

Underwater frequency discrimination in the bottlenosed dolphin (1–140 kHz) and the human (1–8 kHz)

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Frequency difference limens (DLs) were obtained for frequencies (F) from 1 to 140 kHz for the bottlenosed dolphin, *Tursiops truncatus* (Montagu), and from 1 to 8 kHz for two human subjects tested underwater. Discriminations were required between constant-frequency (pure-tone) signals and frequency-modulated signals, using a successive discrimination procedure. Relative DLs (DL/F) for the dolphin generally ranged from 0.002 to 0.004 between 2 and 53 kHz, and never exceeded 0.008 through to 130 kHz; at 1 and 140 kHz, relative DLs increased to 0.014. No responses were obtainable at 150 kHz. These findings demonstrate excellent frequency discrimination throughout the audible spectrum (above 1 kHz) of *Tursiops* and support electrophysiological evidence of highly sensitive frequency detection mechanisms. Results for the humans showed smaller DLs than the dolphin at 1 kHz, approximately equal DLs at 2 kHz, and progressively larger DLs at 4 and 8 kHz. The human underwater thresholds were generally consistent with typical human in-air measurements of frequency DL.

Subject Classification: 65.54, 65.22; 80.50.

INTRODUCTION

Underwater frequency discrimination in the bottlenosed dolphin, *Tursiops truncatus* (Montagu), has recently been studied by behavioral techniques (Herman and Arbeit, 1972; Jacobs, 1972). Herman and Arbeit (1972) tested frequencies (F) between 1 and 36 kHz, using a simultaneous discrimination procedure. A constant-frequency (pure-tone) signal and a frequency-modulated (FM) signal, of the same center frequency as the pure tone, were projected in random sequence at each trial. Responses to the constant-frequency (CF) signal were reinforced. Difference limens (DLs), expressed as relative measures (DL/F), were from 0.002 to 0.003 between 6 and 36 kHz, and increased to 0.006 at 1 kHz. DLs for 50 and 70 kHz were also obtained, but because of limitations in the power amplification stage, the signal levels were reduced much below the levels used from 1 to 36 kHz. The results suggested an increased threshold at 70 kHz but not at 50 kHz. The 70-kHz data were considered very tentative.

Jacobs (1972) measured DLs for frequencies from 0.9 to 90 kHz, using a successive discrimination procedure. Either a CF or an FM signal was presented at each trial, each signal type requiring a different response. Relative DLs ranged from 0.003 to 0.004 between 2 and 20 kHz and from 0.007 to 0.012 for frequencies above and below that range. Unfortunately, the animal died before all planned replications could be completed.

The present study obtained DLs for *T. truncatus* for 14 frequency values between 1 and 140 kHz, using the successive discrimination method. This frequency range covers the complete audibility spectrum above 1 kHz of this species (Johnson, 1967). Additionally, underwater frequency DLs for two humans were obtained for frequencies from 1 to 8 kHz, using procedures very similar to those applied to the dolphin. The similarity of procedures permitted ready comparison of dolphin and human data.

In air, humans are excellent frequency discriminators

(Heffner, Heffner, and Masterton, 1967; Shower and Biddulph, 1931), but have not been tested previously for this capability in water. Hearing underwater occurs primarily by bone conduction (Hollien, 1973). In air, frequency DLs for bone-conducted pure tones are at least as small as for air-conducted pure tones (Corso and Levine, 1965). Consequently, there may be no loss in pitch-discrimination capability underwater.

I. METHOD

A. Bottlenosed dolphin

1. Subject

The subject was an adult female, 9–10 years in age and approximately 141 kg in weight. This animal was the subject in Herman and Arbeit (1972).

