

## A comparison of signal detection between an echolocating dolphin and an optimal receiver

Whitlow W.L. Au<sup>1</sup> and Deborah A. Pawloski<sup>2</sup>

<sup>1</sup> Naval Ocean Systems Center and <sup>2</sup> SEACO Division of SAIC, Kailua, Hawaii 96734, USA

Accepted August 21, 1988

**Summary.** An electronic simulated target apparatus was used in a two-experiment study to compare the target detection performance of an echolocating bottlenose dolphin with an optimal receiver. Random Gaussian noise with a relatively flat spectrum from 20 to 160 kHz was used as a masking source. Experiment I was conducted to establish a technique for estimating the echo energy-to-noise ratio,  $E_e/N$ , at the dolphin's threshold of detection. Dolphins typically vary the amplitude of their emitted signal over a large range making it difficult to estimate  $E_e/N$ . In the first part of experiment I, the simulated echo was a double click, the pulses separated by 200  $\mu$ s, with each pulse being a replica of the dolphin's transmitted signal. A staircase psychophysical procedure was used to obtain the detection threshold, and the echo energy-to-noise ratio based on the highest amplitude click emitted per trial,  $(E_e/N)_{\max}$ , was determined at each reversal point. The second echo type consisted of one of the animal's echolocation clicks, previously measured, digitized and stored in an erasable programmable read-only memory (EPROM). The electronic target simulator was modified so that every time the dolphin emitted an echolocation signal, the EPROM was triggered to produce two pulses separated by 200  $\mu$ s. On any trial, the EPROM signal was played back at a fixed amplitude, regardless of the amplitude of the dolphin's emitted signal. The  $E_e/N$  obtained with the EPROM signal at threshold was found to be 2.9 dB lower than  $(E_e/N)_{\max}$  obtained with the normal phantom target. Therefore an estimate of  $E_e/N$  can be obtained by subtracting 2.9 dB from  $(E_e/N)_{\max}$ .

*Abbreviations:*  $\beta$  response bias;  $d'$  detection sensitivity;  $E_e$  echo energy flux density; EPROM erasable programmable read-only memory;  $N$  noise spectral density;  $p(t)$  instantaneous acoustic pressure;  $P(Y/SN)$  probability of detection;  $P(Y/N)$  probability of false alarm; ROC receiver-operating-characteristics; SE source energy flux density

Experiment II was conducted to obtain isosensitivity data that could be plotted in an ROC (receiver operating characteristic) format. The response bias of the dolphin was manipulated by varying the food reinforcement payoff matrix. In terms of the ratio of correct detections to correct rejections, the payoff matrix was varied over four values: 1:1, 4:1, 8:1, and 1:4. A modified method of constants procedure was used to obtain the dolphin target detection performance data. Each session consisted of two 20-trial blocks in which a strong echo was used in the first block and a weak echo in the second block. The energy-to-noise ratio required by an optimal detector to approximate the dolphin's performance was obtained by determining the appropriate detection sensitivity,  $d'$ , that best fitted the dolphin's data plotted in an ROC format. The results of experiment II indicated that the dolphin required approximately 7.4 dB higher  $E_e/N$  than an optimal detector to detect the phantom target.

### Introduction

An optimal or ideal receiver is a receiver which theoretically yields the best possible performance in signal detection consistent with the input signal-to-noise ratio. Petersen et al. (1954) related the receiver-operating-characteristic (ROC) curves (probability of detection versus the probability of false alarm) to the signal-to-noise ratio at the receiver input required for detection of a signal. They showed that the optimal receiver for the detection of a signal known exactly in white noise was a cross-correlator receiver, in which the input signal plus noise is correlated with a noise-free replica of the known signal. An equivalent receiver is a matched filter whose impulse response is the same

