auditory meatus. The second suggests that echolocation signals are generated in the nasal sinus system and allied soft tissue structures in the forehead, are primarily emitted in a narrow beam focused through the melon, and that the primary sites of sound reception are the lateral sides of the fat-filled lower jaw.

Because the concepts of sound production and reception are inextricably linked in any discussion of dolphin echolocation, a brief review of both will provide a broader frame of reference for the experiment and results reported in this dissertation.

Sound Production

The blowhole, a singular crescent-shaped orifice at the highest point of the head, is the visible element of the dolphin's nasolaryngeal system (Figure 1). It can be sealed off by the valve-like organ just beneath it to prevent water from entering the nasal passage. From the blowhole, the nasal passage continues as a pair of rigid tubes that descend just anterior to the frontal bones of the skull and posterior to the melon, the body of fat which rests on the paired premaxillary and maxillary bones. These bones extend forward from the cranium along with the mesorostral cartilages to form the rostrum. Just beneath the blowhole, a number of sacs or diverticula begin to branch off from the nasal passage. In <u>Tursiops truncatus</u> the vestibular sacs are the first encountered and lie on either side of the blowhole just beneath the skin. Deeper than and ventral to the vestibular sacs are the paired

Figure 1. A schematic representation of the dolphin's nasolaryngeal system. Echolocation signals are believed to originate at the nasal plugs.


Blowhole
Vestibular sac
Tubular sac
Node
Melon
Premaxillary sac
Bony nares
Larynx

anterior and posterior nasofrontal or tubular sacs which are long, narrow, and curve forward and laterally to meet the fatty tissues of the melon. The nasal plugs are paired muscular valves that close off the internal nares at the junction of the tubular sacs. Projections of the nasal plugs, the nodes, invade the tubular sacs. As the nasal passage approaches the bony nares, premaxillary sacs extend forward along the dorsal surfaces of the premaxillary bones. The nasal passage continues down beyond the opening to the Eustachian tube in the lateral wall of each naris and is sealed off at its base by the elongated intranarial larynx. Detailed and comprehensive descriptions of these structures have been provided by Lawrence and Schevill (1956), Green, Ridgway, and Evans (1980), and Ridgway (1983).

While the dolphin's larynx is heavily muscled, it lacks vocal cords and appears to be a major control point for air flow through the respiratory system (Harrison and King, 1965). The identification of the larynx as a sound producing mechanism, however, has been based on dissections like those reported by Lawrence and Schevill (1956, 1965) which reveal specialized and complex structures. Blevins and Parkins (1973) have more specifically proposed that the larynx, even though it lacks the appropriate vocal folds, produces a wide variety of sounds including the "clicks" associated with echolocation. Purves (1967) has argued that mechanical vibrations of the glottis are transmitted to the pharyngeal muscles and emitted into the environment through the rostrum. These investigators, and others (Lilly and Miller, 1961; Schenkaan, 1973; Purves and Pilleri, 1983), have based their arguments on the heavy musculature surrounding the cetacean larynx and the assumption that it should function similarly to the larynx of a terrestrial mammal.

Norris et al. (1961) suggested that echolocation signals originated in the area of the forehead and were beamed through the melon in a highly directional fashion as opposed to being emitted in a wide field of transmission originating in the larynx. Evans and Prescott (1962) recorded the vocalizations of captive animals and forced air through the respiratory systems of excised dolphin heads to examine sound production sites in the larynx and nasal sac system. Their findings specifically implicated the tubular sacs in combination with the nasal plug nodes as the site of production for echolocation clicks. Diercks, Trochta, Greenlaw, and Evans (1971), using hydrophones attached directly to various points on the head of their dolphin determined that sound production was occurring at a location corresponding to the nasal plugs in the nares and that signals were being directed forward from the melon. Norris, Dormer, Pegg, and Liese (1971) employed cineradiography to visualize the movements of air-filled structures in the respiratory tract and nasal diverticula during respiration and vocalization. The resulting images associated movements of the nasal plugs and the absence of airflow through the larynx with the production of "squeals" in the spinner porpoise (Stenella longirostris). Unfortunately, no clicks were produced during their tests. Evans and Maderson (1973) provided further evidence supporting sound production by the nasal plugs moving against the edge of the bony nares. Mead (1975) reviewed the evidence available and concluded that, while the possibility of sound production in the laryngeal region could not be completely eliminated, structures in the vicinity of the nasal plugs were the most likely to be involved.

There is a good deal of evidence indicating that the echolocation signals emitted by dolphins are highly directional and it is believed that the skull, air-filled nasal diverticula, and melon are involved in guiding and beaming the signals forward (Norris et al., 1961; Evans, Sutherland, and Bell, 1964; Norris and Evans, 1967; Norris, Harvey, Burzell, and Krishna Kartha, 1972; Mohl and Andersen, 1973; Au, Floyd, and Haun, 1978; Penner and Murchison, 1970; Au, 1980; Au, Moore, and Pawloski, 1986; and many others). Wood (as noted by Norris, 1964) identified the melon, the soft body of oily-fat in the dolphin's forehead, as an "acoustic lens" capable of focusing sound and transducing it between tissue and sea water. This proposal for the function of the melon has been supported by lipid composition topography (Varanasi and Malins, 1972; Litchfield, Greenberg, Caldwell, Caldwell, Sipos, and Ackman, 1975; Varanasi, Feldman and Malins, 1975; Apfel, Young, Varanasi, Maloney, and Malins, 1985) and by transmission velocity studies (Norris and Harvey, 1974).

The hypothesis for sound production in the nasal system, unlike its opposing model, enjoys experimental support which includes the use of ultrasound (Mackay and Liaw, 1981), electromyographic and air pressure events (Ridgway, Carder, Green, Gaunt, Gaunt, and Evans, 1980), and cineradiographic evidence (Dormer, 1979). Cranford (1985) has employed a technique based on computed tomography to provide the first three-dimensional reconstruction of the odontocete head, specifically the areas involved in sound production and transmission. His computer generated model has made possible detailed descriptions of delphinid cephalic anatomy and will allow accurate measurements of size, shape, and density necessary to investigate sound phonation and transmission theories.

Sound Reception

Lacking external pinnae, the surface opening of the external auditory meatus appears as a small hole approximately 4 cm posterior to the dolphin's eye at each side of the head. The auditory canal typically runs from the surface to the tympanic bulla but may be discontinuous or absent across species or individuals. There is a cartilaginous segment withdrawn below the surface which is believed to be a vestigial structure analogous to the external pinnae of terrestrial mammals. The meatus and its allied cartilaginous structures are not always clearly differentiated from surrounding tissues. The cartilaginous segment ends near the tympanic bone and the canal continues as a funnel-shaped membrane, the tympanic conus, opening to terminate at the tympanic membrane which is reduced in thickness by comparison to terrestrial mammals.

The dolphin's middle and inner ear are encased in the tympanoperiotic bone which is actually two bones that are fused together and consist of an ivory-like material which may be the densest material found in the dolphin's body. Each tympanoperiotic bone is isolated away from the skull by a complex network of small blood vessels and pockets of gas and foam. The bone encased cochlea is surrounded by the peribullary sinus.

On the internal side of the tympanic membrane, extending from its bony edges on the tympanoperiotic bone, the tympanic ligament, a tough cone-shaped structure, is attached by its narrow end to the extended process of the malleus. There does not appear to be any direct connection between the malleus and the tympanic membrane. The ossicular chain in the dolphin is present but differs from that of terrestrial mammals in size, shape and leverage. The joint between the malleus and incus is ankylosed while the joint between the incus and stapes is movable. Detailed and comprehensive descriptions of the auditory system in odontocetes have been provided by Reysenbach de Haan (1957), Fraser and Purves (1960), Morgane and Jacobs (1972), and Purves and Pilleri (1983).

The cochlea in odontocetes is comparable to that of a terrestrial mammal in most respects but there are differences relative to its response to high-frequency sounds (Popper, 1980b). While the number of hair cells in the dolphin cochlea is comparable in number to that of the human cochlea, the ganglion cell to hair cell ratio in Tursiops truncatus is 5:1 as opposed to the 2:1 ratio in humans (Wever, McCormick, Palin, and Ridgway, 1971a; 1971b). Wever et al. have suggested that the large number of ganglion cells provide a greater number of pathways for high-frequency information to the brain. Fleischer (1976) noted more stiffness in the basilar membrane of Tursiops truncatus as compared to terrestrial mammals, as would be expected for an animal adapted for high-frequency hearing. Greater stiffness of the membrane and a stiffness gradient along its length enhances the ability to respond in the higher ranges (von Bekesy, 1960).

The transmission of sound from the surface of the tympanoperiotic bone to the cochlea is not clearly understood. McCormick, Wever, Palin, and Ridgway (1970) and McCormick, Wever, Ridgway, and Palin (1980) rejected the function of the tympanic membrane and ligament in causing motion between the stapes and the cochlear capsule in favor of translational bone conduction.

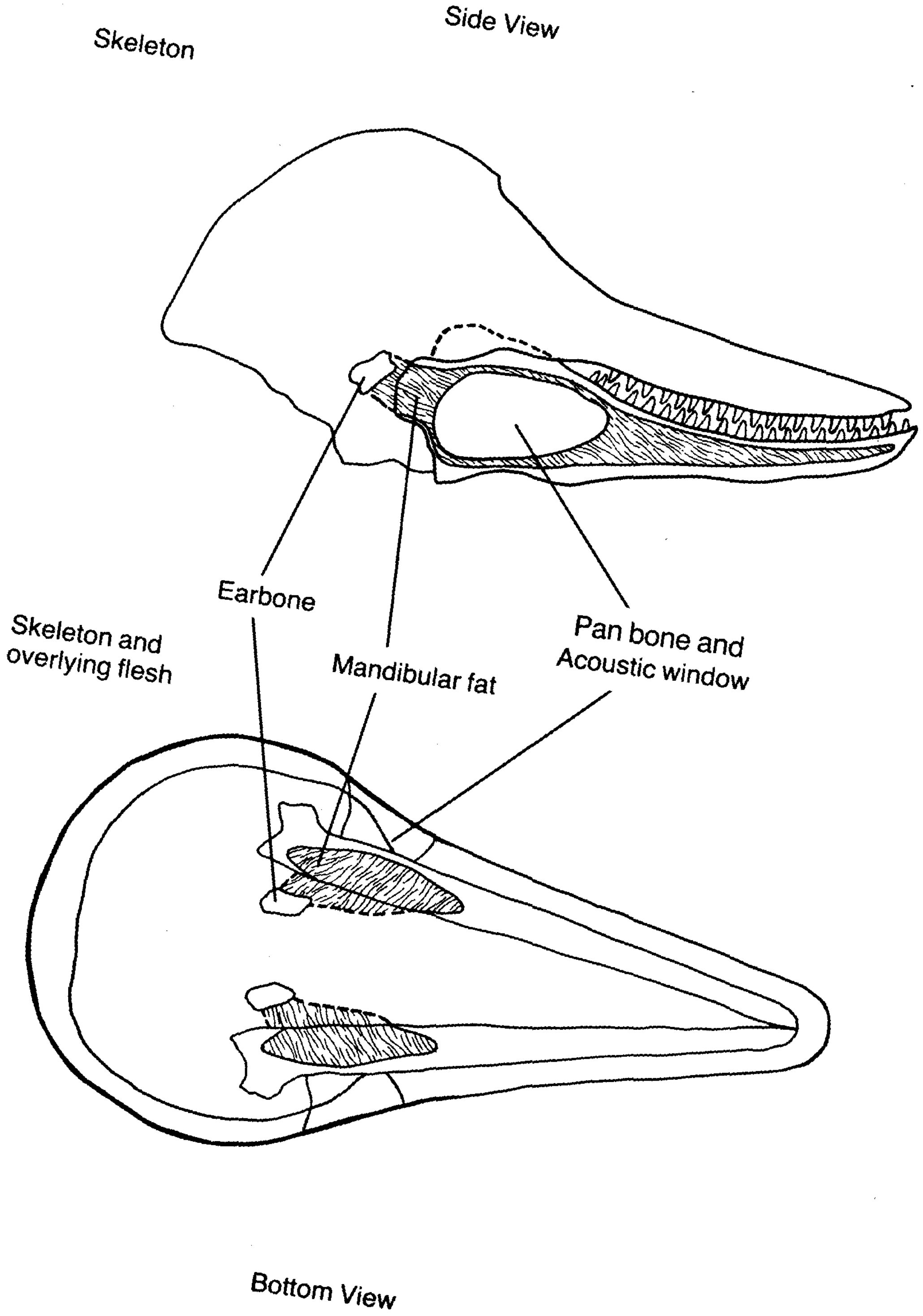
The physics of underwater acoustics in the dolphin's environment are such that sound is readily transmitted through the bone and tissue of the animal's head and body (Johnson, 1986). A major question concerns the manner in which acoustical signals are specifically directed to the auditory bulla. Reysenbach de Haan (1957) argued that the external auditory meatus is vestigial and that sounds are received by means of the ligaments and tissues surrounding it. Fraser and Purves (1960) and Purves and Pilleri (1973, 1983) have argued that the external auditory meatus itself is functional and responsible for the transmission of sound to the tympanic bulla. Purves and Pilleri (1983) remain the strongest supporters for the model of sound generation in the larynx and reception by the auditory meatus and have consistently argued that these mechanisms must certainly function in a manner directly comparable to that of a terrestrial mammal.

Hearing Through the Lower Jaw

The idea that sounds are received via the fat bodies contained in the hollow lower jaw of odontocetes, was first proposed by Norris (1964). He initially suggested that the entire lower jaw of odontocetes acted as a sound reception and wave guide apparatus. He attributed that function to the thinness and hollowness of the lower jaw and the elongated cone-shaped body of fat which occupies its interior, running from the symphysis and extending back beyond the pan bones to a point in the region of the inner ear. His first illustration (p. 330) depicted returning echolocation signals being received along the lower jaw and through the mandibular nerve foramena and transmitted to the inner ear via the fat body of the mandibular canal.

Norris (1968) later provided supporting evidence and revised his argument for the primary site of sound reception during echolocation. According to his theory, returning sound would certainly meet the lower jaw at all points along its surface encountering a variety of tissue structures overlying the bone (Figure 2). Taking into account the reflective properties of muscle-tissue interfaces, the sound would pass most easily through an "acoustic window," an area of oily fat overlying the flared posterior end of the lower jaw, or pan bone. Muscle fibers are absent within this body of fat but the area is well-defined by those that surround it. Norris assumed that high-frequency sounds would again be guided through this area to the bone layer by reflections at the fat-muscle interface. The oval shape of the "acoustic window" directly corresponds to the shape of the thinnest area of the pan bone where sound could pass relatively unimpeded dependent on the angle of incidence. Once through the bone, the sounds would be guided through the mandibular fat body, which is well differentiated from surrounding tissues, again by reflections at the fat-muscle interface, to its termination on the thinnest area of the auditory bulla. In this manner, it was assumed that sound could most easily and effectively be

Figure 2. A schematic representation of the relationship between the dolphin's lower jaw, mandibular fat body, and auditory bulla. According to the "jaw-hearing" theory, returning echolocation signals enter at the acoustic window, pass through the thinnest area of the pan bone, and are guided to the earbone by the mandibular fat body. (This illustration is based on computer-generated images provided by T. Cranford).


Skeleton
Side View
Earbone
Skeleton and overlying flesh
Mandibular fat
Pan bone and Acoustic window
Bottom View

transduced and guided from sea water, past overlying fibers, fat and bone to the auditory bulla. Norris acknowledged the possibility of sound conduction through areas at the base of the melon as had been suggested by the work of Yanagisawa _et al_. (1966) but considered the supporting evidence for an appropriate connection leading over the edge of the rostrum into the fatty tissue of the lower jaw to be inconclusive. He proposed no definition for the manner in which sound is transmitted to the cochlea from the auditory bulla.

Norris's "jaw-hearing" theory, as it has come to be informally called (Norris, 1974), has found support both in the consensus among students of dolphin echolocation that it makes intuitive sense and the results of the experiments of several investigators.

Bullock, Grinnell, Ikezono, Kameda, Nomoto, Sato, Suga, and Yanagisawa (1968) were the first to study dolphin hearing by means of evoked potentials from midbrain auditory structures. Using stimuli that were airborne, waterborne, and directly applied to the animals' heads, responses from the inferior colliculi, medullary auditory centers, and the medial geniculate were recorded. Their series of experiments yielded a number of significant findings among which was the conclusion that the lower jaw is the primary pathway for sound to the cochlea. It is important to note that they additionally reported a marked attenuation of response caused by the shielding of the lower jaw with paper or foam rubber. The melon and the areas around the external auditory meatus were also described as sensitive to sound but to a much lesser degree than the lower jaw. McCormick _et al_. (1970, 1980) used cochlear microphonics to study the dolphin's auditory system. Their mapping of areas of sound sensitivity was in close agreement with that of Bullock et al. and they also concluded that the lower jaw was the primary site of sound reception. Biochemical evidence that the melon and mandibular fat bodies have acoustical properties favorable to echolocation has been provided by Varanasi and Malins (1971, 1972). They have described lipid patterns, isovalerate wax esters, and triglycerides, unique to the melon and the mandibular fat bodies in the lower jaw in odontocetes and have proposed sound velocity functions essential to echolocation for these tissues which would allow signals to pass between tissue and sea water with relatively little loss of energy. The biochemical composition of the tissues of the lower jaw implicated in sound reception, while similar to that of the melon, is distinct from the body fat of the dolphin (Litchfield et al., 1975). Norris and Harvey (1974), in a series of experiments to investigate sound conduction through these fat bodies, clearly demonstrated the passive transmission of sound through the jaws and throats of recently dead specimens.

The most prominent supporters of the larynx-meatus model have not given any ground in their arguments. Purves and Pilleri (1973) discounted the findings of McCormick et al. (1970) with the arguments that the stimulus intensities used, 50 dB above behavioral thresholds, were too high, confounding the use of normal auditory pathways, and that the surgical procedures employed, in fact, damaged the auditory system. Their most recent treatise on cetacean echolocation (Purves and Pilleri, 1983) rejected hearing through the lower jaw as an idea based solely on anatomical inference rather than experimental evidence. Based on the argument that sound waves travel readily through the tissue and bone of the dolphin's head and, therefore, directly to the auditory bulla, Johnson (1986) discounted the existence of any directional pathways. He suggested that the evidence for sound reception through the lower jaw provided by Bullock _et al_. (1968) and McCormick _et al_. (1970) may be misleading since the techniques used allowed the presence of gas-filled spaces in the mouths and throats of the animals tested, not present in the natural state, that may have reflected acoustical signals.

Hypothesis

What has been lacking in the evaluation of the "jaw-hearing" theory is evidence gained from a living animal actively echolocating and listening under controlled conditions. If the theory is correct as proposed, the attenuation of incoming signals at the lower jaw should noticeably hinder a dolphin's ability to echolocate and may cause it to adopt strategies to compensate for that attenuation that would be observable in its behavior. Furthermore, if echolocation signals are produced in the nasal system, the placement of sound attenuating material over the lower jaw to block incoming signals should have no effect on outgoing signals.

The experiment reported in this dissertation provided both behavioral and acoustical evidence concerning those hypotheses. The development and use of a controlled methodology made possible the observation and measurement of the effects of attenuation of sound at the lower jaw in terms of a dolphin's responses, collateral behaviors, and outgoing signals while it performed an echolocation task.

METHOD

Subject

The subject for this experiment was a male Atlantic bottlenose dolphin, Tursiops truncatus (Montagu), named Nemo, estimated to be thirteen years of age at the time that preparations for this experiment were initiated. Captured in Florida waters in 1976, this dolphin was previously trained to perform in public demonstrations but had no former experience as a research subject. At the time of this experiment he was housed in a concrete pool at the Seven Seas Panorama exhibit of the Chicago Zoological Park (Brookfield Zoo) with four (1.3) other dolphins of the same species. This dolphin was selected on the basis of his dominance within the group, which reduced the threat of his being disturbed or displaced by other dolphins during the experiment. Furthermore, he had previous experience in wearing opaque latex rubber suction cups over his eyes and performing an echolocation task during regularly scheduled public demonstrations. Neither the dolphin's diet (7.25 kg/day) nor his performing schedule (2 to 5 shows/day) were altered for the sake of the experiment reported here.

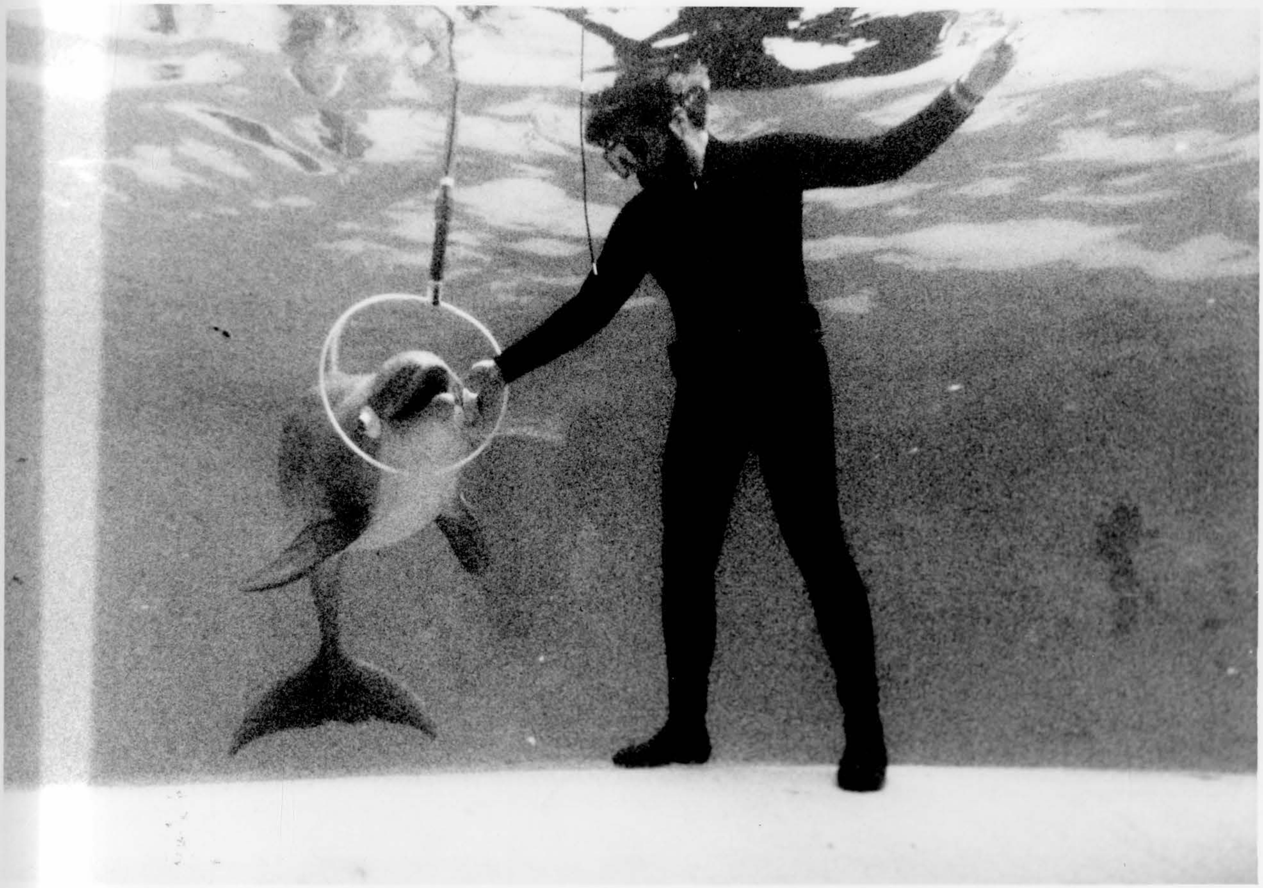
The Seven Seas Panorama pool was an elongated oval-shape measuring 30.48 m l x 7.62 m w x 5.18 m d and held approximately 757,000 liters (200,000 gallons) of manmade salt water. This experiment was conducted in the shallow north end of the pool where the water was approximately 1.68 m deep and the dolphin could be stationed looking over the edge of a slope that led down to the deep center of the pool.