2. Apparatus and stimuli

Testing was carried out in the animal's home tank (Herman and Arbeit, 1972), using a modification of the underwater apparatus described fully in that study. Briefly, two pairs of vertically suspended ropes defined an underwater channel leading to a start paddle. During signal projection, the animal maintained the anterior portion of its body in the approximate 1-m² area (listening area) between the channel exit and the start paddle. A Sumner and Mills J9 transducer, obtained from the Naval Research Laboratory, was positioned 0.5 m beyond the start paddle, and faced the listening area. The CF and FM signals were projected from the J9, while other auditory signals controlling the animal's behavior were projected from a University MM2PPS underwater speaker, located slightly above and behind the J9. Two response paddles were positioned diagonally to the left and right of the listening area.

The CF signals and the center frequency of the FM signals were generated using the sine-wave function of a Wavetek 131A voltage controlled oscillator. A second Wavetek 131A oscillator provided a 2-Hz sine-wave modulation of the center frequency of the FM signals. This

modulation rate yielded minimal threshold variability and the lowest threshold values in the Herman and Arbeit (1972) study, and was also used by Jacobs (1972). The modulation period was calculated by a digital counter. The percentage of frequency variation of the FM signals about their center frequency was controlled by a Hewlett-Packard 350D 110-step decibel attenuator. To insure harmonic-free input to the power amplifier (Hewlett-Packard 467A), the signals were filtered with a Krohn-Hite model 3202R bandpass filter set at $\pm 8\%$ of the signal center frequency.

Between 1 and 120 kHz, the signal voltage applied to the J9 transducer was randomly either 6.4 or 7.1 Vrms; at 130 kHz it was either 9.2 or 9.9 Vrms, and at 140 and 150 kHz it was always 10.6 Vrms. The different voltage levels at a given frequency yielded signal levels from the J9 differing by approximately 1 dB and guarded against intensity cues controlling the animal's responses (cf. Henning, 1966). Additional random variation in the momentary amplitude of all signals was contributed by reflections from the water surface, which was perturbed by orienting movements of the animal or by wind action.

The signal levels from the J9 were measured in the listening area with a Hewlett-Packard 3590A/3594A wave analyzer in conjunction with a Clevite CH-3A hydrophone system. Harmonic distortion of the signals was reliably less than 1%. The noise level of the tank, measured with a Hewlett-Packard 8556A-8552B-141T spectrum analyzer, was -37 dB (re $1 \mu\text{bar}$) at 1 kHz, and decreased by approximately 3 dB/octave to 5 kHz and by approximately 10 dB/octave between 5 and 20 kHz. Above 20 kHz the noise level was within the instrument noise level of -63 dB.

Figure 1 shows the mean in-water signal levels of the

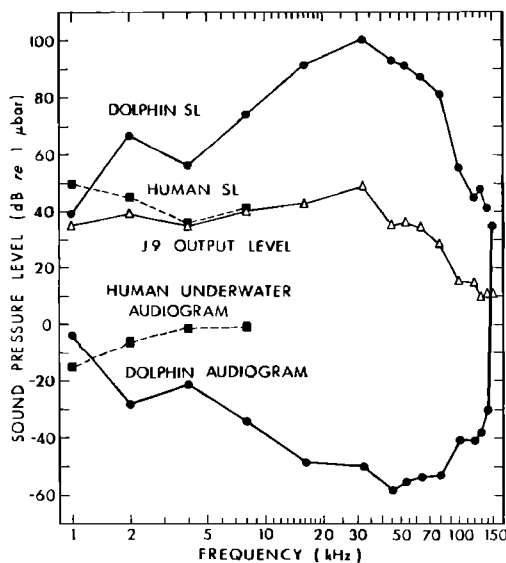


FIG. 1. The sensation levels (SL) at each frequency tested, given as the difference in decibels between the signal level from the J9 and the pure-tone thresholds for the bottlenosed dolphin, from Johnson (1967), and for humans, as derived from Brandt and Hollien (1967, 1969).

TABLE I. Bottlenosed dolphin: The mean relative frequency DL (DL/F) and standard deviation (SD) for each frequency tested, together with the number of testing sessions and number of threshold shifts determining the mean.

