Detection of underwater signals by a California sea lion and a bottlenose porpoise: variation in the payoff matrix

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A sea lion (*Zalophus californianus*) and a porpoise (*Tursiops truncatus*) were trained to report the presence of a pure tone under water in yes–no psychophysical procedures. Signal probability was held constant at 0.50. For the sea lion signal strength and payoff matrix were varied concurrently while only payoff matrix was varied for the porpoise. Payoff matrix was manipulated by changing the amount of reinforcement (number of fish) consequent on the two different classes of correct responses —hits and correct rejections. In terms of the ratio of hits to correct rejections the matrix was varied over three values—1:1, 4:1, and 1:4. In the sea lion signal detection improved as signal intensity increased and was independent of the sea lion's response bias. In the porpoise changes in response bias occurrred as a function of changes in the payoff matrix. Both the sea lion and the porpoise repeatedly demonstrated rapid acquisition of a stable response bias. These experiments demonstrate that varying the payoff matrix may be an effective way to control response bias in experiments dealing with the detection of underwater signals by marine mammals.

Subject Classification: 80.50, 80.60.

INTRODUCTION

Measurement of an animal's ability to make fine discriminations are frequently influenced by biasing factors, and the theory of signal detectability allows one to evaluate independently the contributions to discriminative behavior of an animal's sensitivity and its response bias (Swets, 1973). Animal psychophysicists, engaged in estimating acoustic thresholds in several different marine mammals under a wide variety of acoustic tasks (including passive hearing in air and under water by seals, sea lions, and porpoises and active sonar by the porpoises), have been relatively unaware of the response bias effects resulting from certain reinforcement contingencies (Schusterman, 1974a). It is likely that in such psychophysical experiments the animals were trained to be "conservative, " i.e., to maintain a moderately strict criterion, thus emitting a low rate of false alarms and thereby producing threshold estimates indicative of a relatively high signal/noise ratio (Schusterman, 1974a). However, like rats (Terman and Terman, 1972) and monkeys (Clopten, 1972) in auditory tasks, response bias of the California sea lion (*Zalophus californianus*) can be manipulated by varying signal probability and obtaining a bias-free estimate of discrimination (Schusterman and Johnson, in press).

Another way to manipulate response bias is to change the symmetry of the payoff matrix, i.e., the amount of reinforcement consequent on two different classes of correct responses. Amount of reinforcement on discriminative instrumental conditioning usually leads to differential rates of responding with, for example, the larger amount leading to faster running in rats (Bower and Trapold, 1959) or more key pecks/min in pigeons (Catania, 1963) than does the smaller amount of reinforcement. Swets (1973) has pointed out that during the past 20 years it has been standard procedure in human psychophysics to generate so-called isosensitivity curves, i.e., to manipulate response bias or criterion, by varying the positive and negative reinforcements of the various stimulus-response outcomes (payoff matricies) while keeping stimulus configurations constant. The present experiment investigated the effects of varying the payoff matrix on response bias in *Zalophus* and in the bottlenose porpoise (*Tursiops truncatus*) in underwater auditory tasks paralleling a "yes–no" signal detection paradigm.

I. EXPERIMENT 1: CALIFORNIA SEA LION

A. Method

1. Subject

The experimental subject (Sam) was an eight- to nine-year-old male *Zalophus californianus* who was wild-born and had been in captivity since the age of two years. Prior to the present experiment, Sam had been trained to hold his head under water or in air in a fixed position and to emit a burst of clicks in the presence of a pure tone preceded by a warning light and to remain silent if no tone followed the warning signal (Schusterman, Balliet, and Nixon, 1972; Schusterman, 1974b). In this manner underwater and aerial audiograms were obtained in the California sea lion. Sam had most recently served as a subject in an experiment dealing with bias as a function of acoustical signal probability (Schusterman and Johnson, in press).

2. Sound equipment and measurement

The experiment was conducted in a 3.5 m×11.1 m ×1.2 m concrete pool located above ground. At one end of the pool was a testing platform with a vertical opaque screen with a viewing slot which allowed observation of the behavior of the sea lion, but prevented the sea lion from seeing the experimenter. The platform also housed such testing equipment and materials as attenuators, the speaker-amplifier, fish, etc. Similar conditions for psychophysical experiments on sea lions and seals have been described in detail by Schusterman, Kellogg, and Rice (1965) and by Schusterman *et al.* (1972).

