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TIME RESOLUTION OF THE DOLPHIN SONAR: WHAT IS ACTUAL?

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1. INTRODUCTION

The term "time resolution" refers to the ability of an auditory system to follow temporal changes in the envelope of sound. The "critical interval" of around 300 µs, derived by Velmin and Dubrovskiy [1, 2] from dolphin discrimination of correlated stimuli, appeared to be a sort of compromise between the very high theoretical time resolution of dolphin clicks and a presumed "sluggishness" of the dolphin auditory system. They defined the critical interval as a time interval in which "individual acoustic events merge for a dolphin into an acoustic whole".

Our early results on a dolphin's discrimination between correlated double clicks appeared to be consistent with the critical interval concept, Zanin & Zaslavskiy [3]. Dolphin TP72-78 turned out to be unable to discriminate between correlated double clicks if both interclick intervals fell into a range between 200 and 300 µs (Fig. 1, TP72-78, double clicks, 1). A similar psychometric function for interval discrimination task has been found for human subjects, except that humans displayed poor performance between 5000 and 10000 µs (Fig. 1, human, double clicks). Before this "dead zone", discrimination was based on the difference in frequency spectra of the double clicks. After it, human subjects could detect clicks separately in time. It seemed logical at the time, to assume that the same kind of transition from spectral to temporal discrimination cues could be valid for the dolphin, though at much shorter intervals. Such discrimination model was quite consistent with the critical interval concept, in terms of clicks merging at intervals of less than 200 µs or, vice versa, disintegration of the double click at intervals greater than 300 µs. All the more so that a similar irregularity in the dolphin's discrimination between correlated double clicks had already been interpreted in favor of the critical interval concept, Velmin & Dubrovskiy [2].

The analogy later proved to be wrong. For some reason, the dolphin regularly changed the positive (reinforced) stimulus, as interclick intervals in both double clicks crossed the "dead zone". However, there is no apparent link between frequency characteristics of the double click at intervals shorter than 200 µs, and the temporal ones at intervals greater than 300 µs. Moreover, human subjects never displayed any stimulus preference, and chose a positive one randomly in different experiments.

If the dolphin's choice had been incidental, it would have been possible to get the positive stimulus changed in the time domain, without changing it in the frequency domain. However, when the dolphin was forced to choose a smaller interval instead of a longer one at intervals above 300 µs, he immediately changed the positive stimulus at intervals shorter than 200µs. It looked as though the discrimination criteria were the same in both zones, or at least strongly correlated.

As doubts about the critical interval concept arose we decided to examine how a dolphin would discriminate uncorrelated noise stimuli. We found that a human subject could not distinguish noise double pulses, unless interpulse intervals were long enough (4 - 5 ms) for him to hear pulses separately in time

(Fig. 1, human, noise double pulses). In other words the noise double pulses, that differed in interpulse intervals, were indistinguishable for human subjects in the frequency domain, Zaslavskiy & Ryabov [4].

We expected a dolphin to be unable to distinguish the noise double pulses at intervals shorter than about 260 μs, where pulses presumably merge in an acoustic whole, Velmin & Dubrovskiy [1, 2]. A difference limen on interpulse interval (DLI) and pulse duration (DLD) were measured. Forward and backward temporal masking functions were determined for several noise masker intensities and durations.

2. METHOD

The subjects were three adult male bottlenose dolphins (Tursiops truncatus). The experiments were conducted in a 28 × 13 × 4 m concrete pool using a two-response forced-choice procedure. A vertical net partition between two transducers of 1.2 cm in diameter enabled the experimenter to set a minimum distance (5 - 8 m), from which a dolphin was forced to make his choice. Prior to stimuli presentation the dolphin positioned itself at the far (from the transducers) end of the partition. Having made its choice the dolphin swam to the chosen transducer. The maximum of the amplitude spectrum of clicks and noise pulses was between 110 and 130 kHz. The stimuli were presented simultaneously using the method of constant stimuli. The threshold values were calculated at the 75% correct response level. At the beginning of a training session the dolphin used to choose the stimulus to be reinforced by experimenter as a positive one. As experimental condition were changed the dolphin was allowed to change the positive stimulus if it persistently tried to do so.

