Temporary shift in masked hearing thresholds of bottlenose dolphins, *Tursiops truncatus*, and white whales, *Delphinapterus leucas*, after exposure to intense tones

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(Received 21 July 1999; accepted for publication 2 February 2000)

A behavioral response paradigm was used to measure masked underwater hearing thresholds in five bottlenose dolphins and two white whales before and immediately after exposure to intense 1-s tones at 0.4, 3, 10, 20, and 75 kHz. The resulting levels of fatiguing stimuli necessary to induce 6 dB or larger masked temporary threshold shifts (MTTSs) were generally between 192 and 201 dB *re*: 1 μPa. The exceptions occurred at 75 kHz, where one dolphin exhibited an MTTS after exposure at 182 dB *re*: 1 μPa and the other dolphin did not show any shift after exposure to maximum levels of 193 dB *re*: 1 μPa, and at 0.4 kHz, where no subjects exhibited shifts at levels up to 193 dB *re*: 1 μPa. The shifts occurred most often at frequencies above the fatiguing stimulus. Dolphins began to exhibit altered behavior at levels of 178–193 dB *re*: 1μPa and above; white whales displayed altered behavior at 180–196 dB *re*: 1 μPa and above. At the conclusion of the study all thresholds were at baseline values. These data confirm that cetaceans are susceptible to temporary threshold shifts (TTS) and that small levels of TTS may be fully recovered. [S0001-4966(00)00106-5]

PACS numbers: 43.80.Lb [WA]

INTRODUCTION

The order Cetacea includes the Odontocetes (toothed whales) and the Mysticetes (baleen whales). These animals are marine mammals that are born and spend their entire lives in water. Many cetaceans have exceptional hearing and sound production capabilities (Johnson, 1967; Norris, 1968; Nachtigall, 1986; Watkins and Wartzok, 1985) and employ sound to forage, communicate, and navigate (Green *et al.*, 1994). There is growing concern that human-made sounds from sources such as maritime shipping, geophysical surveys, dredging, offshore drilling and exploration, oceanographic testing, and military testing are a potentially serious auditory problem for cetaceans (Richardson *et al.*, 1995); however, available data are inadequate to allow confident predictions regarding the parameters of sound that should be of concern (Green *et al.*, 1994).

Short exposure to intense sound may produce elevated hearing thresholds or threshold shifts (TSs). If the TS recovers after several minutes, hours, or days it is known as a temporary threshold shift (TTS). By contrast, a permanent threshold shift (PTS) is characterized by no recovery in hearing thresholds. TTS and PTS studies were instrumental in establishing noise exposure limits in humans. Currently, no published TTS or PTS data exist for cetaceans. Green *et al.* (1994) suggested that by measuring TTS in some cetaceans, it may be possible to safely determine maximum levels of sound to which these marine mammals can be exposed without risk of hearing damage. Richardson *et al.* (1995) identified studies of TTS in marine mammals as a ‘‘major data need.’’

This report presents the results of a series of eight experiments designed to measure TTS in bottlenose dolphins (*Tursiops truncatus*) and white whales (*Delphinapterus leucas*) exposed to 1-s pure tones at frequencies between 0.4 and 75 kHz. The data presented here were collected between May 1996 and August 1998 and include and expand upon the original pure-tone TTS data for bottlenose dolphins provided by Ridgway *et al.* (1997) in a technical report. This technical report included TTS data for bottlenose dolphins exposed to 1-s tones at frequencies of 20, 75, and 3 kHz. These tests correspond to experiments I–III of the present report; however, the current study employed a different data analysis technique compared to Ridgway *et al.* (1997), thus some differences in results were obtained from the same raw data (see Sec. III).

The experimental methodology was briefly as follows: A behavioral response paradigm was used to measure masked underwater hearing thresholds in five bottlenose dolphins and two white whales before and immediately after exposure to intense 1-s tones. Thresholds measured before and after exposure were compared to determine if the subject experienced a TTS. Masking noise was used to provide a floor effect in the presence of variable ambient noise in San Diego Bay. Studies of TTS in humans (e.g., Humes, 1980; Parker *et al.*, 1976) have shown that the presence of masking noise results in elevated hearing thresholds and decreases the amount of TTS observed. The relationship between masking

TABLE I. Subject taxa, identification, and signalments.

Species	Animal identification	Gender	Weight (kg)	Length (cm)	Age (yrs)
Tursiops truncatus	APR	F	150	240	12–14
Tursiops truncatus	BEN	M	230	260	33–35
Tursiops truncatus	MUU	F	180	240	19–21
Tursiops truncatus	NEM	M	230	270	31–33
Tursiops truncatus	TOD	F	250	270	38–40
Delphinapterus leucas	MUK	F	550	350	29–31
Delphinapterus leucas	NOC	M	660	400	20–22

noise level and TTS in cetaceans is unknown. To indicate that the threshold shifts presented in this report were measured in the presence of masking noise, we use the term masked temporary threshold shift (MTTS) to identify these data.

I. METHOD

A. Subjects

The subjects for this study consisted of five *T. truncatus* and two *D. leucas* that ranged in age from 12 to 40 years (Table I). These species are members of the superfamily Delphinoidea, which includes more than half of all cetaceans (Ridgway, 1997). Figure 1 shows behavioral audiograms measured for *D. leucas* (Awbrey *et al.*, 1988; Johnson *et al.*, 1989; White *et al.*, 1978) and *T. truncatus* (Johnson, 1967). These species have hearing ranges and sensitivities equivalent to or better than many marine mammals (Fay, 1988; Richardson *et al.*, 1995) and may presumably be impacted by a wide range of anthropogenic acoustic devices.

The test animals were housed in netted enclosures (10 ×10 m to 13×25 m) in San Diego Bay, California. Individual diets consisted of a specific amount of herring, mackerel, capelin, smelt, and squid in order to maintain a healthy weight relative to the animal's age and gender. The amount of food delivered per day was the same regardless of performance or of the number of sessions in which an animal participated during the day. All animals were under constant veterinary supervision in accordance with applicable Federal regulations. The study followed a protocol approved by the Institutional Animal Care and Use Committee under guidelines of the Association for the Accreditation of Laboratory Animal Care. At the time of this study, all subjects were healthy and were not known to have any hearing loss at any of the fatiguing stimulus frequencies. One subject (MUK) had elevated baseline and preexposure thresholds at 40 kHz relative to those at 35 and 45 kHz, indicating a possible preexisting hearing loss at that frequency.

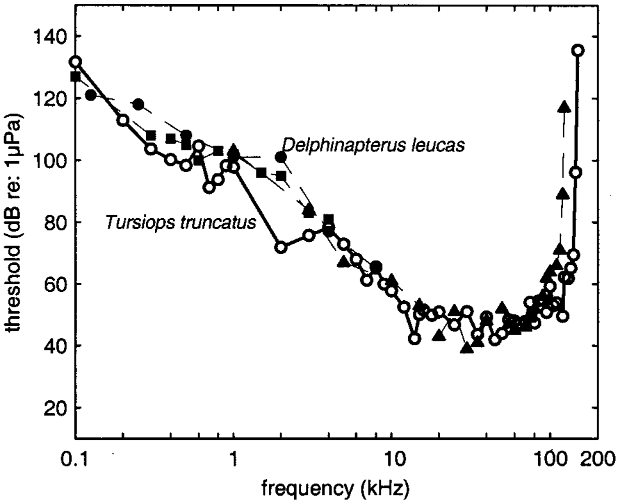

FIG. 1. Behavioral audiograms measured for the bottlenose dolphin, *Tursiops truncatus*. (open circles: Johnson, 1967) and white whale, *Delphinapterus leucas* (filled triangles: White *et al.*, 1978; filled squares: Johnson *et al.*, 1989; filled circles: Awbrey *et al.*, 1988).

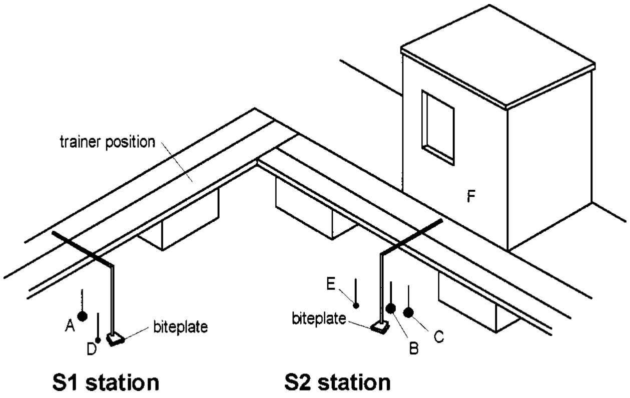

FIG. 2. The test enclosure showing the location of two underwater listening stations, S1 and S2. A—S1 projector, B—S2 projector, C—masking noise projector, D—S1 receiving hydrophone, E—S2 receiving hydrophone, F—equipment shelter.