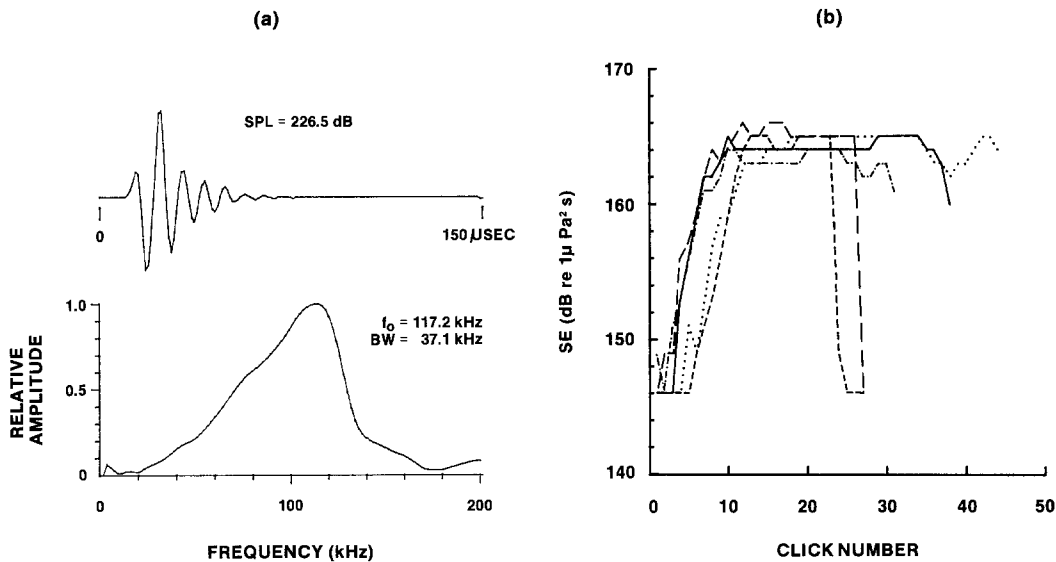


Fig. 1 a, b. a An example of the waveform and frequency spectrum of a bottlenose dolphin echolocation signal. b Typical variations in the source energy flux density for five target present trials involving a reversal, in the study of Au et al. (1988). Different types of lines are used for ease in following the variations in any given trial

as the waveform of the known signal reversed in time. Since the ideal receiver will detect a signal in noise better than any other receiver, the efficiency or effectiveness of a receiver can be compared against that of an ideal receiver.

Mohl (1986) and Troest and Mohl (1986) studied the capability of a pipistrelle bat (*Pipistrellus pipistrellus*) and serotine bats (*Eptesicus serotinus*), respectively, to detect a phantom target in white noise. They measured echo energy-to-noise ratios ( $E_e/N$ ) at threshold of 50 dB for the pipistrelle bat, and 36–49 dB for the serotine bats. These  $E_e/N$ 's were approximately 40–50 dB higher than would be necessary for an ideal receiver. Therefore, these investigators concluded that their results did not support the hypothesis that bats process echoes like a matched filter receiver. In comparison, Au and Penner (1981) and Au et al. (1987) measured  $(E_e/N)_{\max}$  between 7–13 dB for Atlantic bottlenose dolphins (*Tursiops truncatus*) detecting a target in white noise.

The purpose of this study is to compare the target detection performance of an echolocating bottlenose dolphin with that of an ideal or optimal receiver. Bottlenose dolphins typically use short duration, broadband, transientlike click signals for echolocation. An example of an echolocation signal is shown in Fig. 1a. The expression  $E_e/N$  is the ratio of the energy flux density (acoustic energy per unit area) of the echo to the received noise power density. Energy flux density and can be expressed in dB as

$$\text{energy flux density} = 10 \log_{10} \left[ \int_0^{\infty} p^2(t) dt \right] \quad (1)$$

where  $p(t)$  is the instantaneous acoustic pressure in micropascal ( $\mu\text{Pa}$ ). Energy flux density has units of  $\text{dB re } 1 \mu\text{Pa}^2 \text{ s}$ . For an echolocating dolphin, large variations in the source energy flux density (SE) within a click train must be properly considered. Dolphins typically begin an echolocation trial emitting relatively low amplitude clicks which eventually rise to a maximum before tapering off in amplitude at the end of the click train. An example showing the variation in the SE for 5 typical trials in the study of Au et al. (1988) is shown in Fig. 1b. Differences between the minimum and maximum signal levels can be as much as 20 dB. These fluctuations will introduce uncertainty in the estimation of  $E_e/N$ . The use of the average SE will lead to a low estimate of  $E_e/N$ . Au and Penner (1981) and Au et al. (1988) used the maximum SE per trial in calculating the  $(E_e/N)_{\max}$ . This amounted to the most conservative estimate of  $E_e/N$  at the dolphin's detection threshold. In this study, experiment I was performed to determine the relation between the most conservative estimate of  $E_e/N$  with a more realistic and accurate estimate of  $E_e/N$ .

The performance of an ideal receiver can be estimated by determining the isosensitivity curve that best fits the dolphin's performance data plotted in an ROC format. Schusterman et al. (1975) showed that isosensitivity curves of auditory detec-

tion sensitivity in the California sea lion and the Atlantic bottlenose dolphin could be obtained by varying the response bias of the animals. Au and Turl (1984) used the technique of varying the response bias of an echolocating dolphin by varying the food payoff matrix to obtain data that when plotted in an ROC format could be fitted by isosensitivity curves. Experiment II was conducted to obtain phantom target detection data while the response bias of an echolocating bottlenose dolphin was manipulated by varying the food payoff matrix.

