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BEHAVIORAL METHODOLOGY IN ECHOLOCATION BY MARINE MAMMALS

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INTRODUCTION

Despite the fact that a preponderance of the investigations dealing with echolocation by marine mammals has been done with intact animals performing some characteristic behavior, only a single paper written some fifteen years ago (Turner, 1964) has ever dealt in any profound way with problems of behavioral methodology. The 1964 paper by R. N. Turner addressed itself primarily to conditioned responses and included response measures, techniques of target or signal presentation, threshold measurement and reinforcement contingencies. When Turner's paper was published, there had only been a few pioneering studies done on porpoise echolocation and hearing, and by today's standards, these studies were, for the most part, relatively unsophisticated. A recent Russian publication (Lekomtsev and Titov, 1974) attempted to update Turner's work, but in reality the paper served primarily to highlight Russian behavioral procedures to the study of porpoise sonar abilities.

Even though numerous advances in the behavioral analysis of sensory and perceptual capabilities of a wide variety of animal species have been made since the mid 1960's, there has been no attempt to review and evaluate procedural variables in the behavioral study of animal sonar systems. In particular, modern operant conditioning techniques (Skinner, 1961) have become very efficient, and methodological advances have been applied to many problems and many animal species. With these advances has come a marked interest in a relatively new field of animal psychology which has been termed "animal psychophysics" (Blough and Blough, 1978; Stebbins, 1970).

The purpose of this paper is to review and evaluate behavioral techniques used to study echolocation by marine mammals, particularly dolphins, within the context of this new field of animal psychophysics. The goal of these techniques is to establish and maintain stimulus control of an animal's behavior. Stimulus control is essentially a convenient expression for saying that a stimulus change brings about a change in some measurable aspect of behavior. The degree to which a stimulus exerts control over an animal's behavior may be measured in a variety of ways including probability, latency, amplitude, or rate of some specified response and it is usually assumed that a controlling stimulus either signals the animal that a particular class of responses will be reinforced or it signals the animal that a particular class of responses will not be reinforced. Once stimulus control has been established, the experimenter may want to identify the manner in which the animal classifies or dimensionalizes the stimulus. This has been particularly true in recent echolocation experiments in which the controlling aspects of the stimulus targets were interpreted in one way by the experimenter and in quite a different way by the porpoise (Schusterman and Kersting, 1978). In animal psychophysics, the answer to the question about what the porpoise "sees" when it is stimulated with suprathreshold echoes depends on a series of perceptual investigations in which tests of equivalence, transfer or generalization are given. Thus, the porpoise is placed in experimental situations in which different stimulus configurations, as defined by the experimenter, are responded to in the same fashion.

The emphasis in this paper will be on problems associated with the types of indicator responses used by echolocating animals and the ways in which stimulus targets have been presented. In this regard, it should be pointed out that the major difference between a passive hearing task and an active sonar task is that in the former task it is not necessary to preclude the animal's dependence on vision unless visual stimuli are correlated with acoustic stimuli in signalling reinforcement. However, in echolocation tasks the targets invariably have a visual analogue, and if the animal can use visual cues, it may not depend on its acoustic auto-communication cues, i.e., on echoes which return following its own sound emissions. When using marine mammals in echolocation tasks, enucleation has rarely, if ever, been used and the traditional way of occluding or eliminating vision has been to either have the animal work in turbid water or in water where the light level was very low, place a blindfold or eye cups on the animal, use targets which are quite different acoustically but appear visually to be the same, or place the targets behind a visually opaque but acoustically transparent screen. All of these methods have costs and benefits and the technique used will frequently depend on the species under investigation and the type of problem being studied.

This paper will not discuss some procedural problems of echolocation experiments which have been reviewed elsewhere (Turner, 1964; Lekomtsev and Titov, 1974). These include randomization of stimulus presentation and motivation or food deprivation variables.

UNCONDITIONED RESPONSES

In procedures with unconditioned responses, the indicator response appears to require no special training, i.e., it is reflex-like in its action, being directly elicited by a variety of submerged targets and sounds.

Perhaps the first systematic use of reflexes as indicator responses were the experiments by Kellogg (1961) with two Atlantic bottlenose dolphins (Tursiops truncatus) which were conducted in a pool with very limited visibility. Kellogg's targets included: (a) polelike sheet-metal devices, triangular in cross section; (b) BB shot; (c) wooden streamlined shapes which could be silently submerged; (d) food fish, and (e) human swimmers. Kellogg recorded two classes of behavior: (a) bursts of sonar clicks, and (b) changes in movement or swimming patterns. The latter behavior was subdivided into either approach or avoidance responses. These experiments suggested that almost any target "noisely" submerged would elicit echolocation pulses by Tursiops sometimes followed by approach (e.g. fish) or avoidance (human swimmer or long metal pole). Oscillating head movements were frequently noted as the porpoise, emitting clicks, swam toward a hand-held fish. If the water was splashed without submerging a target, then the animals did not sustain their clicks. However, when reflecting targets were submerged, sustained clicking occurred, and it was assumed by the experimenter that the porpoises detected targets and differentiated between them on the basis of the sound signals emitted and the type of swimming movement (approach or avoidance) observed.

In retrospect, it is likely that one of the most vexing problems in Kellogg's experiments was a lack of an objective and quantitative evaluation of the porpoises's behavior under these extremely variable stimulus conditions. On occasion, the experimenter must have been forced to make a subjective judgment as to whether there was indeed an avoidance response or an approach response--particularly if the porpoise did not take the hand-held fish. The fact that Kellogg did not present quantitative data in reporting these unconditioned responses to submerged targets and water splashing supports the notion that the use of unconditioned responses is of limited value in the study of echolocation by marine mammals. Another confounding factor in these experiments

is the possibility that these reflex-like responses habituated with repeated stimulation by similar sounds or similar targets. Habituation of sudden changes in the swimming movements detected visually by the experimenter when relatively loud pure tones were presented may have led to an initial underestimate of the upper frequency limit of hearing in Tursiops (Kellogg and Kohler, 1952; Kellogg, 1953).

CONDITIONED RESPONSES

Unconditioned responses depend on a relatively simple and direct stimulus-response relationship in which echoes from the target or other auditory stimuli elicit the indicator response, which may not be easy to define and quantify. When conditioned responses are used, the experimenter usually chooses some carefully defined motor response which can be readily measured. In classical or Pavlovian procedures, the unconditioned stimulus (US) or reinforcer is contingent on the conditioned stimulus (CS) i.e., the CS and US are paired. In operant or Skinnerian procedures, reinforcement is made contingent on some class of responses. If a stimulus sets the occasion for reinforcing a class of responses, then the stimulus becomes a discriminative stimulus (S^D) and serves as a signal very much as the CS serves as a signal in classical conditioning procedures. Following repeated pairings on the CS and US or the S^D and reinforcement, a highly stereotyped indicator response is elicited or emitted whenever the CS or S^D is presented.

Operant procedures may involve the use of positive or negative reinforcers. When positive reinforcement is used, if the animal makes a response in the presence of an S^D , it receives a reward. When negative reinforcement is used, if the animal makes a response in the presence of an S^D , it avoids an aversive stimulus event.

Classical conditioning in which the US is shock and the CS is an acoustic signal has been used extensively by the Russians to study the sound reception by echolocating porpoises. For example, sound detection thresholds were obtained in the common porpoise (Phocaena phocaena) by pairing auditory stimuli (CS) with shock (US) and measuring a restrained animal's galvanic skin response (Supin and Sukhorunchenko, 1970). In another experiment on restrained bottlenose dolphins the characteristics of directional sound signals in the horizontal plane were investigated by measuring the cardiac component of what the Russians call "motor-defensive conditioned reflexes" (Ayrapet'yants, et al., 1973). All of these experiments have involved passive hearing in porpoises and I do not know of a single experiment that has used classical conditioning procedures to determine the sonar capabilities of

marine mammals. It seems that only operant conditioning procedures have been used to investigate the performance of echolocating marine mammals.