Procedure (Behavioral)

The dolphin was conditioned to perform a discrimination task in a "Go/No-go" paradigm (Schusterman, 1980). Cued by a trainer standing at poolside at the beginning of each trial, the dolphin would leave its starting place at the far end of the pool with a latex rubber suction cup, referred to as an eyecup, mounted over its right eye to take a position with its head inserted through an underwater hoop. The water-filled rubber hoop was 46 cm in diameter and mounted on a PVC extension arm so that it was centered 61 cm below the surface of the water and 1.8 m away from the side of the pool. Once the dolphin was properly positioned in the hoop station, a second trainer standing in the water next to the hoop and wearing a diving mask placed a second eyecup over the dolphin's left eye eliminating all visual cues (Figure 3). One of two targets was then manually lowered into the water at a distance of 3 m for approximately four seconds allowing the dolphin to determine its identity by echolocation. An aluminum cylinder, 76 cm long and 6 cm in diameter, positioned in the water so that its center was aligned with the center of the underwater hoop was used as the "Go" target. A sand-filled rubber ring, 18 cm in diameter, positioned in the water so that it was completely submerged approximately 6 cm below the water's surface was used as the "No-go" target. After the target was withdrawn, the left eyecup was removed and the dolphin was free to report his choice. To indicate the "Go" target, the dolphin left his hoop station immediately to strike a nearby float suspended to his right just above the water's surface before returning to his starting position. To indicate the "No-go" target, the dolphin would remain in his hoop

Figure 3. Dolphin and second trainer positioned for target presentation.

station until the second trainer sounded a hand held "clicker" underwater after a period of anywhere from 9 to 15 seconds which was randomly [illegible] by the second trainer. Once the "clicker" was sounded, the dolphin returned to its starting position (Figure 4). Figure 5 schematically represents the sequence of events in



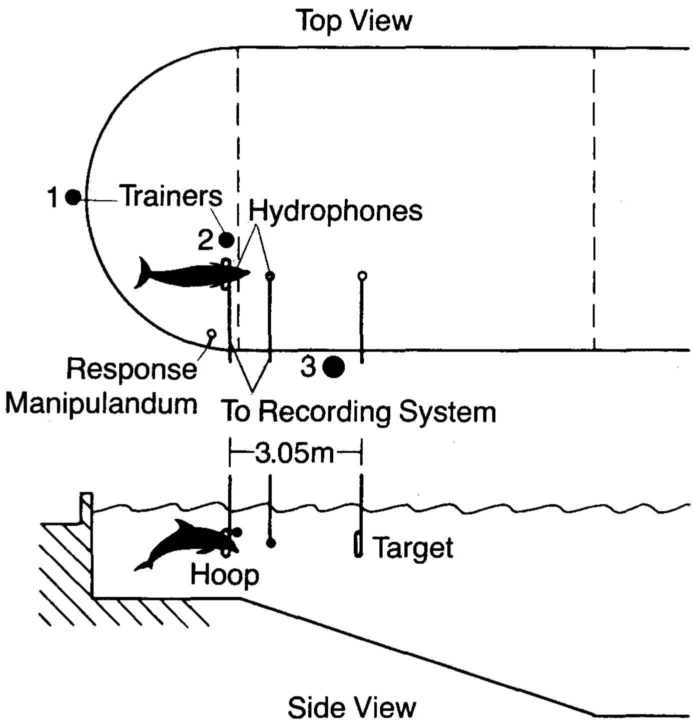
indicate that the dolphin was ready for target presentation. As the appropriate target was lowered into the water [illegible] range, the second trainer looked back in the opposite direction toward the first trainer. The first trainer, simultaneously with the presentation and withdrawal of a target, quietly lowered into the water and removed a plastic float attached to the end of a narrow pole within sight of the second trainer.

station until the second trainer sounded a hand held "clicker" underwater after a period of anywhere from 8 to 15 seconds which was randomly varied from trial to trial by the second trainer. Once the "clicker" was sounded, the dolphin returned to its starting position (Figure 4). Figure 5 schematically represents the sequence of events in a typical trial.

Each session consisted of twenty trials. The order of target presentation was determined by Gellerman tables (Gellerman, 1933) which were adjusted to allow both targets to be presented an equal number of times but never more than three times in a row.

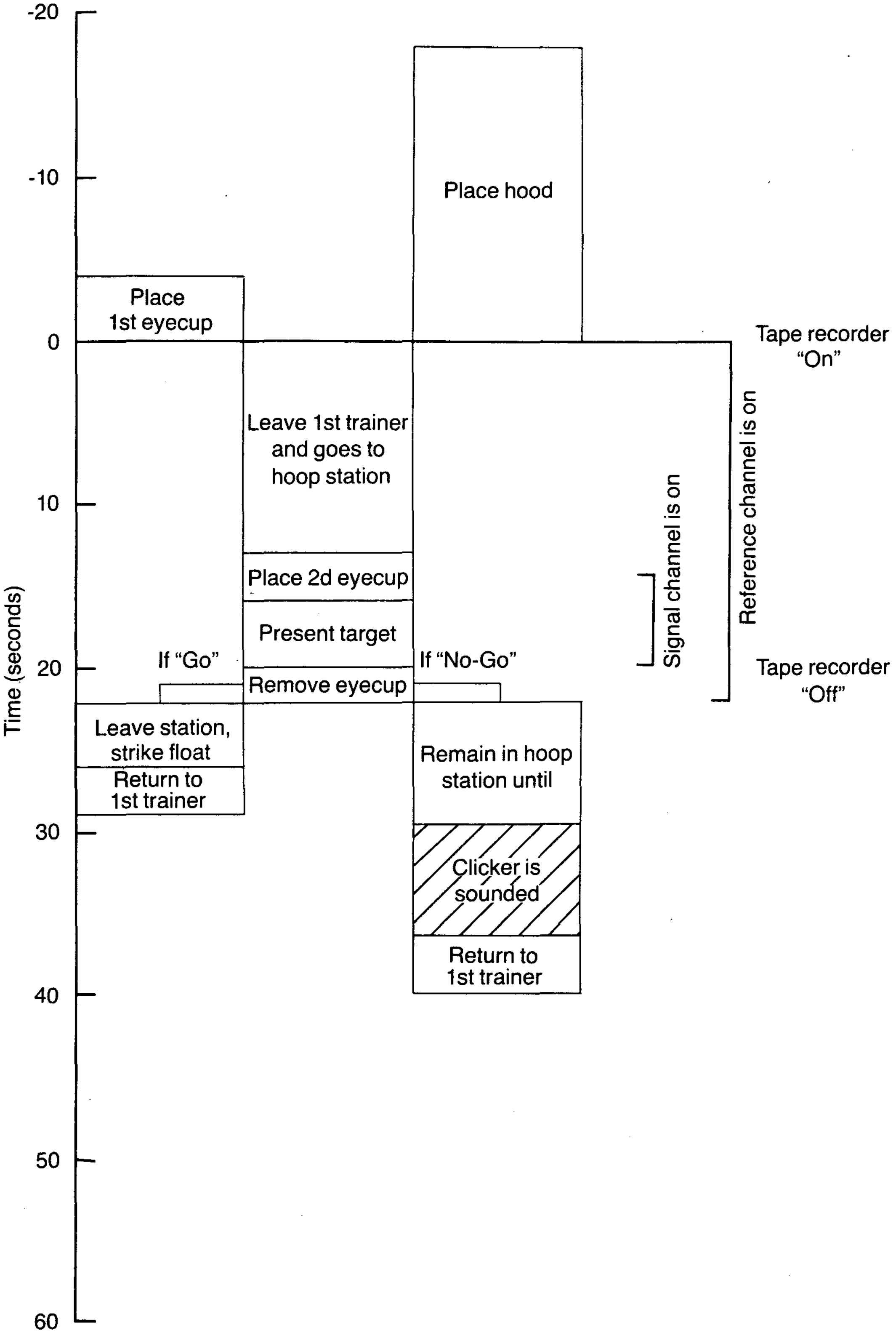
The trainer in the water at the hoop station was unaware of the target condition for each trial and relied on the first trainer for visual indications of target presence and the appropriateness of the dolphin's response. As the dolphin entered the underwater hoop on each trial, the second trainer turned from facing the dolphin's starting position to face the side of the pool with his left hand, holding the "clicker," extended to his side and just above the surface of the water. He used his right hand to position the eyecup and keep it from falling off during target presentation. When the eyecup was properly positioned, the second trainer gave a gesture of the left hand to indicate that the dolphin was ready for target presentation. As the appropriate target was lowered into the water down range, the second trainer looked back in the opposite direction toward the first trainer. The first trainer, simultaneously with the presentation and withdrawal of a target, quietly lowered into the water and removed a plastic float attached to the end of a narrow pole within sight of the second trainer.

Figure 4. Schematic representation of the positions of the dolphin, trainers, and equipment during trials.



Pool Dimensions:
30.48m(L) × 7.62m(W) × 5.18m(D)
757,000 L

Figure 5. Schematic representation of the sequence of events as they occurred during a typical trial.


-20
-10
0
10
20
30
40
50
60
Time (seconds)
Place hood
Place 1st eyecup
Tape recorder "On"
Leave 1st trainer and goes to hoop station
Reference channel is on
Signal channel is on
Place 2d eyecup
Present target
If "Go"
If "No-Go"
Tape recorder "Off"
Remove eyecup
Leave station, strike float
Return to 1st trainer
Remain in hoop station until
Clicker is sounded
Return to 1st trainer

Once the float was removed, the second trainer, who had been watching the dolphin as well as the float, would look above the water's surface to the first trainer for a hand gesture indicating whether the trial had been a "Go" or a "No-go" and proceed appropriately. During and after each trial, the second trainer also reported any collateral behaviors observed as discussed below. At the end of each trial, the second trainer then turned and faced the first trainer until the next trial began to avoid any visual indications of what target might be presented.

The targets were manually presented by a third trainer who additionally acted as record keeper during each session. The targets were each attached to monofilament line and could be interchanged at the end of a pole for presentation. On each trial, the target to be presented was kept out of sight at poolside until the dolphin was underwater and on its way to its hoop station. The third trainer, therefore, was the only one of the three individuals involved that was aware of the target condition prior to each trial. The target was then swung out over the surface of the water and lowered upon a gesture from the second trainer as described above. The third trainer recorded the dolphin's response as well as collateral behaviors reported by the second trainer for each trial.

To investigate the role of the lower jaw in the performance of the task described above, sessions were conducted in which ten of the twenty trials required the dolphin to wear one of two rubber hoods. The ten trials were selected prior to conducting a session and accounted for an equal number of presentations of each target. The hoods were designed to cover the dolphin's lower jaw from the tip of the snout to a few centimeters anterior to the base of the pectoral fins along the gape of the mouth (Figure 6). With the exception of the areas around the external auditory meatus, the hoods covered the sound-sensitive areas over the lower jaw as indicated by Bullock et al. (1968) and McCormick et al. (1970).

The hoods were held in place on the dolphin's head by means of rubber straps around the snout and the back of the head as well as by clusters of small suction cups glued to the interiors of the hoods at strategic points to prevent slippage and to keep the material as close to the dolphin's skin as possible (Figure 7). The suction cups were commercially produced holders for bar soap which are designed to adhere to smooth surfaces.

One of the hoods, used as a control, was constructed from 0.16 cm thick gasless neoprene (Durometer neoprene obtained from the Abbott Rubber Company, 2143 Lunt Avenue, Elk Grove Village, IL 60007). The other hood, used to establish the experimental condition in which acoustical signals would be attenuated at the lower jaw, was constructed from 0.48 cm closed-cell neoprene.

Tests to determine the attenuation values of the neoprene materials used were conducted in a concrete pool designed for making underwater acoustical measurements at the Naval Ocean Systems Center, Hawaii. An ARL-90 element planar transducer was mounted 1.8 m below the surface of the water. A Clevite CH-24 transducer was mounted in line with the ARL-90 at a distance of 2.1 m. Test signals were broadcast through the CH-24. The peak-to-peak amplitudes of the signals received

Figure 6. Dolphin wearing hood and eyecups and stationed as he would be during target presentation.

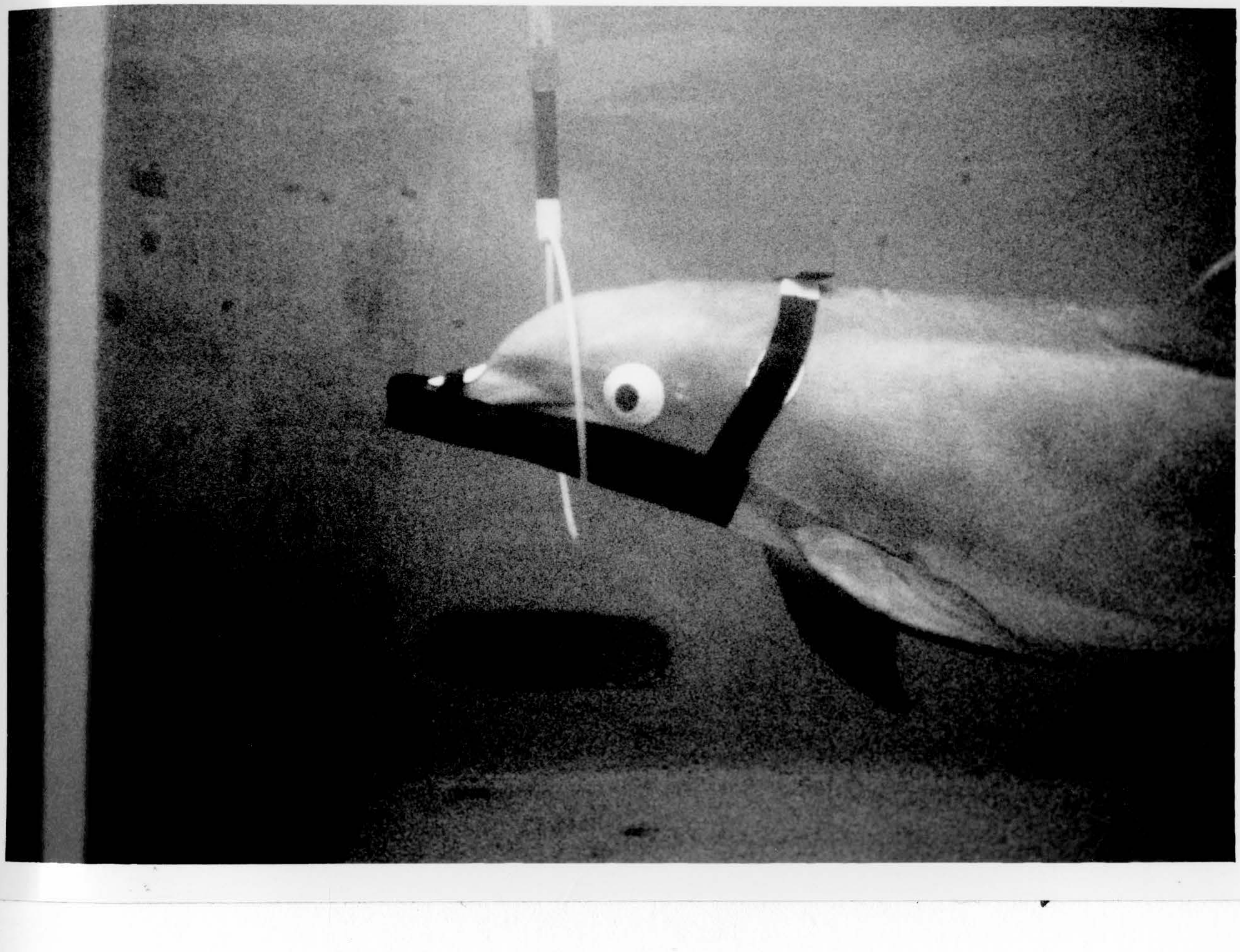
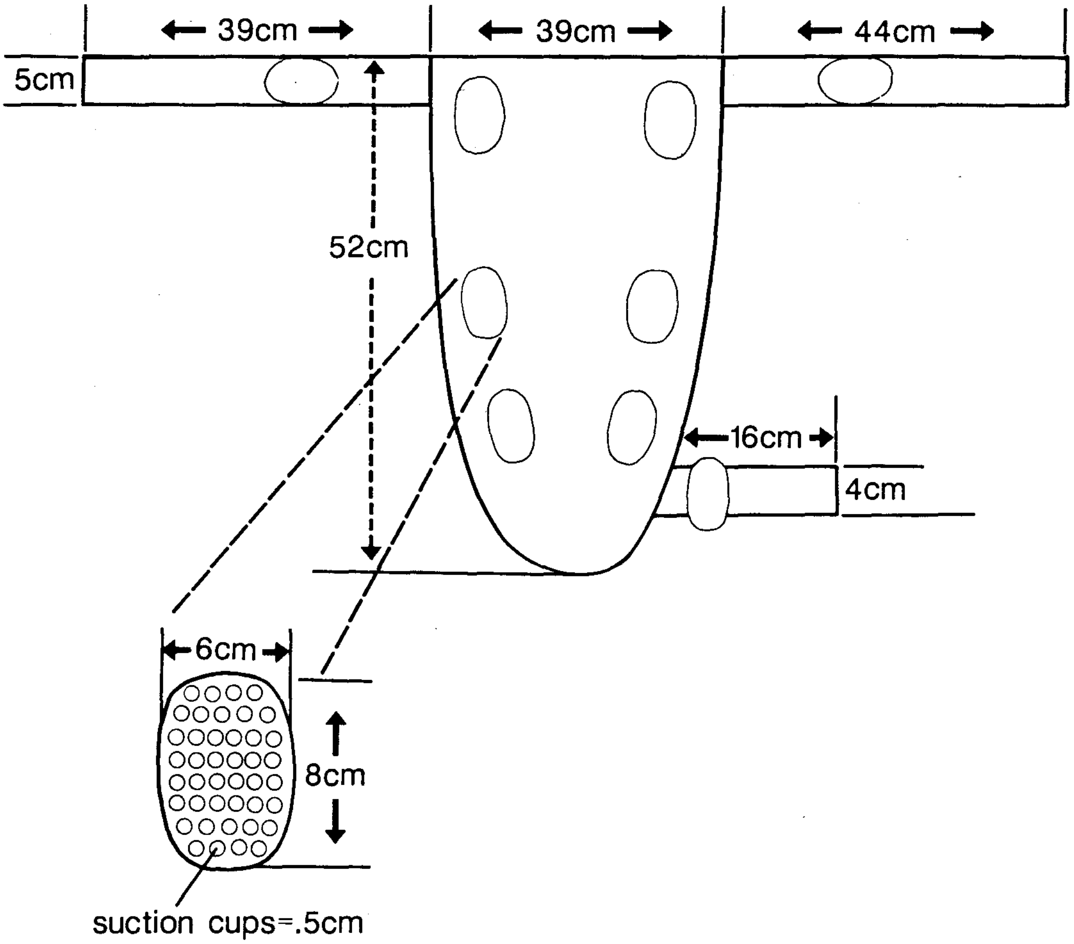


Figure 7. Schematic representation of the hood design.


39cm
39cm
44cm
5cm
52cm
16cm
4cm
6cm
8cm
suction cups=.5cm

with and without a neoprene covering placed over the ARL-90 were compared for the respective materials. Using simulated dolphin echolocation clicks, it was determined that the gasless neoprene had attenuation values of 2.2 dB and 1.2 dB for signals with peak frequencies of 35 kHz and 115 kHz respectively. Similarly, the closed-cell neoprene had attenuation values of 39 dB and 36 dB for signals with peak frequencies of 55 kHz and 115 kHz respectively (Au, personal communications).

In addition to observing and recording the dolphin's responses in the discrimination task, the occurrence of any predetermined collateral behaviors were also noted for each trial. Prior to beginning the experiment, eight behaviors were anticipated and selected for observation based on what was known to be typical of echolocating dolphins and what was known about the behavior of this particular subject. The behaviors selected were headscanning in both the vertical and horizontal planes, holding the head cocked at a noticeable angle in the vertical plane, the emission of air bubbles from the blowhole, the suppression of emitted signals, holding the mouth open, the intentional displacement of hoods or eyecups, and any noticeable variation in the length of response latencies.

To accommodate the dolphin's performing schedule, sessions were conducted with some irregularity at a rate of one or two sessions per day over a period of six months. A baseline session, conducted without the use of a hood, always preceded a pair of sessions involving each of the hoods which were conducted in a counterbalanced (ABC/ACB) order. Each sequence of three sessions beginning with the baseline condition constituted a set. A total of twenty sets were completed. Each of the dolphin's correct responses were reinforced either with food, secondary reinforcers, or combinations of both in keeping with the training regimen familiar to the dolphin (Brill, 1981). Each incorrect response was followed by a brief time-out during which the first trainer would stand motionless and avoid eye contact with the dolphin. During each trial, the remaining dolphins in the group were kept occupied at the opposite end of the pool.

Procedure (Acoustical)

To supplement the behavioral data collected in this experiment and to investigate any changes made in the emitted echolocation signals across conditions, samples of the dolphin's outgoing echolocation signals from each of the three conditions were recorded at intervals throughout the experiment. The number of sessions recorded over the course of the experiment was limited by the manpower available during the sessions and the large amount of data that would result from each recording.

Two hydrophones were in place during all trials recorded. A Celesco LC-10 hydrophone was placed in line with the center of and 1 m in front of the underwater hoop to detect the dolphin's echolocation clicks. An Edo-Western 6166 hydrophone was affixed to the top of the underwater hoop directly over the dolphin's head. The signals recorded by the Edo-Western hydrophone were used to act as a time reference in the analysis of the signals recorded at the LC-10 hydrophone which made it possible to distinguish the subject's signals from any of those that were occasionally emitted by one or more of the other dolphins in the pool during trials.

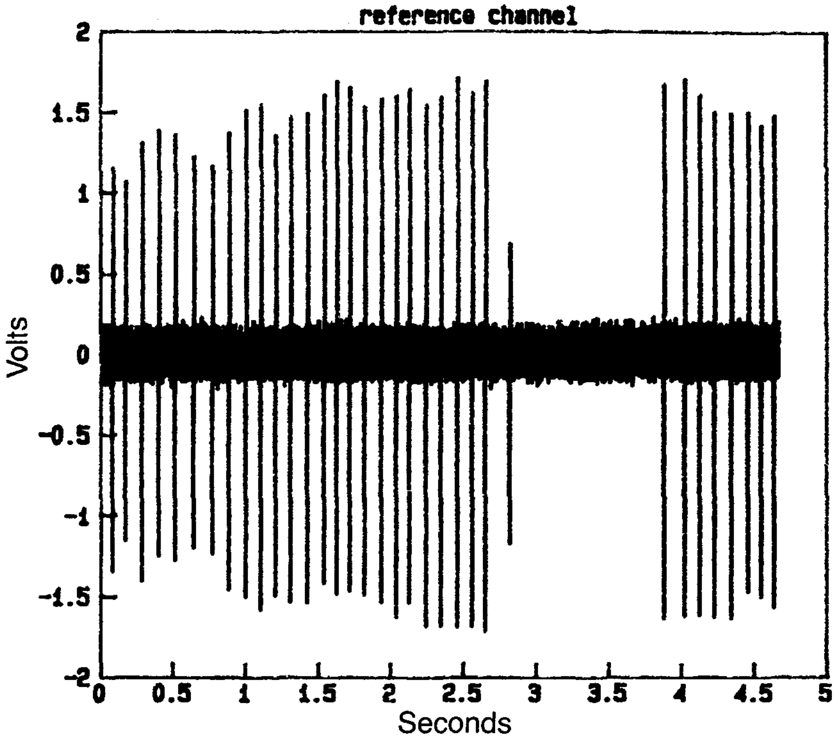
The signals from each hydrophone were amplified with 40 dB of gain, bandpass filtered between 3 kHz and 200 kHz through Krohn-Hite 3550 variable filters, and recorded on two channels of an Ampex FR-1300 portable instrumentation tape recorder. The tape recorder was operated at 152.4 cm/s (60 ips) providing a bandwidth of 280 kHz. To record a trial, the reference channel monitoring the Edo-Western hydrophone was active continuously from the time that the dolphin was cued to go to its station until the time that it reported its choice. The signal channel, monitoring the LC-10 hydrophone, was controlled by a mute switch placed in line between the Ampex tape recorder and the Krohn-Hite filter. The mute switch was opened, allowing the signals from the LC-10 hydrophone to be recorded, from the time that the second eyecup was put into position until it was removed (see Figure 5). It is assumed, then, that the signals recorded at the LC-10 hydrophone were those emitted by the dolphin during the time that it was echolocating on the presented target.

