Discrimination of complex synthetic echoes by an echolocating bottlenose dolphin

David A. Helweg[a)] and Patrick W. Moore
Space and Naval Warfare Systems Center, 53560 Hull Street, San Diego, California 92152

Lois A. Dankiewicz and Justine M. Zafran
Science Applications International Corp., 3990 Old Town Avenue, Suite 208A, San Diego, California 92110

Randall L. Brill
Space and Naval Warfare Systems Center, 53560 Hull Street, San Diego, California 92152

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Bottlenose dolphins (*Tursiops truncatus*) detect and discriminate underwater objects by interrogating the environment with their native echolocation capabilities. Study of dolphins' ability to detect complex (multihighlight) signals in noise suggest echolocation object detection using an approximate 265-μs energy integration time window sensitive to the echo region of highest energy or containing the highlight with highest energy. Backscatter from many real objects contains multiple highlights, distributed over multiple integration windows and with varying amplitude relationships. This study used synthetic echoes with complex highlight structures to test whether high-amplitude initial highlights would interfere with discrimination of low-amplitude trailing highlights. A dolphin was trained to discriminate two-highlight synthetic echoes using differences in the center frequencies of the second highlights. The energy ratio (ΔdB) and the timing relationship (ΔT) between the first and second highlights were manipulated. An iso-sensitivity function was derived using a factorial design testing ΔdB at -10, -15, -20, and -25 dB and ΔT at 10, 20, 40, and 80 μs. The results suggest that the animal processed multiple echo highlights as separable analyzable features in the discrimination task, perhaps perceived through differences in spectral rippling across the duration of the echoes.
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I. INTRODUCTION

Bottlenose dolphins (*Tursiops truncatus*) detect and discriminate underwater objects by interrogating their environment with their native echolocation capabilities. *Tursiops* echolocation signals are clicks approximately 50–100 μs in duration, with peak frequencies typically ranging between 30–100 kHz and fractional bandwidths between 10%–90% of peak frequency (Au, 1980; Houser *et al.*, 1999). Although the outgoing echolocation signals are brief, echoes reflected from objects can be several milliseconds in duration and contain rich structure that encodes information about the object's shape, orientation, and internal composition (e.g., Chapman, 1971; Gaunaurd *et al.*, 1998; Neubauer, 1986; Urick, 1983). The diversity of complex time and frequency-domain structures includes great variability in the amplitude ratio of multiple echo components, called ''highlights'' or ''glints.'' The variance in echo structures between objects, and within objects in aspect-dependent shapes, immediately raises questions of how dolphins exploit the complex timing and relative amplitude of highlight structure to detect and identify objects.

Study of the dolphins' ability to detect multihighlight signals in noise has revealed a temporal integration time of approximately 265 μs (Au *et al.*, 1988; Moore *et al.*, 1984; Vel'min and Dubrovskiy, 1976). The energy of echo highlights appears to be summed within this window and contributes to signal detection, whereas stimulus highlights separated by more than this interval do not contribute to detection performance. Dolphins appeared to detect echoes using a 265-μs window sensitive to the echo region or highlight of highest energy, and low-amplitude echo highlights spaced more than a few hundred microseconds apart did not contribute to detection performance (Au *et al.*, 1988).

However, many large objects with complex structures generate echoes with highlight structure spaced over several milliseconds (e.g., Chapman, 1971; Gaunaurd *et al.*, 1998; Neubauer, 1986; Urick, 1983). For multiple highlights that fall within a single integration window, spectral models can describe discrimination performance. For example, Johnson and colleagues (1988) demonstrated that a dolphin could discriminate a signal with a high-amplitude followed by a low-amplitude highlight from one consisting of a low-amplitude followed by a high-amplitude highlight, even when both highlights appeared within the same putative integration window. Au and Pawloski (1992) demonstrated that a dolphin could discriminate metal cylinders with differences in the wall thickness. Inspection of cylinder echoes revealed multiple highlights within a single integration window, with interhighlight intervals proportional to wall thickness (in tens of μs). These studies indicate that the animal was not simply integrating over the integration window. Instead, spectral