Au et al. (1988) previously used the same animal and phantom echo experimental apparatus to study detection of complex target echoes by *Tursiops*. While there is no controversy on whether or not dolphins processed signals like a matched filter, Au et al. (1988) showed that *Tursiops* process signals like an energy detector with an integration time of approximately 264  $\mu$ s.

## Materials and methods

The study was conducted in Kaneohe Bay, Oahu, Hawaii. The experimental subject was a 7-year old male *Tursiops truncatus* designated Tt-622M. It was born at the Naval Ocean Systems Center facility in Kaneohe Bay.

The dolphin was required to detect a phantom target echo in noise. Target echoes were produced by a microprocessor-controlled electronic target simulator which captured each signal emitted by the dolphin and retransmitted the same signal back to the animal after an appropriate delay to simulate a specific target range. The experimental configuration is depicted in Fig. 2, showing a dolphin in a hoop station and three hydrophones directly in front of the animal. An acoustic screen was located between the hoop and the hydrophones. In the raised

position, the screen blocked the animal's echolocation signals from the hydrophone.

A detailed description of the phantom electronic target simulator is presented by Au et al. (1987). The dolphin's echolocation signals were detected by the first hydrophone (Ceesco LC-10) which triggered an 8-bit analog-to-digital converter to digitize the signal received by the second hydrophone (Brüel and Kjaer 8103) located 1.9 m from the hoop. The analog-to-digital converter operated at a 1 MHz rate, digitized 128 points per signal and stored the data in a static random access memory. The output of the first hydrophone also triggered an external delay generator and flagged the computer (Franklin Ace-1000) that a signal had been detected. After an appropriate delay corresponding to a simulated target range of 20 m, the delay generator flagged the computer to project the stored signal. The number of highlights or glints, the time separation between highlights and the amplitude of each highlight was controlled by the computer. Random Gaussian masking noise was mixed with the stored signal and projected from the third transducer (Naval Research Laboratory F-42D), located 2.4 m from the hoop. The projector was driven by an equalization circuit which flattened the transmit response of the projector allowing it to transmit broadband noise and simulated dolphin signals with a minimum of distortion (Au et al. 1987). The noise had a relatively flat spectrum from 20 to 160 kHz (Au et al. 1987) and was transmitted at a fixed level of 64 dB re 1  $\mu$ Pa<sup>2</sup>/Hz measured at the hoop. This noise level was approximately 5 to 11 dB greater than the ambient noise for frequencies between 80 and 120 kHz (Au et al. 1985). The level of the simulated target echoes was controlled with an adjustable attenuator.

Data of signal parameters such as the number of clicks, peak-to-peak source levels, source energy flux density as well as the click intervals between transmitted clicks were stored in the computer. The  $(E_e/N)_{\max}$  for each trial was also stored in the computer, along with the animal's performance data.

A trial started when the dolphin was directed to swim into the hoop station, with the acoustic screen in the raised position. The masking noise was then projected and the acoustic screen lowered, cueing the dolphin to echolocate. A go/no-go response procedure was used in which the dolphin was required to leave the hoop and strike a paddle for target present trials. Striking

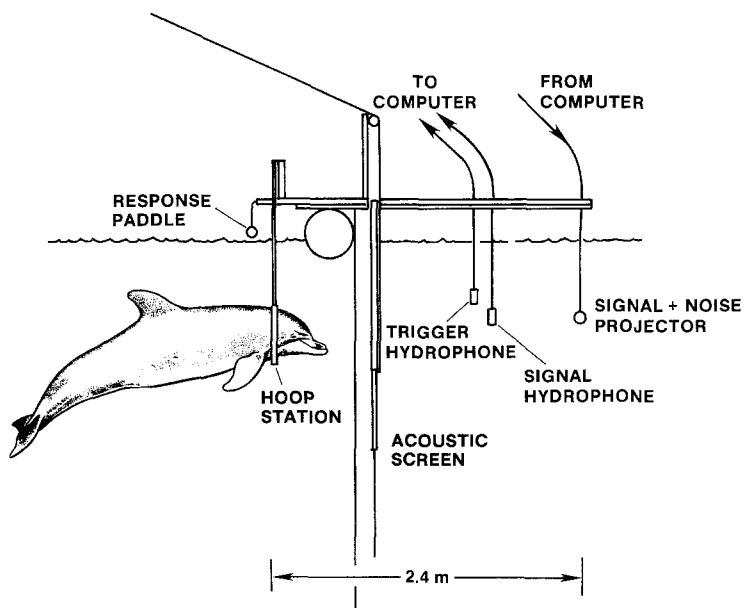


Fig. 2. Experimental configuration showing the dolphin in a hoop station echolocating with a phantom echo electronic apparatus

the paddle activated a bridge tone which provided immediate feedback to the animal that its response was correct. For target absent trials, the animal was required to remain in the hoop until a bridge tone was played three seconds after the trial began. After each trial, the dolphin received a fish reward only if it responded correctly.