RESPONSE MEASURES

Examination of a variety of response measures and their related reinforcement contingencies reveals remarkable similarity among different experimenters in different laboratories around the world in their use of operant procedures to study echolocation in both marine mammals and in bats. Investigators from the Soviet Union and United States have used very different terminology in describing essentially the same procedure. For example, when a Russian researcher says he or she used the "method of motor-food conditioned reflexes in unrestrained dolphins" this is nearly the equivalent of an American researcher saying he or she used "a two-alternative forced-choice procedure",

Retrieval

Typically, this procedure involves the arrangement of reinforcement contingencies such that if the porpoise picks up a single submerged target with its mouth or rostrum and returns it to the experimenter or trainer, then the animal is positively reinforced with a food fish. In theory, at least, the retrieval technique could be used as a way of determining the echo dimensions along which auditory quality is represented in the echolocating porpoise. This could be done by repeatedly presenting a blindfolded Tursiops with a variety of targets differing in some aspect of fine target structure and differentially reinforcing the animal for retrieving targets differing in this single aspect. In fact, however, the retrieval procedure has been used infrequently to study the sonar abilities of marine mammals, and its use has generally been limited to simple detection tasks.

An experiment by C. Scott Johnson (1967) used the retrieval procedure in an attempt to determine the relationship between pulse rate and target range. The targets used in the experiment included a weighted air-filled foam rubber ring and single vitamin pill. Scronce and Ridgway (this volume) failed in their attempt to demonstrate echolocation in a blindfolded gray seal (Halichoerus gyrfus) by requiring the seal to retrieve an air-filled plastic ring 20 cm in diameter situated randomly in one large section of a 10 m diameter redwood tank. Most recently Dziedzic and Alcuri (this volume) studied changes in the click burst of T. truncatus when the task was to retrieve different shaped objects.

Obstacle Avoidance

The most definitive early demonstrations of echolocation in bats were those reported by Griffin and Galambos (1941) in which enucleated bats were required to navigate through a maze of wires. Similar experiments have been done with free-swimming T. truncatus and P. phocaena under a variety of conditions (Busnel et al., 1965; Busnel and Dziedzic, 1967; Kellogg, 1961). The complexity of these obstacle avoidance tasks makes it extremely difficult to determine what aspects of the targets were important for the occurrence of the complex swimming patterns of porpoises which included short and difficult turns in order to avoid colliding with poles, wires and nets. The obstacle avoidance technique is extremely limited from this standpoint and is rarely used today in echolocation experiments with marine mammals where the emphasis is the determination of a well-defined response and a carefully controlled target or signal dimension.

Go/No-Go

Surprisingly, the "go/no-go" procedure has rarely been chosen to measure the echolocation performance of marine mammals despite the fact that it is, perhaps, the most simple and straight forward procedure to study discriminative echolocation. There are several variations of the go/no-go paradigm. In the study of marine mammal bioacoustics, the paradigm operates within the context of a discrete trial procedure in which target or signal presentation is relatively brief and is contingent on the animal's maintaining a reasonable fixed position between target presentations. During a trial, indicated by a sound or a light, the animal orients from its starting position towards the target area. Then it either performs a carefully defined action, e.g. pressing a paddle (a "yes" response) in the presence of a standard target, or it inhibits or withholds the action (a "no" response) in the presence of a comparison target or in the absence of a target. Following the indicator response the animal stays or returns to its starting position. Response measures include the likelihood of a response occurring on each trial and the latencies of "yes" responses. Reinforcement may be programmed so that "yes" responses in the presence of a target are positively reinforced and are extinguished, i.e., are not reinforced in the absence of a target, or reinforcement may be programmed symmetrically so that it follows "yes" responses in the presence of a target ("hits") and "no" responses in the absence of a target ("correct rejections"). Errors (which may be punished with "time-outs" or other aversive events) are of two types: a "yes" response in the absence of a target ("false alarms") or a "no" response in the presence of a target ("misses").

The go/no go procedure is usually employed when targets or

stimuli are presented sequentially and is thus used most extensively in the earlier stages of training when only a single standard target is presented on repeated trials (Lekomstev and Titov, 1974).

One type of go/no-go procedure is exemplified by an experiment on discriminative echolocation (Ayrapet'yants, et al., 1969) in three Black Sea dolphins (Tursiops truncatus), under high and very low illumination. The dolphins were required to tug at a ring in the presence of a standard target (a cylinder 25 mm in length and 110 mm in diameter) and to withhold this response when presented with comparison targets (cylinders 28, 30, 35, 45, 55 and 75 mm in length and 110 mm in diameter). A 5 kHz tone signalled the dolphin to swim "from the starting position at a distance of 20 meters to the experimenter who immersed different targets into the water...." (Ayrapet'yants, et al., 1969). Tugging the ring when the standard target was presented resulted in a fish reward. The manner in which this paper was written makes it difficult to be sure about the reinforcement contingencies, but in my interpretation the contingencies were not symmetrical which means that withholding the "ring-tug response" in the presence of the comparison targets did not result in a fish reward. Following each response, the dolphin was required to swim back to the start position. Eventually, all dolphins accurately differentiated all but the 28 and 30 mm comparison cylinders from the standard 25 mm standard cylinder. The authors state that "it was more difficult to differentiate the 30 mm cylinder which was only 5 mm taller than the positive one. Such differentiation was not absolute (correct answers constituted 70%). Presentation of the 28 mm cylinder, which was 3 mm taller than the positive one, elicited no recognition. Thus, the threshold of differentiation of targets according to height was 5-10 mm" (Ayrapet'yants, et al., 1969).

The Russian experiment highlights some of the least desirable aspects of the go/no-go procedure. With only a single well-defined response, it is sometimes difficult to separate "no" reports from a failure to respond, and there is no measurable latency for the "no" response. Moreover, it would seem that unless the reinforcement contingencies or what signal detection theorists call the payoff matrix was symmetrical there might be a preference for the "yes" response, thereby driving the threshold estimate down. Furthermore, the statistical definition of a "threshold" is sorely missing in this particular paper.

Multiple-Response Forced-Choice Procedures

The multi-response technique which has probably been used most extensively for doing experiments on marine mammal biosonar

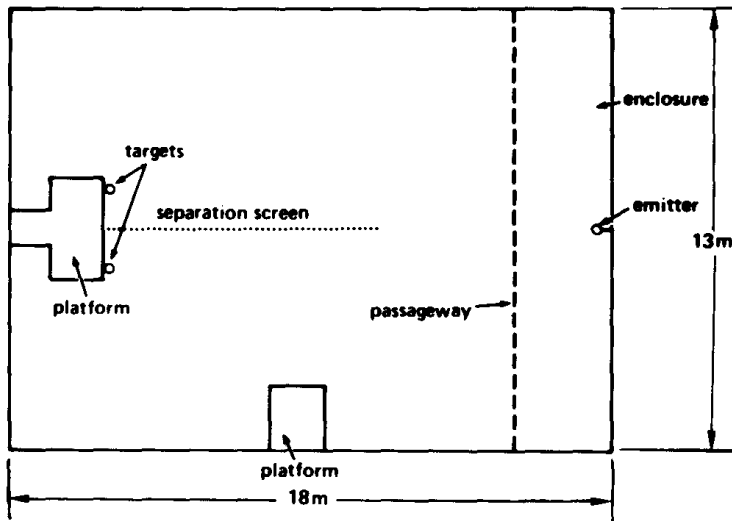


Figure 1. Schematic of a testing tank illustrating the use of the two-response forced-choice procedure with simultaneous target presentation. Prior to the onset of an 8 kHz tone, the dolphin positioned itself in front of the emitter. The targets were lowered silently into the water at two points 2 m apart. In response to the audio signal the dolphin emerged from the enclosure through the passageway and headed for the platform where it detected the targets from a certain distance (adapted from Lekomtsev and Titov, 1974).

is the two-response forced-choice procedure. The major variation on this procedure depends on the simultaneous or successive presentation of targets.