3. RESULTS

3.1 Interpulse interval discrimination

The discrimination of correlated double clicks (Fig. 1, human, double clicks) and noise double pulses (Fig. 1, human, noise double pulses, t = 1200μs) were quite coherent with human subjects' description of the stimuli in the time and frequency domain. The human subjects were incapable of discriminating noise double pulses in the frequency domain which resulted in high DLI at intervals below the "dead zone". The DLI were high enough for the human subjects to perceive pulses of greater interpulse interval separately in time.

In contrast to human subjects, the dolphin retained its ability to discriminate between the noise double pulses at intervals below the "dead zone", where pulses presumably merged for him into an acoustic whole (Fig.1, TP72-78, noise double pulses, t = 85 μs). Obviously, an analogy between human subject and the dolphin, as far as discrimination of double clicks is concerned, does not work.

All the more so that in recurrent experiment with the correlated double clicks, dolphin TP72-78 revealed a new discrimination function similar to that of the noise double pulses (Fig. 1, TP72-78, double clicks, 2). The same continuos discrimination function for correlated double clicks was collected later in experiment with another dolphin (Fig. 2, TM78-90, double clicks).

Measurement accuracy of intervals between noise pulses (10 to 15 %) was predictably lower than that of between correlated pulses (Fig. 1 and 2).

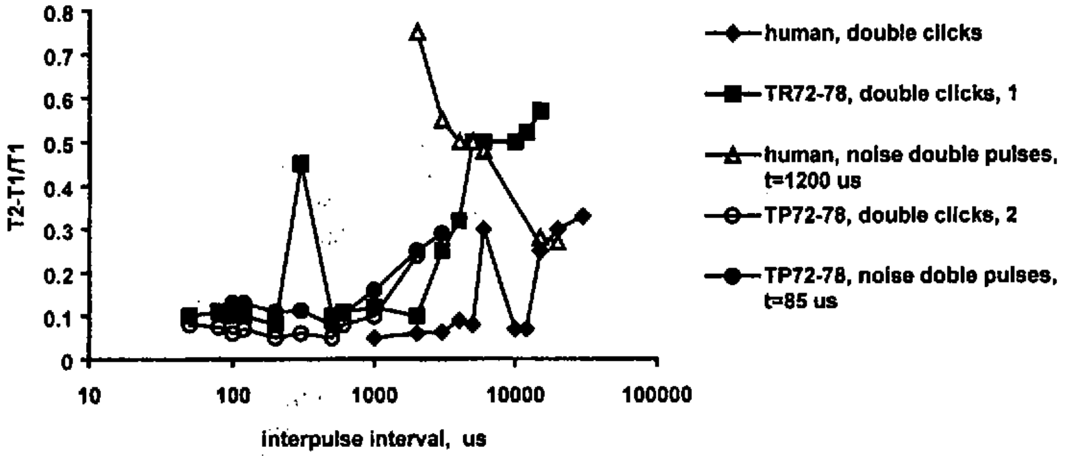

Figure 1. Difference limen on interval versus shorter interpulse interval T. t: noise pulse duration (on the electrical side of a transducer).

There was an abrupt DLI increase at interpulse interval greater than 100 μs for dolphin TL77-79 (Fig. 2, TL77-79, t = 25 μs, 1). The DLI jump at this point was accompanied by change of positive stimulus. At intervals before the DLI jump the dolphin was found to measure interpulse intervals. After 100μs the dolphin discriminated the noise double-pulses by a difference in their duration (from onset of the first pulse to the offset of the second one).