*Experiment I-Estimation of echo energy-to-noise ratio.* Experiment I was conducted to establish a realistic method of estimating  $E_e/N$  at the dolphin's detection threshold. Two different types of echoes were used and the dolphin's threshold determined by an up-down or staircase procedure described in the next paragraph. The first echo type consisted of two clicks, separated by 200  $\mu$ s, which were replicas of each transmitted click. The double click echo with a 200  $\mu$ s separation was used because it was a standard in a previous study (Au et al. 1988) and thereby provided a way to check the dolphin's performance with past results. The amplitude of the echoes was directly proportional with the amplitude of the emitted clicks. With this echo type, the  $(E_e/N)_{\max}$  at threshold was determined. The second echo type consisted of a previously measured and digitized echolocation click from the animal which was stored in an erasable programmable read-only memory (EPROM). The electronic target simulator was modified so that every time the dolphin emitted an echolocation signal, the EPROM was triggered to produce two pulses separated by 200  $\mu$ s. The amplitude of the echo clicks was fixed for each trial independent of the dolphin's signal level, resulting in a fixed  $E_e/N$ . The difference between the threshold  $(E_e/N)_{\max}$  obtained with the normal variable amplitude phantom echo and  $E_e/N$  obtained with the EPROM signal was then determined.

The masked thresholds were determined by varying the signal attenuator in an up-down or staircase procedure designed to produce a 50% correct detection threshold. After each target present trial the attenuator was increased (echo made weaker) if the animal's response was correct or decreased (echo made stronger) if the response was incorrect. Therefore during a session, the signal attenuator was continuously increased and decreased, depending on the animal's responses on the target present trials. Reversal points were values of the local maxima and minima of the signal attenuator during a session. At the start of each session, after the warm-up trials, the attenuator was increased (echo made weaker) in 2-dB steps until the first incorrect target present response was made, and thereafter 1-dB steps were used. The first ten trials of each session were designated as warm-up trials, and the signal attenuator was fixed so that  $E_e/N$  was approximately 10 dB above the animal's previously defined masked threshold. The last ten trials of each session were cool-off trials and the attenuator was adjusted to the same level as in the warm-up trials.

After each session, the masked threshold was computed by averaging the values of the signal attenuator settings at the reversal points. A threshold estimate was considered completed when at least 20 reversals had been obtained over a minimum of two consecutive sessions, and the average reversal values were within 2 dB of each other.

*Experiment II-determination of ROC curves.* Experiment II was conducted to obtain data that could be presented in an ROC format with the probability of detection,  $P(Y/SN)$ , plotted against the probability of false alarm,  $P(Y/N)$ . ROC curves for an ideal receiver can then be fitted to the dolphin data providing an estimate of  $d'$  or  $E_e/N$  required by an ideal receiver in order to achieve similar performance as the dolphin. Each session consisted of 50 trials divided into a 10-trial warm-up, a 20-trial easy-detection with a strong echo and a 20-trial difficult-detection

task with a weak echo. During warm-up trials, the signal attenuator was set approximately 10 dB above a previously determined threshold value. The easy- and difficult-detection tasks were conducted with the signal attenuator set at approximately 6 and 2 dB respectively, above the typical threshold value. Target present and absent conditions were randomized and balanced for the warm-ups and the two 20-trial blocks.

The dolphin's response bias was manipulated by varying the payoff matrix (number of pieces of fish reinforcement for correct responses). Schusterman et al. (1975) found that the response bias of marine mammals could be manipulated without significantly changing the animal's detection sensitivity, by varying the payoff matrix. The animals were manipulated to be conservative in reporting the presence of a stimulus by rewarding them with 4 fishes for each correct rejection versus one fish for each correct detection. Conversely, the animals were manipulated to be liberal by rewarding them with 4 fishes for each correct detection versus one fish for each correct rejection. The payoff matrix was varied in terms of the ratio of correct detection to correct rejection in the following manner: 1:1, 1:4, 1:1, 4:1, 1:1, 8:1. Six consecutive sessions were conducted at each payoff matrix, with the 1:1 payoff being the baseline. Each fish reward (Columbia River smelt) was cut in half to prevent satiation of the dolphin, especially during 8:1 sessions.