Simultaneous Target Presentation. Following the stationing of an animal each of two spatially separated targets are presented near their associated response manipulanda and the animal is reinforced for responding to the "correct" stimulus. Frequently, a vertical partition or separation screen has been placed between the targets so the animal is forced to make its choice at some minimum specified distance (see Figure 1).

Variables affecting the echolocation performance of several species of dolphins, including T. truncatus and D. delphis, have frequently been investigated by the two-response forced-choice procedure using a simultaneous presentation technique. These factors include object detection with noise disturbance (Titov, 1975), angular and range resolution (Bel'kovich et al, 1970; Lekomtsev and Titov, 1974; Murchison, this volume), size discrimination of planometric and stereometric figures (Kellogg, 1961;

Turner and Norris, 1966; Barta, unpublished ms.; Ayrapet'yants et al, 1969), shape discrimination of planometric and stereometric figures made of metal or plastic (Gurevich, 1969; Barta, unpublished ms.; Nachtigall and Murchison, this volume; Bagdonas et al., 1970) and material composition of plates and solid elastic spheres (Evans and Powell, 1967; Dubroskiy et al, 1971).

Perhaps the only disadvantage of the two-alternative forced-choice procedure with a simultaneous presentation of targets is that even with a partition between the targets it is extremely difficult to force a dolphin or seal without eye cups to make its choice at some fixed distance from the targets when the experimenter has difficulty visually tracking the animal in turbid water or at very low levels of light (see Schusterman, 1967).

Successive Target Presentation. A group of American investigators at the Naval Ocean Systems Center (NOSC) in Hawaii have done a wide variety of echolocation experiments by presenting targets on successive trials and requiring the dolphin to respond to one of two spatially separated response manipulanda. In "presence-absence" experiments, a response to one manipulandum (e.g. to the animal's right) is reinforced if a target is present ("yes" response) and a response to the other manipulandum (e.g. to the animal's left) is reinforced if the target is absent ("no" response). In so-called discrimination or recognition experiments, targets usually differing multi-dimensionally control differential responding and the porpoise is reinforced for responding to the manipulanda associated with a specific target. Despite spatially disparate response manipulanda, targets are presented in the same location. Thus, unlike the two-alternative forced-choice method with simultaneous presentation, where stimulus targets and associated response manipulanda have approximately the same relative spatial location (so that different reflected sounds come from different places), the two-alternative forced-choice technique with successive stimulus presentation requires the animal to make a bilateral or spatially different response to different sounding reflected echoes emanating from the same locus in space.

An illustration of this procedure within the context of a detection experiment has been reported by Penner and Murchison (1970), who used it to determine the smallest diameter copper wire that could be detected by an Amazon River dolphin, Inia geoffrensis. The Inia stationed between the response manipulanda (mounted on the opposite side of the pool from the stimulus display) until a trial began with the onset of a 1-sec burst of a 30 kHz tone. Then the Inia swam across the 7.3 diameter tank toward the target area emitting echolocation pulses, and returned to the response manipulanda area. Activation of the "yes" manipulandum in the presence of a target was a hit and the dolphin was reinforced. In the absence of a target activation of the "no"

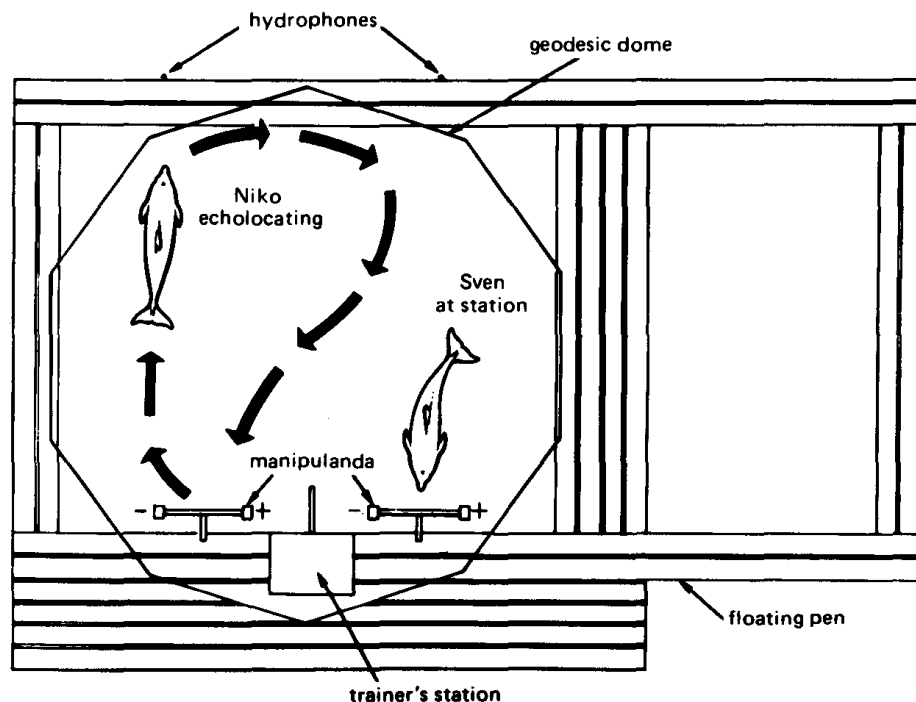


Figure 2. Testing situation showing the use of the two-response forced-choice procedure with successive presentation of targets. Presence of a target was reported on the "yes" manipulandum and the absence of a target was reported on the "no" manipulandum. For further details of this procedure see Murchison (this volume).

manipulandum was a correct rejection and the dolphin was reinforced. Errors (false alarms as well as misses) were never reinforced .

An interesting variation of this procedure was used to calculate the furthest distance at which solid and water filled spheres could be detected by Tursiops (Murchison, this volume). The study used two Tursiops working alternately on the same task (see Figure 2). In an attempt to determine whether cooperative or cueing behavior occurred in this type of paired-porpoise range detection task, Penner (1977) conducted a similar experiment comparing performance when animals worked on alternate trials, simultaneously or alone, and he found that echolocation performance appeared unaffected by these conditions.

Finally, Hammer (1978) and Au and Hammer (this volume) applied the two-alternative forced-choice procedure with successive target presentation to the study of salient target characteristics of different-size cylinders. One set of cylinders (A) controlled A reports and the other set of cylinders (B) controlled B reports (see Figure 3).

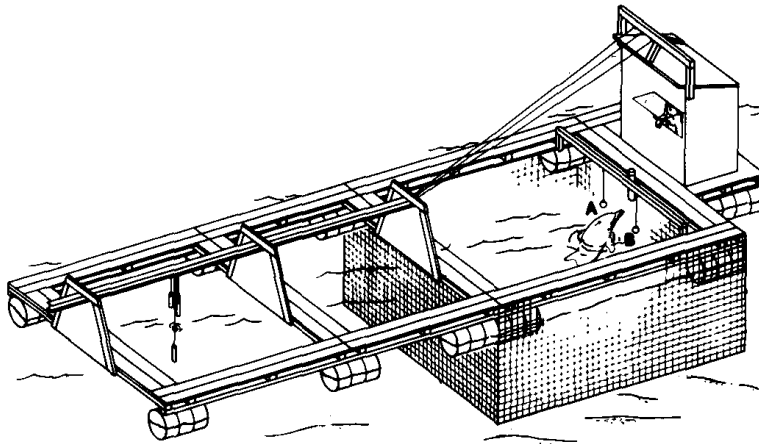


Figure 3. Experimental setting and apparatus showing porpoise stationing, A and B manipulanda, experimenter's shack and the lowering of hollow cylindrical targets attached to monofilament lines mounted on I-beam support.