Extending from below the platform and into the water was a lead zirconate titanate transducer (F50), calibrated by the Underwater Sound Reference Division, Naval Research Laboratory, Orlando, Florida. Alongside of the transducer was a 150-W floodlight. Both were mounted on a 1.3-cm galvanized steel pipe and could be adjusted from the test platform to any desired height above the bottom of the pool. The water level of the pool was always maintained at 91.4 cm. During the entire experiment the transducer was positioned 43.2 cm from the bottom and 172.7 cm from the sides of the pool. The sea lion placed its head on a headrest positioned at a distance of 3.1 m directly in front of the transducer and 43.2 cm above the bottom of the pool (i.e., directly in line with the transducer). An Atlantic Research hydrophone (model LC-50) was used to monitor continuously underwater sounds.

Schusterman *et al.* (1972) provide a full description of the equipment controlling the experimental contingencies and amplifying, attenuating, monitoring, and measuring acoustic signals; ambient noise levels for tones of different frequencies are also given. A 16-kHz tone was used during the course of the experiment. However, since the pool used in the present experiment had different acoustical properties from that previously used, signal and noise measurements were repeated using the same apparatus described by Schusterman *et al.* (1972). The sound pressure levels (decibels *re* 1 μbar) under water of the three different signal intensities for a 16-kHz tone were −7 (strong), −11 (moderate), and −15 (weak). These measurements, as well as the measurements of the standing wave ratio (SWR) and the ambient noise level, were made with an H-56 hydrophone positioned where the sea lion's head would normally be during testing. The ambient noise level in terms of a $\frac{1}{3}$-octave band was −31 dB *re* 1 μbar. However, the signal-to-noise ratios for each signal intensity chosen were not as favorable as the above figures would indicate because of the SWR (a measure of the direct ratio of maximum and minimum or null sound pressure levels). The normal SWR in this tank with a 16-kHz tone of 0.5-sec duration was about 13 dB. Using a slowly moving hydrophone, there was evidence of multipath interference causing resultant signal-level fluctuations in the sound field where the sea lion's head would normally be located. Primary interfering paths were *direct* and *surface* reflected signals. Hydrophone measurement positions were in general accord with expected distance variation for this primarily two-path signal interference at 16-kHz, i.e., approximately 5.1 cm. It was assumed that a sea lion as well trained as Sam would locate the area of maximum intensity within the fluctuating sound field. Observations of the sea lion turning its head to the right when the warning or trial signal was given support this assumption as do Johnson's (1966) observations on a bottlenose porpoise.

3. Procedure

A light was used as a warning signal followed by a pure tone (signal trials) and by "noise" (catch trials). The probability of signal presentation was 0.50. After the sea lion's head was in fixed position a trial was begun by presenting the warning signal for 2.5 sec and sometimes presenting the 16-kHz tone during the final 0.5 sec of 2.5-sec light duration. In order to receive one or more pieces of herring (each piece weighing approximately 13 g), the sea lion was required to emit a burst of underwater clicks ("yes") within 1.5 sec after signal presentation ("hit" or correct detection). If a signal was not presented, the sea lion had to remain silent for 3.5 sec after light onset ("no") in order to receive one or more pieces of herring (correct rejections). Vocalization by the sea lion on a catch trial ("false alarm") was neither positively reinforced nor explicitly punished, and remaining silent on a signal trial ("miss") was also not positively reinforced. The intertrial interval was approximately 10 sec. Under all conditions of the experiment the sea lion was maintained on 20 lb of fish/day; including the amount of fish earned during experimental sessions. The payoffs or the amounts of reinforcement (pieces of fish) were varied in terms of the ratio of hits to correct rejections in the following way: 1:1, 4:1, and 1:4. Thus, in the 1:1 payoff matrix, a hit and a correct rejection both yielded one piece of fish, whereas in the 4:1 payoff matrix a hit yielded four pieces of fish and a correct rejection yielded only one piece of fish. The opposite of this was true for a 1:4 payoff matrix.