To conserve the amount of recording tape being used and to facilitate computer analysis, the signals from both channels originally recorded during the time that the dolphin was echolocating on the target were later reduced by a speed factor of 16 and transferred to a Marantz PMD 360 stereo cassette tape recorder. The Marantz tape recorder and cassettes could then be more easily transported from Brookfield Zoo to the Parmly Hearing Institute, where signal analysis was conducted at a later time.

The best recorded samples of the dolphin's echolocation signals, those that were not contaminated by the presence of the emitted signals of the other animals in the pool, simultaneous whistling by the subject or an equipment failure, were played into a Masscomp computer system for analysis and graphic representation. Samples were submitted at an A/D conversion rate of 40,000 points/sec. This rate allowed for the representation of spectral information up to 320 kHz which was well above the highest frequency of interest.

Once the samples obtained from both channels were graphically represented, the subject's echolocation clicks were identified and extracted by matching the major peaks in each channel based on two factors; the travel time between the hydrophones (approximately 657 usec) which remained constant, and an assigned peak voltage criterion selected to be greater than the peak voltage of the noise observed in the sample in question. Signals that could not be matched were disregarded. Based on the clicks extracted, the following data were generated and stored onto diskettes: 1) the total number of clicks extracted from the sample; 2) the relative times at which the clicks occurred in the sample; 3) the average waveform showing the voltage range at points sampled based on the clicks extracted; 4) a frequency spectrum (Fast Fourier Transform) of the average waveform; 5) the same as 3 and 4 with all clicks normalized by setting the major negative peak at -1v; 6) the average FFT showing the range at each sampled point based the FFT's of each click in the sample; 7) a waterfall display of all waveforms in the sample; 8) a waterfall display of all FFT's in the sample; and, 9) an interclick interval (ICI) histogram. Figures 8a-h illustrate the graphics produced in the process. Peak-to-peak sound pressure levels, -3 dB bandwidths (the spacing between the frequencies measured at the point midway down from the highest peak in the spectrum), and signal duration were determined by hand measurements made on the graphic representations of waveforms and their respective FFT's.

Figure 8a. Graphic representation of a typical sample as recorded in the reference channel on the left and in the signal channel on the right. The trial ID code is shown above the signal channel image.


reference channel
Volts
Seconds
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5

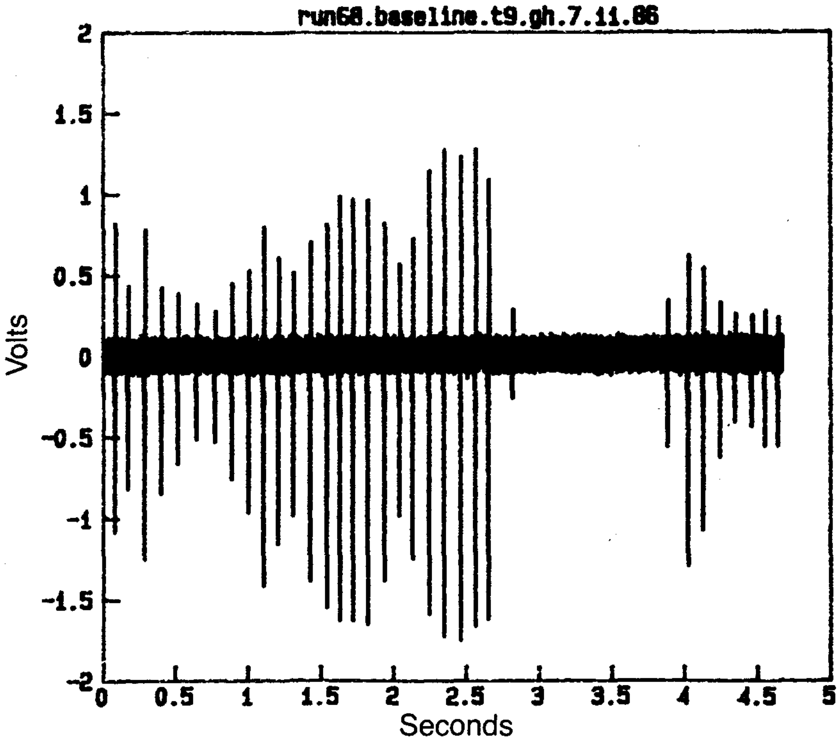
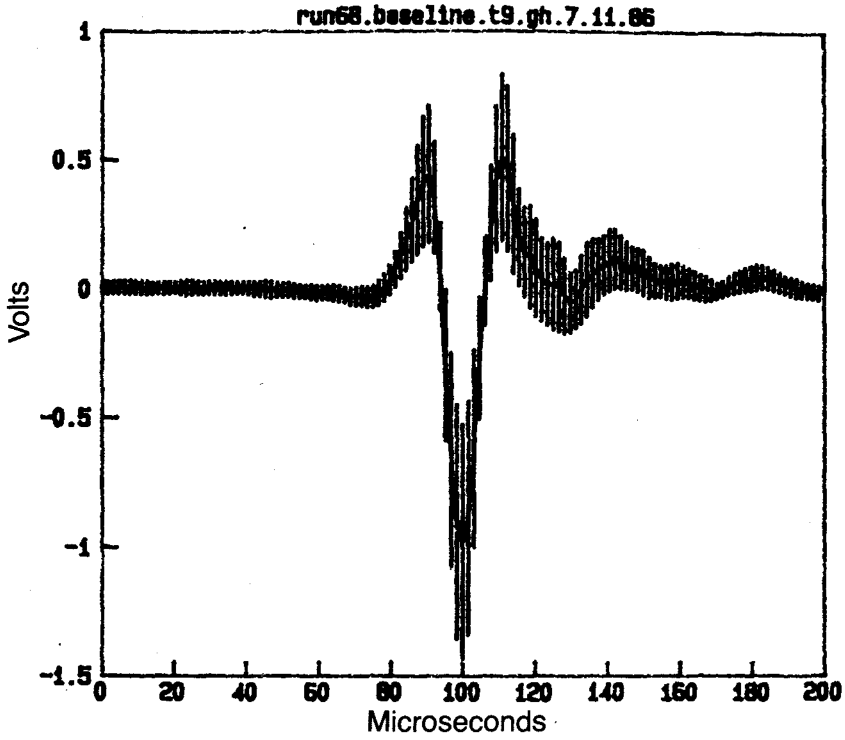

run68.baseline.t9.gh.7.11.86
Volts
Seconds
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5

Figure 8b. A listing of the clicks extracted from the sample and the times of their occurrence in milliseconds relative to the beginning of the sample.

```
Jan 21 19:13 1987  cndtms Page 1


run68.baseline.t9.gh.7.11.86
  1   64.9953
  2   147.822
  3   245.056
  4   341.328
  5   437.445
  6   539.028
  7   647.266
  8   753.417
  9   841.691
  10   923.733
  11   1013.67
  12   1099.18
  13   1198.97
  14   1285.18
  15   1362.75
  16   1439.35
  17   1525.24
  18   1613.67
  19   1705.12
  20   1788.19
  21   1869.84
  22   1960.61
  23   2051.23
  24   2139.63
  25   2219.83
  26   2357.31
  27   3244.60
  28   3356.13
  29   3454.38
  30   3533.02
  31   3625.49
  32   3719.76
  33   3791.59
  34   3873.85
  35   3956.10
  36   4044.75
  37   4136.67
  38   4218.93
  39   4306.65
  40   4393.34
  41   4477.50
  42   4568.86
  43   4651.21
```

Figure 8c. The average waveform derived from the clicks listed in Figure 8b and its corresponding frequency spectrum. Bars on the waveform indicate the amplitude range in the sample.


run68.baseline.t9.gh.7.11.86
Volts
1
0.5
0
-0.5
-1
-1.5
0
20
40
60
80
100
120
140
160
180
200
Microseconds

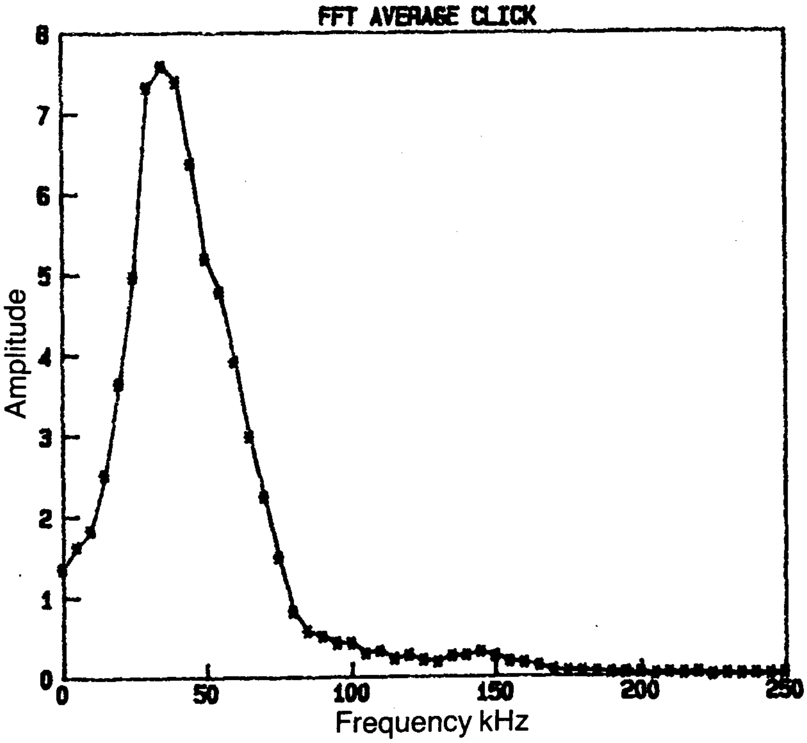
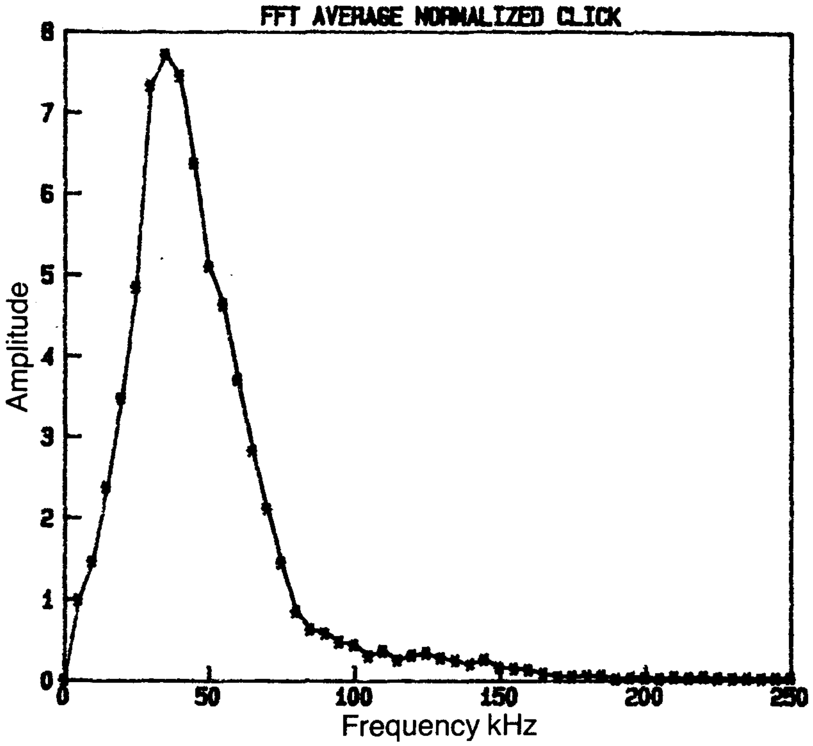

FFT AVERAGE CLICK
Amplitude
8
7
6
5
4
3
2
1
0
0
50
100
150
200
250
Frequency kHz

Figure 8d. The same as Figure 8c but normalizing the sample by placing the major negative peak of each click at -1 volt.


FFT AVERAGE NORMALIZED CLICK
Amplitude
0
1
2
3
4
5
6
7
8
0
50
100
150
200
250
Frequency kHz

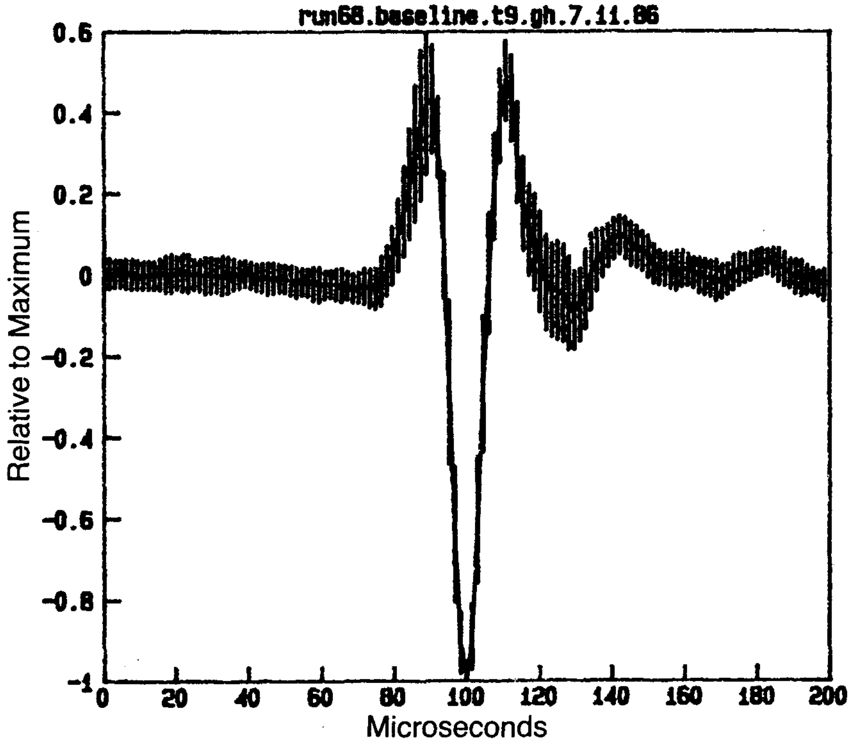

run68.baseline.t9.gh.7.11.86
Relative to Maximum
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
0
20
40
60
80
100
120
140
160
180
200
Microseconds

Figure 8e. The average frequency spectrum with amplitude range bars derived from the frequency spectra of the clicks listed in Figure 8b.

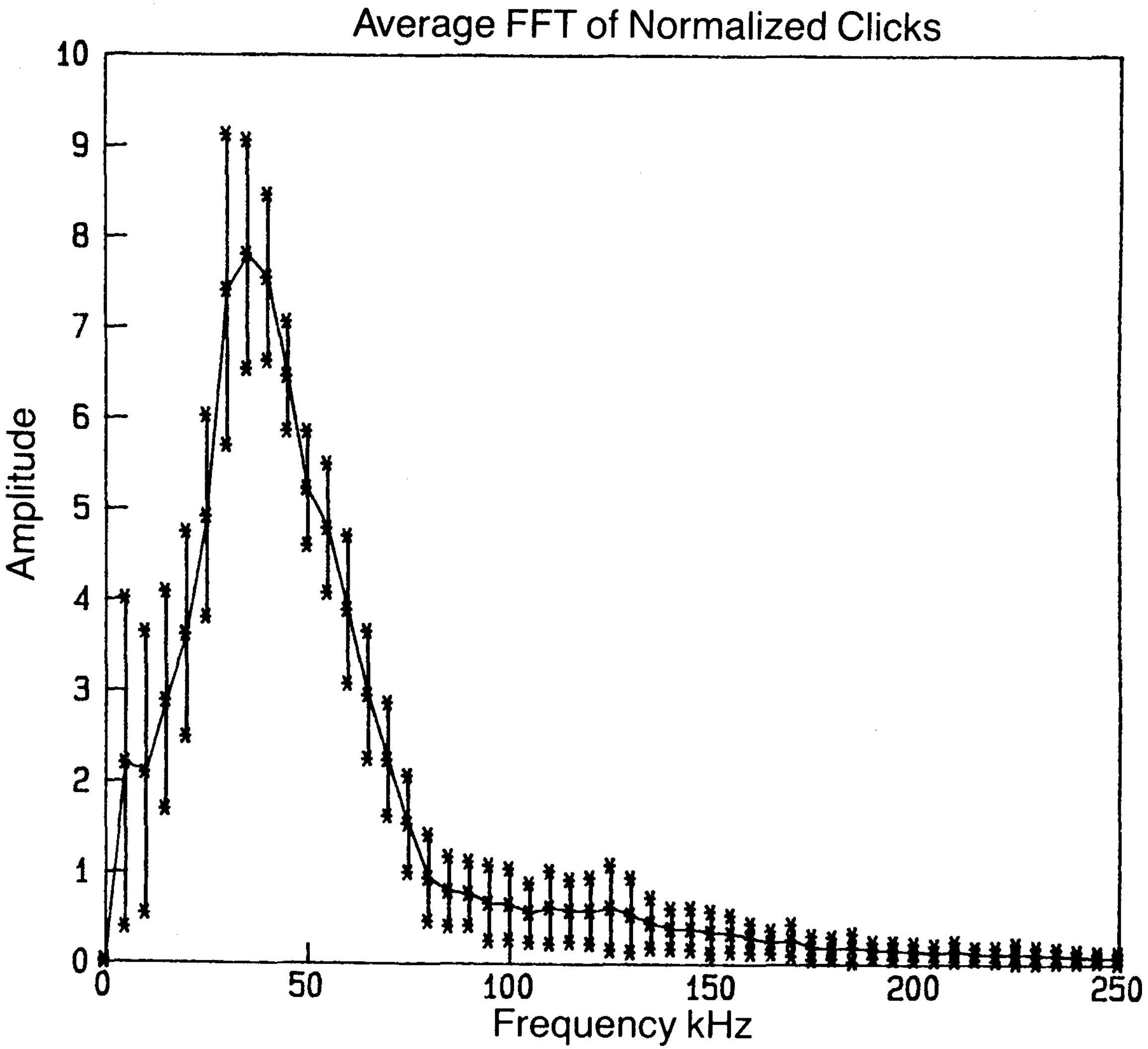
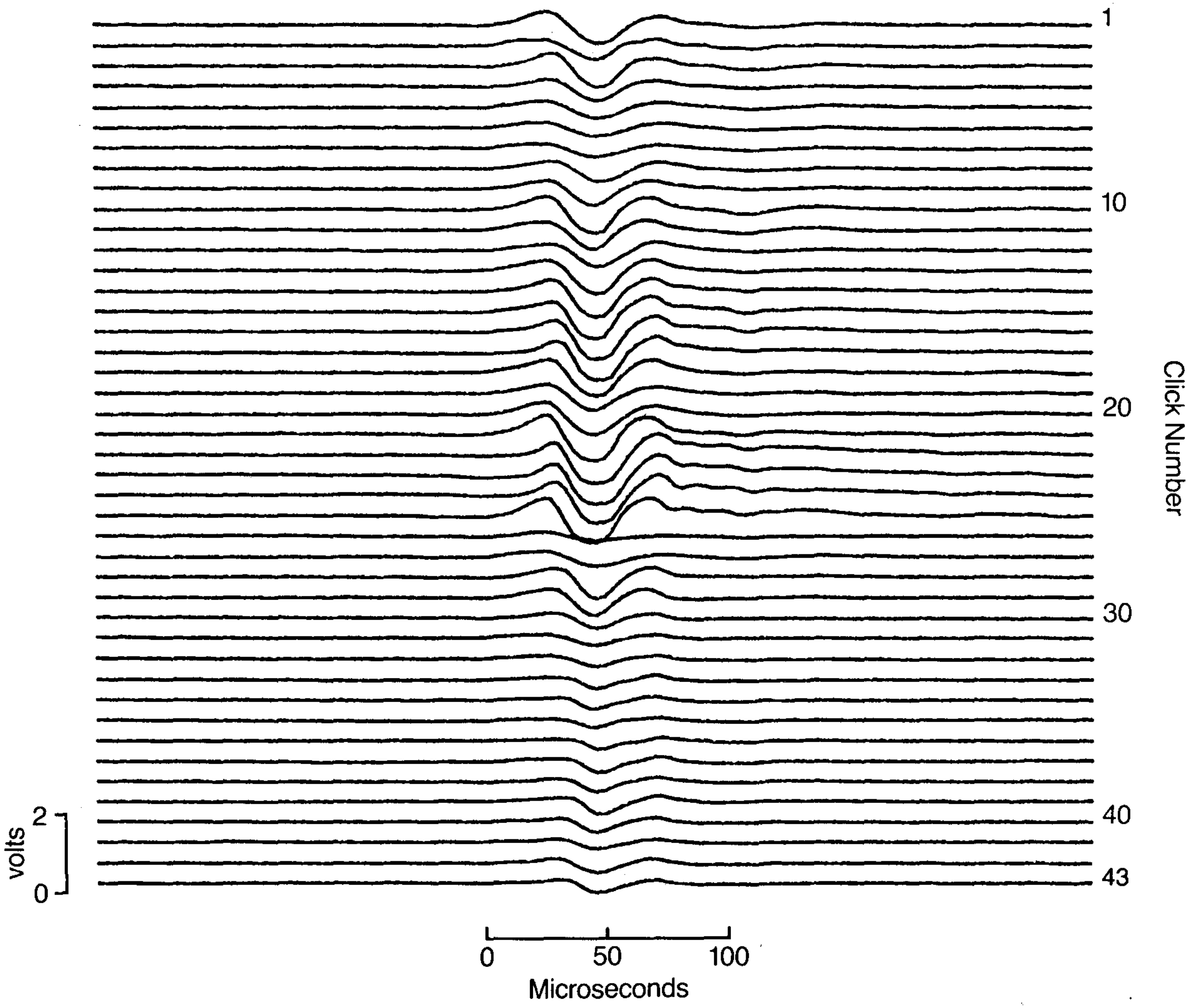

Average FFT of Normalized Clicks

Figure 8f. A waterfall display of all waveforms in the sample. Scales for time and amplitude are shown. Click numbers, as given in 8b, are shown on the right. The actual times between clicks are not represented.



run68.baseline.t9

Figure 8g. A waterfall display of all frequency spectra in the sample. Scales for frequency and amplitude are shown. Corresponding click numbers, as given in Figure 8b, are shown on the right.