Collateral Behavior

As previously indicated, a response-contingent reinforcement procedure within the context of a discrete trial procedure is the method by which echolocation is studied in marine mammals. For example, following the intake of a fish reward, the beginning of the next trial depends upon the dolphin resuming its stationing or starting position. At the start of the trial, the dolphin makes an "observing response" by emitting echolocation pulses at the target, and on the basis of its echo perception, the dolphin makes a choice (e.g. hitting one of two rubber balls mounted on flexible stalks as shown in Figure 3) which results in either a fish reward, no reward, or a time-out period (negative reinforcement). In this type of response-contingent procedure, the form or topography as well as the temporal patterning of each response--stationing → observing → choice → feeding or time-out--are all likely to influence the relationship between the "choice" response, the target variables and the reinforcement in either unknown or at least in rather imprecisely measured ways. Thus, at the start of a trial the dolphin leaves its starting position, swims to its right, begins to emit pulses while swinging its head from side to side as well as up and down, turns its entire body around, swims back to the manipulandum, breaks the water surface by spinning on its vertical axis and terminates the behavioral sequence by striking one of the rubber balls with its rostrum while simultaneously emitting squeaking sounds. Then the dolphin immediately opens its mouth, swallows the fish reward, begins swimming along

the right wall of the tank before returning to station where the animal subsequently begins bobbing its melon and rostrum up and down prior to the start of the next trial. This bewildering array of responses, their sequential dependencies and their duration are, to some extent, important regarding an interpretation of the dolphin's auditory perception of echo complexes.

In a discriminative echolocation experiment with different sized spheres presented simultaneously to an Atlantic bottlenose dolphin, Turner and Norris (1966) called some of these behaviors "collateral behavior" and found a relationship between "disruption of a stable pattern of collateral behavior" and a substantial increase in errors. Moreover, these experimenters could accurately predict incorrect choices or errors on the basis of the dolphin's swimming pattern. Evans and Powell (1967) also used the term "collateral behavior" to refer to all behaviors except target pressing and showed that there was an inverse correlation between "performance scores" (correct target presses) and "scanning rate". They also found that choices of a target (metal plates) were more rapid for easy discriminations as compared to difficult ones, but that this was largely due to the greater head scanning at distances of less than one meter from the plates for the difficult comparisons. Here again we see that responses occurring before the originally conditioned operant were predictive of the animal's performance.

Although Evans and Powell (1967) emphasized various aspects of the observing response in an echolocating dolphin and showed correlations between this behavior and the "terminal" response, Penner and Murchison (1970) noted that an echolocating Inia geoffrensis sometimes swam upside down, jaw gapped, jaw snapped and yawned. In terms of predicting whether their fresh water dolphin would hit the "yes" or "no" manipulandum, Penner and Murchison found that Inia terminated its observing response sooner or later depending on the absence or presence of a target. Similar observations have been reported in echolocation experiments dealing with the effects of distance and reverberation on object detection in Tursiops truncatus (Murchison, 1979).

Collateral behavior in echolocating porpoises may be viewed in the larger context of environmentally induced sequential patterns of behavior. Falk (1961; 1969; 1971) coined the term "adjunctive behavior" in reference to excessive drinking in a hungry rat when the animal was lever pressing on a schedule of intermittent food reinforcement. The distinction between adjunctive or interim activities and terminal responses was first made by Staddon and Simmelhag (1971) who showed that during interfood or intertrial intervals predictable sequential behavior patterns increased and decreased with terminal responses (e.g. a conditioned operant or Pavlovian response) occurring just before the delivery

of food. In a recent review Staddon (1978) has shown that temporal sequences of behavior depend on their interactions with other behaviors that are induced in the situation. Interim activities for an echolocation dolphin would include all aspects of the observing response (pulse emission, head scanning, etc.) as well as head bobbing, jaw clapping, jaw gapping, side swimming, etc. Various measures of the terminal or indicator response might include its form or topography, its duration, and its strength. Any and all of these response measures may be correlated with the "choice" response in an echolocation task and are likely to help in our understanding of the behavior of a porpoise following its analysis of complex echo inputs in relation to its previously stored information.

To illustrate the interaction between interim activities and terminal responses, I will describe one of a series of discriminative echolocation experiments which I conducted at the Naval Ocean Systems Center in Kaneohe Bay, Hawaii. Hollow steel and hollow bronze targets were presented successively to an experienced adult male porpoise (Sven) in a two-alternative forced-choice procedure. Figure 3 shows a schematic diagram of the experimental setting. The dolphin's task was to differentiate echoes from hollow steel and hollow bronze targets--each having two different-sized outer diameters (OD) and wall thicknesses. The targets were described in detail by Hammer (1978). All targets were 17.8 cm long. The smaller OD's were 3.81 cm with a wall thickness of 0.32 cm and the larger OD's were 7.62 cm with a wall thickness of 0.40 cm. Both the large and small steel targets were to be reported on the A or left manipulandum and the large and small bronze targets were to be reported on the B or right manipulandum. In earlier experiments Sven had been trained to report the presence of a target by hitting the A manipulandum and the absence of a target by hitting the B manipulandum. To take advantage of those previously established response contingencies, Sven was first trained to make an A report when presented with either a large or a small hollow steel target submerged about 1.14 m from the surface of the water and to make a B report in the absence of a target. Once Sven perfected this differentiation, both the large and small bronze targets were submerged gradually, i.e., the vertical positions of the bronze targets were initially always closer to the surface of the water than the steel targets. The vertical position of the bronze targets gradually approached that of the steel targets until eventually all targets were presented in the same position. In general, this type of stimulus fading procedure minimizes errors (see below) during the acquisition phase of a learned discrimination.

Figure 4 shows the acquisition of the discrimination between steel and bronze targets regardless of size. Because a fading procedure was used, the number of errors was minimized even when

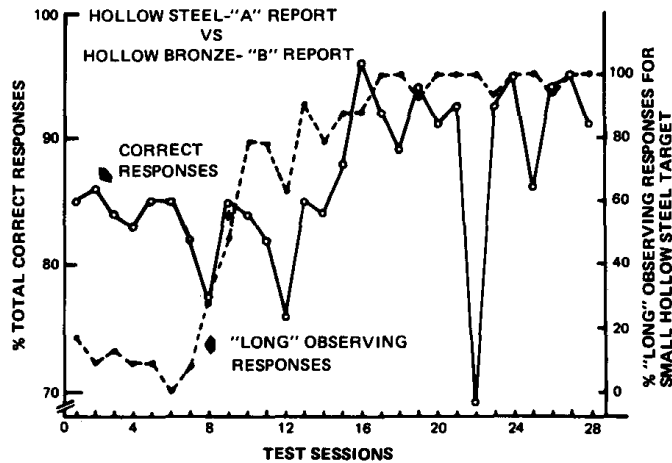


Figure 4. Acquisition of a hollow bronze and hollow steel differentiation regardless of the size of the outer diameter of the targets. "Long" observing responses occurred only in the presence of the small hollow steel target ("A" reports) and were a precursor of a significant increase in total correct responses.

the porpoise was first confronted with the discrimination. Nevertheless, the percentage of total correct responses, i.e., for all four targets, rose significantly from the first 14 test sessions to the last 14 sessions ($p < .01$; sign test). In addition to measuring the terminal choice responses as a function of the type of target presented, we also recorded response latencies and classified observing responses into two categories. The most frequently occurring response was one in which the turn from station toward the target area at the beginning of a trial was quickly followed by another abrupt turn to the manipulanda. During the course of these rapid observing responses, Sven never swam more than two meters from station and the response latencies were invariably less than four seconds. This observing response occurred most frequently in the presence of both bronze targets and the large steel target. However, about one-quarter of the way through the experiment, Sven began to make a different observing response. When he made a complete turn from station toward the target area at the start of a trial, he rolled onto his left side and with his head tucked slightly he faced the target area. Following a pause of between one to two seconds, after swimming at least three meters from station, Sven swung his entire body around in a very deliberate fashion before returning to the manipulanda. The response latencies for these observing responses were usually more than four seconds. These "long" observing responses occurred primarily in the presence of the small steel target. As Figure 4 shows, "long" observing responses were very

infrequent during the first seven test sessions and then increased dramatically. The increased probability of "long" observing responses in the presence of the small steel target was a precursor to the significant increase in total correct responses. Thus, in this experiment, there was a strong interaction between interim activities and terminal responses as a function of specific target stimuli. Moreover, a measure of the interim responses showed that the porpoise was actually differentiating between the large and small hollow steel targets even though the terminal response (A-report) was the same for both echo complexes.