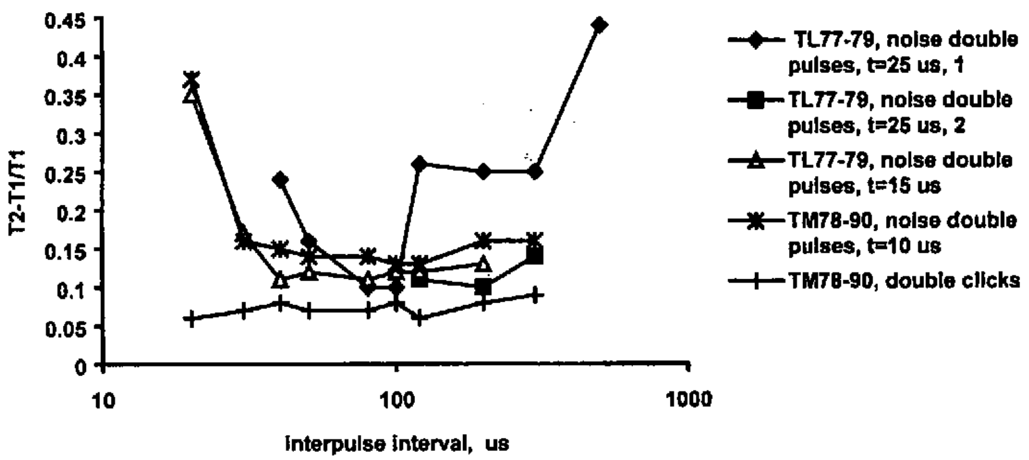

Figure 2. Difference limen on interval versus shorter interval T1. t: noise pulse duration (on the electrical side of a transducer).

It didn't take us long to train the dolphin to use the first temporal cue instead of the second one at intervals greater than 100 μs. That resulted not only in changing of the positive stimulus, but in DLI decrease from about 25% to 10%, (Fig. 2, TL77-79, t = 25 μs, 2). To make the dolphin discriminate the stimuli by the difference in interpulse intervals, we equalized their duration by increasing pulse duration of the shorter double pulse. After the dolphin switched to measuring the interpulse interval, the pulse duration became of no matter to him: the double pulse with a smaller interpulse interval remained positive for him.

The DLI increase, due to approaching the time resolution of the dolphin auditory system, occurred at interclick interval of 30 - 60 μs, much shorter than was predicted by the critical interval concept (Fig. 2).The longer noise pulses comprising the double pulse, the smaller interpulse pause and, as a result, the DLI increase started at a greater interpulse interval. On the acoustical side of the transducer the pulse duration is about 10 -15 μs longer than on an electrical side. Therefore at interpulse interval of 60 μs and the electrical pulse duration of 25 μs the pause between acoustic pulses is only 20 - 25 μs.

3.2 Pulse duration discrimination

One more estimate of the auditory time resolution can be based on the dolphin discrimination between noise pulses by duration. In contrast to the double pulses, there are no periodic ripples in the single pulse amplitude spectrum that could, at least theoretically, identify a positive stimulus for the dolphin. Moreover, the audibility of the pause between pulses sets a limit for the dolphin's capability to measure interpulse interval. At very short intervals the pause became too small for the dolphin to detect it, which resulted in a sharp increase of DLI (Fig. 2).On the other hand, at least at interpulse intervals greater 100 μs, the threshold difference in duration of the double pulses turned out to be higher (Fig 2, TL72-79, t = 25 μs, 1) than DLI (Fig 2, TL72-79, t = 25 μs, 2). Obtainable accuracy seems to be higher at measuring of the time interval between abrupt onsets of noise pulses than between onset and more diffused offset of the noise pulse.

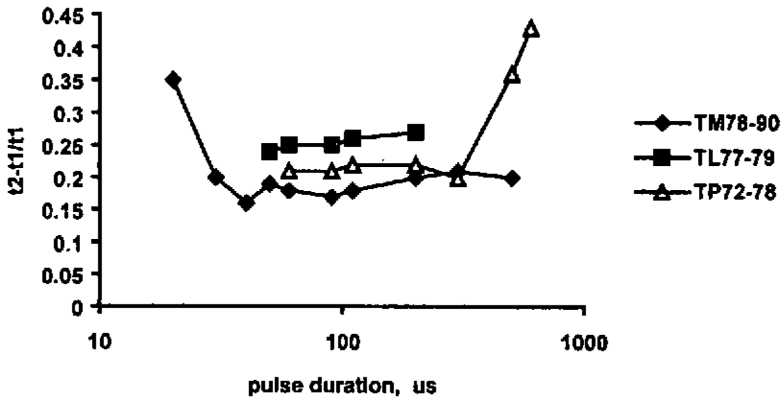

Figure 3. Difference limen on pulse duration (DLD) versus duration of a shorter pulse t1 (on the acoustical side of a transducer).