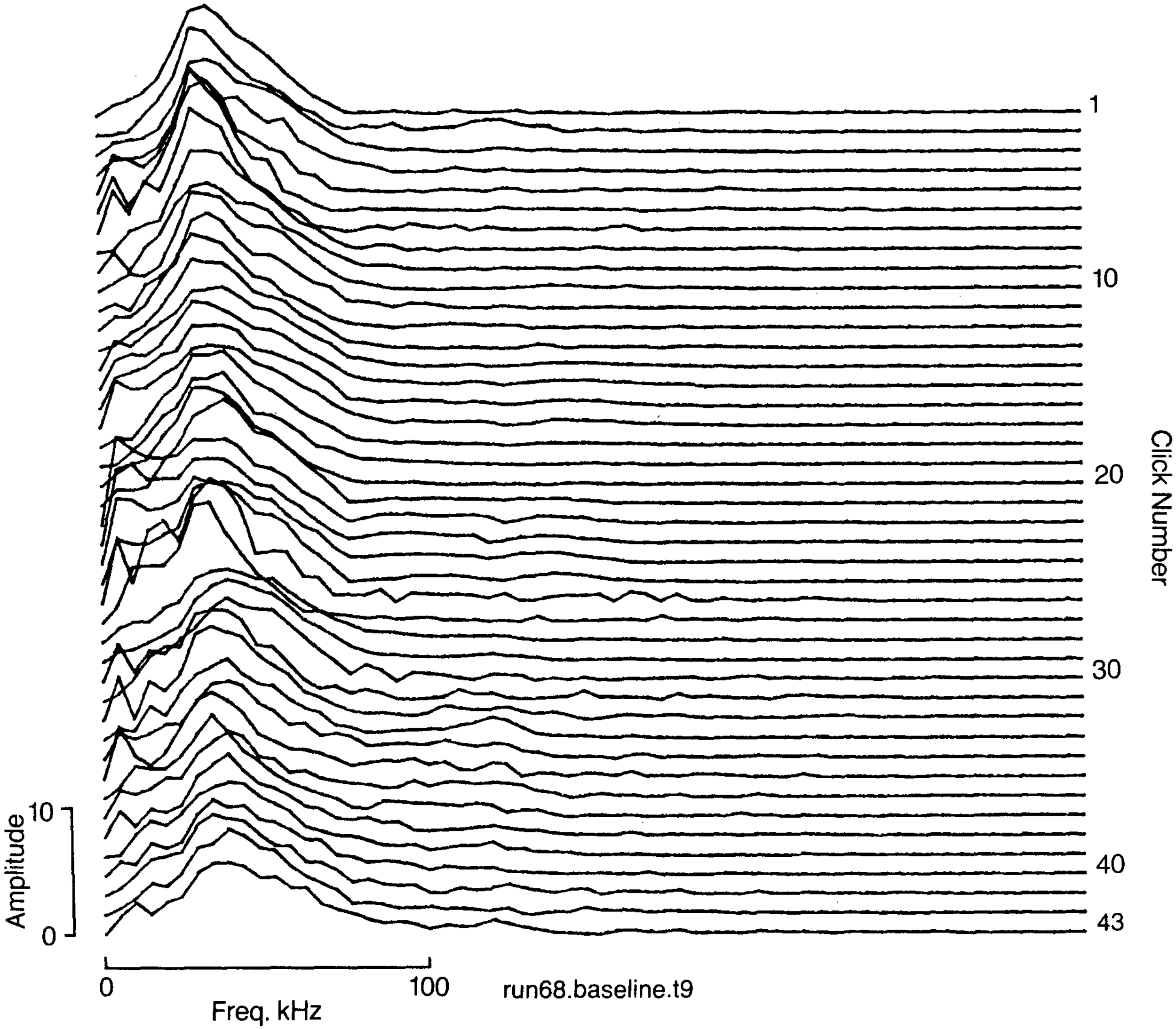
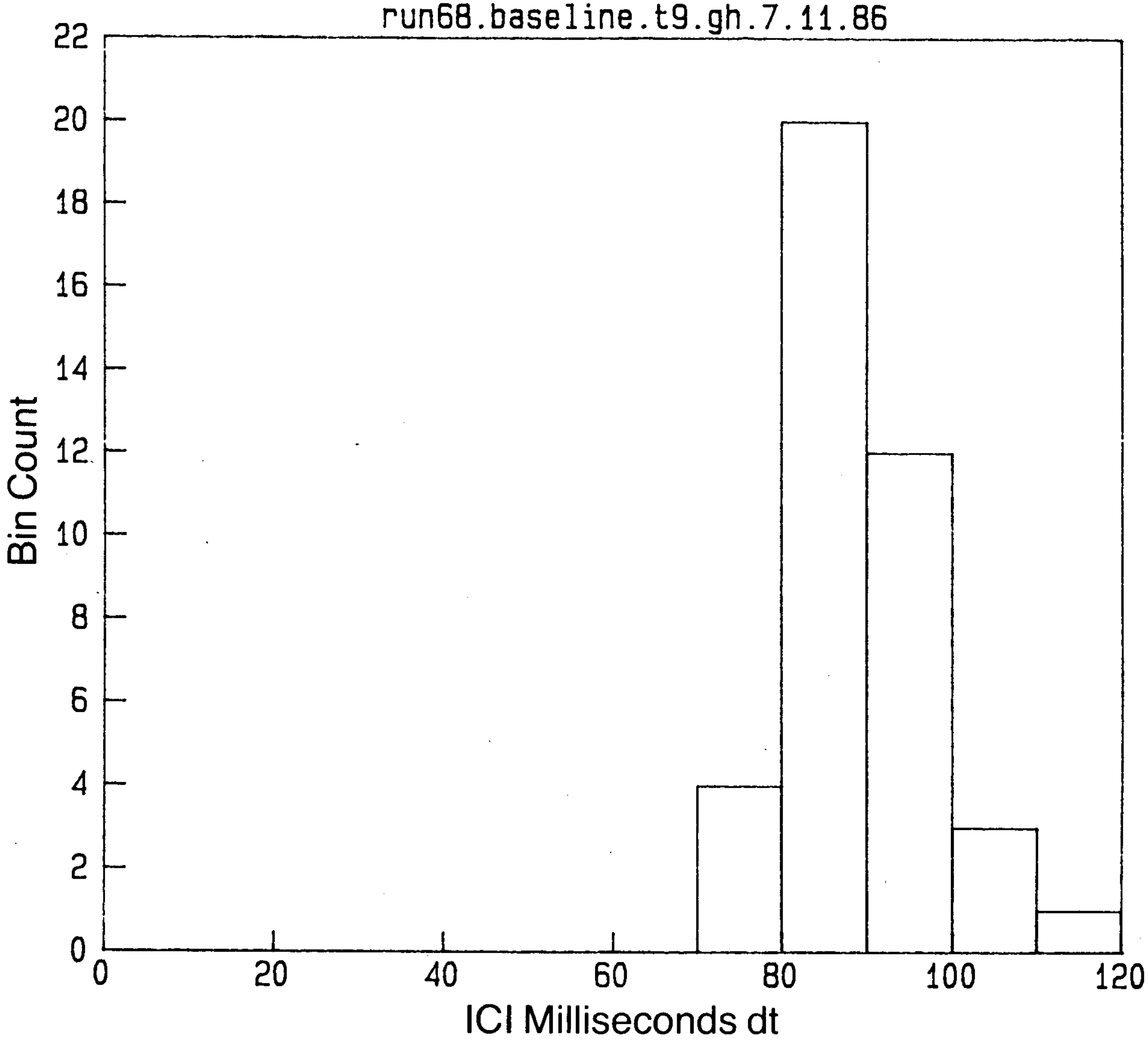

1
10
20
30
40
43
Click Number
Amplitude
10
0
0
100
Freq. kHz
run68.baseline.t9

Figure 8h. An interclick interval (ICI) histogram of all intervals less than 120 msec in the sample.


run68.baseline.t9.gh.7.11.86
Bin Count
0
2
4
6
8
10
12
14
16
18
20
22
0
20
40
60
80
100
120
ICI Milliseconds dt

RESULTS

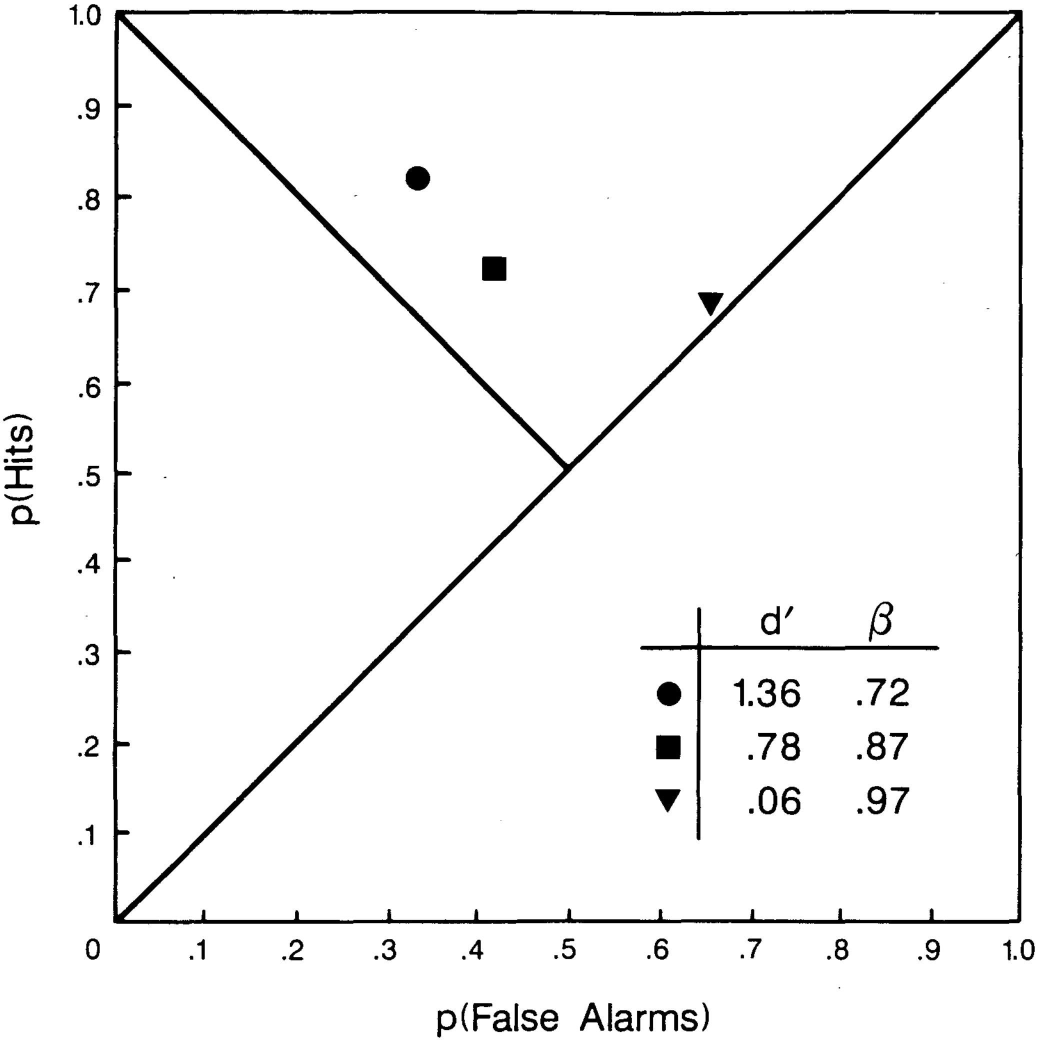
Behavioral Data

To facilitate the evaluation of the behavioral data gathered during this experiment, samples of equal size (N=200 trials) for each condition were employed. The samples taken from the control and experimental conditions represented all of the trials in which the dolphin was required to wear the respective hood. For the baseline condition, ten trials, which included an equal number of presentations of the two targets and approximately half of the errors observed in the session, were selected from each baseline session. The samples described in the following section, therefore, are as defined above unless otherwise specified.

Performance on the Discrimination Task

The dolphin's performance on the echolocation task across conditions was evaluated by application of Signal Detection Theory (Green and Swets, 1966). Figure 9 displays the data in a receiver-operating-characteristic (ROC) format. The ordinate is the probability of "hits," a "Go" response made after a presentation of the aluminum cylinder. The abscissa is the probability of "false alarms," a "Go" response made after a presentation of the sand-filled ring. Values for target sensitivity (d') and response bias (Beta) as defined by Green and Swets (1966) are displayed in the figure as well. Performance clearly

Figure 9. Response data plotted in a receiver-operating-characteristic (ROC) format, the probability of hits versus the probability of false alarms. Values for target sensitivity (d′) and response bias (Beta) are displayed. Performance and target sensitivity diminished across conditions while a relatively unbiased response criterion was maintained. Circle = baseline condition, Square = control condition, Triangle = experimental condition. Each point = 200 trials.


1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
0
p(Hits)
.1
.2
.3
.4
.5
.6
.7
.8
.9
1.0
p(False Alarms)
d′ β
● 1.36 .72
■ .78 .87
▼ .06 .97

fell from well above chance in the baseline and control conditions to just above chance in the experimental condition. The d′ values indicate that target sensitivity was clearly diminished in the experimental condition suggesting that the dolphin had difficulty detecting the target under that condition. Beta values (1.0 = no bias) indicate that a relatively unbiased response criterion was maintained across conditions with a slightly stronger tendency to make "Go" responses in the experimental condition.

Figure 10 summarizes the dolphin's performance in terms of percent correct for each of the three conditions tested over time. Chi-square tests of association (Siegel, 1956) were applied to evaluate the differences in performance on the echolocation task in terms of the proportions of correct responses to incorrect responses. Table 1 summarizes the Chi-square values reported below. The differences in performance across all three conditions ($X^2 = 24.1$, $p < .001$) and between the baseline and experimental conditions ($X^2 = 22.6$, $p < .001$) were significant. Furthermore, the insignificant differences between the baseline and control conditions ($X^2 = 3.8$, $p = .05$) and the significant differences between the control and experimental conditions ($X^2 = 7.6$, $p < .01$) indicate that performance was distinctly affected by the use of the experimental sound-attenuating hood as opposed to being an artifact of the placement of any arbitrary covering over the dolphin's lower jaw.

The control and experimental conditions provided opportunities to directly compare the effect of hood use and non-use within a session, from trial to trial, in contrast to the comparison of different session

Figure 10. Performance in terms of the percent of correct responses per session plotted over time by condition. Baseline = 20 trials/point, Control and Experimental = 10 trials/point. * Indicates tape recorded sessions.

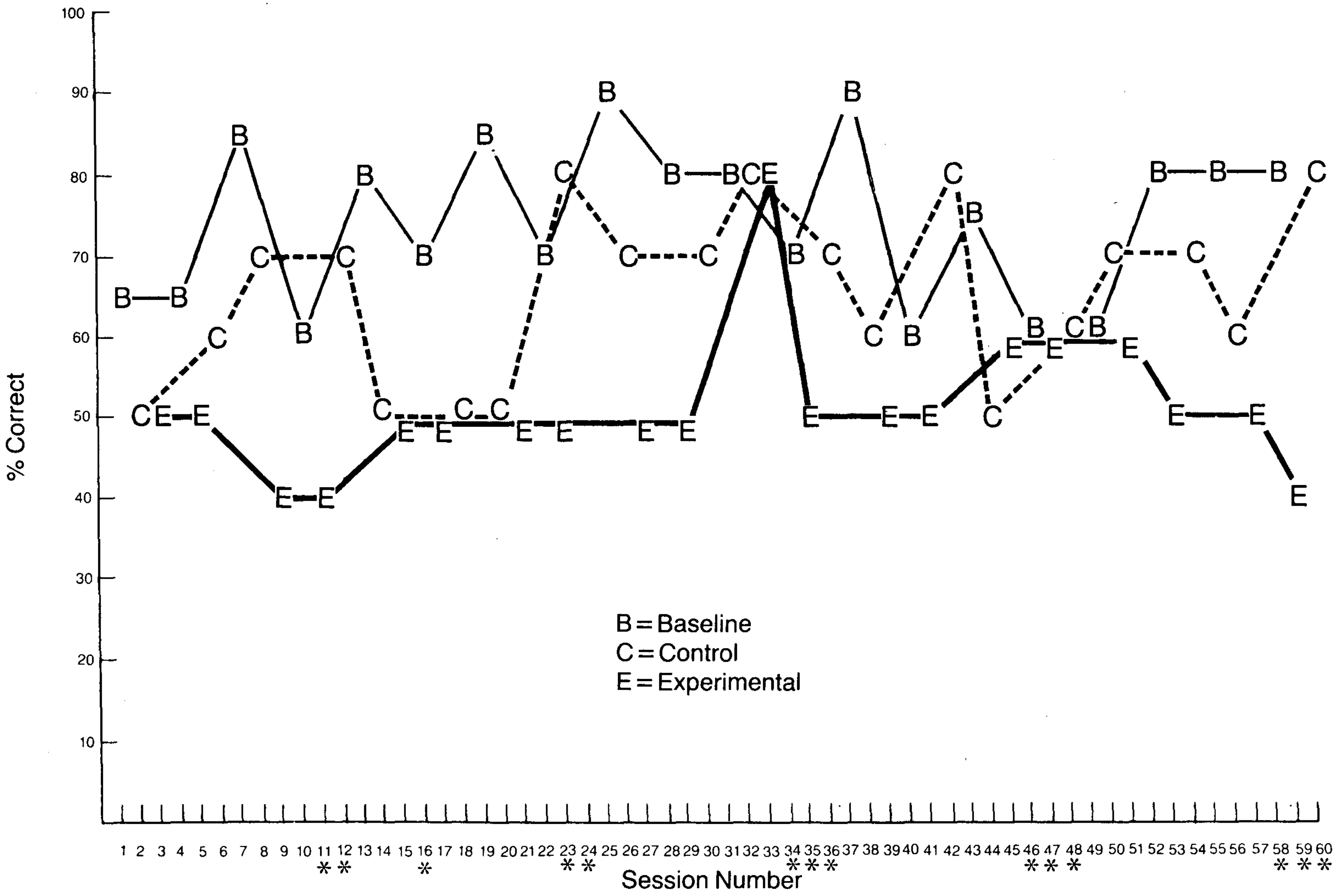

% Correct
100
90
80
70
60
50
40
30
20
10
B = Baseline
C = Control
E = Experimental
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60
* * * * * * * * * * * * * *
Session Number

Table 1

Chi-square values for the difference in performance in terms of the proportions of correct responses to incorrect responses across the conditions indicated.

Baseline	Control	Experimental	N	df	X^2	p
x	x	x	600	2	24.1	< .001
x		x	400	1	22.6	< .001
	x	x	400	1	7.6	< .01
x	x		400	1	3.8	= .05
Hooded vs. Unhooded Trials						
Control Condition			400	1	3.4	> .05
Experimental Condition			400	1	16.9	< .001

types over time. Therefore, to further evaluate the effect of the hoods on performance, Chi-square tests were applied to the differences observed between the trials conducted with and without a hood within the control and the experimental conditions. Figure 11 compares the percent of correct responses made with and without a hood in each session of the control condition and Figure 12 displays the comparable data for the experimental condition. The difference in performance within the control condition was not significant ($X^2 = 3.4$, $p > .05$). However, the difference in performance within the experimental condition was significant ($X^2 = 16.9$, $p < .001$) again suggesting an effect caused by the experimental hood.

Collateral Behavior

Of the eight collateral behaviors that had been anticipated, six were observed and only two of those occurred with any notable frequency (see Appendix I). The occurrences of these collateral behaviors do not appear to be correlated to any particular variable such as test condition, target, or response type.

The suppression of signals and unusually long response latencies were not observed. In the case of the former, it will be noted later that there were, in fact, two tape recorded trials in which no acoustic signals were present.

Headscanning in the vertical plane, holding the head cocked, the emission of air bubbles, and the displacement of hoods each occurred in fewer than 9% of the total number of trials conducted. Headscanning in the horizontal plane was observed in 31% of the trials, with 17% of

Figure 11. The percent of correct responses made with and without a hood per session in the control condition. Each point = 10 trials.

