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DOUBLE-CLICK REPRESENTATION IN THE DOLPHIN AUDITORY SYSTEM

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1. INTRODUCTION

In response to a short acoustic click, most targets return echoes containing many highlights. The time resolution constant for Tursiops clicks of 12 to 15 μs, Au [1], is small enough to resolve these highlights and process the echoes in the time domain. However, the constant seems too small to represent the actual time resolution of the presumably slow dolphin auditory system.

The "critical interval" of around 300 μs, derived by Velmin and Dubrovskiy [2, 3] from experiments on the hearing and echolocation discrimination between correlated stimuli, is thought to be the temporal resolving interval in dolphin sonar. Although it is generally admitted that a time interval of that value is a kind of fundamental constant of dolphin hearing, there is some confusion about its application. Au [1] considers the "critical interval" to be an equivalent of the integration time constant and believes that the actual time resolution of the dolphin sonar is not yet known.

We have learned by experience how wrong one could be at construing results of an experiment with a dolphin, when the waveform and long-term amplitude spectrum of the correlated stimulus could be equally accountable for discrimination. The similarity in the dolphin and human subject discrimination between correlated double clicks provoked us to conclude that the critical interval represented the auditory filter recovery time, Zanin & Zaslavskiy [4]. The same dolphin, however, for which the critical interval has been shown, Velmin & Dubrovskiy [2], as well as two other dolphins, revealed significantly higher time resolution of 25 - 30 μs, when discriminating between uncorrelated noise pulses, Zaslavskiy & Ryabov [5], Zaslavskiy et al. [6], Zaslavskiy & Ryabov [7]. The correlated double clicks that differed in interclick intervals proved to be inadequate stimuli for estimating neither the time resolution nor the filter recovery time.

Therefore we attempted to determine these basic characteristics of the dolphin sonar with the modified correlated double clicks. Mirror image double clicks (Fig. 1, 2) were used to estimate the time resolution of the dolphin auditory system. The smallest interval at which such stimuli are still different for the dolphin can be considered as an estimate of the auditory time resolution.

The frequency domain representation of a double click is a product of an interaction between first and second clicks, that starts at the auditory periphery as an interference in frequency filters. The interference takes place up to some largest interclick interval known as the transition or recovery time of the filter, which is in inverse proportion to its frequency resolution. In order to measure the dolphin auditory filter's recovery time we used double clicks that differed in amplitude spectra but had equal interpulse intervals (Fig. 5). The largest interclick interval at which a dolphin is still capable of discriminating between such double-clicks can be considered as an estimate of the auditory frequency filters' recovery time.

The time resolution and the recovery time seem to represent temporal limits for double click analysis in the time and frequency domains. As a first approximation, these temporal constants can also describe echo processing of real targets by the dolphin.

2. METHOD

The subjects were two male bottlenose dolphins, *Tursiops Truncatus*, TP72-78 and TM78-90. Experiments were conducted in a concrete pool with dimensions of 28 × 13 × 4 m. A two-response forced choice paradigm with simultaneous presentation of stimuli was used. A vertical net partition between two transducers (12 mm in diameter) enabled the experimenter to set a minimum distance of 5 - 8 m to the transducers, from which the dolphin was to make his choice. Prior to the stimuli presentation the dolphin positioned itself at the far (from the transducers) end of the partition. In response to the stimuli the dolphin made its choice and swam to the chosen transducer. A B&K 8103 hydrophone was used to monitor acoustic stimuli. The stimuli were presented at a repetition rate of 5 stimuli per second using the method of constant stimuli. The threshold values were calculated at the 75% correct response level.

3. TIME RESOLUTION OF THE DOLPHIN AUDITORY SYSTEM

Ronken [8] was the first to test mirror image double clicks (Fig.1, upper box) on human subjects. Two pulses of different amplitude were presented in the double clicks in reversed order. Because the stimuli had the same long-term amplitude spectrum, it was assumed that the subject would discriminate between these double pulses as long as he would be able to detect a difference in envelopes or phase spectra.