## Results

### *Experiment I – Estimation of echo energy-to-noise ratio*

Four sessions resulting in 40 reversals were conducted for each of the two echo types. The average and standard deviation of  $(E_e/N)_{\max}$  at the reversal points for the normal variable amplitude phantom echo was

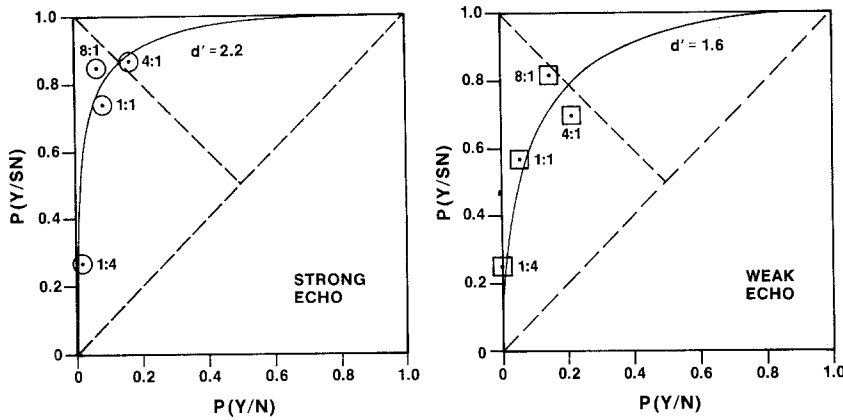
$$(E_e/N)_{\max} = 10.4 \pm 1.1 \text{ dB.}$$

This  $E_e/N$  is approximately the same as the 75% correct response threshold obtained by Au et al. (1988) using a modified method of constants, and 1.8 dB greater than the threshold obtained with the staircase method.

The average and standard deviation of  $E_e/N$  at the reversal points for the fixed EPROM echo was

$$E_e/N = 7.5 \pm 1.5 \text{ dB.}$$

This estimate of  $E_e/N$  can be considered the most accurate estimate since the echo strength for each trial was fixed and did not depend on the level of the dolphin's transmitted signal. There is a 2.9 dB difference between  $E_e/N$  and  $(E_e/N)_{\max}$ , indicating that an accurate estimate of the  $E_e/N$  at the dolphin's threshold may be obtained by subtracting 2.9 dB from  $(E_e/N)_{\max}$ . This adjustment of 2.9 dB is strictly valid only for the dolphin used in this study. Another animal may require a different adjustment to  $(E_e/N)_{\max}$ .



**Fig. 3.** Dolphin performance results plotted in an ROC format along with isosensitivity curves that best matched the results. Ordinate: probability of detection,  $P(Y/SN)$ ; abscissa: probability of false alarm,  $P(Y/N)$

**Table 1.** Dolphin performance results at the different payoff matrix conditions

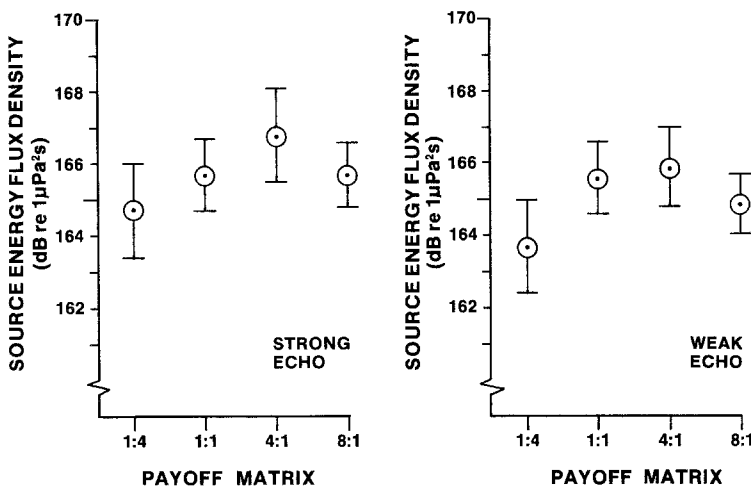
	Payoff matrix	$P(Y/SN)$	$P(Y/N)$	$d'$	$\beta$
Strong echo	1:4	0.267	0.017	1.5	7.8
	1:1	0.739	0.083	2.0	2.1
	4:1	0.867	0.167	2.1	0.9
	8:1	0.850	0.067	2.5	1.8
Weak echo	1:4	0.250	0.000	—	—
	1:1	0.567	0.061	1.7	3.3
	4:1	0.700	0.271	1.3	1.2
	8:1	0.817	0.150	1.9	1.1

*Experiment II – Determination of ROC curves*

The results of the dolphin's target detection performance as its response bias was manipulated are plotted in an ROC format in Fig. 3 and tabulated in Table 1. Also included in Table 1 are the corresponding values of the detection sensitivity ( $d'$ ) and response bias ( $\beta$ ) obtained from tables presented

by Snodgrass (1972). The detection sensitivity,  $d'$ , represents the minimum value of  $E_e/N$  necessary to lead to the performance of an ideal receiver (Elliott 1964). The response bias,  $\beta$ , is a measure of a subject's bias towards the target-present or target-absent responses. A  $\beta$  value of 1 indicates a non-bias subject. Large values of  $\beta$  indicate a cautious or conservative subject and small values of  $\beta$  indicate a liberal subject. The data of Fig. 3 represent 120 trials each for the 1:4, 4:1 and 8:1 payoff matrix. At the 1:1 payoff condition, 360 trials were performed. The ideal isosensitivity curves associated with  $d'$  values of 2.2 and 1.6 for the strong and weak echoes, respectively, are included in Fig. 3. These isosensitivity curves best matched the dolphin's performance in a least-square-error manner.