[a)]Electronic mail: david_helweg@usgs.gov

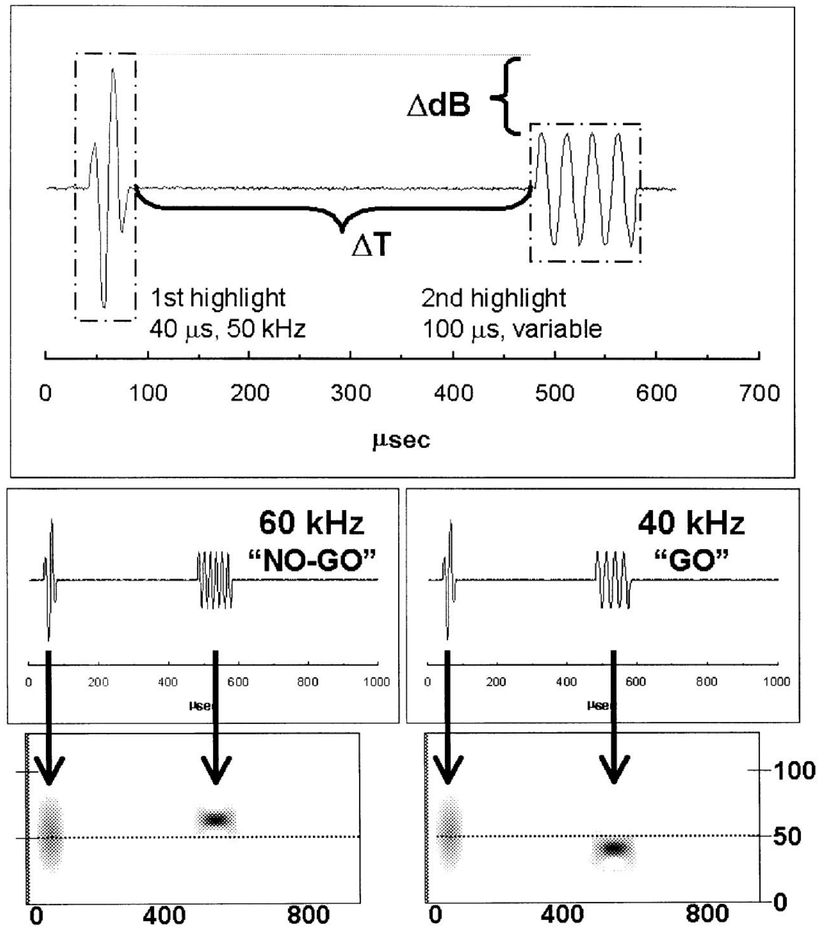

FIG. 1. The synthetic echo stimuli. The top panel illustrates the relationship between the stimulus waveform components and independent variables (ΔdB, ΔT). In this figure, ΔT is 400 μs and ΔdB (energy flux) is zero. The center panels show the ''NO-GO'' waveform on the left and the ''GO'' waveform on the right. They differ only in the frequency of the second highlight, which was 60 kHz for the NO-GO stimulus and 40 kHz for the GO stimulus. The bottom panels are Gabor spectrograms of the stimuli, with frequency on the vertical axis and time aligned with the waveforms.

characteristics generated by the amplitude and timing of multiple highlights were possible acoustic features that may have controlled the dolphin's performance. Johnson *et al.* (1988) demonstrated that the temporal order of click pairs could be discriminated by relative timing of spectral rippling, which was revealed using short-time Fourier transform of the signals. Similarly, Au and Pawloski (1992) suggested that the cylinders of different wall thickness could be discriminated based on differences in spectral rippling within the temporal integration time. Likewise, Moore *et al.* (1984) conducted a backward-masking experiment to replicate the work of Vel'min and Dubrovskiy (1976), and reported results which appeared to support the notion of the critical interval. They suggested, however, that time separation pitch (TSP) might be the underlying mechanism instead of a ''critical interval'' in dolphin hearing. Thus, for multiple highlights that fall within a single integration window, spectral models can describe discrimination performance.

In contrast to within-265-μs mechanisms, the work by Au *et al.* (1988) raises the question of the degree to which dolphin auditory processes are sensitive to information contained in low-amplitude highlights that lie in different temporal integration windows. We investigated this question using synthetic echo stimuli and a computerized echo generator. The use of synthetic echoes allowed absolute experimental control over the amplitude, timing, and spectral relationships among multiple highlights within the synthetic echoes. The work by Au *et al.* (1988) suggests that dolphins may not attend to trailing highlights more than 6 dB below a larger highlight if the time separation is more than about 265 μs. Thus, we tested the dolphin's ability to discriminate two-highlight stimuli differing in the spectra of the trailing highlight, while manipulating the time separation and amplitude ratio of the two highlights.

II. METHODS

A. Subject

The subject was CAS, a 16-year-old female Atlantic bottlenose dolphin housed with several other dolphins in a floating pen complex at the Space and Naval Warfare Systems Center facility in San Diego Bay. CAS had over 5 years of experience as a pyschoacoustical research subject coming into the current study. Based on routine assessments, her hearing was considered normal (Brill *et al.*, 2001).