METHOD OF TARGET PRESENTATION

The development and maintenance of stimulus control in echolocation experiments makes it absolutely necessary to ensure that the animal is appropriately oriented to the target area and that targets are chosen and presented in such a way that target parameters cover a wide range of values including threshold values. Target detectability must be assured if reinforcement contingencies are to produce the desired results of establishing and maintaining stable responding. The spacing of target parameter values around threshold and the sequence of presentation are also crucial considerations in training and maintaining stimulus control. Once established, the degree of stimulus control by an echo complex can be tested or probed by presenting novel targets and finding out the degree to which targets contain similar echo configurations (Hammer, 1978). In general, experimenters using porpoises in studies of echolocation have used traditional psychophysical methods to arrive at threshold estimates.

Observing Response

In an early experiment on discriminative echolocation with different sized spheres (Turner and Norris, 1966), a blindfolded dolphin had to deflect a lever corresponding to the standard sphere in order to collect a fish which was thrown to a specific "zone" or area of the pool. Once the dolphin collected the fish, it oriented to the apparatus to make another response. Obviously, this type of control of the animal's positioning while it echolocates is crude and makes it difficult to specify the properties of the echoes returned to the dolphin which controlled the animal's final choice response. Without controlling the position from which a discrimination is made, it is not even possible to be certain that the intensity of the echo return, depending as it does on the distance between the porpoise and the targets and the manner in which the porpoise faced the targets, is the critical cue in differentiating objects of different target strength (e.g. see Evans and Powell, 1967). Much of the early Russian research

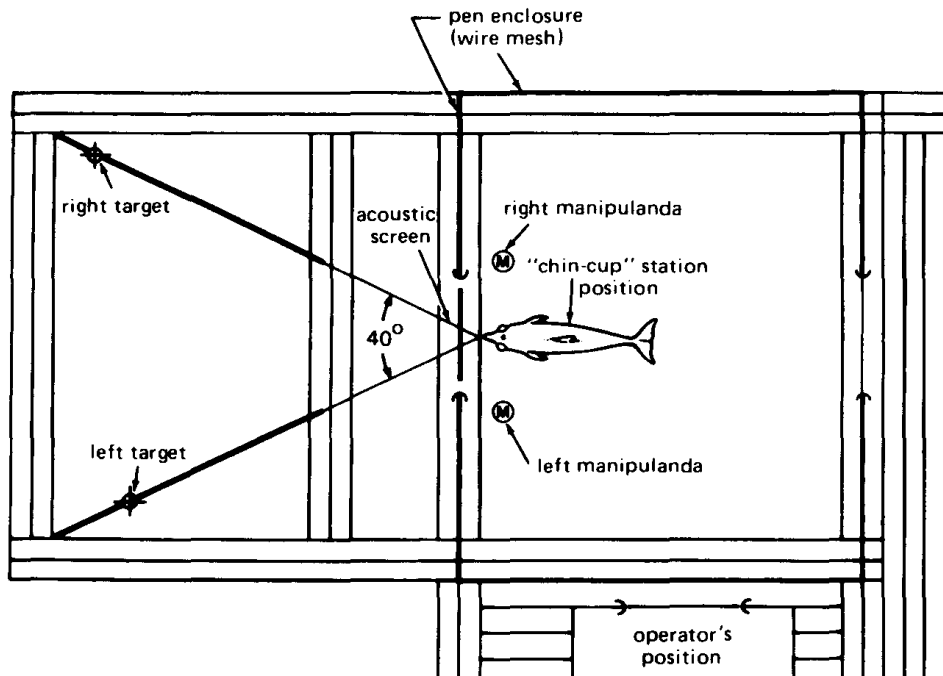


Figure 5. Schematic of a dolphin assuming a fixed stationing position in a chin cup behind an acoustic screen during a range resolution task. The animal's task was to report whether the left or right target was closer and the report was made by striking the appropriate manipulandum. On this trial the correct report is on the left. The two-alternative forced-choice procedure with simultaneous target presentation was used.

suffers from the same problem, i.e., the ambiguous nature of the echo return in relation to the position of the dolphin and the targets at the time the discrimination is made.

During the past few years, much more refined and unambiguous control of an animal's orientation with respect to the targets has been accomplished by making the observing response contingent upon target presentation. In a range resolution task, Murchison (1979) made target presentation (consisting of two identical 7.6 cm diameter polyurethane spheres) contingent on "chin-cup" stationing (see Figure 5). Once the porpoise was stationed in the fiberglass chin cup and the targets were in position, an acoustic screen was dropped and the target display was presented to the dolphin. Thus, the acoustic screen prevented the animal from prematurely scanning the target display and has the potential of allowing the experimenter to make rather precise measurements of pulse emission and the echo return at the relatively precise position of pulse emission (Au, Floyd and Haun, 1978).

HOOP STATION

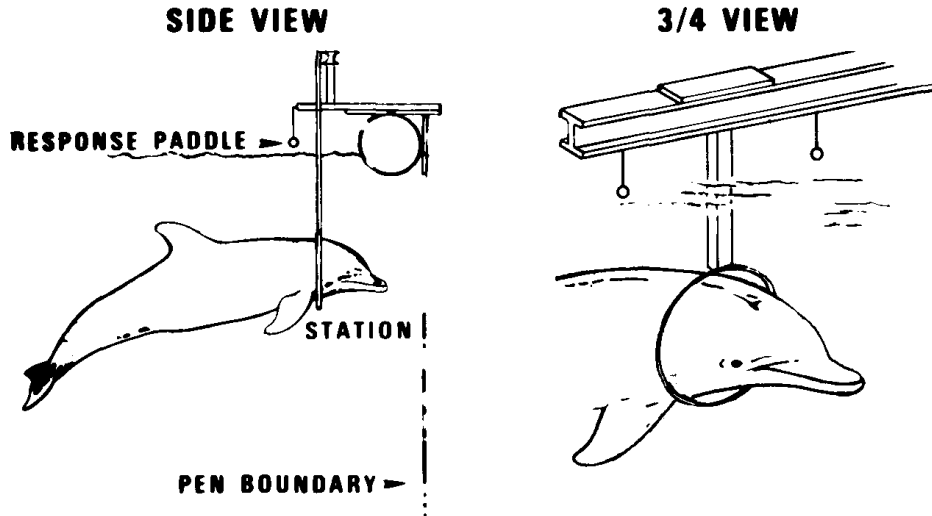


Figure 6. Diagram of an Atlantic bottlenose dolphin (*T. truncatus*) maintaining a fixed position in a water-filled plastic hoop. The dolphin remained in the hoop up to its flippers and when given an audio signal it emitted a burst of echolocating clicks at a target 6 m directly in front of its melon. Following the termination of the last pulse within a burst of pulses, the dolphin backed out of the hoop and reported the presence of a sphere or cylinder by hitting the "A" or "B" response paddle or manipulandum with its rostrum.