As previously noted, three different signal strengths (strong, moderate, or weak) were presented daily in a modified method of constant stimuli. Preliminary work was necessary in order to choose three sound pressure levels under water which would produce d''s of approximately 3.0, 2.0, and 1.0. The d''s are indices of signal detectability and the larger the value the more favorable is the signal/noise ratio (Swets, 1973). Each of the three different signal strengths was mixed on a quasirandom basis from session to session with five catch trials for a total of ten consecutive trials and then repeated four times within each session, for a total of 120 trials/test session. Two test sessions were run/day—separated by approximately 2–3 h. In the sequence of signal strengths, each daily session initially went from high intensity to low intensity. Following the first 30 trials, each block of ten trials containing a given signal strength was presented randomly. A 20-trial warm-up period prior to each test session was given. The warm-up signals were 4–8 dB stronger than the highest intensity test signals and the payoff matrix for the actual test session also prevailed during the warm-up period.

The 1:1 payoff matrix was used as a constant baseline, which was returned to after two or three days following the introduction and termination of each of the other two payoff matrices. The experiment was conducted for 51 days starting with six days of baseline (1:1). Following baseline, the 4:1 matrix was introduced for two days, followed by baseline for two days, followed by the 1:4 matrix for two days. Thereafter, each matrix was run

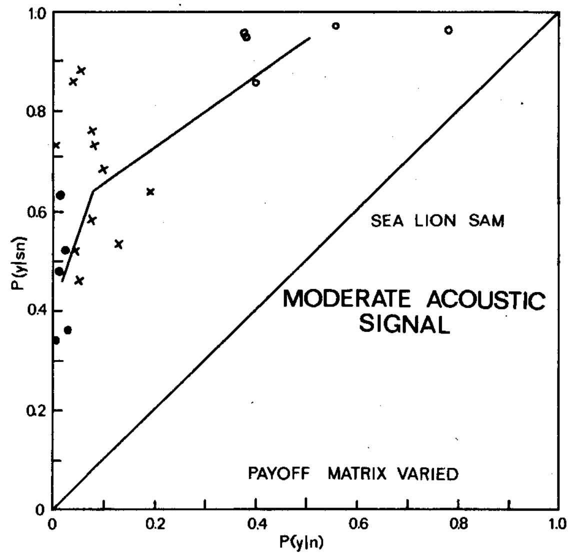

FIG. 1. Conditional response probabilities of a California sea lion as a function of changes in the payoff matrix. The ×'s represent ratios of food reinforcement for hits to correct rejections of 1 : 1. The open circles represent ratios of 4 : 1 and the solid circles represent ratios of 1 : 4. The intensity of the 16-kHz signal was -11 dB *re* 1 μbar under water. Each data point is based on 160 to 240 trials.

for no less than two days and no more than three days. The 4:1 matrix was given five times for a total of 12 days; the 1:4 matrix was given five times for a total of 13 days; and following the initial six days, the 1:1 matrix was given ten times for a total of 20 days.

B. Results and discussion

The significance of the theory of signal detectability is twofold: (1) A number of data points suggesting equal descriminability may be produced by a fixed set of stimulus parameters, and (2) the consequences of responding on a psychophysical task by nonhuman as well as human animals can be manipulated, resulting in the adoption of a wide range of criteria which may be characterized as "strict," "medium strict," "medium," "medium lax," or "lax" (Swets, 1973). Figures 1 and 2 present conditional response probabilities with hits $(y|sn)$ on the ordinate and false alarms $(y|n)$ on the abscissa. The data points are generated for fixed signal strengths when the payoff matrix was changed every two or three days. All but one of the data points in each of the figures (the initial baseline payoff matrix [1:1]) represents between 160 and 240 trials. There are several important features in these figures. First, by changing the payoff matrix from 1:1 to 4:1 or from 1:1 to 1:4, the sea lion's response criterion shifts from "medium strict" to "lax" and from "medium strict" to "strict," respectively. Secondly, the "medium strict" criterion under control of the usual reinforcement contingencies [which presumably was generated when the animal was first trained in psychophysical tasks (Schusterman, 1974a)] remained the same despite ten transitions from the 4:1 and 1:4 payoff matrices. Thus, for example, sea lion Sam never returned from 4:1 (in which it used a lax criterion) to adopt a "medium lax" or even a "medium" criterion when the payoff matrix was 1:1. Third, the variability or scatter of the data points is necessarily large. This is most likely due to signal-level fluctuations in the sound field. However, it should be noted that variability is largest when the payoff matrix is 1:1 and smallest when it is 1:4.