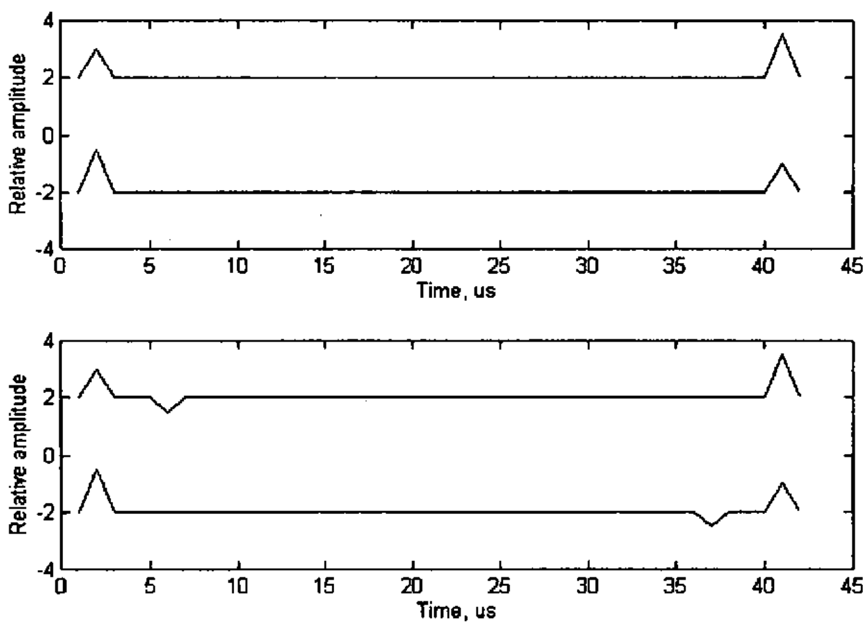

Figure 1. Mirror image stimuli (on the electrical side of a transducer). Upper box: from Ronken [8], lower box: present study.

The dolphin, however, distinguished the stimuli at interclick intervals even shorter than the duration of a click (a transducer reaction to the electrical pulse) and eventually did not reveal any threshold time that could be an estimate of the time resolution, Dubrovskiy [9]. A short-term spectrum discrimination model of such double clicks proposed by Johnson et al. [10] for an interclick interval of 200 μs will hardly work at very short intervals. Clearly, the double clicks discrimination results remain puzzling.

Negative pulses symmetrically added to the double pulse as shown in lower box of Fig. 1 do not violate stimuli property to be mirror reflected, yet produce acoustic stimuli that are different in interclick intervals. At short enough intervals between the negative and adjacent positive pulse, this pair of electrical pulses is transformed into a single click at the acoustical side of the transducer (Fig. 2). Of each double click, one acoustic click is produced by a single electrical pulse, the other - by the pair of electrical pulses of opposite polarity. The additional wave (encircled in Fig. 2) caused by the negative pulse provided a difference in interclick intervals for the acoustic double clicks. The closer the negative pulse to the positive one, the later this wave develops and the smaller the difference.

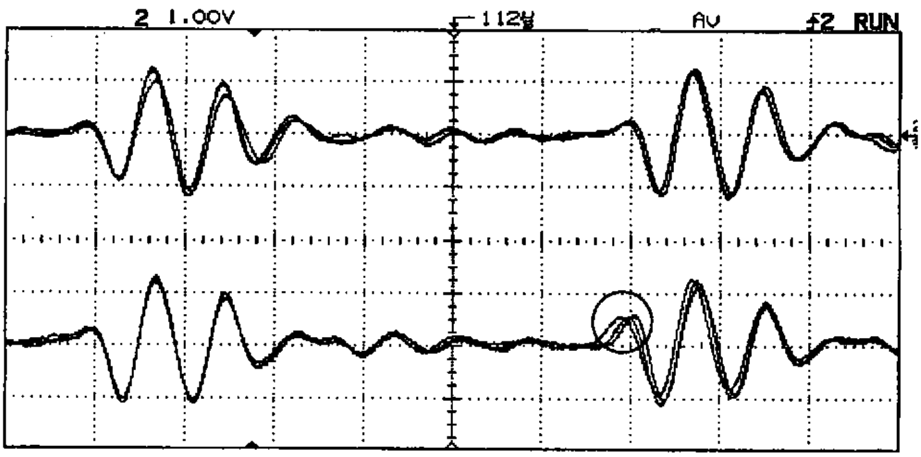

Figure 2. Superimposed acoustic reactions of the transducer to the electrical stimuli shown in lower box of Fig. 1 for intervals between the negative pulse and adjacent to it positive one of 3, 4 and 5 μs.

What is more, the negative pulses equalized amplitudes of the first and the second acoustic clicks. Otherwise it would be rather difficult to force the dolphin to discriminate between intervals. At given amplitude ratios of the electrical pulses, the amplitude spectrum of the first and the second acoustic clicks are practically identical. Within the frequency range of dolphin hearing, minor differences occur below 60 - 70 kHz (Fig. 3). However, at click levels of about 26 dB, as used in the experiment, the low frequency components are likely to be under the detection threshold for the dolphin.