B. Apparatus and sound presentation equipment

1. Apparatus

Figure 2 illustrates the testing environment. The test enclosure, 10×10 m, similar in type to the ''home'' enclosures, was equipped with two underwater listening stations, designated ''S1'' and ''S2.'' Each station was constructed of polyvinyl chloride tubing and supported a biteplate on which the subjects stationed during testing. The stations were located at depths between 1 and 2.5 m, depending on the particular experiment. An underwater video camera was placed above the S1 station to allow the operator to observe the animal's position during low-visibility conditions. Each station was equipped with an underwater sound projector (Fig. 2; projectors A and B) and a receiving hydrophone (Fig. 2; hydrophones D and E). An additional sound source at the S2 station projected masking noise (Fig. 2; projector C). The S1 station was the site for the presentation of a ''start'' signal, or ''S1 signal,'' which was at times elevated for use as the fatiguing stimulus; the S2 station was the site for the hearing tests. The individual hearing test tones are referred to as ''S2 tones.'' The frequencies of the S1 signal and the S2 tones are referred to as the ''S1 frequency'' and ''S2 frequency,'' respectively.

2. Test conditions

Table II lists the S1 and S2 frequencies, the masking noise level, and the sound projectors employed during each of the eight experiments. The parameters of the fatiguing

TABLE II. Combinations of S1 frequency and level, S2 frequency, masking noise level, and sound projectors used in the study. The last column indicates the number of bottlenose dolphins (*Tt*) and white whales (*Dl*) tested at each condition.

Experiment	S1 frequency (kHz)	S1 projector	S1 levels (dB *re*:1 μPa-rms)	S2 frequency (kHz)	S2 projector	Masking noise (dB *re*:1 μPa^2/Hz)	Masking noise projector	*n* (*Tt*/*Dl*)
I	20	ITC 1001	160–197	20, 30, 40	ITC 1032	75	EDC 6166	2/0
II	75	ITC 1042	160–194	75, 85, 100	LC-10	70	EDO 6166	2/0
III	3	ANSSQ62B	160–202	3, 4.5, 6	J9	67	ITC 1001	2/2
IV	10	ITC 1001	180–197	10, 15, 20	ITC 1032	63	J9	2/2
V	20	ITC 1001	180–201	20, 30, 40	ITC 1032	75	ITC 1042	2/2
VI	20	ITC 1001	178–202	30	ITC 1032	63	ITC 1042	2/2
VII	3	ITC 2015	180–201	4.5	ITC 1032	90	ITC 1032	2/2
VIII	0.4	XF4	179–193	0.6	ITC 1001	95	Custom	2/2

stimuli were chosen to be representative of certain sonar signals. Experiments I–IV were designed to measure MTTS at S1 frequencies of 20, 75, 3, and 10 kHz, respectively. Experiment V was designed to replicate experiment I with different subjects. Experiments VI and VII were designed to repeat the 20- and 3-kHz tests, respectively, using different masking noise levels. Experiment VIII featured a 0.4-kHz fatiguing stimulus.

This study was conducted over a 2.3-year period during which time equipment was maintained in an air-conditioned hut adjacent to the test enclosure (Fig. 2, F). During this time, some equipment was repaired and/or replaced, thus multiple pieces of equipment may be listed in Table II for the same task. The S1 signals, S2 tones, and the masking noise are described in more detail next.

a. S1 signals. All S1 signals were 1 s in duration with approximately 0.5-ms rise and fall times. The S1 signal amplitudes were 141 dB *re*: 1 μPa for baseline, preexposure, and recovery sessions (see Sec. I C). The amplitude of the first S1 signal presented during post-exposure sessions was elevated (i.e., was greater than 141 dB *re*: 1 μPa) and served as the fatiguing stimulus. The remaining post-exposure S1 signals were at 141 dB *re*: 1 μPa.

The S1 signals were generated using a programmable function generator (Wavetek model 164 or 178), filtered (Ithaco 4302), amplified (Crown Macro-Tech 2400, Hafler Pro 5000 or P7000, BGW Performance Series 4, or Instruments, Inc. LDV2-5 or S11-24), and used to drive a piezoelectric underwater sound projector (ITC 1001, ITC 1042, ITC 2015, ANSSQ62B, or XF4). The S1 sound projector was positioned directly in front of the subject at a distance of 1 to 2 m (depending on the experiment), at the same depth as the S1 biteplate. The amplitude of each S1 signal presented to the subjects was measured using a receiving hydrophone (B&K 8103) and charge amplifier (B&K 2635), digitized at 320 or 500 kSamples/s (Tucker-Davis AP2, Keithley-Metrabyte DAS-1800, or National Instruments PCI-MIO-16E-1), and saved for later analysis. The sensitivity of the B&K 8103 hydrophone was regularly checked with a B&K 4223 pistonphone. The sound pressure level (SPL) distance correction (from the hydrophone position to the approximate location of the animals' ears) was obtained from experimental measurements conducted prior to testing, without animals present.

At the higher S1 levels the amplifiers and sound projectors were often operating at near-capacity and the ability to specify the S1 level *a priori* decreased; however, recorded S1 amplitudes were generally within 3 dB of the intended level. It is important to note that each individual S1 was recorded so the exact S1 signal level was measured during each exposure. S1 levels cited in this report have units of dB *re*: 1 μPa [root mean square (rms)]; these are received levels at the estimated position of the animals' ears.

b. S2 tones. All S2 tones were 250 ms in duration, including 5-ms rise and fall times. Hearing thresholds were measured at three S2 test frequencies during experiments I–V and at a single S2 frequency for experiments VI–VIII (see Table II). When three S2 frequencies were used, the first was the same as the S1 frequency; the second and third were higher frequencies within one octave of the S1 frequency. If only a single S2 frequency was tested, it was at 1/2-octave above the S1 frequency. The use of multiple frequencies for hearing tests was based on human research showing that TTS may occur at frequencies above that of the fatiguing stimulus, often at a frequency 1/2-octave above (e.g., Dancer *et al.*, 1992; Green, 1976). The order in which multiple S2 frequencies were presented to the subject was counterbalanced between sessions and days.

The S2 tones were digitally generated and output through the D/A converter on a Tucker-Davis QDA2 or National Instruments PCI-MIO-16E-1 multifunction board. The D/A output was filtered (Ithaco 4302 and 4212), amplified (BGW Performance Series 2 or HP 467A), and used to drive an underwater sound projector (Fig. 2, Projector B). A number of different sound projectors were required to cover the range of S2 frequencies used; S2 projectors included piezoelectric spheres (ITC 1001, ITC 1032), piezoelectric cylinders (Celesco LC-10), and a moving-coil type (Chesapeake J9).

The S2 projector was positioned approximately 1.5 m in front of the animal for experiments I–VI and 1.5 m below the animal's ears, projecting upward, for experiments VII and VIII. A receiving hydrophone (B&K 8103, located at the estimated position of the animal's ears), charge amplifier (B&K 2635), and digital signal analyzer (HP 3561A) were used to measure the S2 tone amplitudes and calibrate the sound system prior to testing each day. During the actual hearing tests, this S2 receiving hydrophone was moved to a position above the S2 biteplate and was used to measure the

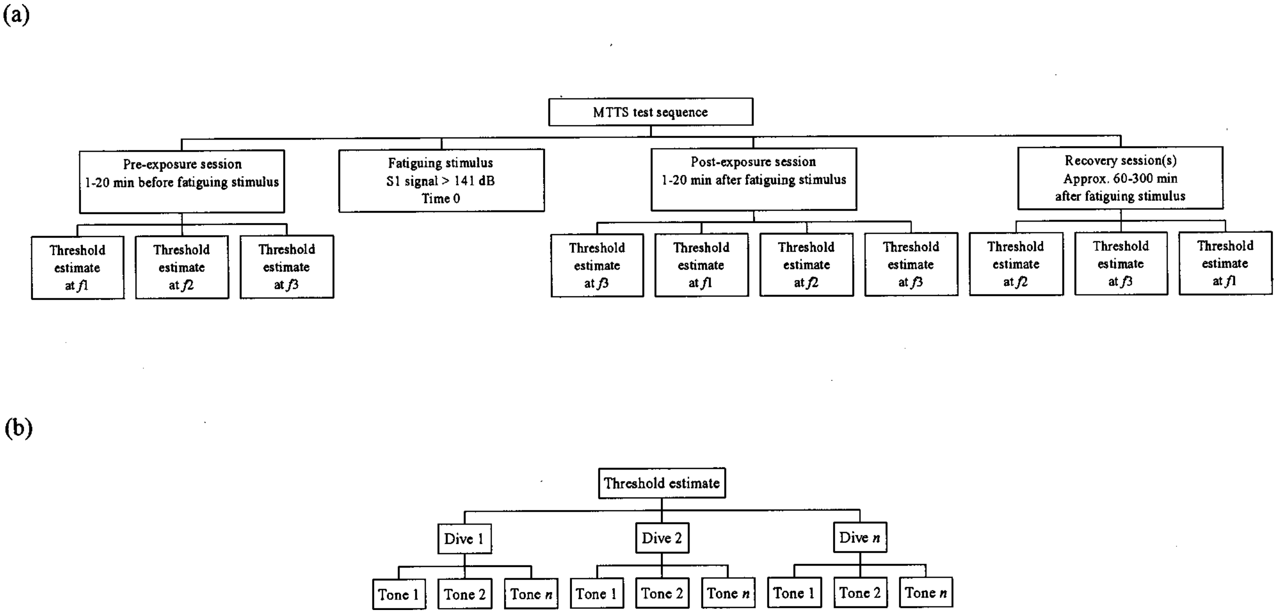

FIG. 3. A block diagram showing (a) the sequence of preexposure, post-exposure, and recovery sessions relative to the presentation of the fatiguing stimulus during MTTS testing when three S2 frequencies (designated f_1, f_2, f_3) were tested, (b) the relationship between multiple dives and multiple S2 tone presentations that make up a threshold estimate (baseline and MTTS testing).