B. Synthetic echo stimuli

A pair of ''synthetic echoes'' was designed to test the research hypotheses. Sample waveforms and Gabor spectrograms are presented in Fig. 1. The waveforms consisted of two highlights. The initial highlight of both stimuli was a 40-μs 50-kHz sinusoid passed through a triangular window. The second highlight was 100 μs in duration, at 60 kHz for the ''NO-GO'' stimulus and 40 kHz for the ''GO'' stimulus (''NO-GO'' and ''GO'' are behavioral response categories and are described below). The 20-kHz difference in frequency was substantial compared with frequency limens reported for bottlenose dolphins in a wide range of paradigms (Jacobs, 1972; Thompson and Herman, 1975); thus, the stimuli were discriminable based on the frequency of the second highlight alone. To control for the effects of ambient noise and to provide a uniform noise background across the frequency range of the test stimuli, the noise floor was controlled by adding 95 dB *re*: 1 Vrms of white noise to the stimuli.

Two variables were manipulated. One, manipulation of the energy flux ratio of the second to the first highlight, permitted evaluation of discrimination performance as the ratio of the two stimulus highlights increased. The relative energy ratio was termed ''ΔdB,'' use of energy flux was based on the assumption that dolphin echo detection is energy based rather than pressure based (Au *et al.*, 1988). The amplitude of the first highlight (50 kHz) was held constant at 135 dB *re*: 1 Vrms. The amplitude of the second highlight (40 or 60 kHz) was manipulated to create the specified ΔdB. A ΔdB of zero meant that the energy flux of the initial highlight was equal to the energy flux of the second highlight. As the amplitude of the second highlight was experimentally decreased, the ΔdB value became more negative. Thus, a stimulus with a ΔdB of -10 dB would have a higher-amplitude second highlight than a stimulus with ΔdB of -20 dB. The ΔdB of the NO-GO and GO stimuli were equated; thus, any change made to the NO-GO stimulus also was applied to the GO stimulus and vice versa. This eliminated energy cues that may have confounded the dolphin's second-highlight frequency discrimination performance if the highlights were summed. Again, note that the ΔdB refers to the ratio of the energy flux of the first and second highlights *within each synthetic echo*, not an amplitude relationship between the GO and NO-GO stimuli.

The second variable that was manipulated was the timing relationship between the initial and second highlights (ΔT). Manipulation of ΔT permitted evaluation of discrimination performance around the 265-μs temporal integration time (Moore *et al.*, 1984; Vel'min and Dubrovskiy, 1976). ΔT ranged from 10 to 400 μs. The initial highlight was 40 μs in duration, and the second highlight was 100 μs in duration. Thus, both highlights were inside the 265-μs temporal energy integration window when ΔT was set to $\leqslant$125 μs. Any ΔT change made to the NO-GO stimulus also was applied to the GO stimulus and visa-versa.

C. Apparatus

1. Digital synthetic echo system

A synthetic echo system (SES) was constructed to detect outgoing echolocation clicks and transmit a single stimulus waveform per detected click. The SES, graphic user interface, data collection parameters, and trial scheduling information were controlled by a LABVIEW Virtual Instrument running a National Instruments PCI MIO-16E-1 multifunction board hosted on a Pentium PC. The digital synthetic echo was generated prior to the start of each trial, mixed with white noise, and stored in RAM. Information available to the dolphin was held constant by permitting only 20 synthetic echoes per trial, regardless of how many clicks the dolphin emitted.

CAS was trained to position her head in a hoop 1 meter below the surface. An acoustically opaque screen (sheet PVC covered with closed-cell neoprene) was placed between the dolphin and the echo projector, which prevented CAS from echolocating the apparatus until the screen was removed. At the start of a trial, the screen was raised. Outgoing echolocation clicks were detected using a Reson TC4013 omnidirectional broadband hydrophone placed 0.5 m from the dolphin's melon. The click channel was bandpass filtered from 16–200 kHz with 40 dB of gain by a DL Electronics 4302 filter/amplifier and cabled to the analog input of the MIO board. When the click exceeded 170 dB *re*: 1 μPa, a digital trigger was sent to the SES software. The trigger generated analog output of a single synthetic echo stored in RAM on board the MIO board. Thus, one echo was projected per click emitted by the dolphin. A target range of 14 m was simulated using a delay of 18 ms between reception of an echolocation click trigger and analog output of the synthetic echo. The synthetic echo was bandpass filtered from 20–100 kHz with 40 dB of gain by a DL Electronics 4302 filter/amplifier and projected to the dolphin with an International Transducer Corporation 5446 transducer located 1.4 m from the dolphin. The digital waveforms were matched to the transmit response of the ITC 5446. Multipath echoes were prevented from reaching the dolphin using a floating horsehair mat placed just below the water surface at the surface reflection point. Prior to data collection, the system was calibrated by projecting synthetic dolphin clicks through the ITC 5446 and measuring received synthetic echoes with a calibrated ITC 6030 omnidirectional hydrophone mounted in the dolphin's stationing hoop.