Frequency (kHz)	No. of sessions	No. of shifts ^a	Relative DL	
			Mean	SD
1	5	84	0.0142	0.0050
2	6	98	0.0043	0.0020
4	7	110	0.0021	0.0010
8	8	132	0.0022	0.0010
16	6	88	0.0028	0.0012
32	10	144	0.0037	0.0019
45	6	98	0.0055	0.0030
53	6	98	0.0040	0.0013
64	6	96	0.0049	0.0022
80	6	102	0.0060	0.0020
100	8	117	0.0080	0.0037
120	11	152	0.0059	0.0058
130	5	68	0.0091	0.0058
140	5	80	0.0140	0.0051
150	2	0 ^b

^aIncludes both ascending and descending threshold shifts.

^bNo responses obtainable.

J9 for the maximum voltage level used at each frequency tested, the pure-tone thresholds for a bottlenosed dolphin from Johnson's (1967) data, underwater pure-tone thresholds for humans, from the mean of the values given in Brandt and Hollien (1967, 1969), and the derived sensation levels for the bottlenosed dolphin and the humans in the present study. The sensation levels were the differences in decibels between the J9 signal levels and the corresponding threshold levels for dolphin and humans. It was assumed that the cited threshold data reasonably represented capabilities of the present animal and of the human subjects. Given this assumption, the sensation levels for the dolphin remained high throughout the frequency region tested, maximum and minimum levels being, respectively, 100 dB at 32 kHz and 40 dB at 1 and at 140 kHz. For the humans, maximum and minimum sensation levels were, respectively, 50 dB at 1 kHz and 36 dB at 4 kHz.

3. Procedure

DLs were obtained for the 14 frequencies of Table I. Each DL was the mean of at least 68 individual threshold shifts, obtained using a threshold tracking procedure (cf., Jacobs, 1972; Herman and Arbeit, 1972).

At each discrete trial of a twice-daily testing session, either a CF signal or an FM signal having the same center frequency as the CF signal was projected from the J9 speaker for 2.5 sec. After a signal terminated, the animal pressed one of the response paddles, the left paddle being correct following the CF signal and the right following the FM signal. CF and FM trials were presented in a quasirandom balanced sequence in blocks of 24 trials, with a maximum of four consecutive trials of one signal type.

At the first FM trial of each session, the FM signal deviated $\pm 6\%$ about its center frequency. Over successive trials, the percentage deviation was reduced fol-

lowing correct responses to both an FM and a succeeding CF trial, and increased again following error responses to either signal type. Changes in the percentage deviation were made by attenuating the sine-wave modulation of the FM center frequency in 5-dB steps for the first 20 trials of a session and in 3-dB steps thereafter. Each shift from a correct response to an error response estimated the descending threshold, while shifts from errors to correct responses estimated ascending thresholds. A session was continued until either ten ascending and ten descending threshold shifts were obtained or 110 trials were completed, whichever occurred first. A minimum of five sessions was completed for each of the 14 frequencies, plus an additional two sessions testing 150 kHz (Table I). The 14 frequencies were tested in counterbalanced ascending and descending series, i. e., 1-140 kHz, 140-1 kHz, with from two to three sessions run at each frequency before proceeding to the next frequency in the series.

The specific events at each trial were as follows. In response to a call sound from the University speaker, the animal entered the listening area through the rope channel and pressed the start paddle, ending the sound. There then followed a 4-sec pause; the CF or the FM signal projected from the J9 speaker for a 2.5-sec duration; a 0.5-sec pause; and a continuous exit sound projected from the University speaker. The animal then left the listening area and pressed a response paddle, ending the exit sound. Pressing the correct paddle immediately produced a short (0.5-sec) "correct" sound from the University speaker, and then a thrown fish reward. There was a 12-sec intertrial interval after correct responses and a 30-sec time-out period after incorrect responses.

B. Humans

1. Subjects

Two experienced SCUBA divers, one 23-year-old male (M.G.) and one 21-year-old female (J.A.), were subjects. Both had normal in-air hearing over the range 250 Hz to 8 kHz, as determined by a standard audiometric test.

2. Apparatus

Testing was carried out in the tank used for the bottlenosed dolphin, but with the dolphin removed. The apparatus and equipment were identical to that described for the dolphin. The start and response paddles were in the water, but were not used by the humans.