background noise (ambient as well as masking) and any sounds produced by the test subjects.

c. Masking noise. A noise-free test environment was not possible in San Diego Bay, therefore band-limited white noise (masking noise) was introduced to help create a floor-effect and to keep thresholds consistent despite variations in ambient noise. Masking noise was presented continuously during a session (i.e., was not turned ''on'' and ''off'' to delineate trials). If ambient noise levels temporarily exceeded the masking noise level, testing was suspended until ambient noise levels again fell below the masking noise.

Masking noise for experiments I and II was generated using a custom-built noise generator. Masking noise for the other experiments was generated using a Wavetek 132 function generator. Masking noise was amplified (HP 467A or BGW Performance Series 4) and output through an underwater sound projector (EdoWestern 6166, ITC 1001, ITC 1032, ITC 1042, Chesapeake J9, or a custom-built piezoelectric sphere). The masking noise projector was positioned approximately 1.5 m directly in front of the subject, at the same depth as the S2 biteplate. The noise spectral density was flat within ± 5 dB (experiments I–IV) or ±3 dB (experiments V–VIII) over the range of S2 frequencies tested.

C. Procedure

During each day of testing, subjects participated in one or more sessions. Each session belonged to one of four categories: (1) baseline, (2) preexposure, (3) post-exposure, and (4) recovery. Baseline sessions were conducted as part of ''baseline testing'' and took place at the beginning of each experiment over several days prior to presentation of the fatiguing stimulus. These sessions provided baseline information regarding hearing thresholds at each S2 frequency with the appropriate level of masking noise to which comparisons of future thresholds could be made. The latter three session types were conducted as part of ''MTTS testing'' and took place within one test day either before or after presentation of a fatiguing stimulus. Preexposure sessions were conducted immediately before exposure to the fatiguing stimulus; post-exposure sessions began immediately after exposure; recovery sessions were conducted beyond one hour post exposure. Figure 3(a) illustrates the relationship between preexposure, post-exposure, and recovery sessions relative to the presentation of the fatiguing stimulus. Within each session, hearing thresholds were estimated at one or more S2 frequencies. Regardless of the session type, the hearing test procedure was essentially the same. The details of this procedure are described next, followed by more detailed descriptions of the four session types.

1. Hearing test procedure

The hearing test procedure was based on the Method of Free Response, or MFR (Egan *et al.*, 1961). In this situation, the listener is presented with a number of brief tones during a relatively long observation period. The time interval between tones is randomized and the listener does not know when the next tone will occur. The listener is provided with a single ''response key,'' which he is instructed to press each time he hears a tone, and to do nothing otherwise.

The MFR was modified appropriately to allow its use with marine mammals. Subjects were trained to produce an audible ''whistle'' if they heard a tone and to remain quiet otherwise (Ridgway and Carder, 1997). The time interval between tones (i.e., measured from onset to onset) was randomized between 5 and 8 s and the animal did not know when the next tone would occur. Each threshold estimate was divided into several observation periods, called ''dives''; each dive consisted of two parts: presentation of the S1 signal at the S1 station, followed by presentation of multiple S2 hearing test tones at the S2 station, as illustrated

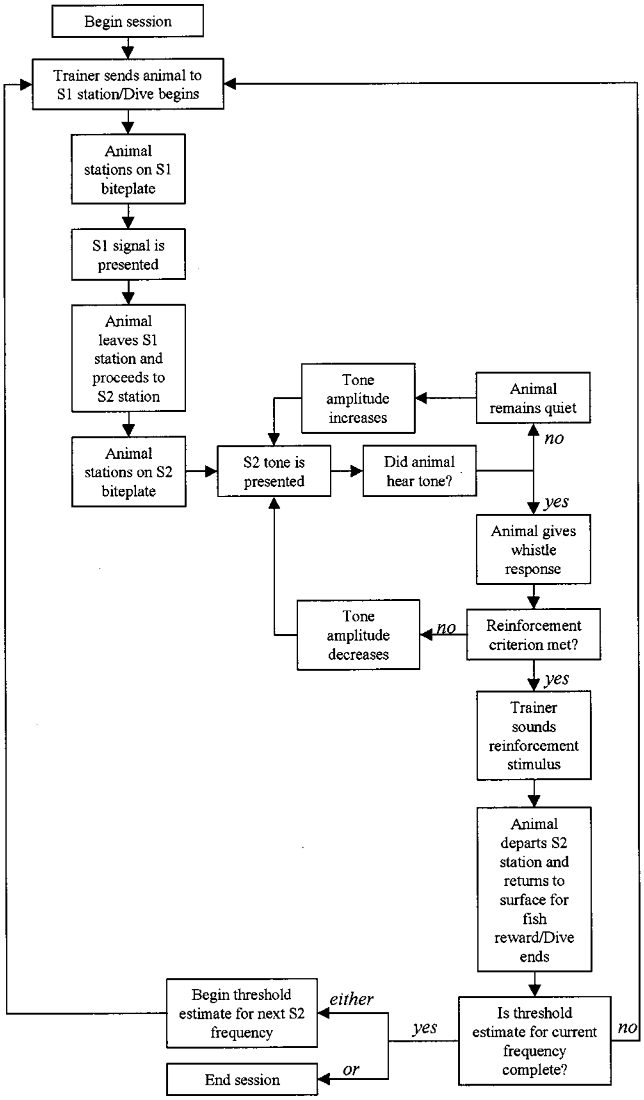

FIG. 4. A flowchart of the hearing test procedure.

in Fig. 3(b). The use of multiple dives was required to allow the animals to periodically surface for air and to receive fish reward.

Figure 4 shows the basic flow of the hearing test procedure. Each dive began with the trainer cueing the animal to the S1 station. The subject was trained to remain on the S1 station until presented with the S1 signal. The underwater camera was used to verify that the animal remained on the station until the signal was presented. Upon hearing the S1 signal, the subject proceeded directly to the S2 station for hearing tests. If the subject left the S1 station during the S1 signal, the dive continued without interruption (the distance moved during the 1-s S1 signal was considered to have a negligible effect on the received level); if the animal left the S1 station before the signal was projected the dive was restarted.

Once the animal was positioned at the S2 station, S2 tones were presented. The amplitudes of the S2 tones were adjusted using a modified staircase procedure (e.g., Cornsweet, 1962; Rosenberger, 1970). If the subject heard a tone and whistled (a hit), the amplitude of the next tone was decreased by 3 dB (experiment I) or 4 dB (experiments II–VIII); if the subject did not hear a tone that was projected and remained quiet (a miss), the amplitude of the next tone was increased by 2 dB. A dive was terminated when the trainer sounded an underwater buzzer, a reinforcement stimulus, which signaled the animal to leave the S2 station and return to the surface for fish reward. Typically, the dolphins remained on the S2 station for an average of 12 S2 tone presentations. The whales remained on the S2 station for an average of 15 S2 tone presentations. Subjects were only reinforced after hits. Following reinforcement, the next dive was then begun, if necessary to complete a threshold estimate.

The time period between 0.05 and 2.05 s immediately following the onset of a tone was designated the ''hit interval'' and was included in the 5–8-s interstimulus interval measured from tone onset to onset. Only whistles occurring within the hit interval were recorded as hits. Any whistle response by a subject not occurring within a hit interval was recorded as a false alarm. Time catch trials (Ljungblad *et al.*, 1982), or no-tone periods, were randomly introduced while the animal was on the S2 station. No-tone periods ranged between 8 and 90 s.

2. Session types

At the start of each experiment listed in Table II, baseline hearing thresholds were measured to establish each subject's masked hearing threshold at the relevant S2 frequencies and masking noise level over several days prior to any exposure to the fatiguing stimulus at the associated S1 frequency. Baseline sessions followed the hearing test procedure outlined above. All S1 signals were presented at 141 dB *re*: 1 μPa during baseline sessions.