D. Threshold estimation methodology

Data were collected using two methods. In phase one, the ΔdB threshold was measured using an up–down staircase method of threshold titration similar to that used by Moore and Schusterman (1987). For phase two, ΔdB was held constant at 75%-correct level, and the boundaries of ΔT were measured using a modified method of constants (Green and Swets, 1966). Finally, in phase three ΔdB and ΔT were jointly manipulated in a 4×4 factorial design using the modified method of constants.

1. Titration paradigm (phase one)

A standard titration method (Green and Swets, 1966) was used to evaluate the ΔdB threshold—the largest ΔdB that the dolphin would tolerate. The amplitude of the initial highlight was held constant at 135 dB *re*: 1 μPa. At the start of each session, ΔdB was set well above the subject's previous threshold (ΔdB was proportional to the energy in the second highlight; thus, more positive values of ΔdB resulted in higher second-highlight amplitudes). After every correct response the ΔdB was decreased by 2 dB, thereby driving the amplitude of the second highlight down (recall that any given ΔdB setting was applied to both ''NO-GO'' and ''GO'' stimuli). Once the dolphin made an error, the first reversal was said to have occurred and the ΔdB was increased by 1 dB. ΔdB were increased in 1-dB steps until the dolphin produced a correct response, the second reversal. The ΔdB were then decreased in 1-dB steps until she produced another error, the third reversal. The session was continued until ten reversals were elicited. The ΔdB threshold was estimated as the average of the values at the ten reversals; thus, each session yielded one threshold estimate. After five training sessions, ΔdB titration sessions were conducted until thresholds within 3 dB were reached on two successive sessions.

2. Method of constants paradigm

Phase two and three testing was accomplished using the method of constant stimuli (Green and Swets, 1966). Each session consisted of a block of ten warm-up trials, followed by four ten-trial test blocks. When practicable, sessions also were terminated with a set of cool-down trials.

First, ΔT was manipulated while holding ΔdB constant at the 75%-correct choice level from the phase one data. This value was selected to allow CAS to demonstrate either increased or decreased choice performance as ΔT was manipulated, while providing a ΔdB level that would assure a good rate of reinforcement. A running estimate of percent correct was calculated for each session using a ten-trial sliding window, and the 75%-correct point(s) were tabulated. The median and semi-interquartile range were derived (Blalock, 1979), and ΔdB was set to the third quartile of the pooled 75%-correct choice data. A set of six ΔT values was tested per session. The dolphin's performance was measured as percent correct for each combination of ΔdB and ΔT.

In the last phase of testing, ΔT and ΔdB were manipulated in a factorial design using ranges for ΔT and ΔdB determined in the first two phases. With $4\Delta T \times 4$ ΔdB levels in the factorial design matrix, and four ten-trial blocks of data per session, four sessions were required to generate one ten-trial block for each level in the 4×4 matrix. Order was counterbalanced across the four sessions. Thus, 28 sessions were run in order to collect seven ten-trial blocks of data for each level. The values of d' were calculated for each ten-trial block, the minimum and maximum values discarded, and an average d' and β were calculated for the pooled 50 trials that remained.

The results of the factorial experiment were analyzed using signal detection parameters d' and β (Green and Swets, 1966), adjusted using an unequal variance model (Hautus, 1995). The receiver sensitivity metric d' is zero at chance performance, i.e., 50%-correct choice in this two-alternative task. To account for unequal variance in responding, threshold was estimated at d' of 1.0 (Green and Swets, 1966). A value of zero for the natural log of the receiver response bias metric β [ln(β), henceforth β] indicates unbiased responding.