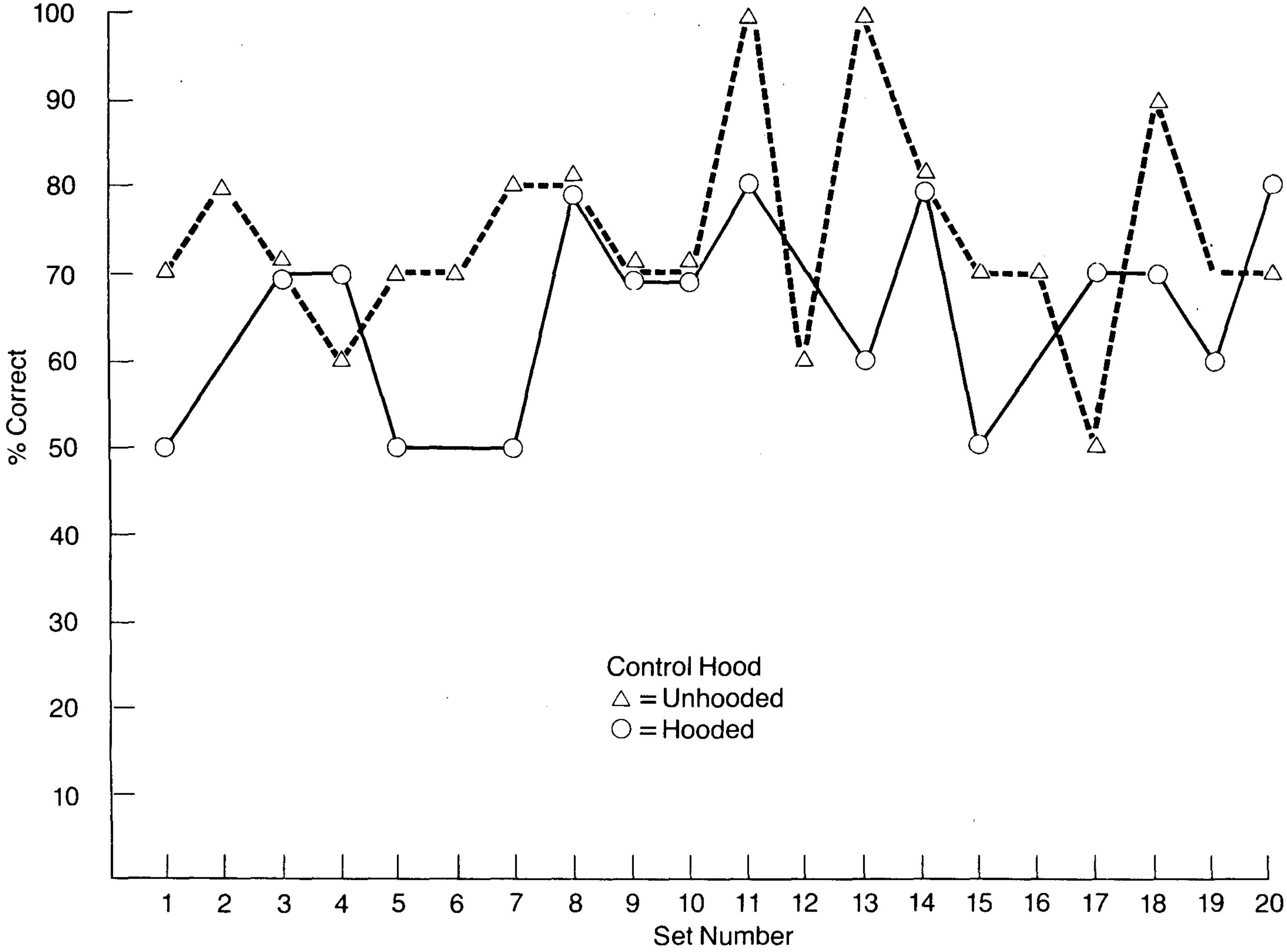
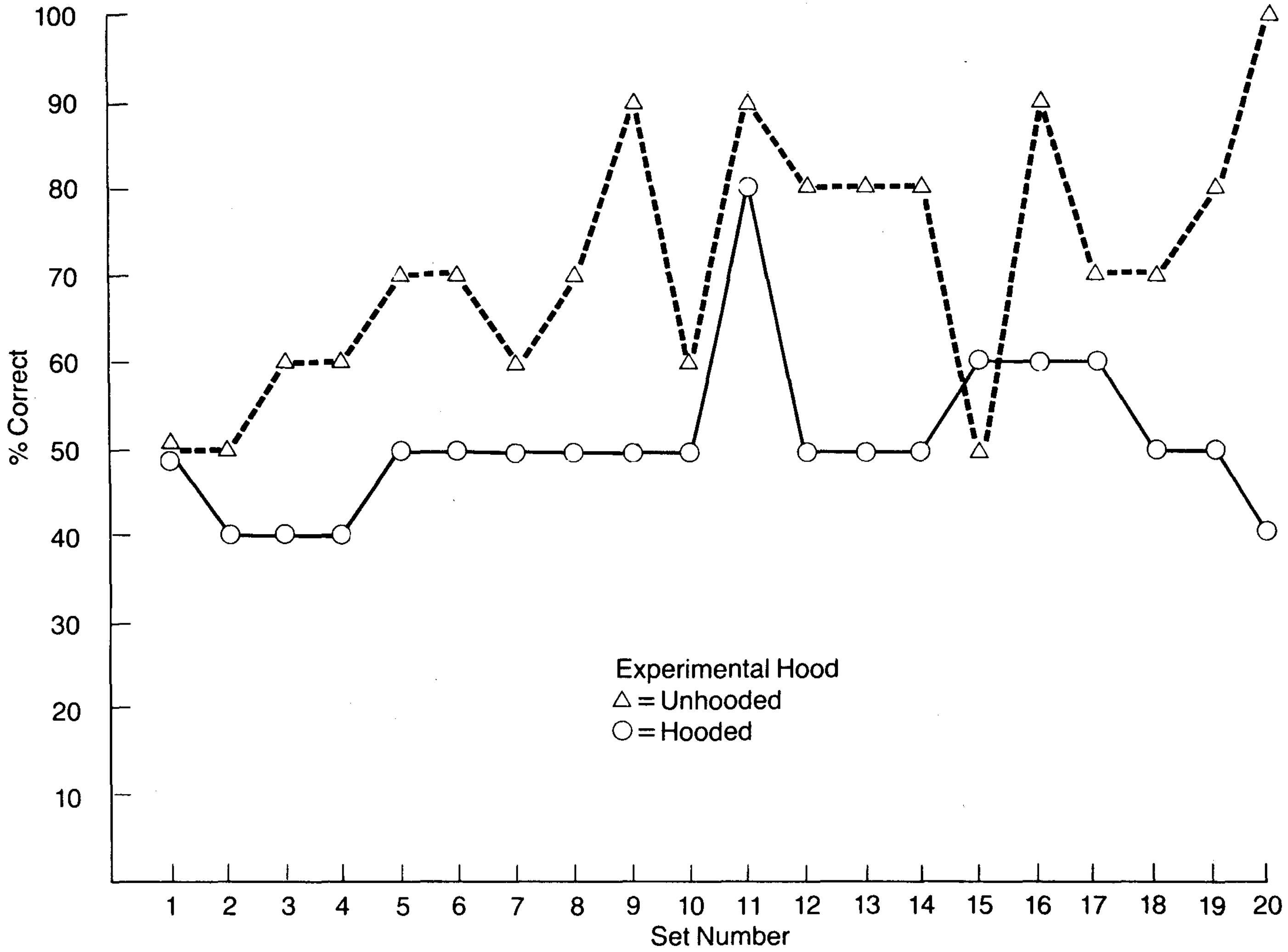

100
90
80
70
60
50
40
30
20
10
% Correct
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
Set Number
Control Hood
△ = Unhooded
○ = Hooded

Figure 12. The percent of correct responses made with and without a hood per session in the experimental condition. Each point = 10 trials.


100
90
80
70
60
50
40
30
20
10
% Correct
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
Set Number
Experimental Hood
△ = Unhooded
○ = Hooded

those observations occurring under hooded conditions. Holding the mouth open was the most frequent collateral behavior observed, occurring in 46% of the trials. The nature of the hood, however, eliminated the possibility of this behavior during hooded trials due to the strap over the dolphin's snout.

General Behavior During Sessions

Nemo's responses during the echolocation task were, for the most part, clear and definite. In making "hits," he often quickly pulled away from the second eyecup to leave his station just prior to the withdrawal of the target and head directly for the response manipulandum. In making "correct rejections," he held his position once the second eyecup was removed, drifting only slightly back and forth and remaining in the plane of the hoop, until the clicker was sounded at which time he would back out of the hoop station and turn to his left, away from the response manipulandum, to return to the first trainer. "False alarms" were often made after a slight delay. Nemo would back away from the hoop and turn toward the response manipulandum and look back toward the second trainer who would ignore him. For trials during which "misses" were made, he would stay in the hoop station for as long as ten seconds beyond the fifteen seconds during which the clicker would be expected and then, after not hearing the clicker, would leave and hit the response manipulandum before returning to the first trainer.

Responses were fairly similar across conditions with one significant exception. During hooded trials, regardless of the type of hood being used, Nemo would slightly thrash his head as he submerged at the beginning of a trial, remain calm while in station, and then thrash again, more vigorously, once he backed away from the hoop station to discard the hood before making a "Go" response or returning to the first trainer after making a "No-go" response. Before the next trial, either the first trainer would have Nemo retrieve the hood or the second trainer would simply pick it up and toss it back depending on who was closer to it.

There were trials in the baseline condition during which the second trainer could observe Nemo following the presentation of a target with head movement in the vertical plane. Once the second eyecup was in place, Nemo would point his snout toward the point of target entry at the water's surface and then lower his head to a horizontal position simultaneous to the presentation of a target. During such times, "buzzing" or rapidly emitted echolocation signals were clearly audible to the second trainer.

A concerted effort made to keep the other four dolphins away from the test area was not always successful. Angie, the oldest female in the group and a frequent companion of Nemo's, would occasionally swim into the area to investigate or Nemo would leave in between trials to swim to the other end of the pool and show interest in Angie or other members of the group. On a few occasions, it proved helpful to keep Angie in the test area. As long as she was close by, Nemo was more attentive to the task at hand and stayed in the test area.

Acoustical Data

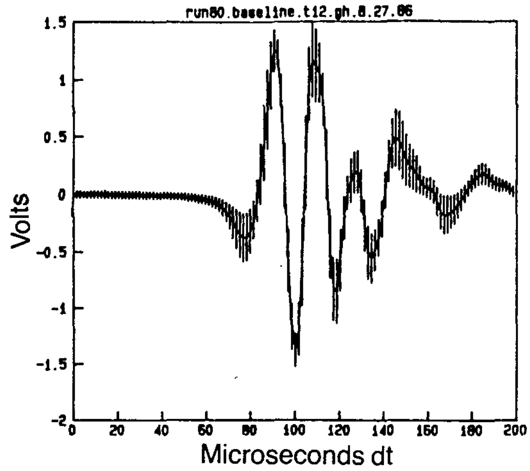
The evaluation of the acoustical data recorded during the course of this experiment sought to examine and compare the amplitudes, peak frequencies, -3 dB bandwidths, interclick intervals (ICI's), and the numbers of echolocation clicks emitted by the dolphin with the assumption that he might employ some noticeable strategy in the emission of his outgoing signals in order to compensate for the attenuation of incoming signals at his lower jaw.

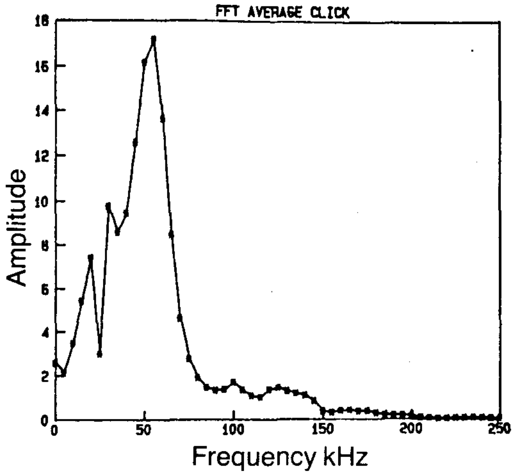
In consideration of the debate over the site of sound production for echolocation signals, a question to be addressed was whether or not the use of either of the two rubber hoods in any way distorted the dolphin's outgoing signals. Figure 13 displays the average waveform and its corresponding frequency spectrum of a representative trial from each of the three conditions tested. In general, there was little variation in terms of the waveforms and signal characteristics examined across conditions. The echolocation signals recorded during this experiment typically had durations of approximately 140-150 usec, peak frequencies between 30 and 55 kHz, -3 dB bandwidths of 30 to 50 kHz, and peak-to-peak sound pressure levels (SPLpp) between 170 and 180 dB re: 1 uPa at 1 m, with few exceptions. It is interesting to note that Diercks et al. (1971) reported a peak frequency of 35 kHz and Evans (1973) reported a peak frequency range of 35 to 60 kHz for the same species (Tursiops truncatus) in a concrete pool which agree with the range reported above.

Table 2 lists the values for SPLpp, peak frequency and -3 dB bandwidth taken from the average waveform and its corresponding

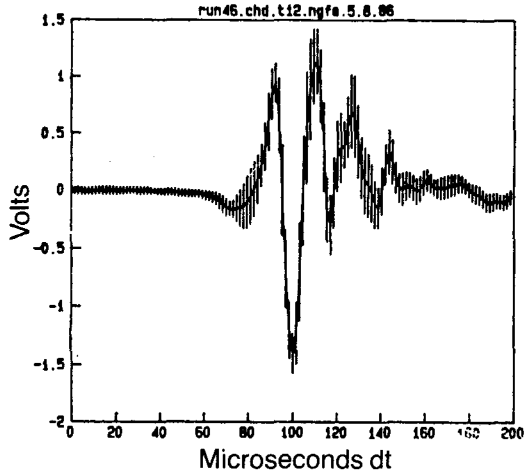
Figure 13. Average waveforms derived from all of the clicks in the sample and their respective frequency spectra shown for each of the three conditions tested.

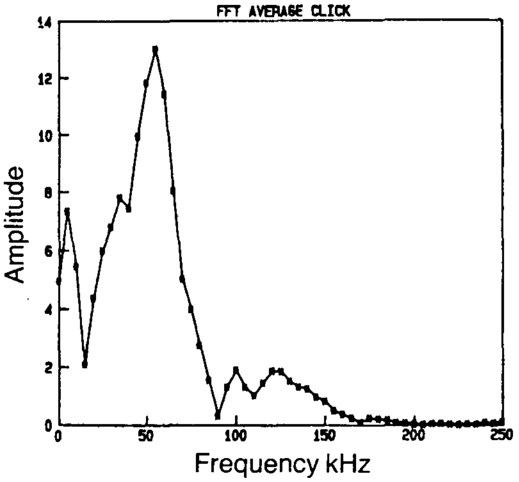
Baseline



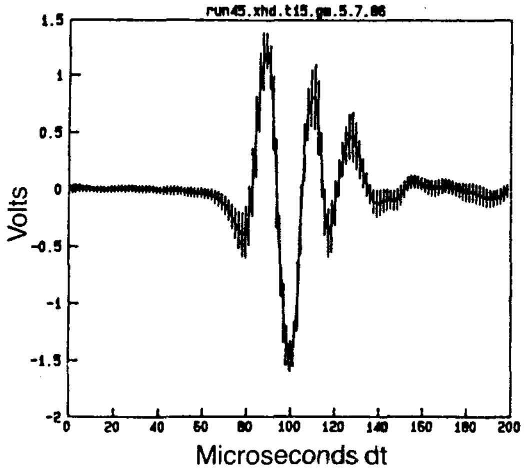


Control Hood





Experimental Hood



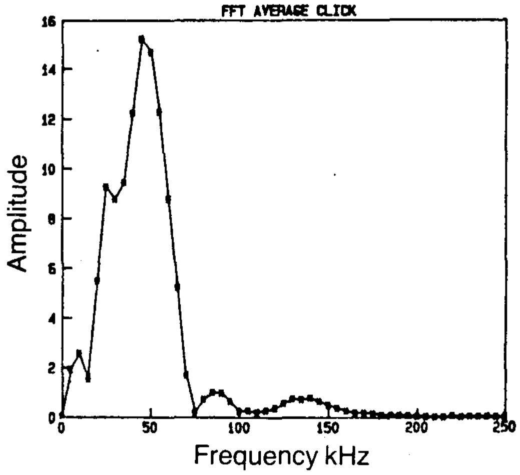


Table 2

Signal characteristic values for each trial in each of the tape recorded sessions. Values for peak-to-peak SPL's, and peak frequencies were taken from the average waveform for each trial. Values for bandwidths were taken from frequency spectra of the average waveforms. Refer to Figure 8. (- indicates unavailable data).

Trial#	SPL re:1uPa	f_p (kHz)	BW (kHz)	# of Clicks
Session 11 Experimental				
3	170.23	41	53	90
5	177.7	46	35	40
7	177.7	30	40	44
15	178.03	45	40	25
17	164.52	50	36	34
19	173.32	45	46	9
20	173.26	45	44	81
Session 12 Control				
5	171.68	55	50	15
9	177.36	55	37	14
10	173.48	55	50	61
12	177.36	55	40	46
14	176.25	56	50	39
18	176.25	55	46	72
Session 16 Baseline				
1	177.36	54	43	129
5	178.03	30	30	41
10	175.84	30	41	80
14	177.7	29	39	59
15	174.01	35	44	84
16	-	-	-	69
17	177.0	30	26	61
18	173.48	30	20	35

Trial#	SPL re:1uPa	f_p (kHz)	BW (kHz)	# of Clicks
Session 23 Experimental				
2	177.7	46	39	8
4	175.84	60	55	81
6	174.01	46	41	47
8	177.0	43	51	115
10	164.67	37	49	11
11	170.91	-	-	2
15	169.57	55	73	9
18	169.49	-	-	24
Session 24 Control				
3	174.26	45	45	31
4	177.18	44	45	44
6	177.0	30	45	47
8	178.03	40	39	30
10	176.63	54	41	26
11	174.51	40	23	38
13	177.36	55	40	28
17	177.0	30	37	23
Session 34 Baseline				
2	174.98	35	37	77
3	176.44	30	37	60
4	177.7	30	35	43
5	177.36	55	35	40
6	177.36	30	28	92
7	178.03	35	23	48
9	172.81	35	42	43
14	174.26	37	53	123
15	174.98	35	35	98
17	176.25	30	42	119
Session 35 Experimental				
2	171.34	35	35	95
3	173.48	35	53	98
8	174.01	35	50	108
9	176.25	35	46	86
11	170.23	37	47	132
12	172.75	36	64	226
14	177.0	30	37	103
16	176.25	40	45	56
18	169.82	30	63	84

Trial#	SPL re:1uPa	f_p (kHz)	BW (kHz)	# of Clicks
Session 36 Control				
3	177.0	30	38	53
5	177.0	55	40	85
6	174.98	35	40	54
8	175.84	35	52	128
9	175.84	55	48	74
11	170.23	30	37	57
14	175.2	35	28	25
15	174.51	35	48	71
17	175.84	40	41	70
19	175.84	40	46	48
Session 46 Baseline				
1	176.63	55	24	73
2	177.36	55	23	54
5	177.36	55	35	57
6	177.36	55	35	36
8	174.01	50	38	75
12	177.7	55	36	67
13	175.42	30	35	93
14	178.34	35	37	165
16	175.42	55	36	48
19	177.0	50	35	63
Session 47 Experimental				
5	177.0	30	45	46
6	177.36	50	34	22
8	176.63	30	30	24
11	178.03	30	40	11
12	177.36	30	30	30
14	175.84	40	37	9
15	177.7	30	33	3
17	177.7	30	36	7
19	170.98	30	44	10
Session 48 Control				
4	177.0	30	38	74
5	178.03	30	15	15
9	176.25	30	20	23
10	176.25	40	45	25
12	177.0	54	37	33
13	176.63	55	35	38
15	174.98	30	57	49
16	-	-	-	19
17	176.44	55	66	39
19	178.65	30	35	19

Trial#	SPL re:1uPa	f_p (kHz)	BW (kHz)	# of Clicks
Session 58 Baseline				
1	178.65	23	23	75
3	169.4	23	34	63
5	174.51	25	45	90
7	170.98	30	44	60
9	178.03	25	45	78
12	176.25	25	45	129
14	176.25	25	53	118
16	177.7	25	28	55
18	175.42	24	35	115
Session 59 Experimental				
3	-	-	-	0
4	178.03	30	38	2
6	172.92	30	35	11
7	174.51	30	27	115
10	175.42	30	25	39
11	162.66	30	14	2
12	171.68	40	45	53
15	173.48	45	20	4
16	-	-	-	0
18	174.26	30	35	98
Session 60 Control				
3	-	-	-	37
5	-	-	-	87
8	178.19	30	40	66
10	177.36	35	55	141
12	178.94	24	34	60
13	176.63	55	42	48
14	172.32	25	40	55
16	177.36	24	23	4
17	176.25	30	40	37
19	177.36	25	30	48

frequency spectrum, and the number of echolocation clicks identified, per trial per recorded session. Note that there are two trials in the last experimental session in which no emitted signals were detected. Table 3 lists the mean values per recorded session based on the values given in Table 2.

Interclick intervals (ICI), the time between one click, or pulse, and its succeeding click, can be defined as the sum of two time components; the two-way transit time for sound between the dolphin and its target plus the processing time (cf. Morozov, Akopian, Burdin, Zaytseva, and Sokovykh, 1972) during which information contained in the incoming signal is being processed by the central auditory system. In this experiment, the two-way transit time between the dolphin and the target was 4 msec and the two-way transit time between the dolphin and the far end of the pool was 30 msec. There has been a good deal of variation reported in the length of the information processing component in ICI's. Au, Floyd, Penner, and Murchison (1974), for example, reported mean values as high as 50 msec over the two-way transit time for the target in the ICI's they measured. Considering those factors and a review of the ICI histograms for the trials recorded in this experiment, 120 msec was chosen as the acceptable maximum ICI. This value allowed for the 30 msec transit time and a liberal processing time. All ICI's greater than 120 msec were assumed to be the intervals between trains of clicks and were excluded from the samples.

Table 4 lists the minimum ICI, mean ICI, and number of ICI's in the sample per trial per recorded session. Histograms using bin widths of 10 msec were generated for each trial. The histograms were then

Table 3

Mean signal characteristic values for each tape recorded session derived from the values given in Table 2. N equals total number of clicks extracted from each session.

Session	SPLpp	f_p	BW	Clks	N
Baseline					
16	176.20	34.0	34.7	69.75	558
34	176.02	35.2	36.7	74.30	743
46	176.66	49.5	33.4	73.10	731
58	175.24	25.0	39.1	87.00	783
					2,815
Control					
12	175.40	55.2	45.5	41.17	247
24	176.50	42.3	39.4	33.38	267
36	175.23	39.0	41.8	66.50	665
48	176.80	39.3	38.7	33.40	334
60	176.80	31.0	38.0	58.30	583
					2,096
Experimental					
11	173.54	43.1	42.0	46.14	323
23	172.40	47.8	51.3	37.13	297
35	173.46	34.8	48.9	109.8	988
47	176.51	33.3	36.6	18.00	162
59	172.87	33.1	29.9	32.40	324
					2,094

Total N = 7,005

Table 4

Values for minimum interclick intervals (ICI), mean ICI, and number of ICI's for each trial in each tape recorded session. N equals total number of ICI's in each trial. (- indicates no ICI's less than 120 msec).

Trial #	Min ICI (msec)	Mean ICI (msec)	N
Baseline			
Session 16			
1	17.5	24.17	128
5	31.48	62.57	37
10	38.55	52.61	76
14	11.25	55.13	54
15	42.11	56.63	77
16	34.47	73.91	63
17	39.41	60.22	59
18	35.86	69.16	29
Session 34			
2	39.25	57.65	74
3	39.56	48.27	57
4	32.42	83.86	38
5	83.5	107.49	36
6	22.09	43.09	90
7	42.81	60.94	39
9	71.83	89.03	40
14	13.04	36.08	120
15	14.61	44.93	96
17	17.67	33.47	117

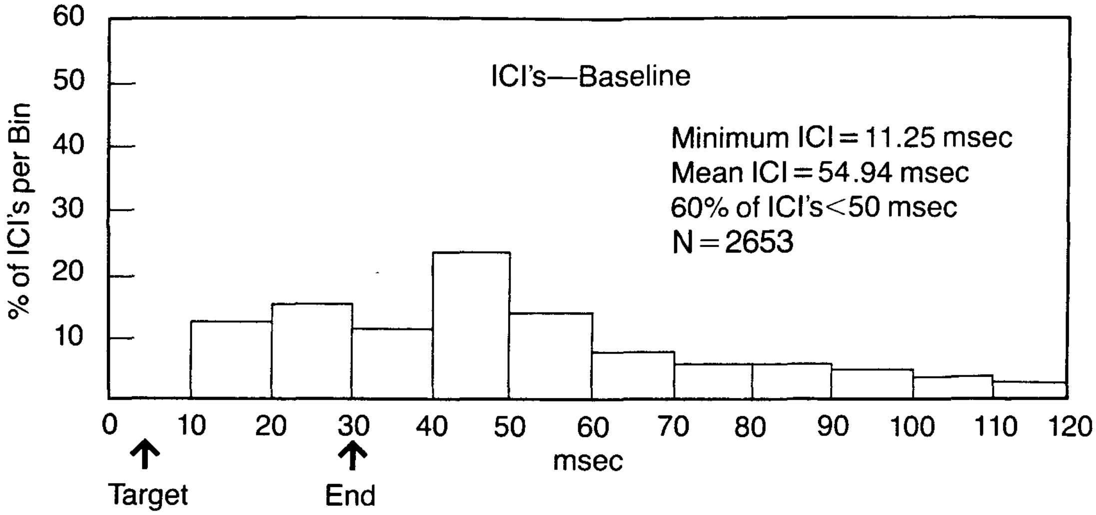
Trial #	Min ICI (msec)	Mean ICI (msec)	N
Session 46			
1	22.86	51.54	70
2	25.4	59.55	47
5	47.94	68.68	54
6	41.71	59.66	28
8	42.23	62.4	74
12	40.13	50.21	63
13	18.06	43.86	88
14	17.9	25.94	157
16	62.43	95.53	45
19	31.59	56.17	56
Session 58			
1	36.0	53.6	72
3	19.29	55.74	58
5	17.22	47.83	81
7	34.42	44.55	53
9	33.5	50.74	71
12	17.55	29.35	128
14	14.63	35.27	113
16	19.65	46.98	52
18	22.67	42.21	113
		Total N =	2,653
Control			
Session 12			
5	66.33	93.7	13
9	18.66	67.05	8
10	33.12	46.27	56
12	22.04	46.3	42
14	42.93	51.09	38
18	30.98	46.91	69
Session 24			
3	29.49	53.25	28
4	36.21	65.49	42
6	44.9	78.17	46
8	39.08	73.41	26
10	39.20	50.19	25
11	46.64	74.84	30
13	19.54	36.81	25
17	28.64	64.54	19