After baseline thresholds had been established for each subject, MTTS testing began [Fig. 3(a)]. During MTTS testing, each subject was tested in the following sequence: preexposure session, post-exposure session, and recovery session (experiments V–VIII only). Preexposure sessions were conducted immediately (normally 1–20 min) before the subject's exposure to the fatiguing stimulus. The procedure was identical to the baseline session procedure. All S1 signals were presented at 141 dB *re*: 1 μPa during preexposure sessions.

Post-exposure sessions were identical to baseline and preexposure sessions with the following exception: the amplitude of the first S1 signal presented during post-exposure sessions was elevated (i.e., was greater than 141 dB *re*: 1 μPa). This single, ''loud'' S1 signal served as the fatiguing stimulus to induce MTTS. The remaining S1 signals during post-exposure sessions were delivered at 141 dB *re*: 1 μPa. The post-exposure threshold at the first S2 frequency was generally obtained within 1–3 min following exposure to the fatiguing stimulus. When three S2 frequencies were tested, thresholds at the remaining frequencies were normally obtained within 20 min after exposure. After all three S2 frequencies had been tested, testing was repeated at the first S2 frequency [see Fig. 3(a)]. The order in which the frequencies were tested was counterbalanced between days, e.g., during experiment I the post-exposure frequencies may have been tested in the order 20, 30, 40, 20 kHz, 30, 40, 20, 30 kHz,

TABLE III. Information about MTTS testing including start dates, animals tested, the number of MTTS test sequences (S) run (i.e., fatiguing stimulus presentations), and the number of thresholds estimated (TE) in the corresponding preexposure, post-exposure, and recovery sessions over the 2.3-year duration of the study.

	Date								
	8/96	10/96	12/96	6/97	9/97	1/98	5/98	6/98	
Animal	EXP I S|TE	EXP II S|TE	EXP III S|TE	EXP IV S|TE	EXP V S|TE	EXP VI S|TE	EXP VII S|TE	EXP VIII S|TE	Total S|TE
MUU	12|57								12|57
APR			8|44						8|44
TOD	15|101	11|82							26|183
BEN				5|29	8|82	5|38	5|40	6|48	29|237
NEM		12|93	9|53	6|35	5|44	7|50	5|39	3|25	47|339
MUK			8|46	6|33	9|91	6|48	5|39	3|24	37|281
NOC			7|40	5|30	8|81	7|56	5|39	4|32	36|278
Total	27|158	23|175	32|183	22|127	30|298	25|192	20|157	16|129	195|1419

and 40, 20, 30, 40 kHz on three successive days. If no MTTS was observed (see Sec. I 3), the S1 level was increased and testing continued the next day. S1 levels were increased by 10-dB steps through 180 dB *re*: 1 μPa, 6-dB steps through 192 dB *re*: 1 μPa, and 2- to 4-dB steps for S1 levels above 196 dB *re*: 1 μPa. If an MTTS was observed, testing was repeated at the same S1 level on subsequent days so that each S2 frequency could be tested immediately after exposure.

Auditory testing of animals using a behavioral response paradigm may be very time consuming, thus the number of S2 hearing test frequencies was limited. Recovery of MTTSs over time (within a few minutes for small levels of MTTS) and declining motivation of the subjects after repeated testing practically limited the number of sessions that could be run in a single day. Therefore, during experiments I–IV, baseline thresholds were measured at all three S2 frequencies; however, preexposure thresholds were only measured for the first S2 frequency to be tested immediately after exposure. For those frequencies with no preexposure thresholds, post-exposure thresholds were compared to baseline values to determine if an MTTS had occurred. As proficiency in the test methodology increased, more sessions were conducted each day, e.g., during experiment V preexposure and post-exposure sessions were conducted at all three S2 frequencies.

Recovery sessions were conducted 60–300 min after exposure to the fatiguing stimulus to confirm that thresholds returned to (or stayed within) baseline levels within the same test day. The procedure was identical to that of baseline and preexposure sessions. Recovery sessions were only conducted during experiments V–VIII. Usually two recovery sessions were conducted at least one hour apart from each other.

3. Threshold estimation and MTTS criterion

Hearing thresholds were defined as the average SPL of the first ten hit-miss or miss-hit reversal points within the staircase data. A subject's threshold at a particular frequency could usually be estimated within 1 to 4 dives, or 20 to 30 total tones [Fig. 3(b)]. Note that this methodology differs from that previously used by Ridgway *et al.* (1997), who estimated thresholds as the average SPL of the five lowest hits. Furthermore, Ridgway *et al.* quantized thresholds into 3-dB bins. Because of these methodological differences, some disagreement may be seen between the results presented here and the earlier data presented by Ridgway *et al.* (1997).

In some cases, it was not possible to obtain ten reversals from previously acquired post-exposure or recovery threshold data [e.g., results previously presented by Ridgway *et al.* (1997) were based on the mean SPL of the five lowest hits and so ten reversal points were not necessarily present]. Post-exposure or recovery threshold data with fewer than five reversal points were excluded from the current MTTS determination. Any MTTSs arising from post-exposure or recovery thresholds based on 5–9 reversals are identified as such Sec. II.

Post-exposure and recovery thresholds were compared to preexposure (or baseline, when preexposure thresholds were not available) hearing thresholds to determine whether an animal experienced an MTTS, defined as a 6-dB (or larger) statistically significant increase. The 6-dB difference was considered the smallest shift that was clearly distinguishable from 3–4 dB variability in baseline thresholds measured day-to-day and session-to-session.

4. Behavioral alterations

In an attempt to document any behavioral reactions to the fatiguing stimuli, detailed notes were recorded regarding each subject's movements, swimming directions, and postures during each session. Each session was videotaped underwater and in-air. The time taken to swim from the S1 station to the S2 station was recorded for each dive. Any acoustic responses by the test subjects were noted as well.

II. RESULTS

A. Threshold shifts

During the 2.3-year test period over which the eight experiments were conducted, there were 195 MTTS test sequences (i.e., presentations of a fatiguing stimulus) and 1419 preexposure, post-exposure, and recovery threshold estimates from the seven test subjects. Table III provides a breakdown of the number of test sequences and the corre-

TABLE IV. S1 exposure levels at which MTTS was observed in dolphins and white whales as well as the magnitude of the shift, the S2 shift frequency, and the number of false alarms committed during threshold estimation at the shift frequency both pre- and post-exposure. Thresholds estimated before and immediately after exposure from which the magnitude of the MTTS was calculated were based on the ten reversals unless noted.

Exp.	S1 frequency (kHz)	Subject	S1 level (dB *re*:1 μPa)	MTTS (dB)	S2 shift frequency (kHz)	No. of false alarms preexposure	No. of false alarms post-exposure
I	20	TOD	193	8	40	0	1
II	75	TOD	182	8	100	0	0
III	3	NEM	194	7[a]	3	0	0
				16[b]	4.5	0	0
				17[c]	6	0	0
		NOC	195	12	4.5	0	0
IV	10	BEN	192	7	15	0	0
		MUK	192	7	20	0	0
V	20	MUK	197	8	40	0	1
			200	6	40	1	0
			201	10	30	0	0
		NOC	200	12	20	0	0
VI	20	BEN	196	6	30	1	1

[a] 7 reversals.
[b] 9 reversals.
[c] 8 reversals.

sponding threshold estimates for each animal by experiment, as well as the dates on which MTTS testing began for each experiment. Eleven MTTSs were observed in six of the experiments. Table IV summarizes the MTTSs observed during each of these experiments. At the conclusion of each experiment, all thresholds were within 3 dB of baseline values; there were no PTSs. Details regarding the levels of the S1 tones that produced the MTTSs, the amount of MTTSs, and the S2 frequencies at which the MTTSs occurred follow.

During experiment I, an 8-dB MTTS at 40 kHz was measured in the oldest dolphin TOD after exposure to a 20-kHz, 1-s tone at 193 dB *re*: 1 μPa. This shift occurred 4 min post-exposure and had recovered (i.e., within 3 dB of baseline/preexposure threshold at that frequency) by the next time she was tested, the following day. During experiment II, TOD also showed an 8-dB MTTS at 100 kHz after exposure to a 75-kHz tone at 182 dB *re*: 1 μPa. This shift occurred 2 min post-exposure and recovered within 11 min. The shifts observed during experiments I and II occurred at frequencies above those of the fatiguing stimuli. No white whales were tested during experiments I and II.

During experiment III, the dolphin NEM had MTTSs of 7, 16, and 17 dB at 3, 4.5, and 6 kHz, respectively, after exposure to a 3-kHz tone at 194 dB *re*: 1 μPa. These shifts occurred at 18, 10, and 5 min post-exposure, respectively. The whale NOC had a 12-dB shift at 4.5 kHz after exposure to a 3-kHz tone at 195 dB *re*: 1 μPa. This shift occurred 15 min post-exposure. Both the animals' thresholds had recovered by the next test day. Note that the post-exposure thresholds for NEM were based on fewer than ten reversals and must be interpreted with some caution. APR, the youngest dolphin tested, showed no MTTS at levels up to 201 dB.