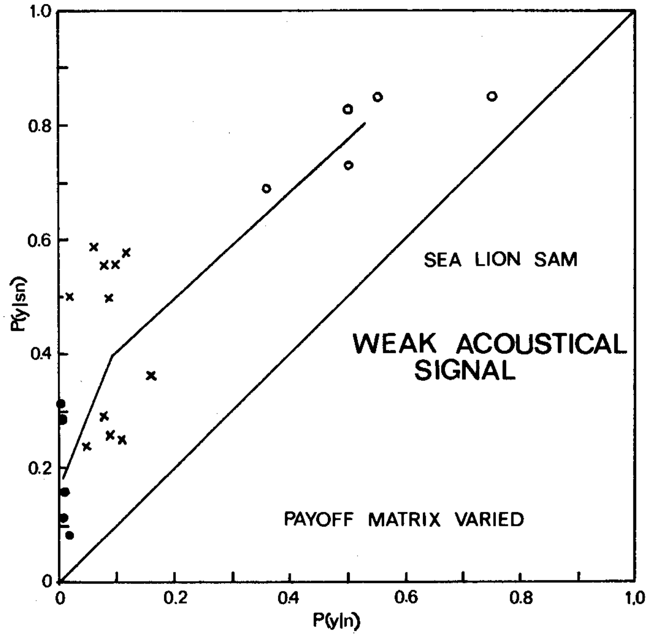

FIG. 2. Figure 2 is similar to Fig. 1, except that signal intensity was -15 dB *re* 1 μbar.

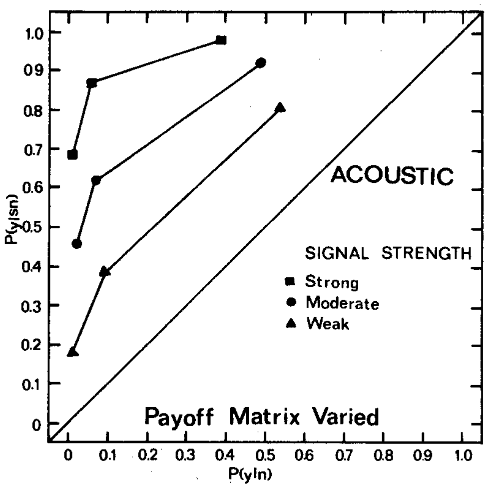

FIG. 3. A family of ROC curves for a California sea lion.

Figure 3 presents isosensitivity curves or what Swets (1973) has recently termed "relative operating characteristic" (ROC) curves. The functions are based on mean values computed from 1040 yes–no responses. In the present experiment stimulus magnitude and amount of reinforcement or payoff matrix were simultaneously varied; therefore, it is important to note that not only do the data plotted in this way show the curvilinear trend predicted by the theory of signal detectability (Swets, 1973), but the curves also show the poikilitic or psycho-

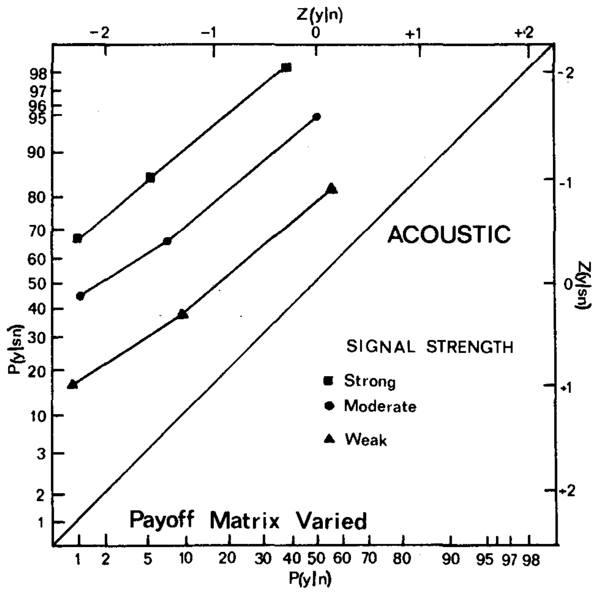

FIG. 4. The same family of ROC curves plotted on two axes marked off on linear normal deviates.

metric function of the dependence of response on stimulus magnitude (Galanter, 1974). Thus, by having varied the amount of reinforcement for different classes of correct responses, all functions swept out, and by increasing the intensity of the signal, the entire function is displaced away from the major diagonal (indicative of chance responding) toward the upper left-hand corner.