Another technique of controlling not only the postural aspect but also the pulse emission aspect of the observing response in an echolocation task has been developed by Schusterman, Kersting and Au (this volume). In a sphere-cylinder discrimination task the porpoise had to position itself in a 41 cm water-filled plastic hoop with its rostrum directly in line with the center of the target located 6 m away and inhibit the emission of echolocation pulses until an audio cue was given (see Figure 6). The preciseness of the observing response just described permitted a determination of the type of signal return the dolphin used to make its differentiation (Au, Schusterman, and Kersting, this volume).

Most recently, Penner and Kadane, in an evaluation of biosonar detection in noise (this volume), were able to record pulse train latencies and response latencies following the last pulse of a train from two bottlenose dolphins who were trained to make a precise postural observing response. Thus, these investigators were and are capable of making relatively exact measurements of

the moment in time in which the dolphins make their decision regarding the presence or absence of a target.

Fading Procedures

Perhaps the most powerful technique currently available which minimizes the number of incorrect responses during the acquisition phase of a detection or discrimination task via echolocation is the technique of fading. In general terms the technique depends on initiating training or stimulus control procedures with an easy detection or discrimination (high signal/noise ratio) and gradually changing some feature of the targets on successive trials so that stimulus control of responding is transferred from one feature or characteristic to another. For example, in the visual mode Schusterman (1965; 1966) showed that sea lions could repeatedly reverse their responses to different visual shapes (circles and triangles) errorlessly if the animals were transferred from a previously well-established size discrimination. These and other experiments suggest that, in a wide variety of species using a wide variety of stimuli, interdimensional training frequently results in less errors than intradimensional training probably because of the greater differences between stimulus configurations in the interdimensional condition (see Castillo and Pinto-Hamuy, 1978, for a recent review of the use of fading procedures).

In, perhaps, the best controlled experiment on discriminative echolocation of planometric shapes, Simmons and Vernon (1971) found that enucleated big brown bats (Eptesicus fuscus) initially could not be readily trained to distinguish between different shaped triangles (made of polystyrene) having the same surface area. However, when the experimenters presented the bats with two triangular targets differing both in size and shape, the discrimination was acquired rapidly. Thereafter, the size dimension was gradually reduced so that eventually only differences in triangular shape controlled responding by the bats.

In a dolphin counterpart to the bat echolocation experiment on fading from a size discrimination to a shape discrimination, Barta (unpublished ms.) and Evans (personal communication) used the type of fading technique first described by Schusterman (1965; 1966). After the successful discrimination of planometric circular targets (made of neoprene cemented to aluminum) differing in size, a blindfolded Tursiops truncatus readily distinguished between equal-size triangles and circles following the fading or gradual elimination of the size dimension.

Several studies on echo ranging in bottlenose dolphins have shown that thresholds were considerably lowered by presenting

progressively more difficult detections or discriminations, i.e., by incorporating fading procedures. Lekomtsev and Titov (1974) report that the detection of a steel sphere 1.1 cm in diameter occurred at a significantly greater range if the separation screen was advanced by successively smaller steps (0.5 m) than if it was advanced by successively large steps (1.0 m). Murchison (1979) showed that in a range resolution study daily sessions of small incremental changes of distance in the near and far targets (ΔR) had to be preceded by large ΔR trials and extensive fading of the ΔR in order to maintain stable responding and the obtaining of reliable estimates of ΔR thresholds.

Probe Trials

In virtually all previously described studies, the behavioral methodologies allowed for interpretation of the dolphin's echolocation capabilities primarily in terms of the systematic covariation between values of target parameters (i.e., size, material, shape, etc.) and performance. These methods are unsuitable for identifying the manner in which dolphins classify target or echo parameters. In animal psychophysics, many investigators depend on generalization tests or test of response equivalence to determine the dimensions along which some sensory quality is represented in a given species or population. One variation on the generalization test which has been used in echolocation experiments is to establish an extremely stable discrimination between two different targets or sets of targets and then, interspersed with trials in which targets from the original or baseline discrimination are presented, the investigator presents novel targets on the "probe" or test trials.

Recent research by Hammer (1978) and Au (Au and Hammer, this volume) serves as a fine illustration of the probe-trial technique. These investigators applied the two-alternative forced-choice procedure with successive target presentation to the study of discriminative echolocation in which the object of the study was to have the porpoise classify echo complexes in terms of response equivalence. An adult male Tursiops, who had been well-trained on a range detection task, was presented with two sets of different-sized cylindrical targets. One set of cylinders (A) controlled responses to the left response manipulandum (A) and the other set of cylinders (B) controlled responses to the right response manipulandum (B) (see Figure 3). In one very interesting experiment, the porpoise was first trained to differentiate between hollow aluminum cylinders and solid coral rock. The animal was then presented with probe trials of different-sized hollow cylinders of glass, bronze and steel and the probability of trials on which the porpoise gave the aluminum response was calculated. On the basis of these ranked probabilities, Hammer and Au found that the porpoise classified glass most like aluminum and steel least like aluminum, regardless of target

size. The results of synthesized broadband dolphin-like signals bounced off the same targets and subjected to a matched-filter analysis indicated a relatively close resemblance to the dolphin's performance on the task.

Psychophysical Procedures

Once maximal stimulus control is attained, then an estimate of the animal's absolute or differential sensitivity is sought. Regardless of the signal or noise parameters involved, the threshold is usually taken as some interpolated stimulus value associated with some arbitrary criterion of detectability or discriminability. Most threshold estimates are arrived at by one of several graphic methods in which a broad range of target or noise values yield a broad range of correct choices extending from chance to perfect performance.

As previously noted, fading procedures are usually incorporated in the application of psychophysical methods to the study of echolocation parameters. Frequently, the dolphin is initially confronted with detections of discriminations with high signal/noise ratios followed by decreasingly lower signal/noise ratios. Thus, in general, the most widely used traditional psychophysical procedure for studying the echolocation abilities of dolphins has been some variation of the descending "method of limits". In order to maintain reliable performance, investigators have frequently used blocks of several trials prior to decreasing the signal/noise ratio.

Titration methods have been used on occasion in order to maintain tight stimulus control in an efficient manner. In titrating (also known as "stair-case" or "tracking"), the signal/noise ratio is decreased (either in terms of single trials or in blocks of trials) until the animal makes an error or reaches some arbitrary error criterion; then the signal/noise ratio is stepped up. Thus, in titration methods, the signal/noise ratio is either decreased or increased, depending on the animal's performance. Murchison (1979) incorporated a titration procedure as a warm-up technique in his study of range resolution in Tursiops truncatus and Barta (unpublished ms.) used a titration procedure to obtain a size discrimination threshold in the same species.

In the psychophysical method of constant stimuli, a set of stimulus values occurs in random order, either in terms of single trials or in blocks or trials. Interestingly, Barta (unpublished ms.), in an attempt to obtain a size discrimination threshold, began with the method of constant stimuli by using comparison target values considerably above threshold and when an asymptotic level of performance had not been attained, he shifted to a

titration method. A recent exception to this trend of using the descending method of limits in psychophysical studies of dolphin echolocation performance is illustrated by an experiment by Penner and Kadane (this volume) on the effects of noise on the detection of a 7.65 cm steel water-filled sphere at a distance of 16.5 m. These researchers, in using a modified method of constant stimuli, randomly presented five levels of white noise (ranging from 67 to 87 dB re 1 μ Pa) in 10-trial blocks and generated a very predictable relationship between noise levels and detectability in two experienced Atlantic bottlenose dolphins.