3. Procedure

DLs were obtained for 1, 2, 4, and 8 kHz, using the threshold tracking procedure described for the dolphin. Sessions began, however, with the FM deviation at $\pm 2\%$, rather than $\pm 6\%$, verbal instructions taking the place of the initial discrimination training required for the dolphin. There were two sessions per day per subject, and during each session from 6 to 11 ascending and descending threshold shifts were obtained. Either two or three sessions were completed at each of the four frequencies for each subject (Table II). Subject M.G. was tested in a counterbalanced ascending and descending series, i. e.,

TABLE II. Humans: The mean relative frequency DL (DL/F) and standard deviation (SD) for each frequency tested, together with number of testing sessions and the number of threshold shifts determining the mean.

Frequency (kHz)	Subject	No. of sessions	No. of shifts ^a	Relative DL	
				Mean	SD
1	MG	2	39	0.0056	0.0030
	JA	2	40	0.0025	0.0014
	Both	4	79	0.0041	0.0039
2	MG	2	42	0.0030	0.0008
	JA	3	59	0.0047	0.0028
	Both	5	101	0.0039	0.0036
4	MG	3	44	0.0024	0.0016
	JA	3	50	0.0045	0.0024
	Both	6	94	0.0035	0.0033
8	MG	2	42	0.0055	0.0044
	JA	2	40	0.0057	0.0018
	Both	4	82	0.0056	0.0052

^aIncludes both ascending and descending threshold shifts.

1-8 kHz, 8-1 kHz, while subject J.A. was tested in a counterbalanced descending and ascending series.

The subject, wearing standard SCUBA gear and a full-body wet suit without head covering, was positioned securely with weights on the tank floor in the listening area. Air pressure in the middle ear was equalized against water pressure before beginning each session. SCUBA breathing noise was eliminated by requiring breath holding before stimulus presentation.

The events at each trial were as follows. Following the offset of a 3-sec call sound from the control speaker, the subject held his/her breath. After a 2.5-sec pause, the CF or the FM signal was projected from the J9 speaker for 2.5 sec. The subject then raised a stick in either the left or right hand. The 0.5-sec "correct" sound was projected from the control speaker if the experimenter observed the left hand raised following a CF signal, or the right hand raised following an FM signal. A 12-sec intertrial interval followed both correct and error responses.

II. RESULTS

A. Bottlenosed dolphin

Table I shows the mean relative DL (DL/F) and standard deviation (SD) for each frequency tested, together with the number of threshold shifts determining the means. Figure 2 compares the mean relative DLs of the present study with those obtained previously by Herman and Arbeit (1972) and Jacobs (1972). Because of the uncertainty of the 70-kHz data of Herman and Arbeit (1972), they were not included in Fig. 2. Also, the data shown for Jacobs (1972) at 0.9, 2, 20, and 50 kHz are in each case the mean of the two threshold estimates reported by Jacobs.

The comparison of the three studies shows the general similarities in the trends of the curves. There is good agreement for the frequency region below 20 kHz, thresholds decreasing abruptly above 1-2 kHz and remaining near their minimum values through to approximately

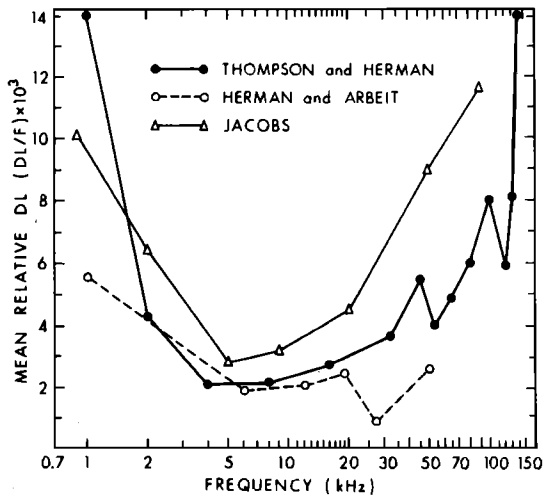


FIG. 2. Mean relative DLs (DL/F) for the bottlenosed dolphin of the present study compared with values obtained previously by Herman and Arbeit (1972) and Jacobs (1972).