Changes in the animal's performance with changes in the payoff matrix were relatively systematic and predictable. As the payoff matrix for correct detections increased from 1:4 to 1:1 and 4:1 the dolphin became progressively more liberal in reporting on the presence of the target, with a sub-



**Fig. 4.** Average and standard deviation of the maximum source energy flux density per trial of the signals used by the dolphin as a function of the payoff matrix

**Table 2.** The average and standard deviation of  $(E_e/N)_{\max}$  from every target present trial and for different payoff matrix conditions

Payoff matrix	Strong echo $(E_e/N)_{\max}$	Weak echo $(E_e/N)_{\max}$
1:4	13.9 ± 1.3 dB	9.1 ± 1.0 dB
1:1	15.3 ± 1.4	10.6 ± 0.9
4:1	16.0 ± 1.3	11.2 ± 1.0
8:1	15.0 ± 1.1	10.2 ± 0.8
Ave	15.1 ± 1.3	10.3 ± 0.9

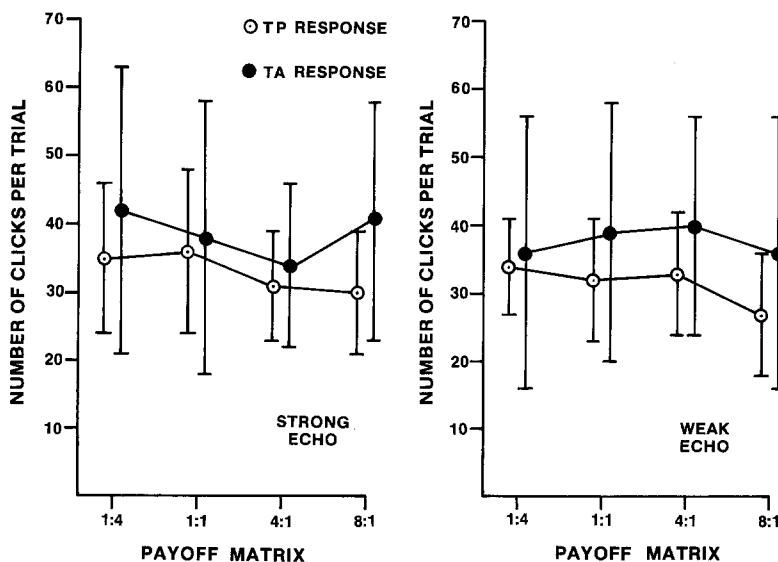
sequent increase in the false alarm rates and a decrease in  $\beta$ . However, even as the dolphin's response bias varied, its detection sensitivity remained relatively constant as can be seen in Fig. 3 and Table 1. As the payoff matrix for correct detection increased to 8:1, the dolphin did not become more liberal than at the 4:1 payoff matrix for both the strong and weak echo cases.

The average and standard deviation of the maximum source energy flux density per trial for the different payoff matrices are shown in Fig. 4. Only "target present" trials are presented in Fig. 4. The mean of the maximum SE per trial ( $\overline{SE}_{\max}$ ) varied less than 2.1 dB for the different payoff matrices. It was minimum at the 1:4 and maximum at the 4:1 payoff condition for both strong and weak echoes. A one-way analysis of variance indicated that the means were significantly different at the 0.01 level for both strong and weak echoes. Applying the *t*-test between pairs of  $\overline{SE}_{\max}$  indicated that the means at the 1:1 and 8:1 payoff for the strong echo were not significantly different and that the

means at the 1:1 and 4:1 payoff for the weak echo were significantly different at the 0.05 level. Differences between the means of all other pairs of  $\overline{SE}_{\max}$  were significant at the 0.01 level.

The average and standard deviation of  $(E_e/N)_{\max}$  for each trial associated with  $\overline{SE}_{\max}$  at the different payoff conditions is given in Table 2. The composite average of  $(E_e/N)_{\max}$  across the various payoff matrix for the strong and weak echoes is also included in Table 2. The difference between the average  $(E_e/N)_{\max}$  for the strong and weak echoes was 4.8 dB, which agreed closely with the 4.0 dB difference in the signal attenuator settings for both echoes.