According to the theory of signal detectability, the data points of Fig. 3, when plotted on double-probability paper with response probabilities transformed into Z units, should yield a straight line with a slope of 1.0 (Green and Swets, 1966). Figure 4 shows that for all acoustic intensities, the functions are quite close to linearity and the slopes do approximate 1.0. As an index of sensitivity it should be noted that the average d' values for the strong, moderate, and weak signals were 2.70, 1.80, and 1.06, respectively.

In all nonhuman animal studies in which either signal probabilities or reinforcement contingencies were varied, the performance as shown, for example, in Figs. 1–4 represented asymptotic performance (Nevin, 1970; Clopton, 1972; Terman and Terman, 1972; Schusterman and Johnson, in press). Schusterman and Johnson found that sea lions on both underwater visual and acoustic tasks achieved asymptotic performance rather slowly when signal probabilities were changed back and forth between values of 0.75 and 0.50, and 0.25 and 0.50. In the present experiment, amount of reinforcement for different classes of correct responses (hits and correct rejections) rapidly changed the conditional probability of incorrect positive responses, i.e., false alarms. In the bottom half of Fig. 5, the probability of a false alarm is plotted as a function of the sea lion's transition from the last day of a baseline payoff matrix (1:1) to the first day of a 4:1 payoff matrix. Transitions going the opposite way, i.e., from 4:1 to 1:1 are shown in the top half of the figure. The rapid shifts in false alarms reflecting changes in response bias as a function of changing payoff matrices was essentially the same for the moderate signal as for the weak signal. Sea lion Sam's baseline criterion remained "moderately strict" each time the animal returned from a 4:1 payoff matrix, and, therefore, the criteria changes to "strict" from "moderately strict" and vice versa (as reflected by false alarms) were necessarily smaller but no less rapid than the criterion changes from "lax" to "moderately strict" (see Fig. 6).

II. EXPERIMENT 2: BOTTLENOSE PORPOISE

A. Method

1. Subject

The experimental subject (Jo) was an adult female *Tursiops truncatus*. The porpoise had been in captivity since 1969 and had been used in several experiments (Murchison and Pepper, 1972; Pepper, Nachtigall, and Beach, 1972) conducted in floating pens in Kaneohe Bay at the Naval Undersea Center in Kailua, Hawaii. Among

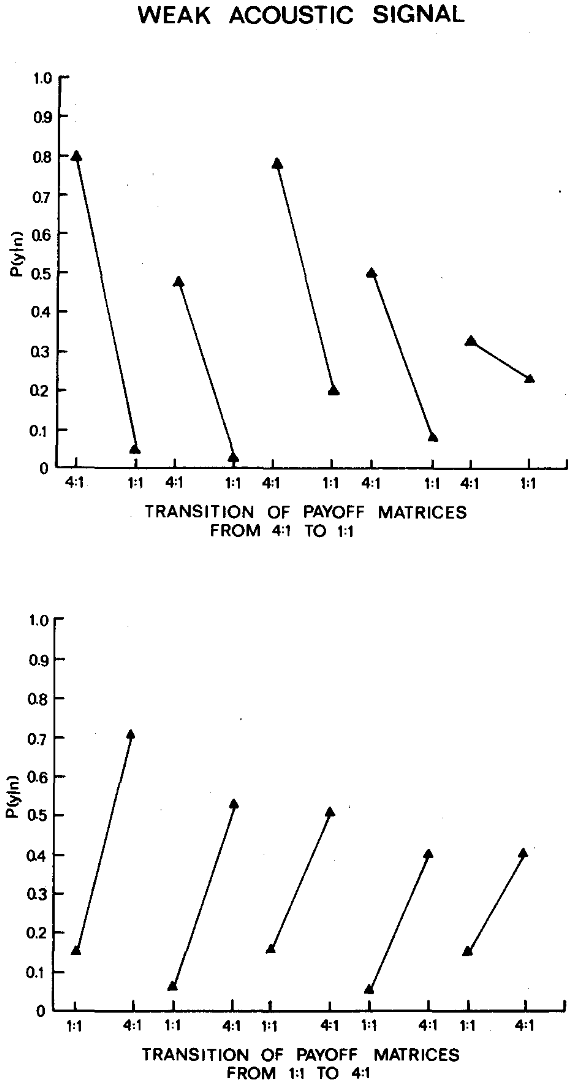

FIG. 5. The change in false alarms $(y\mid n)$ as the sea lion was shifted from ratios of 4:1 to 1:1 (top) and from 1:1 to 4:1 (bottom).