E. Behavioral paradigm

The data collection sessions began with CAS facing the trainer, touching her rostrum against an intertrial station (foam pad) located just above the water surface. Upon presentation of a hand cue, the dolphin would submerge and

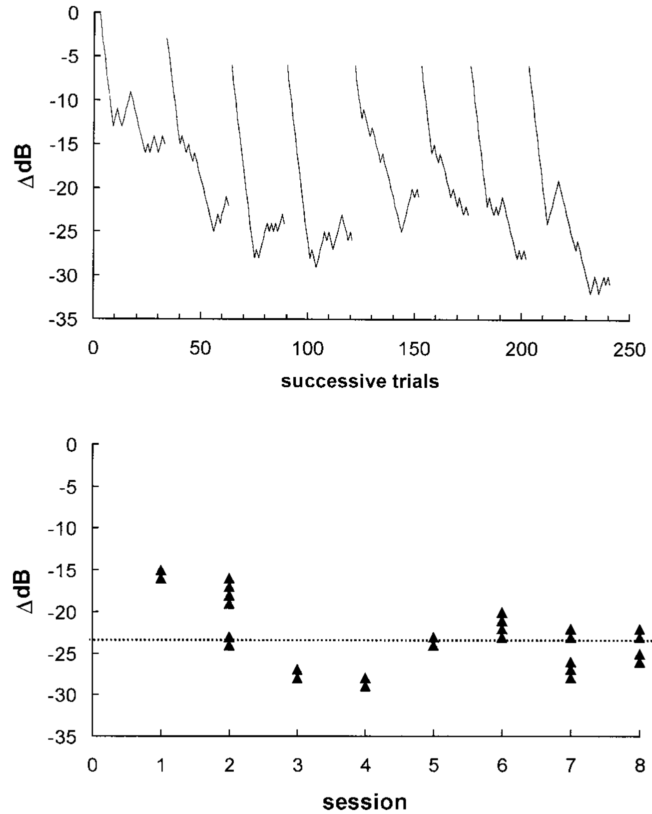

FIG. 2. Determining ΔdB threshold by titration. The top panel shows the raw titration data for each session, plotted as a function of trial number. The bottom panel shows the ΔdB values at the 75%-correct threshold for each session. The median (−22 dB) is indicated by the dotted line.

position her head in the test station hoop. The trainer removed the acoustically opaque screen as a computer operator activated the SES. A 4-s trial period followed, during which time CAS would freely echolocate, receiving up to 20 stimuli in return, and respond. A correct "GO" response was made if she swam out of the hoop and touched a nearby paddle. A correct "NO-GO" response was made if she stayed in the hoop for the 4-s trial duration. Both correct responses were reinforced by a bridging stimulus and a consistent fish reward. Data were collected using a modified Gellermann series (Gellermann, 1933) that had been counterbalanced in ten-trial blocks. Each session was initiated with a ten-trial block of warm-up trials. If CAS's performance was less than 80% correct, the session was terminated and revisited later in the day. One session was run per day.

III. RESULTS

A. Assessment of ΔdB threshold (phase one)

The first phase of measurement was assessment of the ΔdB threshold. ΔT was held constant at 400 μs, which placed the two highlights in separate 265-μs integration windows. Eight ΔdB titration sessions were run and the ΔdB threshold session results are presented in Fig. 2. The top panel illustrates the ΔdB values at which the reversals occurred for each session. CAS's minimum ΔdB was −32 dB. This corresponds to a value of 96.5 dB *re*: 1 Vrms for the second highlight, approximately 1.5 dB above the white-noise floor. A sliding ten-trial window was passed over the

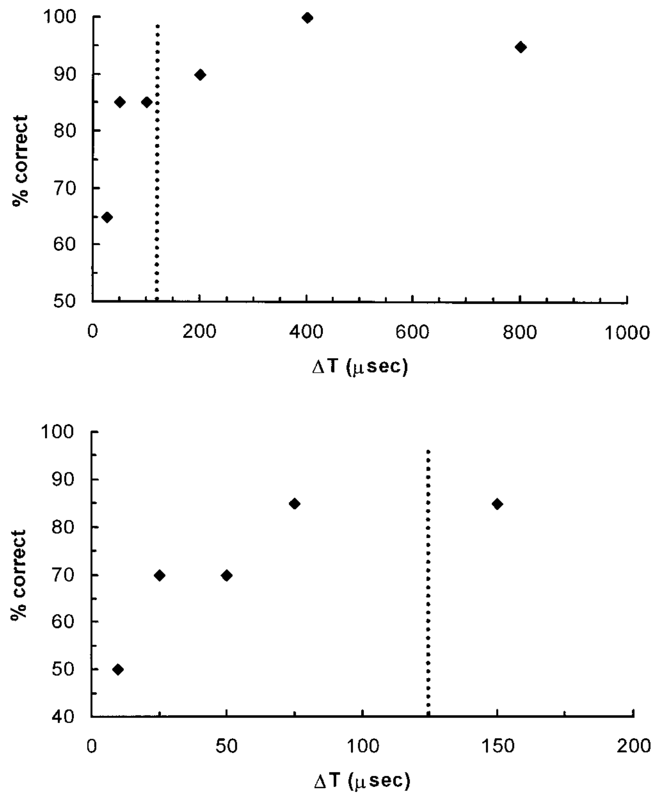

FIG. 3. Determining the limits of ΔT. The top panel summarizes CAS's performance on the first set of ΔT values ($n=20$ per value), and the bottom panel summarizes her performance on the second set ($n=20$ per value). ΔdB was held constant at -19 dB. In each panel, the dotted vertical line indicates the approximate ΔT transition from single to multiple (nonoverlapping) 265 μs temporal integration windows.