The average number of clicks used per trial is shown in Fig. 5 as a function of the payoff matrix. The clicks were separated into two categories, those related to target present (go) and those related to target absent (no-go) responses. There were large variations in the number of clicks emitted per trial as can be seen by the large standard deviations in Fig. 5. The number of clicks per trial related to target absent responses showed considerably more variation than those related to target present responses. A two way classification analysis of variance test with repeated measurements and unequal sample sizes indicated a significant difference at the 0.01 level between the number of clicks associated with target present and target absent responses for the strong and weak echo cases. The differences between the number of clicks emitted at the different payoff conditions were significant at 0.05 level for the strong echo and not significant for the weak echo.



**Fig. 5.** Average and standard deviation of the number of clicks emitted by the dolphin per trial as a function of the payoff matrix. Number of clicks emitted for target present (TP) and target absent (TA) responses

## Discussion

An optimal receiver having a  $d'$  of 2.2 for the strong echo, and 1.6 for the weak echo, will approximate the dolphin's behavioral performance. The echo energy-to-noise ratio,  $(E_e/N)_{op}$ , for this optimal receiver can be calculated from the definition of  $d'$  given in the equation

$$d' = \sqrt{2(E_e/N)_{op}} \quad (2)$$

The echo energy-to-noise ratio in dB is

$$(E_e/N)_{op} = 10 \log(d'^2/2). \quad (3)$$

Therefore, for an optimal receiver approximating an echolocating dolphin

$$(E_e/N)_{op} = \begin{cases} 3.8 \text{ dB} & (\text{strong echo}) \\ 1.1 \text{ dB} & (\text{weak echo}). \end{cases}$$

An estimate of the echo energy-to-noise ratio for the dolphin at the two different echo conditions can be obtained by subtracting 2.9 dB from the average value of  $(E_e/N)_{max}$  shown in Table 2. The difference in  $E_e/N$  between the dolphin and an optimal receiver can be expressed as

$$(E_e/N)_{dol} - (E_e/N)_{op} = \begin{cases} 8.4 \text{ dB} & (\text{strong echo}) \\ 6.3 \text{ dB} & (\text{weak echo}). \end{cases}$$

Averaging the differences for the strong and weak echoes we conclude that an optimal receiver would outperform the dolphin by approximately 7.4 dB. The differences between an optimal receiver and the dolphin should be the same for both type of echoes. The 2.1 dB discrepancy in the experimental results is well within the range of error with biosonar experiments.

The 7.4 dB difference between a dolphin and an optimal receiver is considerably smaller than the 40–50 dB obtained by Mohl (1986) and Troest and Mohl (1986) for two species of bats. However, Mohl stated that his results are likely clutter limited caused by echoes from the electrostatic speaker. On the other hand, Troest and Mohl (1986) compared their results obtained with and without noise and found that the bats in their experiment were not clutter limited if masking noise was used. Yet the results of both experiments were similar, indicating that their bats were relatively insensitive to echoes masked by noise or clutter.

The results of experiment I with the fixed EPROM signal indicate that dolphins do not process echoes like a matched filter. The animal adapted to the EPROM signal instantly and without any erratic behavior upon its introduction. The variations of  $E_e/N$  at threshold across sessions was

similar to variations for the normal phantom echoes. The  $E_e/N$  at threshold was, on the average, lower than  $(E_e/N)_{max}$  by 2.9 dB.

The average number of clicks emitted per trial and the average of the maximum source energy flux density did not vary much for the different payoff matrices, indicating that the dolphin was relatively consistent in its attempt to detect the phantom echo at the different payoff matrix conditions. For the target absent responses, the averages of the number of clicks emitted at the different payoff matrices were significantly different for the strong echo but not for the weak echo. The average number of clicks for the target present responses varied at most by only 7 clicks per trial (between the 1:4 and 8:1 payoff matrix for the weak echo). Au and Turl (1984) found that their dolphin exhibited a tendency to expend the most effort (as measured by the number of clicks emitted) in detecting the targets when the payoff matrix was at both the 1:4 and 4:1 values. They also found considerably more fluctuation in the number of clicks used for the different payoff conditions. However, the low value of  $\overline{SE}_{max}$  at the 1:4 payoff (2.2 dB down from the maximum at the 4:1 payoff) suggests a slight tendency by the dolphin not to expend as much effort in detecting the target at the 1:4 payoff condition since the reward condition favored the target absent response.