Experiment IV produced MTTSs of 7 dB after exposure to 10-kHz tones at 192 dB *re*: 1 μPa in both the dolphin BEN (15-kHz shift frequency, 4 min post-exposure) and the whale MUK (20-kHz shift frequency, 13 min post-exposure). BEN's threshold recovered within 16 min, MUK's threshold had recovered by the next time she was tested, the following day.

During experiment V, the whale MUK had an MTTS of 8 dB at 40 kHz after exposure to a 20-kHz tone at 197 dB *re*: 1 μPa. This shift occurred 15 min post-exposure and had fully recovered by the next time she was tested, five days later. MUK also had MTTSs of 6 dB at 40 kHz (2 min post-exposure, recovered within 6 min), and 10 dB at 30 kHz (2 min post-exposure, recovered within 17 min) after exposure to 20-kHz tones at 200 and 201 dB *re*: 1 μPa, respectively. The whale NOC also had an MTTS of 7 dB at 20 kHz 2 min after exposure to a 20-kHz tone at 200 dB *re*: 1 μPa. This shift increased to 9 dB 5 min after exposure, and to 12 dB 16 min post-exposure. NOC's threshold recovered to within 5 dB by the last recovery session of the day and was fully recovered by the next opportunity for testing three days later.

The dolphin BEN had a 6-dB MTTS at 30 kHz during experiment VI after exposure to a 20-kHz tone at 196 dB *re*: 1 μPa. This shift occurred 2 min post-exposure and recovered within 5 min. No threshold shifts were observed during experiments VII (3 kHz S1, 90 dB *re*: 1 μPa^2/Hz masking noise, maximum S1 of 201 dB *re*: 1 μPa) or experiment VIII (0.4 kHz S1, 95 dB *re*: 1 μPa^2/Hz masking noise, maximum S1 of 193 dB *re*: 1 μPa).

Table IV also provides the number of false alarms that occurred during the pre- and post-exposure thresholds estimated at the S2 frequency where MTTS was observed. The numbers are representative of the very low false alarm occurrences seen throughout baseline and MTTS test sessions. Generally, each threshold estimate (10 reversals) for a given S2 frequency was complete within an average of 30 S2 tone presentations. Usually two or fewer false alarms were committed during any threshold estimate. A total of 195 MTTS test sessions were conducted over the eight experiments.

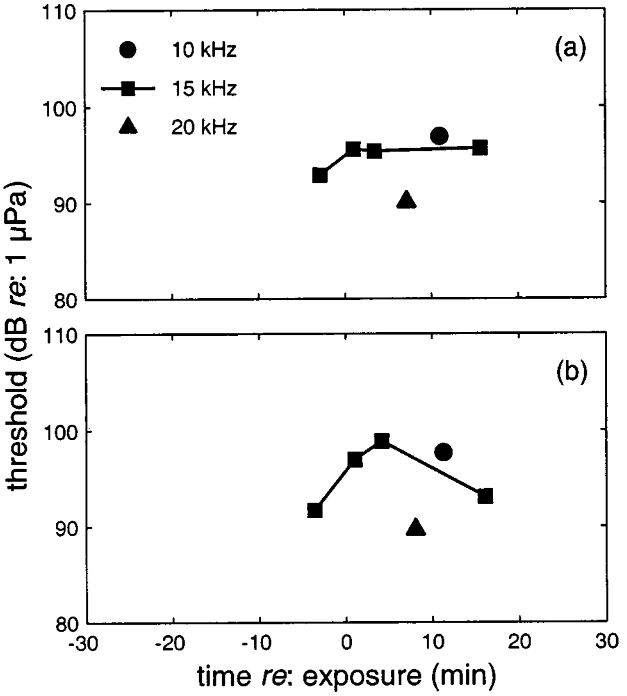

FIG. 5. Hearing thresholds measured from the dolphin BEN during experiment IV before and after exposure to 10-kHz tones at (a) 180 dB *re*:1 μPa (no MTTS) and (b) 192 dB *re*:1 μPa (7-dB MTTS at 15 kHz). Baseline thresholds were 97, 93, and 87 dB *re*:1 μPa at 10, 15, and 20 kHz, respectively.

Eleven of those sessions produced MTTSs (Table IV). In those 11 sessions, a total of 99 thresholds were estimated in preexposure, post-exposure, and recovery sessions combined. Three or more false alarms were committed in only 11 of 99 threshold estimates. Eight thresholds during which three or more false alarms were committed occurred during experiment V (BEN—three false alarms at 20- and 40-kHz preexposure to 181 dB; MUK—three false alarms at 30 kHz pre- and post-exposure to 200 dB, and at 30 kHz recovery to 201 dB; NOC—four false alarms at 40 kHz preexposure and three false alarms at 30 and 40 kHz post-exposure to 197 dB). The remaining three thresholds with three or greater false alarms occurred during experiment VIII (BEN—seven false alarms during preexposure at 600 Hz and three false alarms in two recovery sessions to 191 dB).

Figures 5 and 6 are some representative plots of masked hearing thresholds estimated during MTTS testing presented as a function of time relative to the fatiguing stimulus (time 0). Figures 5(a) and (b) show masked hearing thresholds measured from the dolphin BEN during experiment IV, before and after exposure to 10-kHz S1s at 180 and 192 dB *re*: 1 μPa, respectively. The abscissa is time relative to the exposure and the ordinate is the measured threshold. Baseline masked thresholds were 97, 93, and 87 dB *re*: 1 μPa at 10, 15, and 20 kHz, respectively. Figure 5(a) shows essentially flat thresholds at 15 kHz despite the fatiguing stimulus exposure at time zero. Figure 5(b) shows a 7-dB MTTS approximately 4 min after exposure and the eventual recovery, within approximately 16 min. For both Fig. 5(a) and (b), preexposure thresholds at 15 kHz and post-exposure thresholds at 10 and 20 kHz were within 3 dB of the baseline values. Note that the data for the S1 at 180 dB *re*: 1 μPa were chosen for comparison because this was the other occasion when 15-kHz thresholds were measured immediately before and after exposure with this subject during experiment IV (see Sec. I C 2).

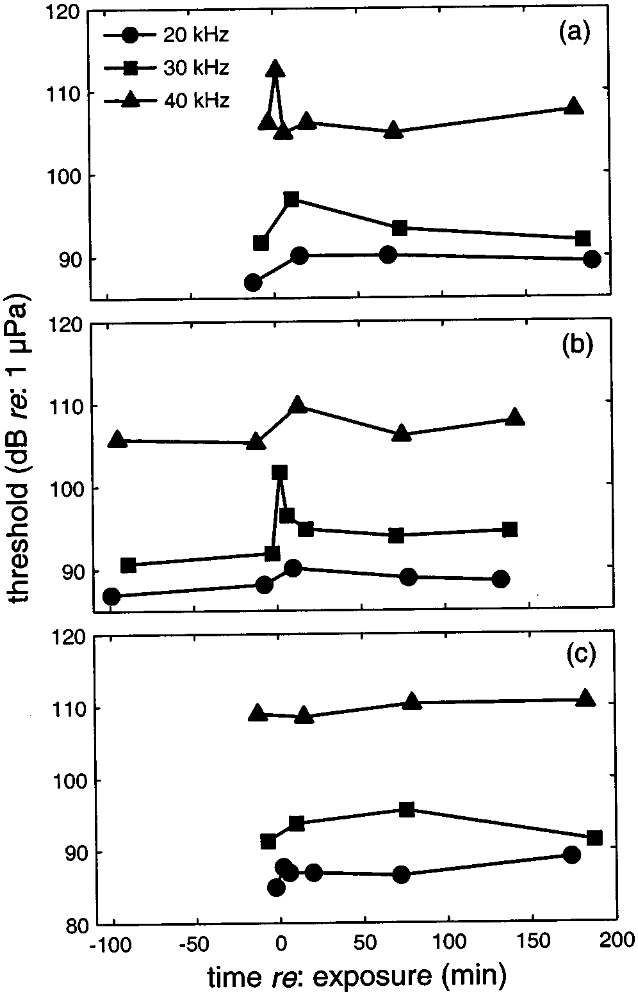

FIG. 6. Preexposure, post-exposure, and recovery thresholds measured for the whale MUK during experiment V. Exposures were to 20 kHz Sls at (a) 200 dB *re*:1 μPa (6-dB MTTS at 40 kHz), (b) 201 dB *re*:1 μPa (1-dB shift at 30 kHz), and (c) 200 dB *re*:1 μPa (no MTTS). Baseline thresholds were 87, 93, and 109 dB *re*:1 μPa at 20, 30, and 40 kHz, respectively.