The amplitude difference between the first and the second acoustic clicks was well above the threshold for the dolphin only at a 2 μs interval between negative and adjacent positive electrical pulses (Fig. 3, the lowest spectrum). By changing acoustic click amplitudes it was easy to alter the dolphin's choice of positive double click. The dolphin always chose a double click in which the first acoustic click was smaller than the second one. By contrast, at intervals of 3 to 5 μs the random variation of the acoustic click amplitudes produced no effect on the dolphin's choice: the double click of a shorter interclick interval was always positive for him.

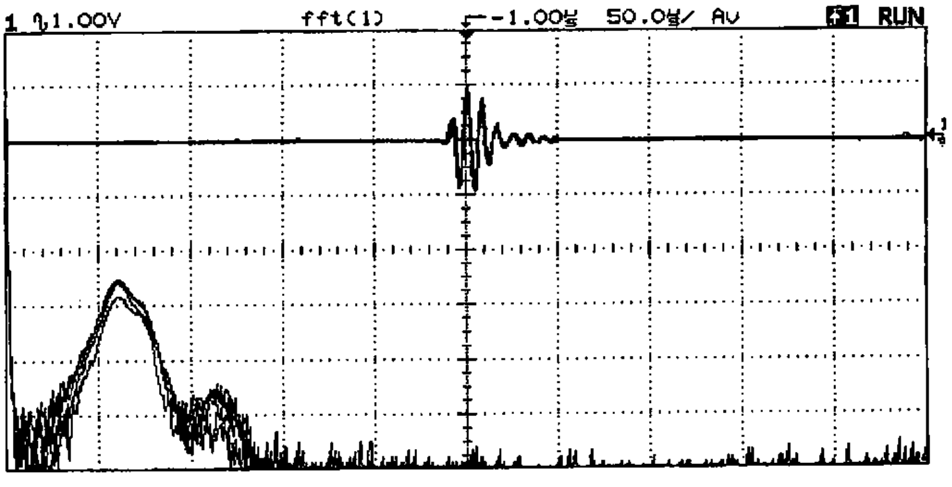

Figure 3. Superimposed acoustic reactions of the transducer to a single electrical pulse of 1μs and a pair of electrical pulses of opposite polarity (from lower box of Fig. 1) and their amplitude spectra. Sensitivity: 10 dB/div. Interpulse interval in the pair: 2 (the lowest spectrum), 3, 4 and 5 μs.

It is noteworthy that within the frequency range from about 70 to 130 kHz, where the amplitude spectra of the acoustic clicks are practically identical (Fig. 3), the phase spectra coincide as well. This made it very difficult, if possible at all, for the dolphin to extract any differences in the short term amplitude spectra of the stimuli.

Therefore, neither long nor short term spectrum discrimination cues were available for the dolphin. The negative pulses eliminated all possible discrimination cues in the frequency domain and produced the acoustic stimuli, that were different for the dolphin in the time domain alone.

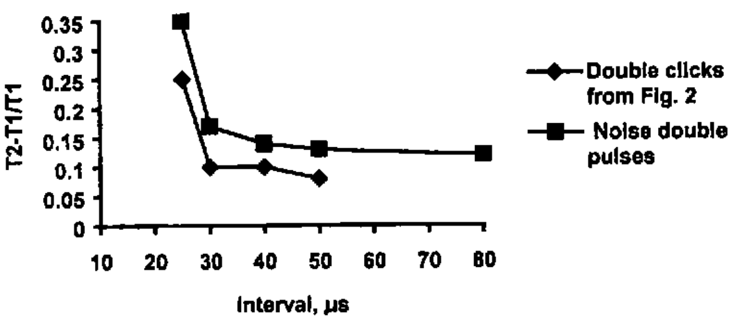

Figure 4. Difference limen on interval between the double clicks of Fig. 2 and between noise double pulses (from Zaslavskiy & Ryabov [7]) versus shorter interclick interval T1. Dolphin TM78-90.

The dolphin was found to distinguish such stimuli at approximately 10% difference in interclick intervals (Fig. 4).

DLI between the clicks of the mirror image stimuli is practically the same function of an interval as that of between the noise pulses (Fig. 4). The lack of coincidence is only to be expected because a measurement accuracy of intervals between noise pulse is lower than that of between correlated clicks. The only discrimination cue applicable to both kinds of the stimuli is a difference in interclick interval. The increase of DLI at intervals shorter than 25-30 μs indicates an approach to the time resolution of the dolphin auditory system.