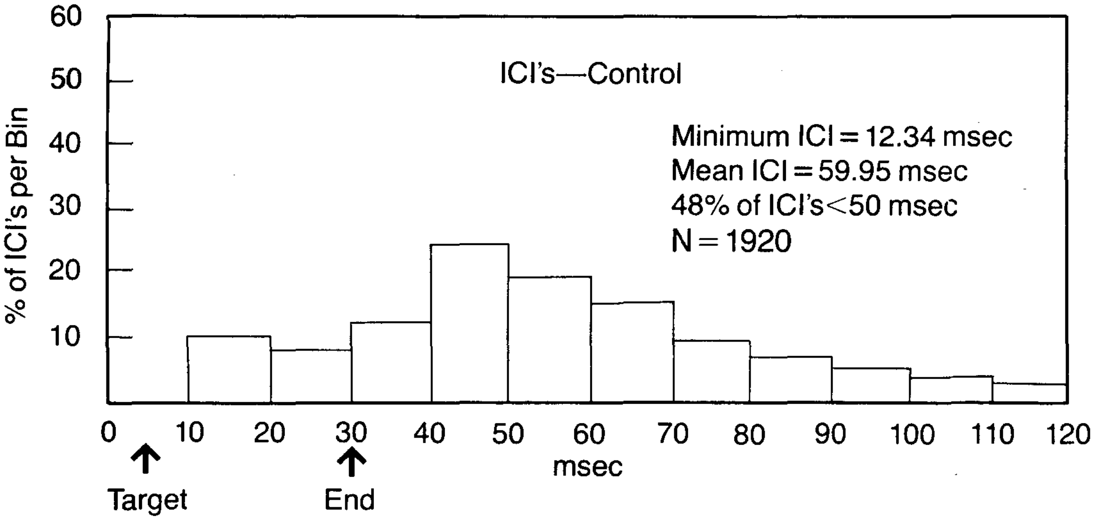
Trial #	Min ICI (msec)	Mean ICI (msec)	N
Session 36			
3	46.46	82.65	44
5	28.79	46.46	83
6	26.33	50.43	49
8	12.92	37.38	127
9	35.42	60.27	70
11	40.33	64.61	52
14	39.69	68.34	23
15	35.05	58.27	66
17	46.93	66.0	69
19	51.44	73.34	37
Session 48			
4	16.6	39.76	61
5	70.35	88.04	8
9	59.8	87.38	12
10	72.98	93.25	20
12	52.41	72.12	28
13	53.2	89.66	33
15	56.6	80.21	37
16	43.79	62.34	14
17	49.89	71.86	31
19	56.17	60.47	2
Session 60			
3	52.4	68.58	34
5	14.12	37.84	84
8	17.65	27.74	62
10	12.34	35.58	140
12	33.87	42.27	59
13	42.54	58.38	47
14	13.6	44.27	82
16	-	-	-
17	39.28	53.94	33
19	14.50	25.78	46
		Total N =	1,920

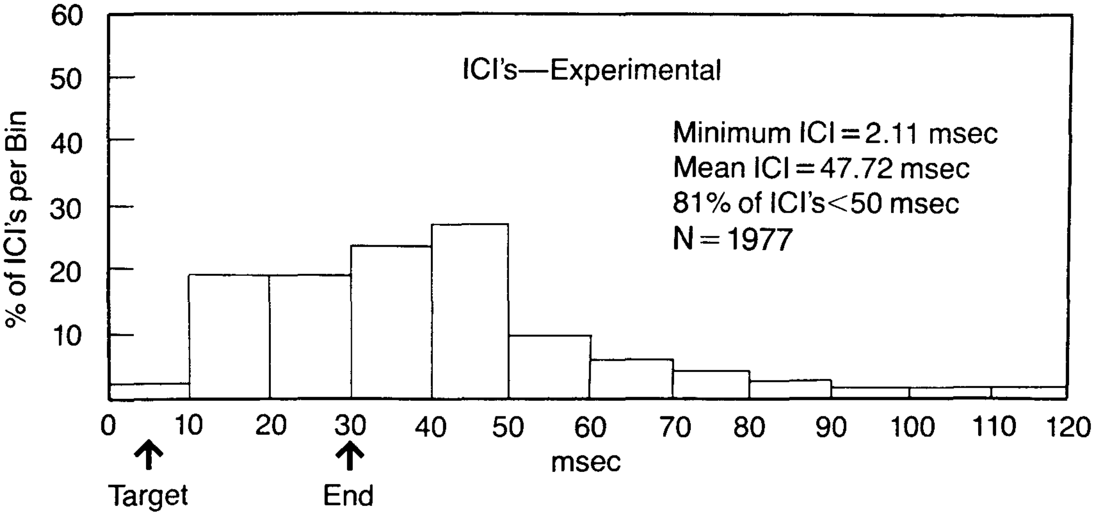
Trial #	Min ICI (msec)	Mean ICI (msec)	N
Experimental			
Session 11			
3	2.1	33.07	88
5	35.16	48.86	38
7	5.64	35.02	39
15	25.12	42.93	23
17	19.08	32.01	29
19	64.59	95.11	3
20	17.62	34.08	79
Session 23			
2	43.78	71.99	6
4	37.38	45.62	80
6	41.06	48.84	43
8	16.67	24.38	114
10	40.6	54.15	9
11	-	-	-
15	40.53	44.86	8
18	30.14	43.97	21
Session 35			
2	12.66	36.96	94
3	14.03	36.46	94
8	15.42	39.53	107
9	26.29	50.29	84
11	11.54	33.74	131
12	12.39	19.98	201
14	31.38	38.9	102
16	58.72	77.59	55
18	15.63	26.22	82
Session 47			
5	4.46	29.83	42
6	31.39	50.78	20
8	17.25	49.01	20
11	57.5	65.14	9
12	49.95	62.27	28
14	71.33	86.75	6
15	67.19	67.19	1
17	59.02	83.67	5
19	8.5	10.82	9

Trial #	Min ICI (msec)	Mean ICI (msec)	N
Session 59			
4	44.47	76.99	3
6	45.49	49.12	9
7	9.96	30.83	109
10	30.0	43.6	34
11	66.11	66.11	1
12	22.81	41.88	51
15	34.3	40.55	3
18	21.22	42.09	97
		Total N =	1,977

Figure 14. ICI histograms for the baseline, control, and experimental conditions represented in terms of the percent of ICI's which fell into each 10 msec bin. Arrows indicate two-way transit times for the target and the far end of the pool. Values for the minimum ICI, mean ICI, percent of ICI's less than 50 msec, and total number of ICI's for each condition are shown.


ICI's—Baseline
Minimum ICI = 11.25 msec
Mean ICI = 54.94 msec
60% of ICI's<50 msec
N = 2653
% of ICI's per Bin
60
50
40
30
20
10
0
10
20
30
40
50
60
70
80
90
100
110
120
msec
Target
End


ICI's—Control
Minimum ICI = 12.34 msec
Mean ICI = 59.95 msec
48% of ICI's<50 msec
N = 1920
% of ICI's per Bin
60
50
40
30
20
10
0
10
20
30
40
50
60
70
80
90
100
110
120
msec
Target
End

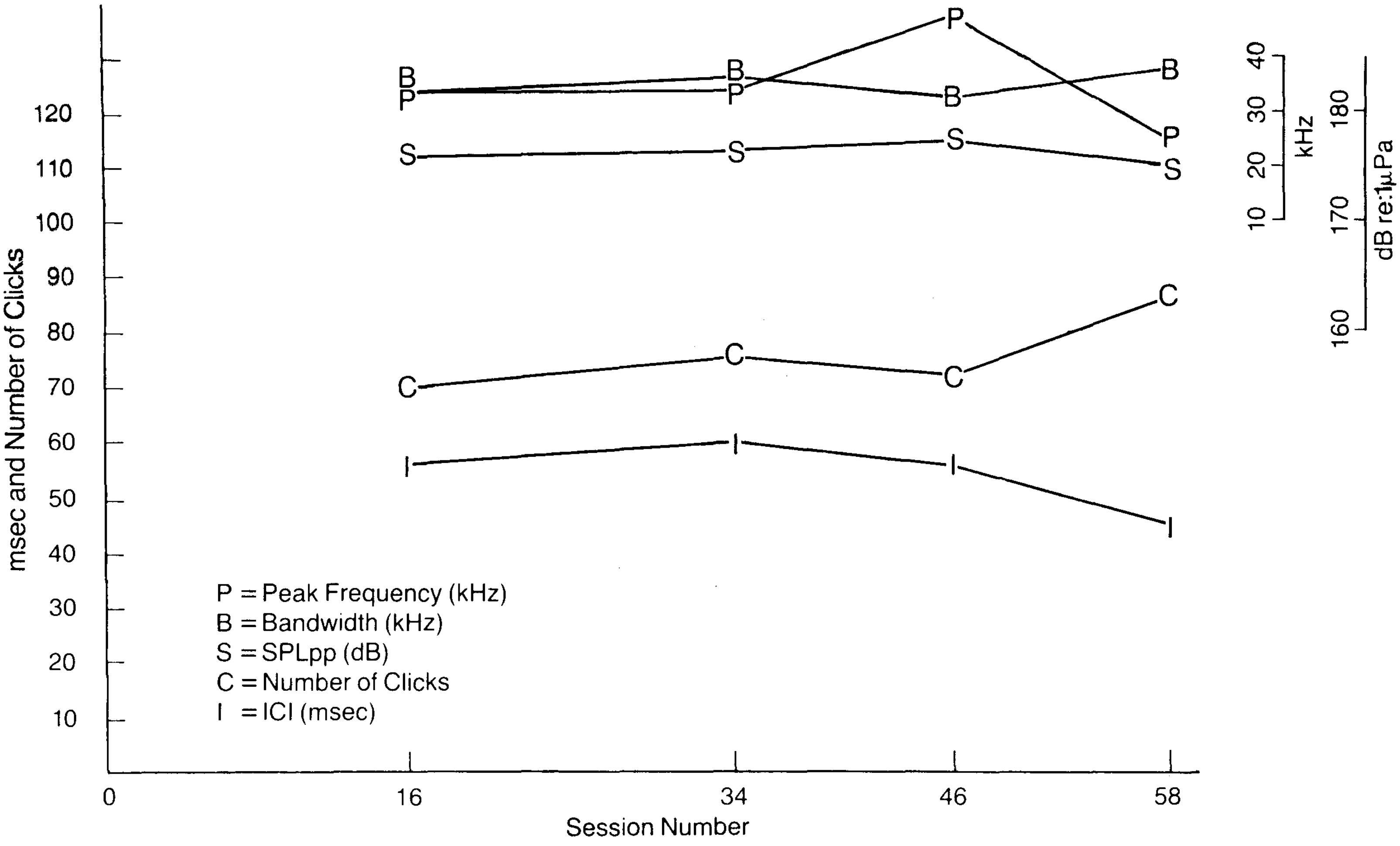

ICI's—Experimental
Minimum ICI = 2.11 msec
Mean ICI = 47.72 msec
81% of ICI's<50 msec
N = 1977
% of ICI's per Bin
60
50
40
30
20
10
0
10
20
30
40
50
60
70
80
90
100
110
120
msec
Target
End

compiled into a single histogram for each condition tested. Figure 14 displays those histograms in terms of the percent of all ICI's per condition falling into each 10 msec bin. The respective values for the minimum ICI, mean ICI, and the percent of ICI's falling below 50 msec are also listed in the figure. The ICI distributions for all three conditions tested peak in the 40-50 msec bin. The distributions for the baseline and control conditions are very similar. In contrast, the distribution for the experimental condition is skewed with 81% of the ICI's falling below 50 msec. It is the only one of the three conditions with ICI's in the 0-10 msec bin and a minimum ICI value, 2.1 msec, less than the two-way transit time to the target.

Figures 15 to 17 plot comparisons of the mean values of the signal characteristics examined for each recorded session in the baseline, control, and experimental conditions, respectively. The most notable variations occur with respect to the mean number of clicks in the control and experimental conditions. The number of clicks follows a "W" pattern over sessions in both conditions with a more prominent rise in number as well as shorter ICI's in the experimental condition.

Figure 18 summarizes the mean signal characteristic values across conditions. In this figure it can be more easily seen that the most notable change across conditions occurs in temporal parameters, namely the lower average number of clicks per trial in the hooded conditions. Finally, Figure 19 combines the performance and acoustical data plotted over a time continuum.

Figure 15. Mean values for peak frequency, -3 dB bandwidth, peak-to-peak SPL re: 1 uPa, ICI, and number of clicks per trial plotted as a function of time for the tape recorded sessions in the baseline condition.



Baseline Signal Data (Mean Values per Session)

Figure 16. Mean values for peak frequency, -3 dB bandwidth, peak-to-peak SPL re: 1 uPa, ICI, and number of clicks per trial plotted as a function of time for the tape recorded sessions in the control condition.

Control Signal Data (Mean Values per Session)

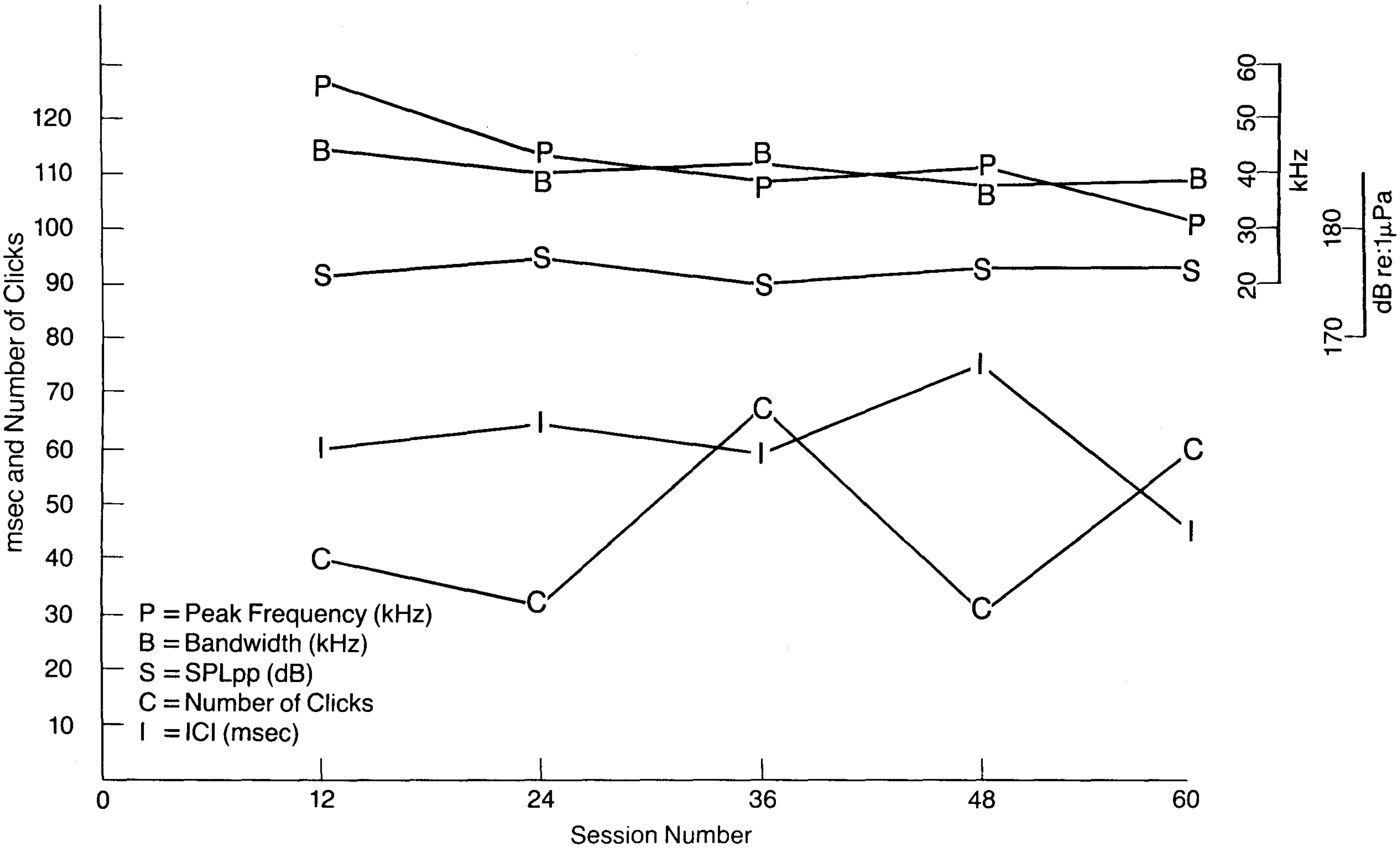


Figure 17. Mean values for peak frequency, -3 dB bandwidth, peak-to-peak SPL re: 1 uPa, ICI, and number of clicks per trial plotted as a function of time for the tape recorded sessions in the experimental condition.

Experimental Signal Data (Mean Values per Session)

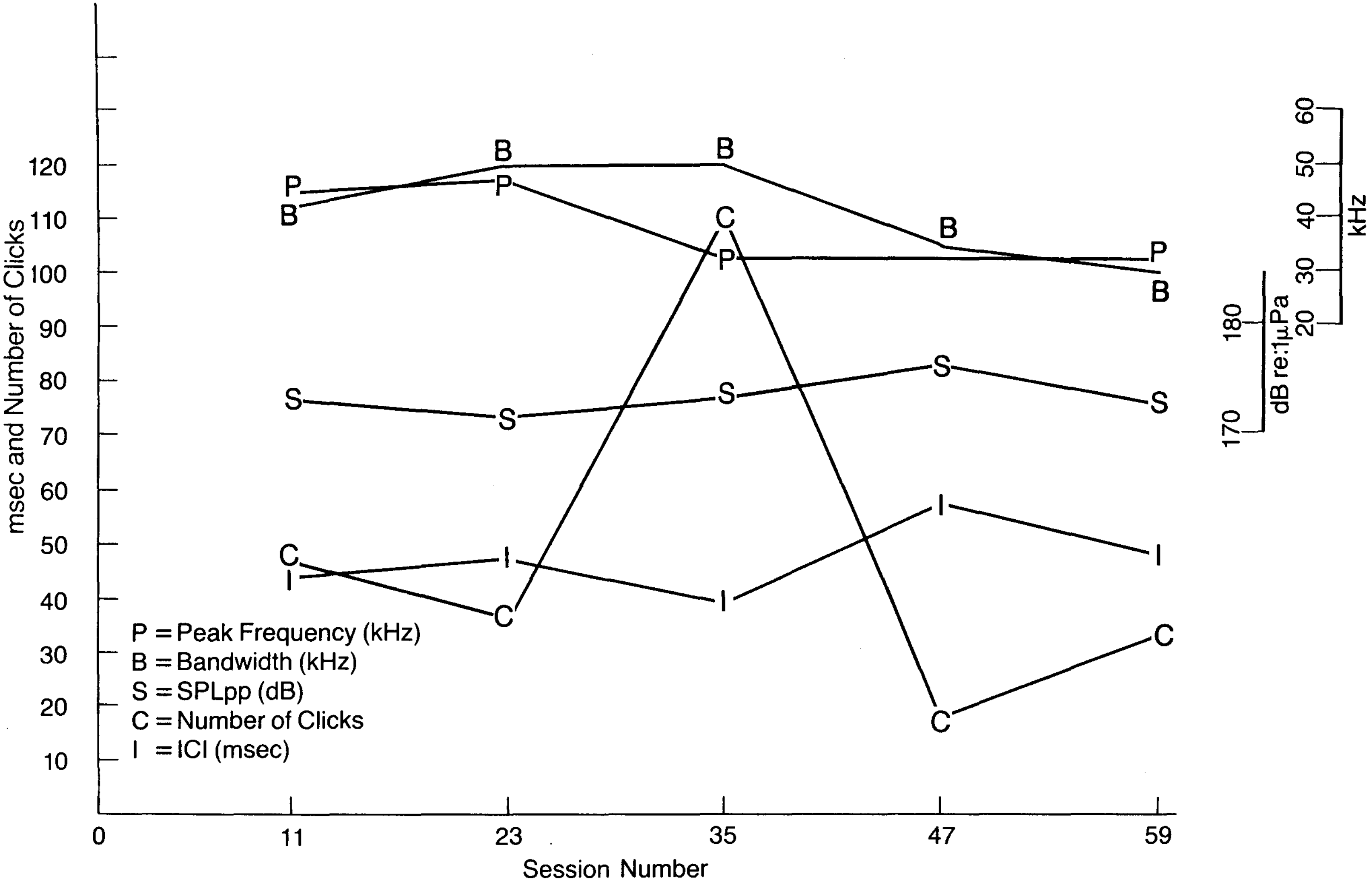


Figure 18. Mean values for peak frequency, -3 dB bandwidth, peak-to-peak SPL re: 1 uPa, ICI, and number of clicks per trial in the tape-recorded sessions plotted as a function of condition tested.