data for each session, and the ΔdB values at the 75%-correct threshold were extracted, presented in the bottom panel of Fig. 2. Overall, the median threshold was -22 dB, with a semi-interquartile range of 3 dB.

B. Assessment of ΔT boundaries (phase two)

In the second phase of measurement, we held ΔdB constant at -19 dB (third quartile), and manipulated ΔT to determine the dolphin's performance boundaries. Warm-up blocks were run with ΔT at 400 μs, and two ten-trials blocks were run for ΔT at 25, 50, 100, 200, 400, and 800 μs. The overall percentage of correct responses for each session in phase two is presented in the top panel of Fig. 3. CAS's performance at the 50-μs level was well above chance; thus, we ran a second set of blocks with the warm-up ΔT at 150 μs, and tested at 10, 25, 50, and 75 μs. The results are summarized in the bottom panel of Fig. 3. With ΔdB held constant at -19 dB, CAS's performance approached chance level as ΔT was decreased below 50 μs, but performance remained at or above 85% correct above 75 μs. Recall that ΔT less than 125 μs placed both highlights within a single separate integration window. CAS's results clearly indicate no significant decrement in performance as the highlights transitioned between separate and single critical intervals.

TABLE I. Values of d' for each combination of ΔdB and ΔT ($n=25$ per cell).

		ΔT (μsec)			
		10	20	40	80
ΔdB	-10	1.68	2.90	3.16	3.81
	-15	1.06	2.58	2.93	3.05
	-20	0.74	0.96	1.31	2.81
	-25	0.18	0.41	0.70	1.29

C. Factorial test: ΔdB vs ΔT (phase three)

The results of phases one and two provided estimates of ΔdB and ΔT that described the boundaries of CAS's discrimination performance. In the third phase, we conducted a factorial experiment to evaluate CAS's performance within these limits. For the warm-up block in each session, ΔdB was set at -19 dB and ΔT at 160 μs. ΔdB was tested at -10, -15, -20, and -25 dB. ΔT was tested at 10, 20, 40, and 80 μs. Average d' and β were calculated for the pooled 50 trials for each factorial level. Results of the factorial testing will be described using the combination of$\{\Delta \mathrm{dB}, \Delta T\}$. CAS's performance on the warm-up and cool-down trials $\{-19, 160\}$ was near perfect, with a d' of 3.2 and virtually no response bias ($\beta=0.06$). For test blocks, her response bias remained minimal and nonsystematic, with an average false-alarm probability of 0.17 and β of -0.02. The test results are presented in Table I and in graphical form in the top panel of Fig. 4. The horizontal line in the top panel of Fig. 4 indicates a d' threshold of 1.0. Sensitivity was highest

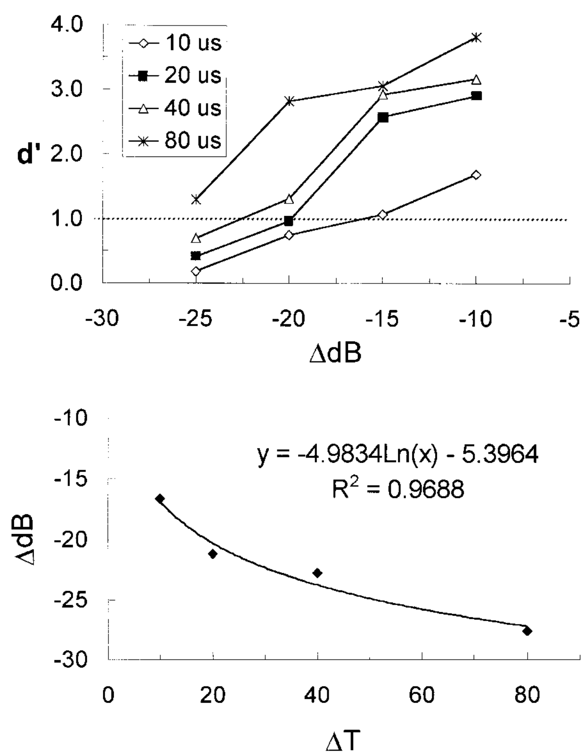

FIG. 4. Derivation of an iso-sensitivity function for $\Delta\mathrm{dB}\times\Delta T$. The top panel shows the results of the factorial experiment in which ΔdB and ΔT were jointly manipulated. ΔdB was estimated for each ΔT curve at d' equal to 1.0. The iso-sensitivity function is presented in the bottom panel, with the best-fit exponential curve.