4. FREQUENCY DOMAIN REPRESENTATION OF A DOUBLE-CLICK

To measure the dolphin auditory filter's recovery time we used the double clicks shown in Fig. 5. One double click was composed of two equal unipolar pulses, the other - of two pulses of opposite polarity (on the electrical side of a transducer). At equal interclick intervals amplitude spectra of the pairs are rippled with the same period. However, maxima of one spectrum correspond to minima of the other (Fig. 5, lower box). It was expected that beyond some interclick interval, determined by frequency resolution of the auditory system, the dolphin would fail to discriminate the double clicks.

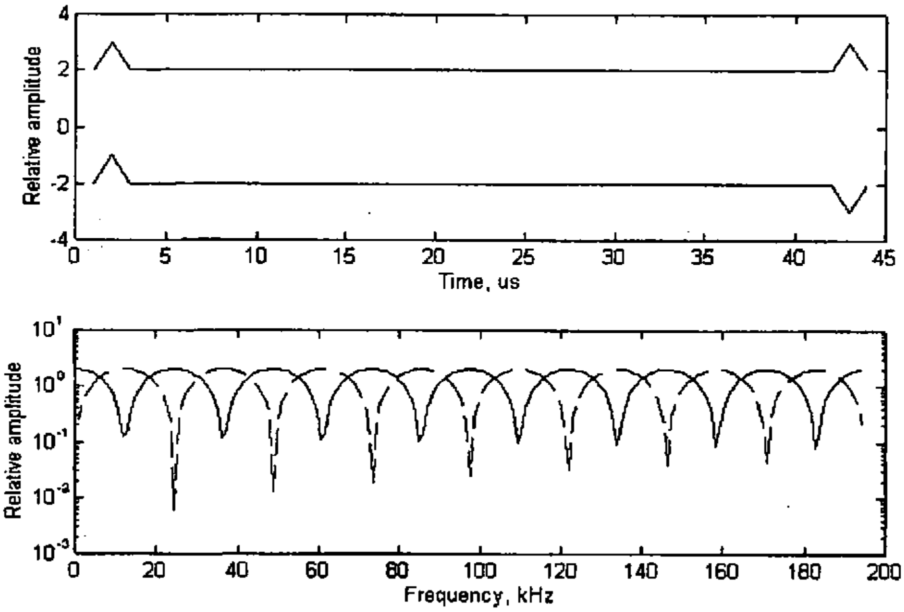

Figure 5. The stimuli on the electrical side of a transducer (upper box) and their amplitude spectra (lower box) drawn with solid and dashed lines respectively.

The largest interclick interval at which the dolphins were able to discriminate double clicks shown in Fig. 5 was found to be 100 -110 μs (Fig. 6).

At a 100 µs interval, the ripples in amplitude spectrum of the double click are separated by a span of 10 kHz. That can be considered as the estimate of frequency resolution of the dolphin sonar for a double click.

We compared the double clicks discrimination by the dolphin and human in the low frequency range from 8 to 20 kHz, Zaslavskiy et al. [11]. It came as a complete surprise that the dolphin's threshold interval at low frequencies turned out to be the same as at high frequencies (Fig. 6, TM78-90, 8-20 kHz).

For two human subjects with normal hearing, the threshold interval reached 500 µs (Fig. 6, human subjects, 8-20 kHz), though one human subject with "absolute" hearing could recognize the double clicks at intervals up to 2000 µs. Significant difference in the threshold intervals shows that an analogy in perception of the double-clicks by the dolphin and the human being can be rather fallible.

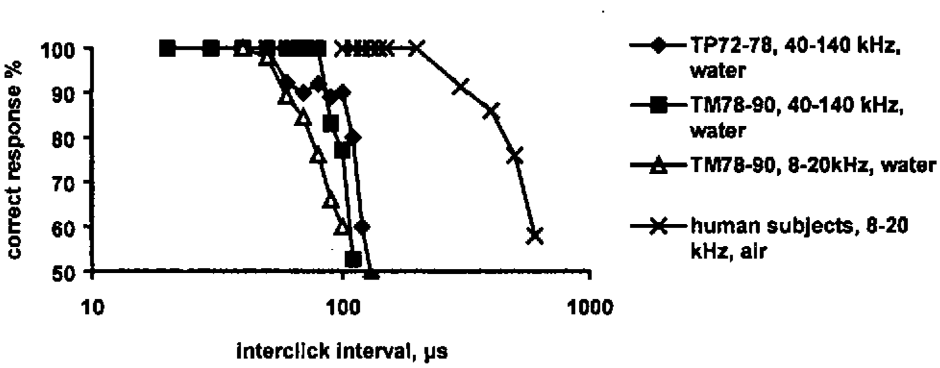

Figure 6. Discrimination of the double clicks (Fig. 5) by the dolphins and the human subjects as a function of an interclick interval. Dolphin designation and frequency range of the stimuli are shown in the legend.