20 kHz. In the frequency region from 20 to approximately 50 kHz, there are some discrepancies, Herman and Arbeit (1972) and the present study showing either continued minimal sensitivity or else only a gradual decrease in sensitivity, while Jacobs' (1972) data indicate a doubling of the threshold from 20 to 50 kHz. The two threshold estimates given by Jacobs at 50 kHz were 0.007 and 0.011, with the mean of these shown in Fig. 2. The lower threshold value, however, would be more in keeping with the results of Herman and Arbeit and of the present study.

At the upper frequency end, the present results show no pronounced threshold shift until 140 kHz, although the variability increased markedly above 100 kHz (Table I). No response could be obtained from the animal at 150 kHz. This was an expected result, since the signal level from the J9 at 150 kHz was below Johnson's (1967) threshold level for this frequency (Fig. 1). Also, Bullock *et al.*'s (1968) physiological estimate of the upper frequency limit of hearing of *T. truncatus* was 150 kHz.

Thresholds were somewhat lower in the Herman and Arbeit (1972) study than in the present one, though the same animal was used in both studies. It may be that the simultaneous comparison method used by Herman and Arbeit (1972) was a simpler discrimination task than the successive comparison procedure used here, resulting in lowered thresholds. Jacobs (1972) also used successive comparisons. His somewhat elevated thresholds in comparison with the present findings might reflect different abilities of the different animals tested, or the relatively unpracticed state of Jacobs' animal. As was noted, Jacobs did not complete all planned replications because of the death of the animal.

B. Humans

Table II shows the mean relative DL and SD for each frequency for individual subjects and for both subjects combined. The number of threshold shifts determining each mean are also shown.

Figure 3 compares the human in-water thresholds with the present threshold values for the dolphin and with the mean human in-air results obtained by Shower and Biddulph (1931). Shower and Biddulph also used an FM technique to determine thresholds.

The human underwater thresholds were only slightly elevated relative to the mean human in-air thresholds. This close correspondence of human in-water and in-air thresholds is impressive given the strenuous in-water testing conditions and the different psychophysical techniques used. Human underwater pitch sensitivity was superior to dolphin sensitivity at 1 kHz, was roughly comparable at 2 kHz, and became progressively poorer at 4 and 8 kHz.

III. DISCUSSION

The present results confirmed and extended over a wider frequency range the prior behavioral evidence (Herman and Arbeit, 1972; Jacobs, 1972) of excellent pitch discrimination capability in the bottlenosed dolphin *T. truncatus*. Bullock *et al.* (1968) predicted a behavioral potential for fine frequency discrimination on the basis of finding large waveform and amplitude changes in evoked potentials from the inferior colliculus after very small frequency changes in applied signals. The frequency discrimination capabilities of *T. truncatus* are probably reflected in a number of its adaptations for high-frequency hearing, particularly the enormous size of the cochlea in comparison with the vestibular portion of the labyrinth and the domination of the eighth nerve by the cochlear portion (Reysenbach de Haan, 1957).

Relative frequency DLs for the dolphin in the present study were from 0.002 to 0.004 over the frequency range from 2 to 53 kHz (there was no apparent reason for the rise to 0.006 at 45 kHz), and never exceeded 0.008 through to 130 kHz. At the extreme frequencies tested,