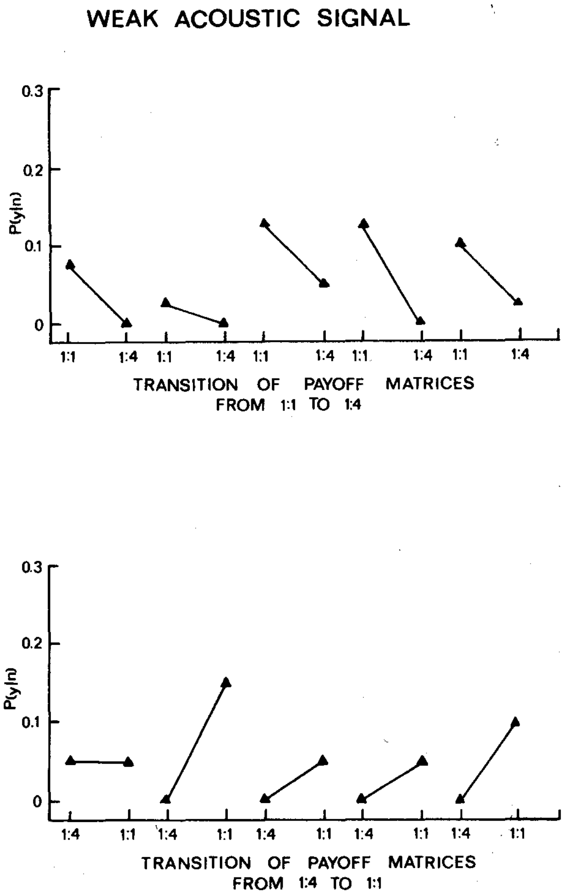

FIG. 6. The change in false alarms ($y \mid n$) as the sea lion was shifted from ratios of 1 : 1 to 1 : 4 (top) and from 1 : 4 to 1 : 1 (bottom).

the experiments Jo had participated in was one dealing with amount of reinforcement. Even when forced away from its initial spatial preference, the porpoise almost immediately demonstrated a consistent response to the manipulation which paid off four fish instead of one fish (Nachtigall, personal communication).

2. Sound equipment and procedure

The experiment was conducted in a 6.1-m^2 floating pen enclosure in 7.6 m of water with a mud and silt bottom (see Steele, 1971, for details). There were other porpoises in adjoining enclosures. Access to the pen was by means of a pier projecting into Kaneohe Bay. Located at the foot of the pier was a converted signal corps communication van with a clear glass window facing the pier area. The van housed relay equipment and equipment controlling the amplification and the attenuation of the acoustic signals. One experimenter worked in the van while a second experimenter worked at penside. Three different pure tones were used throughout the experiment. The tones were a 1-kHz "call tone," a 3-kHz "feeder tone," and an 8-kHz signal tone. The tones were presented under water via a University UW-30 underwater speaker which has a relatively flat response between 100 Hz and 10 kHz with a 360° dispersion pattern. The impedance is 8Ω, with a maximum power rating at 25 W.

The call tone and feeder tone were generated by specially constructed audio oscillators of fixed frequency. The 8-kHz signal was generated by an Eico model 377 signal generator and the signal was fed into a Hewlett–Packard model 353A attenuator. The 8-kHz signal was 5.0 sec in duration. The signal was amplified by a Bogan, model BT-20A, amplifier and then fed to the underwater speaker. The speaker was submerged 0.32 m under water at the opposite end of the pen from a submerged "bite" bar.

Upon presentation of the call tone, the porpoise was required to station in a relatively fixed position with its jaw on the bar suspended 20.3 cm below water and located approximately 3.7 m in front of the speaker. Initially, the porpoise positioned itself in a straight line between the bite bar and the speaker. However, after some experience, especially with relatively low signal-to-noise ratios, the animal began to gradually change its position until, at the start of the experiment proper, its jaw was at about a 65° angle to the bite bar and the tip of its jaw was almost directly on a straight line with the speaker. Since there is good reason to believe that porpoises receive sounds under water through their jaws (Norris, 1968), the animal had presumably located an area within the sound field with the most favorable signal-to-noise ratio. A bar was suspended across the enclosure on a steel "I" beam, pivoted at one end to allow it to be swung into place before a test session. Located 0.91 m to the left of the bite bar, along the I beam, was a 360° random motion microswitch that served as the response manipulandum. When the 8-kHz signal was presented, the porpoise had to swim to the microswitch and strike a rubber ball suspended from the device which was approximately 1.3 m above the water surface. In order to make the response, the animal had to leap up to reach the ball with its jaw, exposing about one third of its body. During training, correct responses were immediately reinforced with the sounding of the feeder tone followed by one Columbia River smelt.