Thus, beyond an interval of 100 - 110 µs, interaction between the first and the second clicks in the auditory system is not sufficient to produce detectable differences between the double clicks in the frequency domain for the dolphin.

It is noteworthy that in initial experiments the dolphins, both rather experienced at target discrimination, could not discriminate between the double clicks from Fig. 5 at interclick intervals longer than 50 - 60 µs. This fact seems to be in a favor of the time domain echo processing in the dolphin.

5. DISCUSSION

The actual time resolution of the dolphin hearing of 25 - 30 µs proved to be different from the auditory filter's recovery time. It may indicate that the dolphin is capable of choosing between narrow and broad band signal processing. Clearly, the choice between temporal and spectral discrimination cues is possible only within a range of interpulse intervals between the time resolution of the auditory system and the auditory filter's recovery time.

The reverse of a backward masking function at 100 µs found for one dolphin, Velmin & Dubrovskiy [2], seems to support this suggestion. The amount of backward masking for the dolphin dropped to almost absolute threshold level as a delay between signal and masker decreased from 100 to 10 μs. The second dolphin from the same study has shown normal increasing backward masking up to a level of 36 dB. It is clear that for intervals under 100 μs the dolphins implemented sort of opposite discrimination cues. One cue provides improvement in performance with increasing of the time interval, whereas the other gives better results at smaller intervals. The first dolphin likely switched to the frequency domain discrimination cue, while the second dolphin continued to discriminate the correlated double clicks in the time domain.

High time resolution of the auditory system suggests that target discrimination cues are available for the dolphin in the time domain. At the same time, at least in the experimental condition it is possible to force the dolphin to process signals in the frequency domain, provided conditions for frequency analysis are fulfilled.

Coincidence of the recovery time of the auditory filters at audio and echolocation frequencies (Fig. 6) appears to contradict a duplex theory of the dolphin hearing, Dubrovskiy [9]. According to Dubrovskiy's classification the main distinct property of the active hearing is "essential difference in auditory processing mechanisms of clicks sequence falling within or outside the critical interval". We did find substantial difference between auditory processing of the double clicks at high frequencies of "active" auditory subsystem and at low frequencies of "passive" subsystem.

The irregularities in the dolphin's performance at double click discrimination have contributed much to developing the critical interval concept, Velmin & Dubrovskiy [3]. In our early study, Zanin & Zaslavskiy [4], we attributed DLI increase at intervals from 200 to 300 μs to the dolphin transition from the frequency domain discrimination below this "dead zone" to the time domain analysis above it, However, there is no interference between two consequent clicks in the dolphin auditory system at intervals greater than 100 - 110 μs that can produce a difference between double clicks in the frequency domain. This time interval is the utmost limit behind which a double click disintegrates for the dolphin in two separate acoustic events. At broad band analysis such disintegration takes place at the time resolution of the dolphin auditory system of 25 - 30 μs.

A short-term spectral analysis of the double clicks shown in upper box of Fig. 1, has been performed at interclick interval of 200 μs, Johnson et al. [10]. Yet again, at intervals greater than 100 - 110 μs there is no interference between two consequent clicks that could provide a difference in short term spectra. At the auditory time resolution as high as 25 - 30 μs the dolphin can discriminate the double clicks of 200 μs interclick interval simply by difference in amplitudes of the first and the second clicks.

There are a lot of speculations on the involvement of time separation pitch (TSP) cue in target discrimination. The TSP concept in the dolphin echolocation is based on an assumed similarity of dolphin and human auditory representation of a double click, Au [1], Johnson at al. [10], Au and Hammer [12], Moore et al. [13]. In reality, however, there is a significant difference in double click perception in the dolphin and human being even within an audio frequency range. A shorter recovery time of the dolphin auditory filter at audio frequencies (Fig. 6) suggests much lower, compared to the human being, frequency resolution for a double click. Besides, the mirror-image double clicks of Fig. 1 having the same frequency spectrum could hardly generate a different TSP for the dolphin. Even the double clicks shown in Fig. 5 are likely to produce the same TSP because they have equal interclick intervals and, as a result, equal periods of the ripples in amplitude spectra.

The time resolution of the dolphin auditory system proved to be more than ten times shorter than its integration time, Zanin et al. [14], Au et al. [15]. A time resolution of 25 - 30 μs, the filter's recovery time of

100 - 110 μs and an integration time of 300 - 500 μs represent three independent processes in the dolphin hearing.

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