PROCEDURAL PROBLEMS

I have already focused in on some fairly important problems related to the behavioral methods used in the study of echolocation in marine mammals. These have included the desirability of explicitly controlling in precise measurable ways various aspects of observing responses, indicator or terminal responses and ways of measuring what the animal "sees" when it is stimulated with suprathreshold echoes. There are other related problems that I would like to deal with in my concluding remarks, and these include learning, response bias, and the subtle difference between the recognition or discrimination of targets and the detection of targets.

Baseline Behavior

There have been several measurements of thresholds related to such target parameters as distance, size, resolution, wall thickness, etc. which have resulted in considerably detailed data on the echolocation capabilities of several species of porpoises (see the papers by Moore, Murchison and Nachtigall in this chapter). In all the psychophysical experiments reviewed, it usually takes months before stable asymptote or baseline is achieved. Several psychophysical studies have reported learning effects over a relatively long period of time (e.g. see Turner and Norris, 1966, and Lekmotsev and Titov, 1974).

The continued learning effect on the echolocation capability of a bottlenose dolphin is clearly illustrated in an experiment reported by Lekmotsev and Titov (1974). Following several days of training, the dolphin could reliably detect a lead sphere 5.0 cm in diameter at a distance of 11 m. After two additional months of training, the dolphin reliably detected an 0.8 cm sphere of the same material at the same distance, a greater than fourfold increase in detection acuity.

In perceptual experiments of echolocation in which generaliza-

tion techniques are used, it is extremely important, as Hammer (1978) has pointed out, that probe trials be "superimposed" on unchanging baseline behavior. It is meaningless to attempt to interpret responses to novel targets either in terms of sound emission parameters or echo return parameters if response to the original training targets are no longer reliable.

Detection, Recognition and Discrimination

In the literature of animal sonar systems, sometimes the terms "detection", "discrimination", and "recognition" are used interchangeably. However, traditional, as well as operational, use of these concepts in the psychophysical literature suggests a distinction between these concepts (Galanter, 1962). Classically speaking, detection (in echolocation tasks) should refer to the problem of how much echo strength is necessary in order for an animal to reliably differentiate the target or signal from the ambient noise. Recognition and discrimination, on the other hand, assume detectability and refer to the question of how distinctive or how similar echoes emanating from two or more targets are from each other. Even a cursory review of the literature leads me to believe that relatively few investigators working on animal sonar systems have realized that behavioral methods, particularly in terms of a whole host of variables dealing with the animal's previous training experience, critically determine the way in which an animal perceives the common as well as the distinctive or salient features of different target-reflected echoes.

In an experiment on shape discrimination in bats (Myotis oxygnathus), the animals were first food reinforced for approaching squares and not triangles (presented simultaneously) of equal surface area (Konstantinov and Akhmarova, 1968). After learning this discrimination to a high degree of accuracy, when the nonreinforced triangle was replaced with a circle, the probability of the bats still approaching the square remained unchanged. Later, when the square was presented simultaneously with both the circle and the triangle, performance still remained relatively unchanged. A similar experiment was conducted under water with T. truncatus and the results were essentially the same, i.e., the introduction of a new target presented simultaneously with the previously reinforced target did not effect performance deleteriously (Barta, unpublished ms.). These results might be expected if during or following original learning it was primarily the presence of distinctive echo characteristics from the positive or reinforced target which controlled responding and not the distinctive echo characteristics of the negative or nonreinforced targets or the echo characteristics which both positive and negative targets had in common. However, the results are surprising if it is understood

that during and following original training both positive and negative targets were equally or nearly equally effective in controlling discriminative performance (Mackintosh, 1974). The question of what would have happened in these and other similar experiments if the positive target were replaced and a novel target was paired with the negative target seems never to really have been considered. My guess is that performance would have deteriorated. It would appear, therefore, that the animals in these experiments were listening for distinctive echoes from the positive target and that echoes from other targets acquired the status of background or ambient noise similar to the situation that prevails in detection experiments.

Perhaps the clearest example of a dolphin being trained inadvertently to listen for distinctive echoes reflected from one set of targets and not another comes from the work of Hammer (1978). As previously mentioned, Hammer's Atlantic bottlenose dolphin (Sven) had previously been trained in a series of detection tasks to report the presence of a target to its left and the absence of a target (ambient noise) to its right, and was then trained by Hammer in a two-alternative forced-choice procedure to report the presence of small and large hollow aluminum cylinders (A targets) to its left (A response manipulandum) and to report the presence of small and large solid coral rock (B targets) to its right (B response manipulandum). After the porpoise had perfected this baseline differentiation, Hammer conducted a series of experiments in which he used probe trials to determine what characteristics the probe targets had in common with the baseline targets of rock and aluminum. In almost all instances, probe targets--even hollow aluminum targets with a wall thickness of only 0.16 cm difference from the standard hollow aluminum targets--were classified as the standard solid rock targets, i.e., as B targets or ambient noise. These results suggest that most targets were classified as ambient noise because the dolphin, Sven, was listening for a salient portion of the echo complex to make its differentiation and that in the absence of the salient or distinctive feature, Sven reported on the B manipulandum. Since Sven's previous training probably played a crucial role in the way the dolphin reported on the A and B manipulandum, I suspect that if Hammer had trained Sven to report solid rock cylinders on A and hollow aluminum cylinder on B, most of the probe targets would have been classified as aluminum, or, in other words, as ambient noise. Thus, Hammer's results and his interpretations may have strongly depended simply on the way he constructed the original or baseline reinforcement contingencies.

I tested the hypothesis that Sven made his classification on the basis of a distinguishing feature or features emanating from the A targets and on the basis of irrelevant features or ambient noise emanating from the B targets in the following way. First,

I trained the dolphin to differentiate between successively presented small and large hollow steel cylinders (A targets) and small and large hollow bronze cylinders (B targets). The dolphin perfected and continued this baseline behavior during each test session for 56 of the 64 trials, but during the other eight trials, "compound probe" trials were presented. On these compound probe trials, instead of presenting a single A or B target, both the large and small A targets were presented side by side approximately 4-8 cm apart. If Sven was listening for a specific echo feature from a single A target (large or small) in order to report A, this feature, according to my hypothesis, should be blocked or in some way masked or negated by the presence of both the large and small A targets and Sven should classify such reflected echoes as irrelevant noise and report on the B manipulandum. If, on the other hand, Sven was indeed distinguishing the A target features from the B target features, then reflected echoes from two A targets should be classified as A and reported as such. During eight compound probe trials with both A targets, Sven classified all such presentations as B ($p < .01$, binomial test); thus confirming the hypothesis. A control procedure in which compound probes consisted of large and small B targets (hollow bronze) resulted in 7 of 8 B reports ($p < .05$, binomial test).

These experiments clearly demonstrate the importance of considering both the previous training and the current behavioral techniques in use in interpreting results from so-called "discriminative" echolocation tasks. Apparently the way echolocating dolphins perceived and classify echo complexes from specified targets depends, not only on previous experience, but also on the manner in which these targets are presented in relation to the specific responses required by the experimenter, i.e., the response-contingent reinforcement procedures. It might very well be the case that bilateral responding to different echo complexes emanating from the same location in space (as is the case in the two-alternative forced-choice procedure with successive presentations) has a different effect on the processing of echo information by dolphins than does bilateral responding to different echo complexes emanating from different locations.