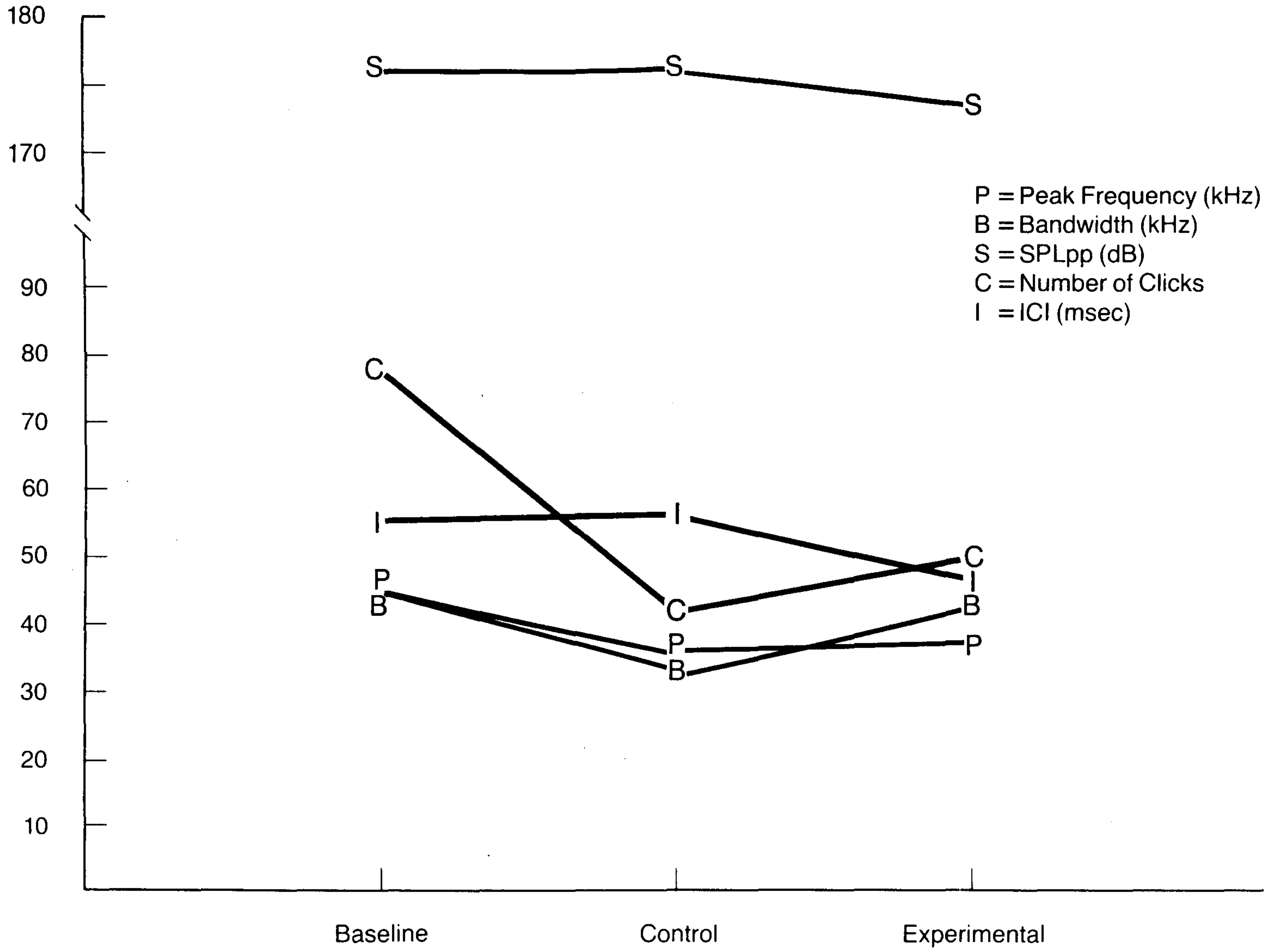
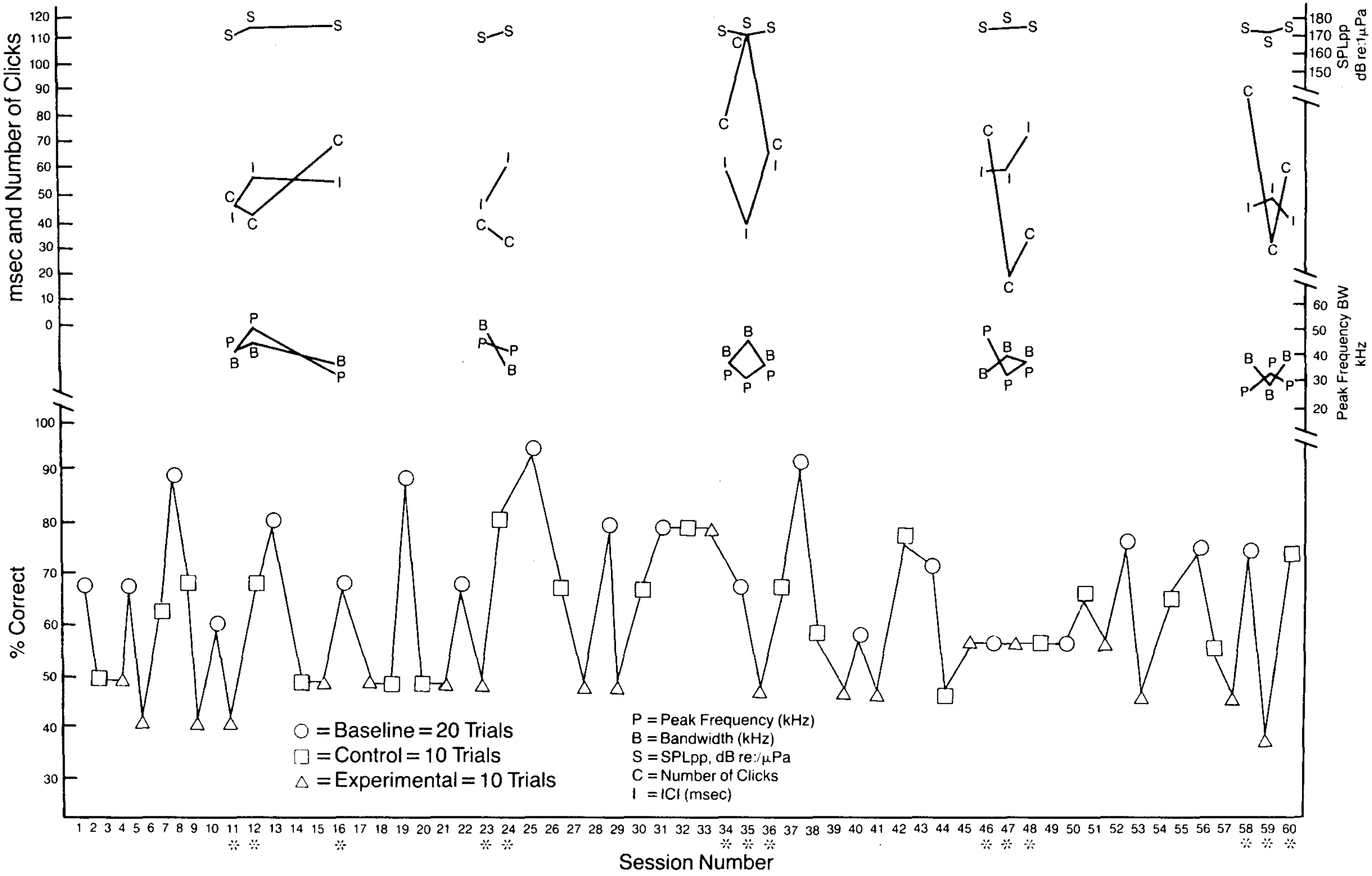

180
170
90
80
70
60
50
40
30
20
10
S
S
S
C
C
C
I
I
I
P
P
P
B
B
B
P = Peak Frequency (kHz)
B = Bandwidth (kHz)
S = SPLpp (dB)
C = Number of Clicks
I = ICI (msec)
Baseline
Control
Experimental

Figure 19. Performance data in a continuum and acoustical data plotted simultaneously as a function of time. * Indicates tape recorded sessions.


msec and Number of Clicks
120
110
100
90
80
70
60
50
40
30
20
10
0
% Correct
100
90
80
70
60
50
40
30
SPLpp
dB re:1µPa
180
170
160
150
Peak Frequency BW
kHz
60
50
40
30
20
S
C
I
P
B
○ = Baseline = 20 Trials
□ = Control = 10 Trials
△ = Experimental = 10 Trials
P = Peak Frequency (kHz)
B = Bandwidth (kHz)
S = SPLpp, dB re:/µPa
C = Number of Clicks
I = ICI (msec)
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60
Session Number

DISCUSSION

The attenuation of acoustical signals at the lower jaw of a dolphin (_Tursiops truncatus_) significantly hindered its performance in an echolocation task performed under controlled conditions as would be predicted by Norris's (1968) "jaw-hearing" theory. Observed collateral behaviors did not reveal any strategies used to compensate for such attenuation. Echolocation signals recorded across conditions clearly showed that emitted pulses were unaffected by the application of neoprene materials over the lower jaw and that the only notable changes in signal characteristics occurred with respect to the number of clicks and the length of ICI's. The data resulting from this experiment provide the first direct evidence of its kind relative to this theory.

It should be noted, however, that it would be unwarranted to assume that the use of the experimental hood completely eliminated the reception of acoustical signals by the dolphin or that the lower jaw and mandibular fat bodies represent the only acoustical pathway to the inner ear. There were means possible by which the dolphin in this experiment could have received potentially meaningful, albeit subtle, signals that would have bypassed the barrier to the lower jaw that was imposed. Since this experiment was conducted in a concrete pool, the nature of the dolphin's surroundings (see Figure 4) were such that his echolocation signals could have returned from points behind him by means of several reflective pathways. Yanagisawa _et al_. (1966) and Bullock _et al_. (1968) identified areas on the dolphin's melon as being sensitive to incoming sound and the role of the melon in sound reception has been previously proposed and discussed (cf. Dreher, 1969; Johnson, 1986). This experiment made no attempt to attenuate any acoustic signals above the line of the gape of the mouth. Finally, sound reception through the external auditory meatus itself or the tissues that surround it cannot be completely ruled out. If, however, the dolphin in this experiment was receiving subtle acoustic cues relevant to the task that it was performing, they were of no benefit to his performance in the experimental condition. Further behavioral experimentation would be required to determine what role, if any, the melon or upper portion of the dolphin's head has in sound reception and to determine if performance under conditions comparable to those imposed in this experiment would improve if tested over a much greater number of trials.

Given those considerations, it remains clear from the performance data in this experiment, as evaluated by both Chi-square tests and Signal Detection Theory, that a significant effect on performance in the echolocation task was caused by the use of the experimental sound attenuating hood. The most direct argument for the effect of the experimental hood is represented in the comparison between the trials conducted with and without a hood in both the control and experimental conditions (see Figures 11 and 12). The implication of these data is that the dolphin did as well in performing the discrimination task from trial to trial with the control hood as he did without it whereas a significant difference in performance from trial to trial in sessions involving the experimental hood is evident. This finding helps to eliminate the potential criticism that novelty or some form of discomfort on the part of the dolphin in wearing any type of material over the lower jaw would account for a disruption in his ability to echolocate.

Low false-alarm rates, less than .30, have been typical for several species of marine mammals in the results of echolocation experiments conducted, particularly those intended to measure acoustic detection thresholds (Schusterman, 1974). Schusterman pointed out that when faced with an a priori signal presentation probability of .50, the animals in the studies he reviewed consistently adapted the conservative Neyman-Pearson criterion; keeping the proportion of false alarms at a constantly low value. He suggested that the animals' strategies were influenced by the need for stimulus control imposed by the investigator in the conditioning process which emphasized the report of hits as opposed to the report of false alarms. In all of the cases reviewed by Schusterman, the probability of target presence was equal and the payoff for correct responses was the same.

Au and Penner (1981) reported results for target detection in noise by Tursiops truncatus which departed from the Neyman-Pearson criterion with higher false alarm rates. In their experiment, the level of masking noise, and, therefore, the degree of difficulty in detecting the target, was randomly varied. Au and Penner suggested that the randomization of difficulty caused the departure from the Neyman-Pearson criterion that they observed.

The Beta values presented in Figure 9 indicate, as has been mentioned, a relatively unbiased response criterion, as defined by Green and Swets (1966), across conditions. The false alarm rates falling between .30 and .70 in Figure 9 are high in comparison to those reviewed by Schusterman (1974) and, like those reported by Au and Penner (1981), do not suggest the utilization of a Neyman-Pearson criterion. In this experiment, the probability of target presentation was equal and target range and depth were constant. It is reasonable to assume that, given Nemo's experience during the length of time he had spent residing in the Seven Seas Panorama facility prior to this experiment and the experience he acquired as a result of the preparatory training involved, he approached the discrimination task at hand by employing a signal of predetermined characteristics regardless of the condition under which he was being tested. Due to the nature of the training regimen used with the dolphins at the Seven Seas facility (Brill, 1981), there was variation in the form of reinforcement administered for each correct response. The randomization of the use of a hood from trial to trial in the control and experimental conditions may be analogous to a randomization of the difficulty in detecting a target. Similarly, the increased difficulty in target detection in the experimental condition, as indicated by the d' values in Figure 9, may explain the slightly stronger tendency in making false alarms that was observed in that condition as compared to the baseline and control conditions.

The collateral behaviors that had been anticipated prior to the conduction of the experiment and noted during trials did not occur with frequencies sufficient enough to provide any meaningful information (see Appendix I). It had been hoped that such behaviors would reveal directly observable indications of any strategies used by the dolphin to compensate for any difficulties in echolocating while wearing the hoods.

The most frequently observed collateral behavior, holding the mouth open while echolocating, could only be observed during trials in the baseline condition. This behavior had been included among the anticipated collaterals because Nemo was known to frequently echolocate with his mouth open while blindfolded during public demonstrations. If sound reception by the mandibular fat bodies is an advantage to an echolocating dolphin, which has been shown to be the case in this experiment, holding the mouth open would be helpful. Exposing the soft tissues in the interior of the mouth would provide access to a pathway to the mandibular fat bodies that bypasses the thin layer of bone in the flared posterior ends of the mandible. If, on the other hand, holding the mouth open during echolocation were necessary to a dolphin, the performance rates in the control and experimental conditions where the dolphin's mouth was kept closed should have been very similar. They were not.

A good deal of headscanning behavior had been anticipated. Dolphins typically swing their heads from side to side and occasionally up and down while echolocating (Schevill and Lawrence, 1956; Kellogg, 1960; Norris _et al_., 1961). It is believed that such motion is used to direct the beam of emitted signals as well as to assist in localizing on the source of the echoes to which the animal is attending. Some fine-tuning or filtering of the incoming signals may also be accomplished by the change of the angle of incidence, and, therefore, the density of bone through which the signal must pass, at the pan bones (Norris, 1968). One of the reasons for using a hoop station in this experiment, as opposed to a chin rest or bite bar, was to allow the freedom of movement necessary for headscanning should the dolphin have found it necessary. The low rate of headscanning that was observed in this experiment may be attributable to two factors. The first is that Nemo had learned where the targets would be located eliminating the need to search or determine an echo source. The other is that any scanning of his outgoing beam may have been accomplished internally without any visible movement of the head (Ayrapet'yants, Voronov, Ivanenko, Ivanov, Ordovskiy, Sergeyev, and Chillingiris, 1973; Evans, 1973). Familiarity with and the geometry of the target positions would also explain the lack of head movement in the vertical plane. Au _et al_. (1986) have reported that the transmission and receiving beam axes in _Tursiops truncatus_ lie on a 5° angle above the line of the gape of the mouth. Nemo's depth and horizontal head position and the range and depth of the targets would have easily allowed target detection without any vertical head movement. The low rate of headscanning that occurred was not directly attributable to the use of either hood and may have had more to do with listening to the acoustic activities of pool mates during trials.

There were two trials in the experimental condition that were tape recorded and revealed no detectable echolocation clicks in either channel. There was no report of the suppression of acoustic signals, echolocation clicks, from the trainer in the water during those trials. It is likely that the trainer in the water was hearing acoustic signals that were being emitted by one or more of the other dolphins residing in the pool and mistook them as signals being produced by Nemo. Based on personal experience during this experiment and a number of other occasions, it is difficult to be certain of the source of the acoustic signals that one can hear dolphins making underwater in a concrete pool. The lack of signal production during those two trials is most likely the result of frustration and/or complacency as indicated by Nemo's chance performance in the experimental condition overall and in the last session of that condition in particular (see Figure 10). Similar behavior as seen in the breakdown of conditioned responses and the simulation of echolocation behavior in the absence of emitted signals by dolphins as target detection became increasingly difficult has been previously reported (Au and Penner, 1981).

Again, familiarity with the test situations gained by the dolphin prior to the experiment may explain the low frequencies of collateral behaviors observed.

Norris et al. (1961), Evans (1973), Norris and Harvey (1974), Au et al. (1986) and others have provided evidence that echolocation signals are emitted from the area of the forehead above the line of the gape of the mouth and are focused forward in a directional manner. If the signals emitted by dolphins during echolocation originate in the larynx and are radiated in an omnidirectional field without being focused forward through the melon as others already cited in the introduction of this manuscript have suggested, then placement of hoods on Nemo's lower jaw should have blocked and distorted his emitted signals. The comparison of average waveforms and their respective frequency spectra from each of the conditions tested in this experiment provided in Figure 13 clearly show that Nemo's emitted signals were unaffected by the presence of either of the hoods at his lower jaw. In examining Figure 13, it is difficult, at best, to determine which of the three waveforms presented was taken from a particular condition without the benefit of appropriate identification. It is clear, then, that Nemo was able to emit useful echolocation signals in all three conditions and that those signals were being emitted from an area or areas above the line of the gape of the mouth. Such evidence supports the assumption that the hoods were, in fact, affecting the reception of echolocation signals and not their emission.

The average peak-to-peak amplitude, peak frequency, bandwidth, and interclick intervals (ICI's), and number of clicks or pulses per trial were the signal characteristics examined and compared in this experiment. Several investigators have provided evidence that dolphins exert control over the characteristics of their emitted signals as they echolocate (Turner and Norris, 1966; Norris, Evans, and Turner, 1967; Norris _et al_., 1972; Evans, 1973; Au, 1980). It had been anticipated that Nemo would make significant alterations in the characteristics of his outgoing echolocation signals, particularly with respect to amplitude and repetition rates, in an effort to compensate for the attenuation of incoming signals at the lower jaw. The results reported in the preceding section indicate that spectral parameters were stable across conditions while some variations occurred in temporal parameters as reflected in the number of clicks emitted and the lengths of the ICI's.

A preliminary report made while this experiment was still in progress and data analysis was incomplete (Brill, in press) suggested the possibility that Nemo was using shorter bursts composed of fewer clicks and longer ICI's in the hooded conditions as opposed to the baseline condition. The complete body of data resulting from this experiment, however, indicates a lower average number of clicks per trial in the hooded conditions with a shorter ICI in the experimental condition.

An echolocating dolphin will typically increase its click repetition rate and, conversely, decrease the length of ICI's as it homes in on its target (Busnel and Dziedzic, 1967; Evans and Powell, 1967; Norris _et al_., 1967; Morozov _et al_., 1972), a strategy that provides more echoes and, therefore, more information regarding the object of interest. Norris (1964) suggested that the repetition rate may be related to the degree of discrimination desired by the dolphin at any given moment. Au _et al_. (1982) have pointed out that interclick intervals almost always exceed the two-way transit time to the target implying that the echo from one click is received by the dolphin before the next click is emitted. Murchison (1980) has proposed that interclick intervals used by echolocating odontocetes are behaviorally controlled by the animal and are relative to its "search image," the type of returning signal expected from a familiar target.

Compared to the baseline condition (refer to Figure 10), Nemo had little trouble compensating for the use of the control hood. With the exception of a brief drop to chance, his performance rates in that condition rose quickly over time to approach the rates in the baseline condition. The average ICI's and the distributions of the ICI's for the baseline and control conditions are similar (see Figure 14). The fact that the ICI histograms presented in Figure 14 all show peaks in the

40-50 msec bin indicates that Nemo relied most frequently on an interval that allowed for the return and processing of all returning echoes. An ICI of 40-50 msec would accommodate both the greatest two-way transit time in the test environment, 30 msec for the far end of the pool, and a reasonable length of processing time.

However, with the exception of one high-scoring session (refer to Figure 19, Session 33), Nemo's performance in the experimental condition did not improve over time. The shorter ICI's evident in the skewed distribution for this condition (see Figure 14) and the somewhat lower average number of clicks are possibly indicative of a reaction to the absence of some expected information or search image. It is possible that the acoustic information available to Nemo in the baseline and control conditions was being obscured, if not eliminated, in the experimental condition by virtue of the use of the sound attenuating hood. To compensate, then, Nemo appears to have relied on shorter ICI's in an effort to gain more information and shorter bursts may have been the result of some difficulty in processing that information in the experimental condition.

The tape recorded hooded sessions (sessions 34-36, see Fig. 18) immediately following the high-scoring experimental session (session 33) show an increase in the average number of clicks per trial that is much more dramatic in the experimental condition. The fact that the increase occurs in both conditions may be coincidental. The fact that it occurs so dramatically in the experimental condition may indicate that it was a successful strategy in the preceding high-scoring session. Even so, the next set of tape recorded sessions (sessions 46-48) show a drop in the average number of clicks and success in the experimental condition was never repeated.

As previously described, the hoods left the area around the external auditory meatus exposed, yet a dramatic difference in performance on the echolocation task caused by the experimental hood was observed. If the external auditory meatus or its surrounding tissues provide a functional acoustic pathway to the inner as has been proposed, its effectiveness, as well as the effectiveness of the lower jaw, may be frequency dependent. It is clear from the results of this experiment that the frequencies of Nemo's outgoing signals fell in the range between 30 kHz and 55 kHz. The electrophysiological experiments of Bullock _et al_. (1968) and McCormick _et al_. (1970) suggested that the area around the external auditory meatus was sensitive to frequencies below 20 kHz whereas the lateral surfaces of the lower jaw were sensitive to frequencies above 20 kHz. Renaud and Popper (1975) observed that their psychophysical data for sound localization by _Tursiops_ _truncatus_ likewise suggested a dependency on the external auditory meatus for localization on acoustic signals below 20 kHz and a dependency on the lower jaw for localization on signals above 20 kHz. Since Nemo's signals were well above 20 kHz, the area around the external auditory meatus was of no benefit in sound reception. Therefore, it is likely that the area of the lower jaw was the primary site of sound reception during echolocation in this experiment.

Suggestions for Further Research

The availability of new evidence for sound reception through the lower jaw of a dolphin generates several questions of immediate interest which would be worthy of further investigation, some of which have been implied earlier in this dissertation.

Verification of the findings of this experiment through replication with additional subjects would be of obvious value. Of greater benefit would be a replication conducted over a more extensive period of time. In such a replication, the question of usable, subtle acoustic cues could be pursued. In addition, a longer test period may reveal more information regarding learned strategies which compensate for the attenuation of incoming signals.

Signal transmission sites above the line of the gape of the mouth could be investigated by adapting the same methodology used in this experiment, as had similarly been considered by Chun (personal communication). It would be of interest to determine whether or not outgoing signals could be rendered useless to the dolphin by covering the melon and/or upper rostrum with an appropriate barrier, how the resulting waveforms differed in their characteristics, and whether or not the dolphin is capable of emitting a usable echolocation signal from the tip of the upper rostrum as has been suggested by the recordings made by Evans (1973).

If the echolocation process can be disrupted by acoustically blocking the lower jaw, how much of an area need be blocked to cause a significant effect? The imposition of acoustical barriers of various and appropriate shapes and sizes would make possible the behavioral mapping of areas on the head of a dolphin that are critical to a dolphin for sound reception. It would be of use to determine how well such a behavioral map would correspond to the physiological maps described by Bullock _et al_. (1966) and McCormick _et al_. (1970).

Finally, an exact determination of sound reception in the areas of the lower jaw of a dolphin defined by Norris (1968) as "acoustic windows" would invite the possibility of adapting some of the techniques used in human auditory psychophysics for use with dolphins. The ability to direct calibrated signals to the acoustic windows, thereby transmitting them directly to the inner ear, would allow the extensive investigation of the dolphin's ability in the discrimination of specific signal characteristics under well controlled conditions.

REFERENCES

Apfel, R.E., Young, R.E., Varanasi, U., Maloney, J.R., & Malins, D.C. (1985). Sound velocity in lipids, oils, waxes, and their mixtures using an acoustic levitation technique. J. Acoust. Soc. Am., 78, 868-870.

Au, W.W.L. (1980). Echolocation in signals of the Atlantic bottlenose dolphin (Tursiops truncatus) in open waters. In R.-G. Busnel & J.F. Fish (Eds.) Animal sonar systems (pp. 251-282). New York, NY: Plenum Publishing Corp.

Au, W.W.L., Floyd, R.W. & Haun, J.E. (1978). Propagation of Atlantic bottlenose dolphin echolocation signals. J. Acoust. Soc. Am., 64, 411-422.

Au, W.W.L., Floyd, R.W., Penner, R.H., & Murchison, A.E. (1974). Measurement of echolocation signals of the Atlantic bottlenose dolphin, Tursiops truncatus Montagu, in open waters. J. Acoust. Soc. Am., 56, 1280-1290.

Au, W.W.L., Moore, P.W.B., & Pawloski, D. (1986). Echolocation transmitting beam of the Atlantic bottlenose dolphin. J. Acoust. Soc. Am., 80, 688-691.

Au, W.W.L., & Penner, R.H. (1981). Target detection in noise by echolocating Atlantic bottlenose dolphins. J. Acoust. Soc. Am., 70, 687-693.

Au, W.W.L., Penner, R.H., & Kadane, J. (1982). Acoustic behavior of echolocating Atlantic bottlenose dolphins. J. Acoust. Soc. Am., 71, 1269-1275.

Ayrapet'yants, E. Sh., Voronov, V.A., Ivanenko, Yu. V., Ivanov, M.P., Ordovskiy, D.L., Sergeyev, B.F., & Chillingiris, V.I. (1973). Physiology of the sonar system in Black Sea dolphins. J. Evol. Physiol. and Biochem., 9, 364-374.

Bekesy, G. von (1960). Experiments in hearing. New York, NY: McGraw-Hill.

Blevins, C.E., & Parkins, B.J. (1973). Functional anatomy of the porpoise larynx. Am. J. Anat., 138, 151-164.