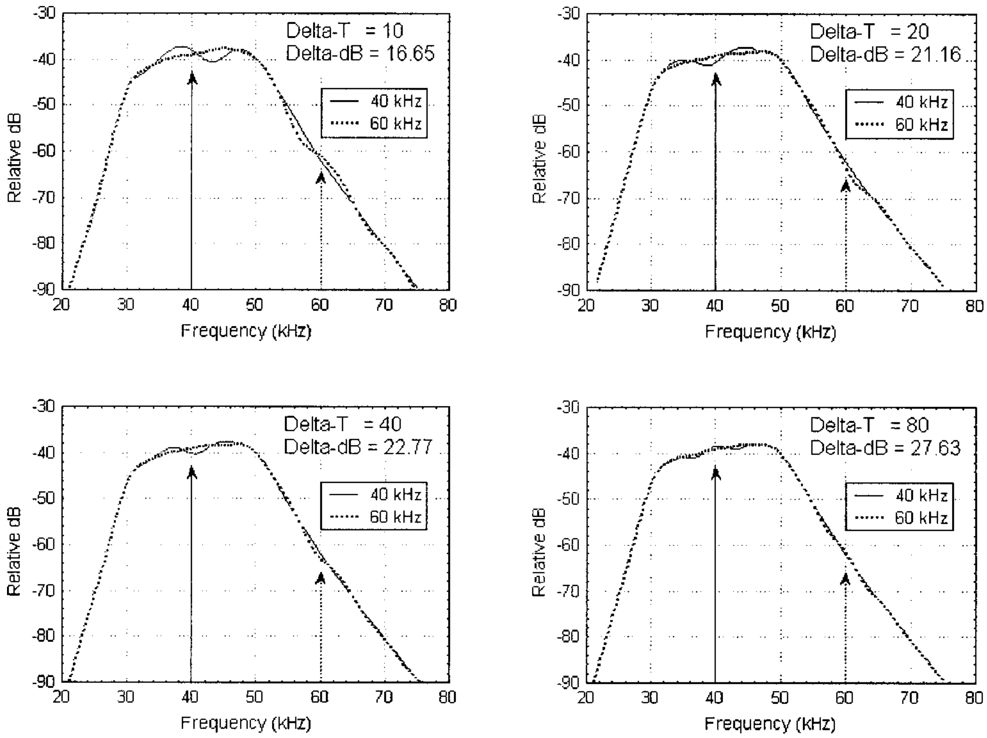

FIG. 5. Spectra of the stimuli, one for each combination of ΔdB and ΔT predicted from the iso-sensitivity function derived in the factorial experiment. Frequency resolution was 488 Hz per FFT bin. The NO-GO spectra (60-kHz second highlight) are represented by dotted lines, and the GO echoes (40-kHz second highlight) by solid lines.

at {−10, 80} and lowest at {−25, 10}. To fuse the results into a single function, we estimated the ΔdB value at d' equal to 1.0 by linear fit to each ΔT curve. The resulting iso-sensitivity function is presented in the bottom panel of Fig. 4. The function is well-behaved, described well by a natural logarithmic function ($\Delta\mathrm{dB} = -4.9834 \cdot \ln(\Delta T) - 5.3964, R^2 = 0.969$). The results clearly demonstrate the relationship between the energy and timing features of the synthetic echoes, with the dolphin requiring increasing separation between the first and second highlight to maintain discrimination sensitivity as the energy in the second highlight decreased.

IV. DISCUSSION

The first phase of measurement was an assessment of the ΔdB threshold. ΔT was held constant at 400 μs, with the initial stimulus component held constant at 135 dB *re*: 1 Vrms and the white-noise floor at 95 dB *re*: 1 Vrms. CAS's median threshold was −22 dB. Her maximum ΔdB was −32, which corresponds to a value of 96.5 dB for the second highlight, approximately 1.5 dB above the white-noise floor. Thus, ΔdB was limited by the white-noise floor and not by the amplitude relationship of the first and second echo highlights. This contrasts with the detection results reported by Au *et al.* (1988), which would have predicted that CAS's choice performance would decline at ΔdB of about −6 dB since the initial highlight would have "captured" the 265-μs temporal integration window, reducing attention to low-amplitude trailing highlights.