Response Bias

When sonar targets are presented successively in order to determine a threshold, e.g., the maximum range at which a given sized object is detected by a dolphin on 50 percent of the trials (see Murchison, this volume), response bias may affect the threshold estimate. The bias can be manifested either as a position preference in a forced choice procedure or as a preference for responding or not responding in a go/no-go procedure. A bias in

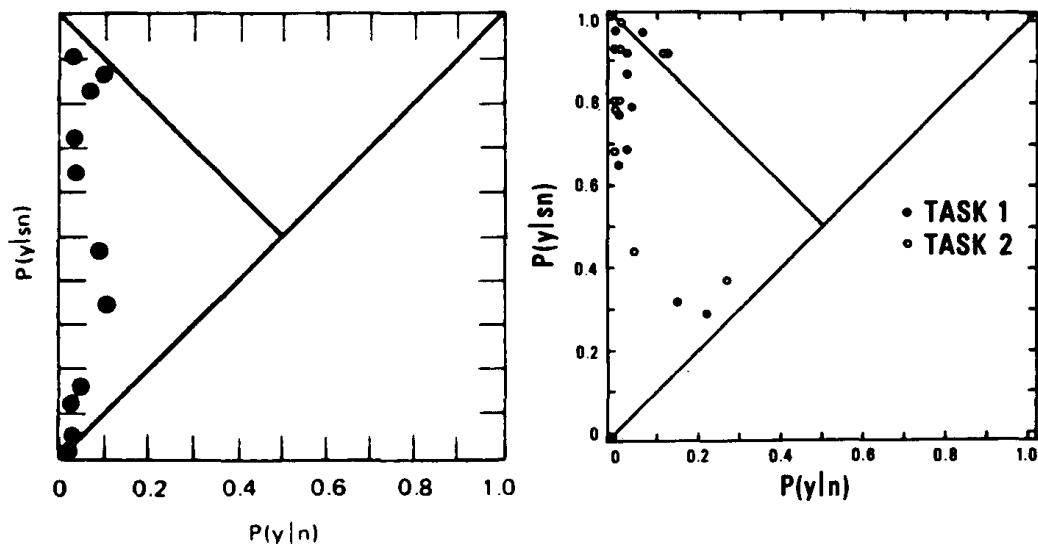


Figure 7. Hits or $P(y|sn)$ plotted against false alarms or $P(y|n)$ for echolocating Amazon River porpoise in a size detection task (left panel) and two echolocating Atlantic bottlenose dolphins (*T. truncatus*) in a maximum detection range task (right panel).

favor of a "no" response would result in an increased threshold while a bias in favor of a "yes" response would result in a decreased estimated threshold. The theory of signal detectability is a relatively recent approach which permits one to evaluate independently the contributions to discriminative behavior of an animal's sensitivity and its response bias (Swets, 1973). Schusterman (1974) has pointed out that in some echolocation experiments biases introduced by training conditions and reinforcement contingencies have led to underestimates of sensitivity.

Figure 7 presents conventional signal detection plots with "hits" ($y|sn$) on the ordinate and "false alarms" ($y|n$) on the abscissa. The data were originally plotted as ogives and involved an Amazon River dolphin in a size detection task (Penner and Murchison, 1970) and two Atlantic bottlenose dolphins performing on two range detection tasks using different sonar targets (Murchison, this volume). The data points lie between the upper left-hand corner (perfect detection) and the major diagonal (chance detection). Points lying along the minor diagonal (the line

drawn from the upper left-hand corner to the major diagonal) would represent "zero" bias since the two possible types of error (false alarms and misses) would be equally probable. Both graphs show that all three echolocating dolphins (regardless of the task) have a strong and relatively consistent bias against making false alarms. This is particularly true of the Amazon River dolphin. The sensitivity index, called d' , is a measure of sensory effects uncontaminated by bias and represents the distance of a data point from the major diagonal. The signal detection arrangement of plotting hits in relation to false alarms is a convenient way to display response bias and to estimate its interaction with apparent sensitivity to stimulus events. A careful inspection of the right panel of Figure 7 shows that the smallest d' values also yielded the weakest bias against making false alarms. This analysis suggests that for the two echo ranging detection tasks by Tursiops there is an interaction between response bias and apparent sensitivity to the strength of the returning echo.

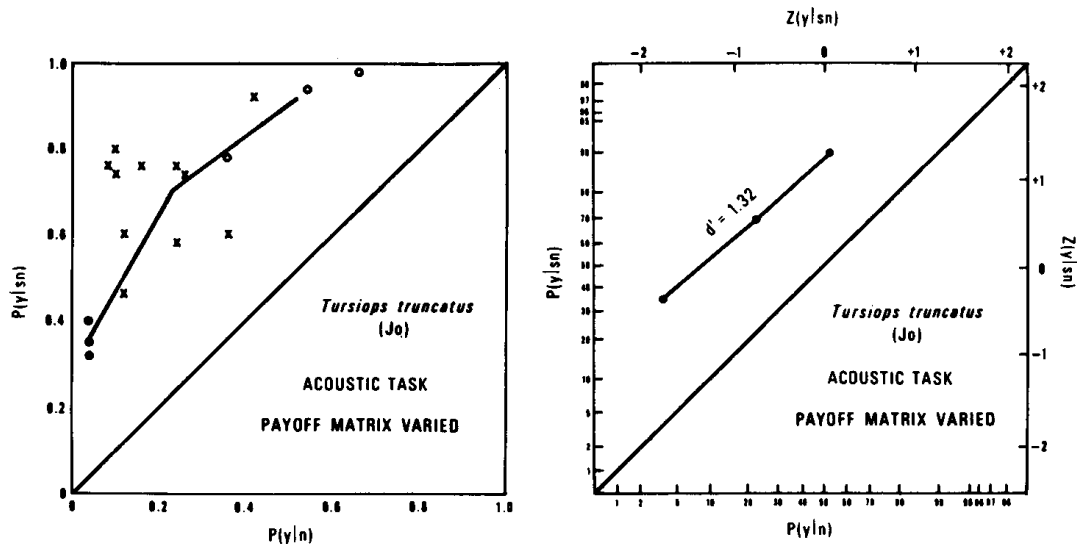


Figure 8. ROC functions for an Atlantic bottlenose dolphin (T. truncatus). The animal attempted to detect an 8-kHz signal varying between -9 to -11 dB re 1 μ bar with ambient noise varying by as much as 15 dB. Each data point in the left plot is based on 100 trials. The x's represent ratios of number of fish rewards for hits; correct rejections of 1:1. The open circles represent ratios of 4:1 and the solid circles represent ratios of 1:4. The right plot shows the same data plotted on Z-score coordinates.

Several recent studies with marine mammals have shown that in underwater passive hearing tasks with acoustical signals having a relatively low signal/noise ratio, variation in such nonsensory variables as signal probability, amount of reinforcement and probability of reinforcement, resulted in highly predictable changes in response bias without appreciably altering their ability to detect the acoustic signal (Schusterman, 1976; Schusterman, 1974; Schusterman and Johnson, 1975; Schusterman, Barrett and Moore, 1975). If signals of similar strength are repeatedly presented while the amount of reinforcement for "yes" and "no" responses is varied, then a series of data points along a "receiver operating characteristic" (ROC) or "isosensitivity" curve are produced. Figure 8 shows ROC curves for a dolphin. The curves were generated by holding signal strength constant (the ambient noise levels were relatively unstable) and varying the number of fish for hits and correct rejections. According to the theory of signal detectability, when the averaged data points in the left panel of Figure 8 are transformed into standard deviation units or Z-scores, they should yield an ROC curve parallel to the major diagonal as shown in the right panel of Figure 8 (Green and Swets, 1966).

In order to obtain a threshold estimate uncontaminated by response bias, one could extrapolate a d' value from a family of ROC curves where the curves cross the minor diagonal, i.e., at the point of zero bias. Unfortunately, ROC curves have not, as yet, been generated from dolphin performance on echolocation tasks. It seems that a signal detection approach would certainly further the understanding of signal processing in echolocating marine mammals by disentangling the effects of bias (e.g. motivation and attention) from psychophysical data dealing with their sonar receiver, i.e., the peripheral and central mechanisms of their auditory system.

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