Brill, R.L. (1981). R.I.R. in use at the Brookfield Zoo: random and interrupted reinforcement redefined in perspective. In J. Barry & R. Brill (Eds.), *Proceedings of the Annual Conference of the International Marine Animal Trainers Association, 1981, Niagara Falls, New York*. Boston, MA: New England Aquarium.

Bullock, T.H., Grinnell, A.D., Ikezono, E., Kameda, K., Nomoto, M., Sato, O., Suga, N., & Yanagisawa, K. (1968). Electrophysiological studies of central auditory mechanisms in cetaceans. *Z. Vergleich. Physiol.*, *59*, 117-156.

Busnel, R.-G., & Dziedzic, A. (1967). Resultats metrologigues experimentaux de l'echolocation chez le *Phocaena phocaena* et leur comparison avec ceux de certaines chauves-souris. In R.-G. Busnel (Ed.), *Animal sonar systems, biology and bionics* (pp. 307-335). Jouy-en-Josas, France: Laboratoire de Physiologie Acoustique.

Cranford, T.W. (1985). Quantitative morphology of delphinid cephalic anatomy. Paper presented at the Sixth Biennial Conference on the Biology of Marine Mammals, Vancouver, B.C., Canada.

Diercks, J.J., Trochta, R.T., Greenlaw, R.F., & Evans, W.E. (1971). Recording and analysis of dolphin echolocation signals. *J. Acoust. Soc. Am.*, *49*, 1729-1732.

Dormer, K.J. (1979). Mechanisms of sound production and air recycling in delphinids: cineradiographic evidence. *J. Acoust. Soc. Am.*, *65*, 229-239.

Dreher, J.J. (1969). Acoustical holographic model of cetacean echolocation. In A.E. Metherell, M.A. El-Sum, & L. Larmore (Eds.), *Acoustical holography* (pp. 127-137). New York, NY: Plenum Press.

Evans, W.E. (1973). Echolocation by marine delphinids and one species of fresh-water dolphin. *J. Acoust. Soc. Am.*, *4*, 191-199.

Evans, W.E., & Maderson, P.F. (1973). Mechanisms of sound production in delphinid cetaceans: a review and some anatomical considerations. *Amer. Zool.*, *13*, 1205-1213.

Evans, W.E., & Powell, B.A. (1967). Discrimination of different metallic plates by an echolocating delphinid. In R.-G. Busnel (Ed.), *Animal sonar systems, biology and bionics* (pp. 363-398). Jouy-en-Josas, France: Laboratoire de Physiologie Acoustique.

Evans, W.E., & Prescott, J.H. (1962). Observations of the sound production capabilities of the bottlenose porpoise: a study of whistles and clicks. *Zoologica*, *47*, 121-128.

Evans, W.E., Sutherland, W.W., & Bell, R.G. (1964). The directional characteristics of delphinid sounds. In W.N. Tavolga (Ed.), Marine bio-acoustics, vol. 2 (pp. 353-372). New York, NY: Pergamon Press.

Fish, M. Poland (1949). Marine mammals of the Pacific with particular reference to the production of underwater sound. ONR Technical Report No. 8.

Fleischer, G. (1976). On bony microstructures in the dolphin cochlea, related to hearing. N. Jb. Geol. Palaont. Abh., 151, 166-191.

Fraser, F.C., & Purves, P.E. (1960). Hearing in cetaceans: evolution of the accessory air sacs and the structure and function of the outer and middle ear in recent cetaceans. Bull. Brit. Mus., 7, 1-140.

Gellerman, L.W. (1933). Chance orders of alternating stimuli in visual discrimination experiments. J. Genetic Psych., 42, 206-208.

Green, D.M., & Swets, J.A. (1966). Signal detection theory and psychophysics. Huntington, NJ: Robert E. Krieger Publishing Co.

Green, R.F., Ridgway, S.H., and Evans, W.E. (1980). Functional and descriptive anatomy of the bottlenosed dolphin nasolaryngeal system with special reference to the musculature associated with sound production. In R.-G. Busnel & J.F. Fish (Eds.) Animal sonar systems (pp. 199-238). New York, NY: Plenum Publishing Corp.

Griffin, D.R. (1958). Listening in the dark, the acoustic orientation of bats and men (2nd ed.). New York, NY: Dover Publishing, Inc.

Griffin, D.R., & Galambos, R. (1941). The sensory basis of obstacle avoidance by flying bats. J. Exp. Zool., 86, 481-506.

Harrison, R.J., & King, J.E. (1965). Marine mammals. London: Hutchinson & Co.

Johnson, C.S. (1986). Dolphin audition and echolocation capacities. In R.J. Schusterman, J.A. Thomas, & F.G. Wood (Eds.), Dolphin cognition and behavior: a comparative approach (pp. 115-136). Hillsdale, NJ: Lawrence Erlbaum Associates.

Kellogg, W.N. (1960). Auditory scanning in the dolphin. Psych. Rec., 10, 25-27.

Kellogg, W.N. (1961). Porpoises and sonar. Chicago, IL: University of Chicago Press.

Lawrence, B., & Schevill, W.E. (1956). The functional anatomy of the delphinid nose. Bull. Mus. Comp. Zool. Harvard, 114, 103-151.

Lawrence, B., & Schevill, W.E., (1965). Gular musculature in delphinids. Bull. Mus. Comp. Zool. Harvard, 133, 1-65.

Lilly, J.C., & Miller, A.M. (1961). Sounds emitted by the bottlenose dolphin. Science, 133, 1689-1693.

Litchfield, C., Greenberg, A.J., Caldwell, D.K., Caldwell, M.C., Sipos, J.C., & Ackman, R.G. (1975). Comparative lipid patterns in acoustical and nonacoustical fatty tissues of dolphins, porpoises and toothed whales. Comp. Biochem. Physiol., 50B, 591-597.

Mackay, R.S., & Liaw, H.M. (1981). Dolphin vocalization mechanisms. Science, 212, 676-678.

McCormick, J.G., Wever, E.G., Palin, J., & Ridgway, S.H. (1970). Sound conduction in the dolphin ear. J. Acoust. Soc. Am., 48, 1418-1428.

McCormick, J.G., Wever, E.G., Ridgway, S.H., & Palin, J. (1980). Sound reception in the porpoise as it relates to echolocation. In R.-G. Busnel & J.F. Fish (Eds.) Animal sonar systems (pp. 449-467). New York, NY: Plenum Publishing Corp.

Mead, J.G. (1975). Anatomy of the external nasal passages and facial complex in the Delphinidae (Mammalia: Cetacea). Smithsonian Contributions to Zoology, no. 207, 1-72.

Mohl, B., & Andersen, S. (1973). Echolocation: high-frequency component in the click of the harbour porpoise (Phocoena phocoena L.). J. Acoust. Soc. Am., 54, 1368-1372.

Morgane, J.P., & Jacobs, N.S. (1972). Comparative anatomy of the cetacean nervous system. In R.S. Harrison (Ed.), Functional anatomy of marine mammals, vol. I (pp. 117-244). New York, NY: Academic Press.

Morozov, V.P., Akopian, A.I., Burdin, V.I., Zaytseva, K. A., & Sokovykh, Yu. A. (1972). Frequency of the following of location signals of dolphins as a function of distance to the target. Biofizika, 17, 139-144.

Murchison, A.E. (1980). Detection range and range resolution of echolocating bottlenose porpoise (Tursiops truncatus). In R.-G. Busnel & J.F. Fish (Eds.), Animal sonar systems (pp. 43-70). New York, NY: Plenum Press.

Nachtigall, P.E. (1980). Bibliography of echolocation papers on aquatic mammals published between 1966 and 1978. In R.-G. Busnel & J.F. Fish (Eds.) Animal sonar systems (pp. 1029-1069). New York, NY: Plenum Publishing Corp.

Norris, K.S. (1964). Some problems of echolocation in cetaceans. In W.N. Tavolga (Ed.), Marine bio-acoustics (pp. 317-336). New York, NY: Pergamon Press.

Norris, K.S. (1968). The evolution of acoustic mechanisms in odontocete cetaceans. In E.T. Drake (Ed.), Evolution and environment (pp. 297-324). New Haven, CN: Yale University Press.

Norris, K.S. (1969). The echolocation of marine mammals. In H.T. Andersen (Ed.), The biology of marine mammals (pp. 391-423). New York, NY: Academic Press.

Norris, K.S. (1974). The porpoise watcher. New York, NY: W.W. Norton and Co., Inc.

Norris, K.S., Dormer, K.J., Pegg, J., & Liese, G.J. (1971). The mechanisms of sound production and air recycling in porpoises: a preliminary report. In T. Poulter (Ed.), Proceedings of the 8th annual conference on biological sonar and diving mammals (pp.113-129). Menlo Park, CA: Stanford Research Inst.

Norris, K.S., & Evans, W.E. (1967). Directionality of echolocation clicks in the rough-toothed porpoise Steno bredanensis (Lesson). In W.N. Tavolga (Ed.), Marine Bioacoustics, vol. 2 (pp. 305-316). New York, NY: Pergamon Press.

Norris, K.S., Evans, W.E., & Turner, R.N. (1967). Echolocation in an Atlantic bottlenose porpoise during discrimination. In R.-G. Busnel (Ed.), Animal sonar systems, biology and bionics (pp. 409-437). Jouy-en-Josas, France: Laboratoire de Physiologie Acoustique.

Norris, K.S., & Harvey, G.W. (1974). Sound transmission in the porpoise head. J. Acoust. Soc. Am., 56, 659-664.

Norris, K.S., Harvey, G.W., Burzell, L.A., & Krishna Kartha, T.D. (1972). Sound production in the freshwater porpoises Sotalia and Inia in Rio Negro, Brazil. In G. Pilleri (Ed.) Investigations on cetacea, vol. 4 (pp. 251-259). Benetelli, AG, Berne.

Norris, K.S., Prescott, J.H., Asa-Dorian, P.V., & Perkins, P. (1961). An experimental demonstration of echolocation behavior in the porpoise, Tursiops truncatus (Montagu), Bio. Bull., 120, 163-176.

Penner, R.H., & Murchison, A.E. (1970). Experimentally demonstrated echolocation in the Amazon river porpoise, Inia geoffrensis (Blaineville). In T. Poulter (Ed.), Proceedings of the 7th annual conference on biological sonar and diving mammals (pp. 17-38). Menlo Park, CA: Stanford Research Institute.

Popper, A.N. (1980a). Sound emission and detection by delphinids. In L.M. Herman (Ed.), Cetacean behavior: mechanisms and behavior (pp. 1-52). New York, NY: John Wiley and Sons, Inc.

Popper, A.N. (1980b). Behavioral measure of odontocete hearing. In R.-G. Busnel & J.F. Fish (Eds.), Animal sonar systems (pp. 469-481). New York, NY: Plenum Publishing, Inc.

Purves, P.E. (1967). Anatomical and experimental observations on the cetacean sonar system. In R.-G. Busnel (Ed.) Animal sonar systems, biology and bionics (pp. 197-269). Jouy-en-Josas, France: Laboratoire de Physiologie Acoustique.

Purves, P.E., & Pilleri G.E. (1973). Observations on the ear, nose, throat, and eye of Platanista indi. In G.E. Pilleri (Ed.), Investigations on cetacea, vol. V (pp. 13-57). Benetelli AG, Berne.

Purves, P.E., & Pilleri, G.E. (1983). Echolocation in whales and dolphins. New York, NY: Academic Press.

Renaud, D.L., & Popper, A.N. (1975). Sound localization by the bottlenose porpoise Tursiops truncatus. J. Exp. Bio., 63, 569-585.

Reysenbach de Haan, F.W. (1957). Hearing in whales. Acta Otolaryngol., Suppl., 134, 1-114.

Ridgway, S.H. (1983). Dolphin hearing and sound production in health and illness. In R.R. Fay & G. Gourevitch (Eds.), Hearing and other senses: presentations in honor of E.G. Wever (pp. 247-296). Groton, CN: Amphora Press.

Ridgway, S.H., Carder, D.A., Green, R.F., Gaunt, A.S., Gaunt, S.L.L., & Evans, W.E. (1980). Electromyographic and pressure events in the nasolaryngeal system of dolphins during sound production. In R.-G. Busnel & J.F. Fish (Eds.) Animal sonar systems (pp. 239-249). New York NY: Plenum Publishing Corp., Inc.

Schenkaan, E.J. (1973). On the comparative anatomy and function of the nasal tract in odontocetes (Mammalia, Cetacea). Bijdragen tot de Dierkunde, 43, 127-159.

Schevill, W.E. (1956). Evidence for echolocation by cetaceans. Deep Sea Research, 3, 153-154.

Schevill, W.E., & Lawrence, B. (1956). Food-finding by a captive porpoise (Tursiops truncatus). Breviora Museum Comp. Zool., 53, 1-15.

Schusterman, R.J. (1974). Low false-alarm rates in signal detection by marine mammals. J. Acoust. Soc. Am., 55, 845-848.

Schusterman, R.J. (1980). Behavioral methodology in echolocation by marine mammals. In R.-G. Busnel & J.F. Fish (Eds.) Animal sonar systems (pp. 11-41). New York, NY: Plenum Publishing Corp., Inc.

Siegel, S. (1956). Nonparametric statistics: for the behavioral sciences. New York, NY: McGraw-Hill.

Turner, R.N., & Norris, K.S. (1966). Discriminating echolocation in porpoise. J. Exp. Anal. Behav., 9, 535-544.

Varanasi, U., & Malins, D.C. (1971). Unique lipids of the porpoise (Tursiops gilli): differences in triacylglycerols and wax esters of acoustic (mandibular and melon) and blubber tissues. Biochem. Biophys. Acta., 231, 415-418.

Varanasi, U., & Malins, D.C. (1972). Triacylglycerols characteristic of porpoise acoustic tissues: molecular structures of diisovaleroylglycerides. Science, 176, 926-928.

Varanasi, U., Feldman, H.R., & Malins, D.C. (1975). Molecular basis for formation of lipid sound lens in echolocating cetaceans. Nature, 255, 340-343.

Wever, E.G.,, McCormick, J.G., Palin, J., & Ridgway, S.H. (1971a). The cochlea of the dolphin, Tursiops truncatus: general morphology. Proc. Nat. Acad. Sci., 68, 2381-2385.

Wever, E.G., McCormick, J.G., Palin, J., & Ridgway, S.H. (1971b). The cochlea of the dolphin, Tursiops truncatus: hair cells and ganglion cells. Proc. Nat. Acad. Sci., 68, 2908-2912.

Yanagisawa, K., Sato, G., Nomoto, M., Katsuki, Y., Ikezono, E., Grinnell, A.D., & Bullock, T.H. (1966). Auditory evoked potentials from brain stem in cetaceans. Fed. Proc. Physiol., p. 464. (abstract #1539)

APPENDIX I

APPENDIX I

The list below provides a definition and the frequency of occurrence for each of the eight collateral behaviors observed during the experiment reported. The behaviors are listed according to the numbers used to identify and record their occurrences during trials. Frequency is expressed as the percent of the total 600 trials conducted.

1. Horizontal Headscanning 31%

   Repeated movements of the head from side to side while echolocating on a target.

2. Vertical Headscanning 7%

   Repeated up and down movements of the head while echolocating on a target.

3. Head Cocked Vertical 17%

   Holding the head at an angle in the vertical plane while echolocating on a target.

4. Air Bubbles 8%

   Release of air bubbles from the blowhole while echolocating on a target.

5. Suppression of Emitted Signals 0%

   The absence of audible echolocation signals during target presentation.

6. Mouth Open 46%

   Holding the mouth agape while echolocating on a target.

7. Displacement of Hoods or Eyecups 2%

   Voluntary displacement of hoods or eyecups during a trial.

8. Response Latencies 0%

   Delays in leaving the hoop station to report target condition noticeably longer than the expected 4-7 seconds.

APPENDIX II

APPENDIX II

Problems in Designing a Methodology

The conditions imposed by the configuration and status of the Seven Seas Panorama facility at the Chicago Zoological Park (Brookfield Zoo) required the development of a methodology that would overcome several problems inherent in testing a dolphin's echolocating ability while depriving it of the use of its major sensory modes. Conducting training and data collection sessions in between regularly scheduled dolphin performances presented the need for equipment that was portable and that could be quickly assembled, used, and then broken down and stored, as well as being unobtrusive to the other dolphins in the pool. Conditions in the test environment such as water clarity, the close proximity of targets, and low levels of ambient noise required effective controls for visual and auditory cues. The need to record the dolphin's outgoing signals meant the provision of some assurance that the recorded signals were those of the dolphin concerned and not those that might be emitted by of one or more of the other dolphins in the pool. Finally, requiring a dolphin to cooperate while both blind and deaf created the need for an overall method that would minimize, if not eliminate, any fear or frustration that the dolphin might otherwise experience.

Initial concepts for the design were based on the desire to avoid the use of eyecups to block visual cues while employing some means of attenuating acoustical signals at the dolphin's lower jaw. We had learned by experience that our dolphin would not easily accept blindfolds along with some disruption of his echolocating ability. Norman Chun of Naval Ocean Systems Center, Hawaii, had loaned us a covering made of neoprene, cork, and fiberglass that fit the top of a dolphin's head from the blowhole to the tip of the snout along the gape of the mouth for exploratory use. Chun (personal communication) had been considering the possibility of attenuating the outgoing signals of an echolocating dolphin and had thus built this covering. Held in place by a chin strap, much like the dolphin version of a football helmet, our dolphin, Nemo, accepted the covering and swam around the pool to retrieve lead-filled rings which were regularly used in demonstrations of echolocation during public performances. When required to wear the covering and together with opaque eyecups, however, Nemo put his head underwater, shook violently until the covering floated free, and then proceeded to retrieve his rings. After returning the rings and having his eyecups removed, Nemo immediately left his trainer to retrieve the covering and emphatically threw it out of the water. Norris et al. (1961) and Norris (1974) had reported a similar response from dolphins that had worn neoprene coverings over the top of the head or the lower jaw. It appeared that the possibility of blocking both sensory modes simultaneously as well as employing a method that would allow the dolphin to move about freely while echolocating on a designated target would have to be abandoned.

Another need was the manner in which returning echolocation signals could be attenuated at the lower jaw. Earl Murchison (personal communication), also of Naval Ocean Systems Center, Hawaii, had, at one time, considered behaviorally testing the sound transmission and reception sites on an echolocating dolphin and had made a fiberglass shell that covered the entire head from the tip of the snout to the eyes. He made this shell available for use while designing this experiment. Murchison's proposal was to mount the shell underwater, train a dolphin to insert its head into the shell and echolocate through it. Sound attenuating materials could then be attached to the shell in the appropriate areas rather than to the dolphin itself. After a good deal of consideration, this idea was abandoned due to the difficulty that would have been encountered in manufacturing a shell that would be free of gas bubbles and in successfully arguing that the shell did not somehow affect the echolocation process, with or without coverings.

As plans developed, it was decided that a discrimination task would be the method of choice since the presentation of some target on every trial would act as a control for passive listening which could otherwise be used by the dolphin to detect the presence or absence of a singular target. Under the assumption that eyecups would not be used, training the dolphin for a discrimination task with visually identical targets was considered. The first choice was to use a poly-vinyl-chloride (PVC) cylinder that would either contain or not contain an aluminum cylinder. While it proved easy enough to get our dolphin to recognize the presence of the of the PVC cylinder, we could not establish his ability to detect the presence of the aluminum cylinder within.

Unexpectedly, we had a difficult time establishing a useful discrimination. Nemo did well at simple detection but, for some reason, did not readily learn a discrimination. By this time, we had chosen to use eyecups and a "Go/No-go" design. After abandoning the PVC and aluminum idea, we went to presenting an aluminum cylinder and a rubber cylinder of the same as well as different sizes, and then to an aluminum cylinder and a fiberglass sphere. In each case, Nemo acknowledged the presence of a target but made no distinction between them. Finally, we chose to present the aluminum cylinder as the "Go" target, which it had been intended to be from the start, and a sand-filled ring as the "No-go" target with an added advantage. In contrast to the cylinder which was lined up with the center of the hoop station on each presentation, the sand-filled ring would be presented in a position above the center of the hoop. With that combination, Nemo began to show evidence of recognizing a difference between the target conditions.

In between the training required to establish the desired echolocation task, the method by which acoustical signals could be attenuated at the lower jaw was being developed. After abandoning the shell method and committing to the use of eyecups, it was decided to use two hoods, control and experimental, that would be worn directly by the dolphin. The original design was such that the hood covered the entire lower jaw as well as the area around the external ear. In use, however, that design proved to be too cumbersome in the water and would have allowed the possibility of reflections around the external ear to act as a confounding variable. The shape of the hood was reduced to cover only the lower jaw from the tip of the snout to near the bases of the pectoral fins.

The major difficulty in designing the hood was finding a usable means by which it would be held in place on the dolphin. The use of straps over the lower jaw and the back of the head were obvious elements necessary in the design. Underwater, however, the hood billowed away from the dolphin's head and easily slid off. Attaching a pair of eyecups to the inside of the hood to hold it in place had been considered but that proved to be uncomfortable for Nemo. The solution was to use commercially available bathroom soap dishes whose surfaces were covered with small rubber suction cups. Cutting the small suction cups from the backsides of several soap dishes and gluing them into place on the interior of the hood provided the solution. With the hood strapped into place on the dolphin, the small suction cups held the hood close enough to the skin and prevented it from sliding off as it had before.

Nemo did not resist wearing the hood and swimming into his hoop station as long as his vision was not impaired. The training strategy was to eventually introduce the wearing of the hood into the required echolocation task that Nemo had learned. The first experiences in requiring Nemo to wear a hood and eyecups simultaneously were not successful and might best be described as disastrous. His initial responses were similar and more pronounced than those he gave to the helmet described above. He would thrash his head violently to free himself of the hood and then would often leave his trainers and swim out to the center of the pool to get as far away from the situation as possible. His frustration was such that the mere sight of the hood was enough to cause him to leave and prematurely end a training session. The training process eventually required that more care and time be taken in slowly introducing Nemo to the combination of hood and eyecups.

Aided by the invaluable time commitment and patience of the Seven Seas training staff, a decision was made to step back in the training process and gradually make Nemo comfortable with the combination of hood and eyecups. The hood was used like a toy to be played with in all sessions, both performances and training, and would be placed on him for brief periods of time. Nemo's improvement was seen in the training sessions for this experiment as he began again to comfortably approach his station wearing the hood in place. At that point, the eyecups were cautiously reintroduced one at a time. The first eyecup was accepted readily being placed on Nemo while his head was out of the water at the beginning of each trial just prior to applying the hood. The placement of the second eyecup was carefully approximated over a number of sessions starting with the second trainer in the water holding it so that Nemo could see it as he approached his underwater hoop station, to gradually moving it closer to his head, to touching Nemo well behind the eye, to placing the eyecup over the eye briefly, and to finally securing it in place long enough to conduct a discrimination trial.

APPROVAL SHEET

The dissertation submitted by Randall L. Brill has been read and approved by the following committee:

Richard R. Fay
Professor of Psychology and Otolaryngology, Loyola University of Chicago

Raymond H. Dye
Assistant Professor of Psychology, Loyola University of Chicago

Kenneth S. Norris
Professor of Natural History, University of California at Santa Cruz, Santa Cruz, California

William A. Yost
Professor of Psychology and Otolaryngology, Loyola University of Chicago

The final copies have been examined by the director of the dissertation and the signature which appears below verifies the fact that any necessary changes have been incorporated and that the dissertation is now given final approval by the Committee with reference to content and form.

The dissertation is therefore accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Sept 2, 1988
Date

Richard R Fay
Director's Signature