The dolphin used in this study seemed to be naturally biased in the conservative direction. The conservative response bias is consistent with the behavior of *Tursiops* in other signal detection studies (Schusterman 1974; Murchison 1980; Au and Snyder 1980; Au and Turl 1984). The largest value of  $P(Y/N)$ , 0.217, was obtained at the 4:1 payoff condition with the weak echo. Au and Turl (1984) obtained  $P(Y/N)$  values between 0.470 and 0.600 for the 8:1 payoff conditions. They also did not find any difference in the dolphin's performance with the 1:4 and 1:1 payoff matrix. In this study, there were considerable differences in the dolphin's performance at 1:4 and 1:1 payoff conditions. At the 1:4 payoff condition,  $P(Y/N)$  was 0.01 and 0.00 for the strong and weak echo, respectively. The lowest  $P(Y/N)$  obtained by Au and Turl (1984) was approximately 0.10 to 0.18 at the 1:1 and 1:4 payoff conditions, indicating that the dolphin in our study was more conservative.

Our results show a difference of approximately 7.4 dB between the dolphin and an optimal receiver. Therefore, our results cast some doubts on the accuracy of the beluga results presented by Turl et al. (1987). They performed a comparative study between *Tursiops* and *Delphinapterus leucas* in de-

tecting targets in the presence of masking noise and found that the beluga was approximately 8–13 dB better than the dolphin. The *Tursiops* used in this study (Au et al. 1988) and by Turl et al. (1987) had virtually the same detection threshold;  $(E_e/N)_{\max}$  at the 75% correct response threshold was within 1 dB for both animals. This would indicate that the beluga is as good or better (a physical impossibility) than an optimal detector. Perhaps the beluga discovered some way to reduce the received noise by spatially filtering the target echo from the masking noise as it did by using a surface reflected path in an earlier experiment (Penner et al. 1986).

*Acknowledgements.* The authors would like to express their appreciation to Paul Nachtigall, William Friedl and Forrest Wood of the Naval Ocean Systems Center for reviewing this paper and making many helpful comments.

## References

- Au WWL (1980) Echolocation signals of the Atlantic Bottlenose Dolphin (*Tursiops truncatus*) in open waters. In: Busnel R-G, Fish JF (eds) Animal sonar systems. Plenum, New York, pp 251–282
- Au WWL, Carder DA, Penner RH, Scronce BL (1985) Demonstration of adaptation in beluga whale echolocation signals. *J Acoust Soc Am* 77:726–730
- Au WWL, Martin SW, Moore PWB (1987) Phantom electronic target for dolphin sonar research. *J Acoust Soc Am* 82:711–713
- Au WWL, Moore PWB, Pawloski DA (1988) Detection of complex echoes in noise by an echolocating dolphin. *J Acoust Soc Am* 83:662–668
- Au WWL, Penner RH (1981) Target detection in noise by echolocating Atlantic Bottlenose Dolphins. *J Acoust Soc Am* 70:687–693
- Au WWL, Snyder KJ (1980) Long-range target detection in open waters by an echolocating Atlantic Bottlenose Dolphin (*Tursiops truncatus*). *J Acoust Soc Am* 68:1077–1084
- Au WWL, Turl CW (1984) Dolphin biosonar detection in clutter: variation in the payoff matrix. *J Acoust Soc Am* 76:955–957
- Elliott PB (1964) Appendix 1-Tables of  $d'$ . In: Swet J (ed) Signal detection and recognition by human observers. John Wiley, New York, pp 651–684
- Mohl B (1986) Detection by a pipistrelle bat of normal and reversed replica of its sonar pulses. *Acustica* 61:75–82
- Murchison AE (1980) Detection range and range resolution of echolocating bottlenose porpoise (*Tursiops truncatus*). In: Busnel R-G, Fish JF (eds) Animal sonar systems. Plenum, New York, pp 43–70
- Penner RH, Turl CW, Au WWL (1986) Target detection by the beluga using a surface-reflected path. *J Acoust Soc Am* 80:1842–1843
- Petersen WW, Birdsall TG, Fox WC (1954) The theory of signal detectability. *Trans IRE, PGIT*, 4:171–212
- Schusterman RJ (1974) Low false-alarm rates in signal detection by marine mammals. *J Acoust Soc Am* 55:845–848
- Schusterman RJ, Barrett R, Moore RWB (1975) Detection of underwater signals by a California Sea Lion and a Bottlenose Porpoise: variation in the payoff matrix. *J Acoust Soc Am* 57:1526–1532
- Snodgrass JG (1972) Theory and experimentation in signal detection: Part 1. Life Science Associates, Badwin, New York
- Troest N, Mohl B (1986) The detection of phantom targets in noise by serotine bats: negative evidence for the coherent receiver. *J Comp Physiol A* 159:559–567
- Turl CW, Penner RH, Au WWL (1987) Comparison of target detection capabilities of the beluga and bottlenose dolphin. *J Acoust Soc Am* 82:1487–1491