Figure 6 shows preexposure, post-exposure, and recovery thresholds measured for the whale MUK during experiment V. As in Fig. 5, the abscissa is time relative to the exposure and the ordinate is the measure threshold. Figures 6(a), (b), and (c) show thresholds measured before and after exposure to 20-kHz S1s at 200, 201, and 200 dB *re*: 1 μPa, on three test days (the intended S1 level was 200 dB *re*: 1 μPa). Baseline masked thresholds were 87, 93, and 109 dB *re*: 1 μPa at 20, 30, and 40 kHz, respectively. Figure 6(a) shows a 6-dB MTTS at 40 kHz and Fig. 6(b) shows a 10-dB shift at 30 kHz. Both shifts were measured within 2 min after exposure and recovered within approximately 6–17 min. Recovery thresholds were within 3 dB of preexposure thresholds at all S2 frequencies. No MTTS is seen in Fig. 6(c)—all thresholds were within 4 dB of preexposure thresholds.

Figure 6 illustrates the sequence in which the S2 frequencies were tested: in Fig. 6(a), preexposure thresholds

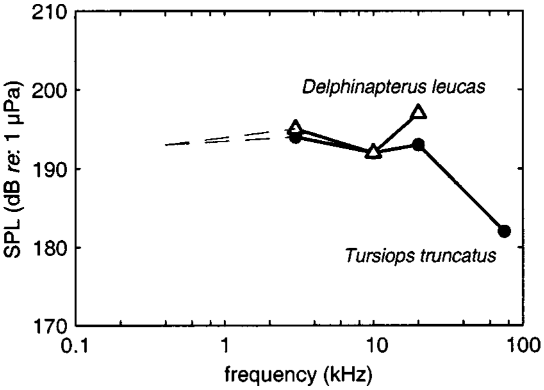

FIG. 7. Minimum fatiguing stimulus levels required to induce MTTS at each frequency, regardless of shift frequency or masking noise level. No MTTS was observed at 0.4 kHz at the highest level achieved, 193 dB *re*:1 μPa.

were measured in the order 20, 30, 40 kHz, then post-exposure thresholds were measured in the order 40, 40, 30, 20, 40 kHz, so that 40 kHz was tested immediately before and after exposure. Similarly, Figs. 6(b) and (c) show thresholds at 30 and 20 kHz, respectively, measured immediately before and after exposure. It is interesting to note that MTTSs (according to our criteria) were only observed in the thresholds measured immediately after exposure, while smaller (<6 dB) TSs appear to occur at some of the frequencies tested later [e.g., 30 kHz in Fig. 6(a) and 40 kHz in Fig. 6(b)]. Higher TSs may have been seen if these frequencies were tested sooner; however, there appear to be no TSs at 20 kHz even when it was tested immediately after exposure. Also of note is the 6-dB threshold shift at 40 kHz, compared to 10 dB at 30 kHz, and no shift at 20 kHz, even though MUK appeared to have elevated baseline and preexposure hearing thresholds at 40 kHz.

Figure 7 shows the minimum fatiguing stimulus levels that produced MTTS at each of the S1 frequencies for both *Tursiops* (filled circles) and *Delphinapterus* (open triangles). These data are pooled at each S1 frequency regardless of the shift frequency or masking noise level. The dashed line indicates that no MTTSs were observed after exposure to the 0.4-kHz fatiguing stimulus at the highest level achieved, 193 dB *re*: 1 μPa.

B. Behavioral reactions

As the S1 level gradually increased each day during MTTS testing, animals began to exhibit alterations in their trained behaviors. In this report we define a behavioral alteration as a deviation from an animal's trained behaviors as a result of exposure to intense sound. This is in contrast to field observations, where the reaction of naïve animals to novel stimuli is often difficult to interpret; a behavioral reaction in these circumstances may occur at levels corresponding to the animal's detection of the sound, rather than a level which may produce TTS (Green *et al.*, 1994). In the present study, changes began at levels below those that induced MTTS and continued as S1 signals increased to MTTS levels. Of the 195 MTTS test sequences, behavioral alterations were recorded for 129 of them.

Some of the most dramatic behavioral alterations were observed in the seconds immediately following exposure to the louder S1 signal and can be described as a general disorientation. The calm, smooth departure from the S1 station in the direction of the S2 station was replaced with an abrupt, quick departure from S1 usually in the direction opposite S2. Dolphins sometimes swam erratically around the test enclosure and performed tail slaps and jaw pops (Connor and Smolker, 1996; Finneran *et al.*, 2000; Smolker and Richards, 1988). Whales quickly backed off the S1 station and also circled the enclosure, often vocalizing as they swam. The male subjects often replied to the S1 with series of pulse bursts. In a more aggressive display, one dolphin (NEM at 3 kHz, 194 dB *re*: 1 μPa) attacked the S1 station after hearing the louder S1 signal. Several animals seemed not to recognize the loudest S1 signals as the tonal cue to go to S2 and, after having swum around the enclosure, voluntarily returned to the S1 station and required a second S1 signal (at 141 dB *re*: 1 μPa) before they would proceed to the S2 station.

The most apparent consequence of these behavioral alterations was an increase in the travel time between the S1 and S2 stations. We looked at a random sample of 15 S1–S2 time intervals over a minimum of three test days for each animal during each experiment ($n=420$) to determine the average time it took to swim between the S1 and S2 stations during baseline testing. The average S1–S2 time was 14 s (*s.d.* 2.4). We looked at the S1–S2 travel time in the dive during which the fatiguing stimulus was presented for 125 of the MTTS sequences in which altered behavior was observed (four of the times were not available). At the higher S1 levels as animals began to deviate from their trained behaviors the average S1–S2 travel time increased to 28 s (*s.d.* 42.4). A linear regression was performed on the S1–S2 times sampled during baseline and immediately following the fatiguing stimulus in the altered behavior sequences during MTTS testing ($n=545$). S1–S2 time intervals were significantly higher immediately after exposure to the louder S1 levels than during baseline testing [$F(1{,}544)=45.89$, $p<0.001$]. Figure 8 shows the mean S1–S2 time interval for each animal over the eight experiments both during baseline and during the dive immediately following the fatiguing stimulus for the MTTS test sequences in which altered behavior was observed.

A fairly common example of a behavioral alteration was the reluctance to return to the S1 station for dives following the fatiguing stimulus. This apparent reluctance was exhibited in several ways: (1) an animal might ignore the trainer's cue to go to the S1 station and instead proceed directly to the S2 station for hearing tests; (2) an animal might not station properly on the S1 biteplate (e.g., biting only the outermost edge or at an angle); or (3) an animal might leave the S1 station early before actually hearing the S1 signal.

Another common behavioral alteration was that of ''breaking station'' or leaving the S2 station prematurely (not under the direction of a trainer). Breaking station after a louder S1 signal usually occurred after only one or two trials and was suspected to be caused by a hypersensitivity to tones following the louder signal. After several instances in which animals broke station at S2 following louder S1 signals, we

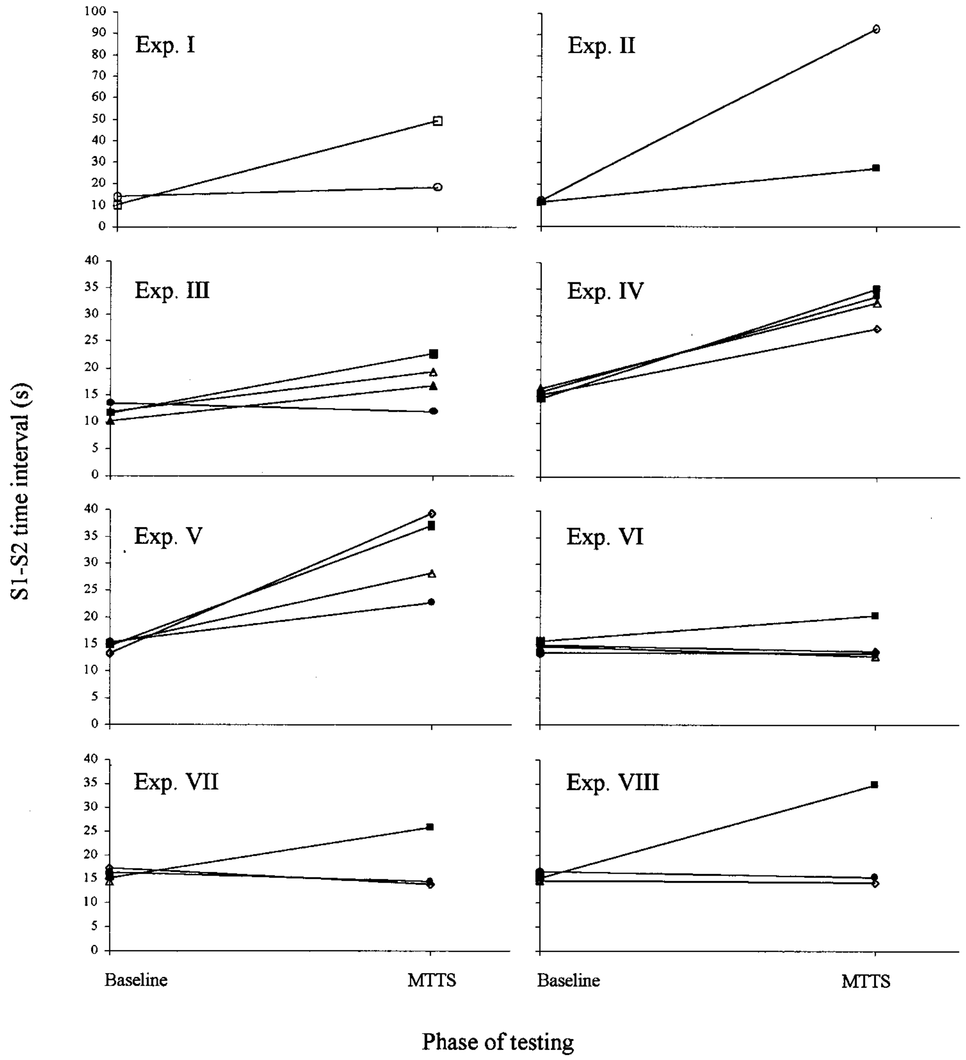

FIG. 8. The mean S1–S2 time interval for each animal over the eight experiments both during baseline and during the dive in which the fatiguing stimulus was presented for MTTS test sequences in which altered behavior was observed (open square: MUU; open circle: TOD; closed square: NEM; open triangle: MUK; closed triangle: APR; closed circle: NOC; open diamond: BEN).