The experimenter controlled the call tone, signal tone, and feeder tone from a switch box located penside. The switches activated Davis relay equipment that in turn switched the various signals to the underwater speaker. After the porpoise remained stationary above the bite bar, a trial was begun by presenting the call tone. The call tone duration was controlled by the experimenter and was terminated when the animal assumed the stationing position at the bite bar. As soon as the animal stationed, the 8-kHz tone was presented on half of the trials. In order to receive one or more smelt, the porpoise was required to leave the bar and hit the ball (yes) within 5 sec of signal presentation (hit). If a signal was not presented, the porpoise had to hold its rostrum on the bite bar for 5 sec (no) in order to receive one or more smelt (correct rejection). Breaking station and striking the ball on catch trials (false alarm) was not reinforced and maintaining its rostrum on the bite bar for 5 sec following termination of the signal tone was also not reinforced (miss). On less than 1% of the trials, the porpoise left the bite bar without striking the ball. On all such occasions the trial was repeated. The intertrial interval was approximately 15 sec. Through-

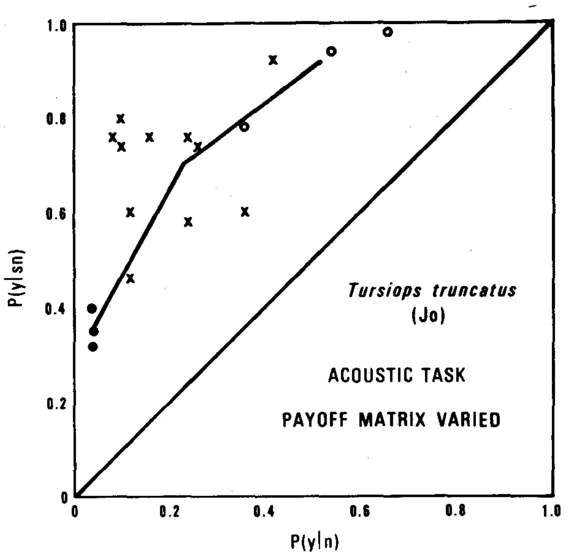

FIG. 7. Conditional response probabilities of a porpoise as a function of charges in the payoff matrix. The ×'s represent ratios of food reinforcement for hits to correct rejections of 1 : 1. The open circles represent ratios of 4 : 1 and the solid circles represent ratios of 1 : 4. The intensity of the 8-kHz signal varied between −9 to −11 dB *re* 1 μbar under water with ambient noise varying by 15 dB but never exceeding −15 dB *re* 1μbar. Each data point is based on 100 trials.

out the period of experimentation, the porpoise was maintained on 15 lb/day, including the amount of fish earned during experimental sessions.

Following one week of preliminary work, a sound pressure level was chosen, which would yield a *d'* value of approximately 1.0.

The sound pressure level (decibels *re* 1 μbar) at the bite bar varied between −9 and −11 when measured with a clevite CH-30 hydrophone used in conjunction with a USNOTS Series II sound measuring set. The measuring system has a flat frequency response up to 150 kHz. A Kron-Hite model 3202 filter used as a bandpass filter was inserted into the sound measuring system. The output of the sound measuring set was monitored with a portable oscilloscope (Tektronix 323). The major natural underwater noise in Kaneohe Bay comes from snapping shrimp (*Alpheus californianus*). Ambient noise measurements performed by the Navy Undersea Center showed that the peak noise levels between 7.5 and 8.5 kHz fluctuated a great deal (about 15 dB), but did not exceed −15 dB *re* 1 μbar. These measurements were made with the spectrum analyzer filter bandwidth set at 100 Hz. In order to minimize sources of noise other than that provided by the snapping shrimp, the experimenter at penside monitored underwater sound during testing by means of a hydrophone. Although relatively few disturbances occurred, when they did testing stopped until the noise levels returned to "normal." The disturbances were of two types: either motor boats or sounds emitted by other porpoises (usually whistles).