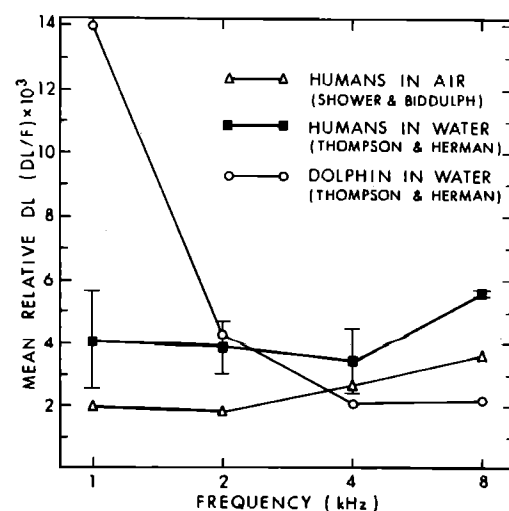


FIG. 3. Mean human in-water relative DLs (DL/F) compared with threshold values for the bottlenosed dolphin of the present study (1-8 kHz) and with mean human in-air thresholds obtained by Shower and Biddulph (1931). The specific thresholds for each of the two subjects in the present study are given by the range indicators around the mean threshold.

1 and 140 kHz, relative DLs increased to 0.014. The variation in capabilities at the different frequencies was not related to the differences in sensation levels (40–100 dB *re* 1 μ bar) noted in Fig. 1, the correlation between sensation level and relative DL being only 0.05 ($p > 0.05$). Also, for humans at least, sensation levels above 20–40 dB do not affect frequency DLs (Shower and Biddulph, 1931; Small and Brandt, 1963).

Among other species, capabilities for discriminating frequency changes as small as 0.2%–0.4% have been found only for humans in air, in the frequency range 1–8 kHz (e.g., Corso and Levine, 1963; Shower and Biddulph, 1931), or in water, in the frequency range 1–4 kHz (Fig. 3). Frequency discrimination in the harbor seal (Mohl, 1967), another marine mammal, is at least three times as coarse as that of the bottlenosed dolphin at frequencies of 2 kHz and above. The same is true for all nonhuman terrestrial mammals tested for frequency discrimination (summarized in Heffner, Heffner, and Masterton, 1971), as well as for the goldfish (Fay, 1970) and pigeon (Price, Dalton, and Smith, 1967). However, some animals which would be expected to have good frequency discrimination capabilities, such as the echolocating bat or the passerine song birds, have not yet been behaviorally tested.

The excellent frequency discrimination capability of the bottlenosed dolphin throughout a major portion of the frequency spectrum of its echolocation signals (see Evans, 1973) could be useful in several important echolocation tasks. These include the detection of relative target movement through an analysis of Doppler shifts, the recognition of target quality through observing selective absorption of different frequencies by different targets, and the estimation of target distance through observing the relative degree of attenuation of higher frequencies in the returned signals. Fine frequency discrimination in the sonic region may be useful in the identification and discrimination of the unique signature whistles of conspecifics or of other odontocete cetaceans, as reported in some recent studies (e.g., Caldwell, Caldwell, and Hall, 1973).

Human underwater frequency DLs did not differ substantially from typical in-air values (Shower and Biddulph, 1931). Since the middle ear mechanisms are relatively ineffective underwater because of impedance mismatches, sound arrives at the cochlea primarily through bone conduction (Hollien, 1973), resulting in decreased sensitivity to weak signals (Brandt and Hollien, 1967, 1969) and a loss of differential time or intensity information across the two ears (Anderson and Christensen, 1969; Feinstein, 1973; Norman, Phelps, and Wightman, 1970). However, Corso and Levine (1963) found that, in air, bone conduction did not raise frequency discrimination thresholds, and Flurr and Adolfson (1966) demonstrated that bone-conducted pure-tone thresholds were not increased in a dry hyperbaric environment relative to a dry 1-atm environment. Flurr and Adolfson concluded that there was no loss in cochlear or neural function under increased atmospheric pressure. Together, the Corso and Levine (1963) and Flurr and Adolfson (1966) findings imply that frequency

discrimination, which takes place at the cochlear level and perhaps beyond (Teas, 1970), should not be affected by the bone-conduction pathway underwater, given that the signal level is sufficiently high. As was noted, the in-water signals of the present study were estimated to be a minimum of 36 dB above human in-water thresholds, a sensation level sufficient in air to yield asymptotic frequency discrimination thresholds in humans (Shower and Biddulph, 1931; Small and Brandt, 1963).

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