began initiating S2 tone presentation at levels 4–6 dB below threshold for trials immediately following the louder S1. Instances of breaking station at S2 were greatly diminished. Further support for a hypersensitivity effect as a result of exposure to louder signals was evidenced by several cases of negative TTS, i.e., lower post-exposure thresholds (Hodge and McCommons, 1966; Marshall and Brandt, 1974; Silbiger, 1965). It has been suggested that negative TTS may be a good predictor for levels that are approaching those that elicit TTS. In this study, both whales and dolphins often experienced slight increases in hearing sensitivity, decreases in threshold, following louder S1s. On most occasions, the improvement in sensitivity was still within the ''normal'' threshold variation of 3–4 dB. On one occasion the whale NOC had a 7-dB increase in hearing sensitivity at 6 kHz after exposure to a 3-kHz tone at 193 dB *re*: 1 μPa. This negative shift occurred 2 min post-exposure and recovered within 14 min.

Figure 9 shows the minimum fatiguing stimulus levels at which the dolphins and white whales began to display altered behavior at each S1 frequency. These levels ranged from 178–193 dB *re*: 1 μPa. In general, the white whales tolerated louder levels better than the dolphins and were more subdued in their behavioral reactions.

III. DISCUSSION

This report presents the first direct evidence of TTS in odontocetes. Using 1-s signals between 3 and 75 kHz, MTTSs between 6 and 17 dB were induced in dolphins and white whales. Because of the limited amount of data and intersubject variability, pooling the data (regardless of shift

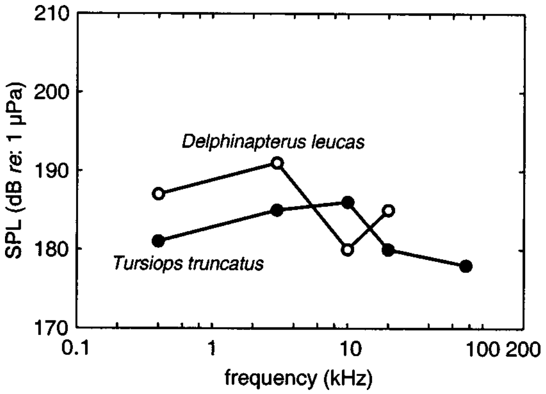

FIG. 9. Minimum fatiguing stimulus levels required to produce behavioral alterations at each frequency.

frequency or masking noise level) and reporting the minimum S1 levels that induced MTTS seems to be the most attractive way of presenting the data. These data are shown in Fig. 7. The levels of fatiguing stimuli necessary to induce MTTSs in the test subjects were consistently within the range of 192 to 201 dB *re*: 1 μPa. The exceptions occurred at the 75-kHz fatiguing stimulus frequency, where one dolphin exhibited an MTTS after exposure at 182 dB *re*: 1 μPa and the other dolphin did not show any shift after exposure to a maximum level of 194 dB *re*: 1 μPa, and at 0.4 kHz, where no subjects exhibited shifts after exposure to maximum levels of 193 dB *re*: 1 μPa. The shifts that were observed most often occurred at frequencies above that of the fatiguing stimulus. The single occasion on which a negative MTTS was observed occurred at an S1 level just below that which caused a positive MTTS in the same animal (NOC, 3-kHz fatiguing stimuli of 193 dB *re*: 1 μPa and 195 dB *re*: 1 μPa, respectively). At the conclusion of the study all thresholds were within 3 dB of baseline/preexposure values.

Hearing thresholds were measured using a unique method (based on the MFR) that featured a vocal response emitted by the test subjects. The modified MFR employed in this study allowed thresholds to be very quickly measured from the test subjects following exposure to the fatiguing stimulus. The first threshold estimate following exposure was routinely obtained within 1–3 min of the exposure, e.g., Figs. 5 and 6. This is particularly important in studies of small TSs, since recovery from small TTSs may be rapid (e.g., Kryter, 1994).

As seen in Table III, four of the subjects (BEN, NEM, MUK, and NOC) were used in the majority of the experiments. Ideally, naïve subjects of varying age and gender would be used in every experiment; however, availability of trained marine mammals for studies such as this precluded this as an option, a problem inherent to most marine mammal studies. Furthermore, the difficulty of maintaining trained behaviors in the face of aversive stimulus presentation further restricted our subject pool. Ultimately, we were limited not only by which animals were available to us, but also by which animals would continue to do the task. A related difficulty is that individual differences between subjects is especially pronounced when working with a small sample size. With the exception of testing at 3 and 20 kHz, these results are based on an *n* of 2 for each species. This fact makes it difficult to establish absolute levels that will cause a reliable TS in these marine mammals; these data are most useful as a basis to estimate maximum exposure levels below which no large TTSs are likely to occur.

Studies of TTS in humans (e.g., Humes, 1980; Parker *et al.*, 1976) have shown that the presence of masking noise results in elevated hearing thresholds and decreases the amount of TTS observed. We employed masking noise out of necessity: the test location in San Diego Bay has rather high, and variable, ambient noise. There are currently no data concerning the relationship between masking noise and TTS in cetaceans. Preexposure hearing thresholds for the test subjects ranged from approximately 20–40 dB above those measured in *Tursiops* and *Delphinapterus* in quiet conditions, thus we must acknowledge that larger shifts may have been seen without the masking noise. No MTTSs were seen during repeated testing at 3 kHz with a higher masking noise level (experiment VII), which also seems to support this statement. The limited data from this study do not support additional conclusions. A more systematic effort with a larger sample size is likely needed to fully explore the effects of masking noise on TTS in cetaceans.

The number of false alarms committed throughout these experiments was low, indicating that the subjects were very conservative. The intent of this study was not to establish absolute thresholds or to compare these thresholds to those obtained elsewhere. More important to this study was that the thresholds be stable and repeatable and that the number of false alarms committed be consistent throughout the study. The fact that the number of false alarms committed post-exposure showed little variability to those committed during preexposure eliminates a change in response bias as a confound for a change in hearing thresholds. Of course it is possible that the occasions on which there were no false alarms committed in either pre- or post-exposure session (see Table IV) could mask a change in response bias, both being arbitrarily high, although this seems unlikely.

Deviations from the animals' trained behaviors were observed at S1 levels approaching those that produced MTTS. These behaviors continued at S1 levels which produced MTTS; however, this may have been due to order effects. The lowest SPLs at which these altered behaviors were observed ranged from 178–193 dB *re*: 1 μPa for the dolphins and 180–196 dB *re*: 1 μPa for the white whales. The abundance of baseline data and the animal's previous test history were paramount in establishing a standard by which ‘‘altered'' behaviors were registered. The trainers' familiarity with the test subjects and the degree of close observation and recording made it possible to not only document behavioral changes, but to relate them directly to the presence of the acoustic signal. Each session was videotaped both underwater and in air. Movements, swimming directions, and postures were recorded during each baseline and MTTS session. The interval it took the animal to swim between the S1 and S2 underwater stations was timed. Animal acoustic responses just after the S1 were noted as well.

One of the fundamental goals in studying TTS in marine mammals is the identification of acoustic stimulus parameters that affect hearing loss. The peak pressure, total energy, frequency content, rise time, and duration may all be significant with regard to auditory fatigue and TTS, yet the relative importance of and interaction between these properties is unknown. TTS research may often be forced to strike a balance between employing acoustic signals representative of those used operationally by military or industrial sources (which have immediate application to the establishment of safe noise exposure guidelines), or idealized sources that allow one to better explore the effects of the various parameters noted above. For this study, we used 1-s tonal signals at frequencies of 0.4, 3, 10, 20, and 75 kHz. These frequencies were selected in part for their prevalence in military sonars and other anthropogenic acoustic sources. The fatiguing stimulus duration was fixed at 1 s. This duration had the advantage of being short enough that the animal's position was essentially constant throughout the exposure, thus making estimates of the received level particularly accurate. The disadvantage of the S1 signal duration was that relatively high SPLs were required to produce TTS. The high SPL and very short rise time may have contributed to the behavioral alterations (producing a startle or annoyance response) at the higher S1 levels. Future studies employing longer tone durations should allow TTS to be observed at lower stimulus levels, where behavioral reactions may not be as pronounced; however, longer tone durations produce additional complexities in estimating the received level for a moving subject, especially if the animal surfaces for air. Even brief interruptions in the noise exposure may allow the ears to recover and decrease the amount of TTS observed. Future studies of TTS in marine mammals should also employ impulsive sources such as those commonly encountered in marine seismic surveys and military testing.