3. *Payoff matrix*

A 10–20-trial warm-up period preceded each test session. There was one test session per day consisting of 100 trials. The warm-up signals were 1–4 dB stronger than the test signal which was held constant. The payoff matrix for the actual test session also prevailed during the warm-up period.

The payoff matrix was varied in the porpoise experiment as it was in the sea lion experiment. The amount of reinforcement (number of fish) was varied in terms of the ratio of hits to correct rejections in the following way: 1:1, 4:1, and 1:4. The 1:1 ratio was used as a constant baseline, which was returned to after one or two days following the introduction and termination of the other two payoff matrices. The experiment was conducted for 16 days starting with five days of baseline. Following baseline, the 1:4 matrix was run for two days, followed by two days of baseline, followed by two days of the 4:1 matrix. Thereafter, each matrix was run for one day.

B. Results and discussion

Figures 7 and 8 present ROCs for the porpoise. The data show rather unambiguously that changes in response bias as a function of changes in payoff matrix were relatively systematic and in the predicted direction. As anticipated, there was a good deal of variability in terms of sensitivity between test days (see Fig. 7), and this was undoubtedly a function of the relatively unstable ambient noise level.

Interestingly though, as was the case with the sea lion, daily changes in sensitivity of the porpoise were largest when the payoff matrix is 1:1 and smallest when it is 1:4.

In general, the results of the porpoise experiment were quite similar to those of the sea lion experiment. Perhaps, the most important similarity was that detec-

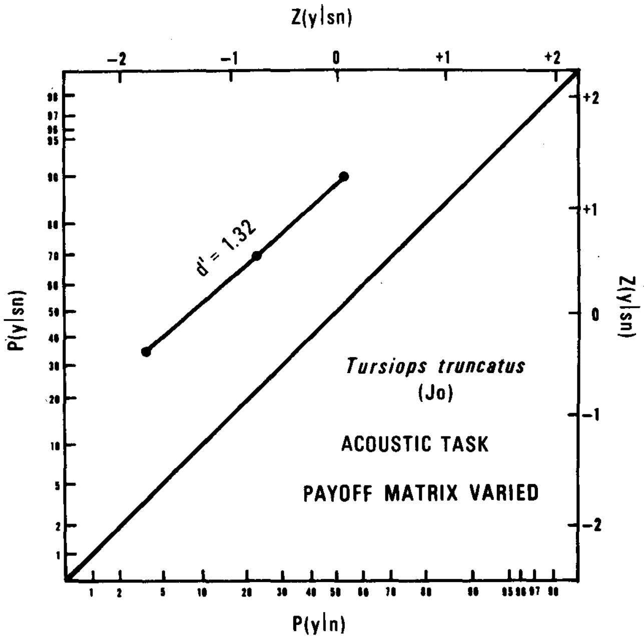

FIG. 8. An ROC for a porpoise based on the mean values shown in Fig. 7. The data points are plotted on normal–normal coordinates.

tion of pure tones under water, in terms of the sensitivity index of d', was independent of changes in response bias when that bias was varied systematically by manipulating amount of reinforcement for different classes of correct responses. Both *Tursiops* and *Zalophus* shifted bias rapidly. Discrimination of the amounts of reinforcement consequent on the two different classes of correct responses occurred during the 10–20-trial warm-up period. The major difference between the two animals was that the sea lion maintained the same criterion ("medium strict") during baseline, whereas the porpoise had much less bias during baseline. It seems likely that this difference in bias under the baseline condition was a function of each animal's original training. In the case of *Zalophus*, reinforcement contingencies were implicitly (if not explicitly) designed so that the animal would maintain a "medium strict" criterion (Schusterman, 1974a). In setting up the reinforcement contingencies for training the porpoise, there was no such implicit or explicit aim.

Comparing the effects of repeated changes in signal probability (Schusterman and Johnson, in press) with that of repeated changes in the payoff matrix suggests that in sea lions and porpoises amount of reinforcement leads to more rapid acquisition of stable response bias, i.e., bias at an asymptotic level of responding, than does signal probability.

There have been two other signal detection experiments with animals (rats) in which response bias changed systematically as the amount of positive reinforcement for different classes of correct responses was varied while sensitivity remained relatively uneffected (Huckle, 1972, as cited by Galanter, 1974; Hume, 1974). Thus, it would seem that the theory of signal detectability deals effectively with the asymptotic discriminative behavior of a wide range of animals subject to differential stimulation and differential reinforcement (Nevin, 1970).

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