In the second phase of measurement, ΔdB was held constant at −19 dB, and ΔT was manipulated to determine the dolphin's performance boundaries. Discrimination performance approached chance level as ΔT was decreased below 50 μs, but performance remained at or above 85% correct from 75–800 μs. The results clearly indicate no significant decrement in performance as the highlights transitioned between multiple or single temporal integration intervals. These results suggest an echo-feature discrimination window that in some sense can operate independently of the energy integration detection process.

The third phase was a factorial study with ΔdB tested at −10, −15, −20, and −25 dB, and ΔT tested at 10, 20, 40, and 80 μs. No evidence of response bias was observed. Sensitivity was highest at {−10, 80} and lowest at {−25, 10}. The data supported a well-behaved iso-sensitivity function indicating that the dolphin required increasing energy in the second highlight within each echo to maintain discrimination sensitivity as the separation between the first and second highlight decreased.

The dolphin's ability to discriminate the synthetic echoes was a function of her sensitivity to the center frequency of the second echo highlight. At 40 kHz, the frequency limens of the bottlenose dolphin auditory system is at most 1% (or about 400 Hz; see Thompson and Herman, 1975), thus the 40-versus 60-kHz discrimination was straightforward. The acoustical feature(s) of the stimuli that controlled her choice performance are unknown. Time separation pitch (Au and Pawloski, 1992) likely was not a cue, because the time separation (ΔT) between the highlights was equated for the GO and NO-GO stimulus waveforms.

The distribution of spectral energy contains differences that could have cued her responses (Au and Pawloski, 1992;

Hammer and Au, 1980; Johnson *et al.*, 1988; Moore *et al.*, 1984). Using frequency cues, a parsimonious description of CAS's decision rule is an ''A versus Not-A'' detection—that is, perform a paddle press (GO) if a 40-kHz signal is detected, otherwise remain in the hoop (NO-GO). To illustrate this concept, we applied a symmetric filter with center frequency of 40 kHz and Q of approx. 2.2 (see Au and Moore, 1990) to stimuli created using the iso-sensitivity function generated in the factorial experiment. The filtered spectra are presented in Fig. 5, depicting four combinations of ΔdB and the ΔT predicted from the natural logarithmic fit to the experimental data $[\Delta\mathrm{dB} = -4.9834 \cdot \ln(\Delta T - 5.3964)]$. For purposes of illustration, the spectral bandwidth was set to 488 Hz, to be consistent with the frequency limens reported by Thompson and Herman (1975). Notice the spectral ripple centered around 40 kHz. This ripple is most pronounced in the $\{\Delta T = 10\ \mu\mathrm{s},\ \Delta\mathrm{dB} = -16.65\ \mathrm{dB}\}$ waveform and gradually attenuates towards the average level as ΔT was increased and ΔdB was decreased. The ΔT and ΔdB values were derived from an iso-sensitivity function, however, so the ripple should have remained more constant to persist as the sole cue.

In summary, unlike the energy integration observed in the *detection* thresholds of complex stimuli (Au *et al.*, 1987; Vel'min and Dubrovskiy, 1976), it appears that in a *discrimination* task the animal may perceive the within-echo components as separable analyzable features. The dolphin's performance was high with multiple highlights both within a single integration window or distributed across several integration windows (e.g., with ΔT greater than 125 μs). Temporal smearing of features, implicit in an energy integrator, did not appear to limit discrimination performance because the dolphin was able to discriminate low-amplitude highlights in close proximity to uninformative high-amplitude highlights. Moreover, as separation between highlights increased, sensitivity to lower-amplitude highlights increased, thereby improving the likelihood that the animal could detect lower-amplitude trailing echo features, such as those generated by target resonance (Gaunaurd *et al.*, 1998). Thus, the energy integration detection mechanism does not necessarily ''lock on'' to high-amplitude features at the expense of reduced sensitivity to lower-amplitude features in trailing integration windows, as can be inferred from detection of complex echoes (Au *et al.*, 1988).

Based on the results provided here, dolphins can isolate and process brief acoustic features that lie within and between energy integration windows of the echo detection system. Such performance would permit the dolphin auditory system to attend to lower-amplitude echo features (unmasked by ambient noise) related to objects of interest while rejecting higher-amplitude features related to reverberation and clutter, an adaptive capability in the high-clutter high-reverberation littoral niche occupied by bottlenose dolphins.

ACKNOWLEDGMENTS

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