IV. CONCLUSIONS

A behavioral response paradigm was used to measure masked underwater hearing thresholds in five bottlenose dolphins and two white whales before and immediately after exposure to intense 1-s tones at frequencies of 0.4, 3, 10, 20, and 75 kHz. The levels of fatiguing stimuli necessary to induce MTTSs in the test subjects were generally within the range of 192 to 201 dB *re*: 1 μPa. The exceptions occurred at the 75-kHz fatiguing stimulus frequency, where one dolphin exhibited an MTTS after exposure at 182 dB *re*: 1 μPa and the other dolphin did not show any shift after exposure to maximum levels of 193 dB *re*: 1 μPa, and at 0.4 kHz, where no subjects exhibited shifts after exposure to a maximum level of 193 dB *re*: 1 μPa. The shifts that were observed most often occurred at frequencies above that of the fatiguing stimulus. Dolphins began to exhibit altered behavior at levels of 178–193 dB *re*: 1 μPa and white whales displayed altered behavior at 180–196 dB *re*: 1 μPa and above. At the conclusion of the study all thresholds were at baseline values. These data confirm that cetaceans are susceptible to TTS and that small levels of TTS may be fully recovered.

ACKNOWLEDGMENTS

We thank Tricia Kamolnick, Jennifer Carr, Monica Chaplin, Lauryn Crosthwaite, Jack Gonzales, and Mark Todd for their assistance with animal training and other technical aspects of the project. Software for computer control of stimuli and recording of animal responses was developed by William Root and was modified by Wesley Elsberry for this project. Tim McBride and Cy Frazier of Program Executive Officer for Undersea Warfare [PEO(USW)], Dr. Frank Stone of N45, and Dr. Robert Gisiner of Office of Naval Research (ONR) gave us frequent encouragement during the work and provided helpful technical review at various stages. Stacie Andersen, Kim De Paul, Tom Fong, and Michelle Reddy were also helpful in facilitating this work. A custom-built noise generator was provided by Dr. Whitlow Au. Funding was provided by PEO(USW), Naval Air Systems Command (NAVAIR), Major Range Test Facility Base (MRTFB), and ONR. James Finneran was supported by a National Research Council Research Associateship.

Awbrey, F. T., Thomas, J. A., and Kastelein, R. A. (**1988**). ''Low-frequency underwater hearing sensitivity in belugas, *Delphinapterus leucas*,'' J. Acoust. Soc. Am. **84**(6), 2273–2275.

Connor, R. C., and Smolker, R. A. (**1996**). '' 'Pop' goes the dolphin: A vocalization male bottlenose dolphins produce during consortships,'' Behaviour **133**, 643–662.

Cornsweet, T. N. (**1962**). ''The staircase method in psychophysics,'' Am. J. Psychol. **75**, 485–491.

Dancer, A. L., Henderson, D., Salvi, R. J., and Hamernik, R. P., eds. (**1992**). *Noise-Induced Hearing Loss* (Mosby Year Book, St. Louis, MO).

Egan, J. P., Greenberg, G. Z., and Schulman, A. I. (**1961**). ''Operating characteristics, signal detectability, and the method of free response,'' J. Acoust. Soc. Am. **33**, 993–1007.

Fay, R. R. (**1988**). *Hearing in Vertebrates: A Psychophysics Databook* (Hill-Fay, Winnetka, IL).

Finneran, J. J., Oliver, C. W., Schaefer, K. M., and Ridgway, S. H. (**2000**). ''Source levels and estimated yellowfin tuna (*Thunnus albacares*) detection ranges for dolphin jaw pops, breaches, and tail slaps,'' J. Acoust. Soc. Am. **107**, 649–656.

Green, D. M. (**1976**). *An Introduction to Hearing* (Lawrence Erlbaum, New Jersey).

Green, D. M., DeFerrari, H. A., McFadden, D., Pearse, J. S., Popper, A. N., Richardson, W. J., Ridgway, S. H., and Tyack, P. L. (**1994**). *Low-Frequency Sound and Marine Mammals: Current Knowledge and Research Needs* (National Academy, Washington, D.C.).

Hodge, D. C., and McCommons, R. B. (**1966**). ''Reliability of TTS from impulse-noise exposure,'' J. Acoust. Soc. Am. **40**(4), 839–846.

Humes, L. E. (**1980**). ''Temporary threshold shift for masked pure tones,'' Audiology **19**, 335–345.

Johnson, C. S. (**1967**). ''Sound detection thresholds in marine mammals,'' in *Marine Bio-Acoustics*, edited by W. N. Tavolga (Pergamon, New York), Vol. 2, pp. 247–260.

Johnson, C. S., McManus, M. W., and Skaar, D. (**1989**). ''Masked tonal hearing thresholds in the beluga whale,'' J. Acoust. Soc. Am. **85**(6), 2651–2654.

Kryter, K. D. (**1994**). *The Handbook of Hearing and the Effects of Noise* (Academic, San Diego).

Ljungblad, D. K., Scoggins, P. D., and Gilmartin, W. G. (**1982**). ''Auditory thresholds of a captive Eastern Pacific bottle-nosed dolphin, *Tursiops spp.*,'' J. Acoust. Soc. Am. **72**(6), 1726–1729.

Marshall, L., and Brandt, J. F. (**1974**). ''Temporary threshold shift from a toy cap gun,'' J. Speech Hear Disord. **39**(2), 163–168.

Nachtigall, P. E. (**1986**). ''Vision, audition, and chemoreception in dolphins and other marine mammals,'' in *Dolphin Cognition and Behavior: A Comparative Approach*, edited by R. J. Schusterman, J. A. Thomas, and F. G. Wood (Lawrence Erlbaum, Hillsdale, NJ), pp. 79–113.

Norris, K. S. (**1968**). ''The evolution of acoustic mechanisms in odontocete cetaceans,'' in *Evolution and Environment*, edited by E. T. Drake (Yale University, Connecticut), pp. 298–323.

Parker, D. E., Tubbs, R. L., Johnston, P. A., and Johnston, L. S. (**1976**). ''Influence of auditory fatigue on masked pure-tone thresholds,'' J. Acoust. Soc. Am. **60**, 881–885.

Richardson, W. J., Greene, Jr., C. R., Malme, C. I., and Thomson, D. H. (**1995**). *Marine Mammals and Noise* (Academic, San Diego).

Ridgway, S. H. (**1997**). ''Who are the whales?,'' Bioacoustics **8**, 3–20.

Ridgway, S. H., and Carder, D. A. (**1997**). ''Hearing deficits measured in some *Tursiops truncatus*, and discovery of a deaf/mute dolphin,'' J. Acoust. Soc. Am. **101**(1), 590–594.

Ridgway, S. H., Carder, D. A., Smith, R. R., Kamolnick, T., Schlundt, C. E., and Elsberry, W. R. (**1997**). ''Behavioral responses and temporary shift in masked hearing threshold of bottlenose dolphins, *Tursiops truncatus*, to 1-second tones of 141 to 201 dB *re* 1 μPa,'' Tech. Rep. No. 1751, Naval Command, Control and Ocean Surveillance Center, RDT&E Division, San Diego, CA.

Rosenberger, P. B. (**1970**). ''Response-adjusting stimulus intensity,'' in *Animal Psychophysics: The Design and Conduct of Sensory Experiments*, edited by W. C. Stebbins (Appleton-Century-Crofts, New York), pp. 161–184.

Silbiger, H. R. (**1965**). ''Temporary threshold shifts due to single clicks,'' J. Acoust. Soc. Am. **38**, 937–938.

Smolker, R., and Richards, A. (**1988**). ''Loud sounds during feeding in Indian Ocean bottlenose dolphins,'' in *Animal Sonar: Processes and Performance*, edited by P. E. Nachtigall and P. W. B. Moore (Plenum, New York), pp. 703–706.

Watkins, W. A., and Wartzok, D. (**1985**). ''Sensory biophysics of marine mammals,'' Mar. Mamm. Sci. **1**(3), 219–260.

White, M. J., Jr., Norris, J., Ljungblad, D., Baron, K., and di Sciara, G. (**1978**). ''Auditory thresholds of two beluga whales (*Delphinapterus leucas*),'' Hubbs/Sea World Research Institute Tech. Rep. 78-108.