Theoretically, the noise pulses can be recognized by their energy though at threshold of discrimination a difference in energy appears to be too small for the dolphin to detect it. We eliminated such possibility by varying of the pulse intensity randomly from trial to trial. It was surprising that the dolphin was capable of distinguishing pulses by their duration at a difference in their intensity of 30 - 40dB, even at the threshold difference in durations.

The difference limen on duration of the noise pulses (Fig. 3) was found to be about 20%.

The dolphin successfully discriminated between a single noise pulse and double pulse by their duration. In other words it did not matter to him whether amplitude spectrum of the stimulus was regularly rippled (double noise pulse) or had just random variation (single pulse). Both of these stimuli could be positive for the dolphin for durations as short as 30 μs. No other cues, except for the time domain ones, can be accountable for the discrimination of such stimuli.

3.3 Temporal masking

Originally, the dolphin sonar time resolution was determined as a delay corresponding to a certain threshold level of a backward masking, Velmin & Dubrovskiy [1]. We conducted the temporal masking study using the same experimental procedure although instead of using the correlated masker and signal, the noise masker and even noise signal were used.

The results (Fig. 4) clearly indicate that the masking threshold strongly depends on the masker intensity. The threshold delay dropped dramatically with reducing masker level from 46 dB to 27 dB, Zaslavskiy et al. [5], for the same dolphin that was previously used in Velmin and Dubrovskiy study [1]. Another well-trained dolphin TM78-90 has shown better performance at the same masker lever of 46dB than dolphin TP72-78, but similar dependence on the masker level was observed for him as well. At the levels of 27, 39 and 47dB a backward masker did not affect detection of the signal if the delay was greater than 20, 60 and 300 μs correspondingly.

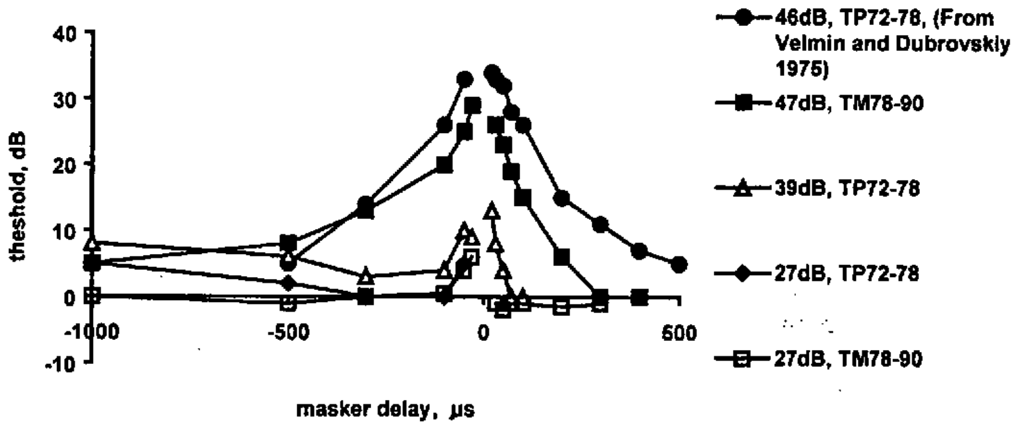

Figure 4. Threshold level of the signal versus masker delay. Positive delay: backward masking, negative delay: forward masking. Signal and masker are imitations of dolphin clicks. Masker level and the dolphin's designation are shown in the legend.

The same kind of the threshold delay dependence on masker level occurred for the noise masker and noise signal (Fig. 5). In addition to the masker intensity, the amount of backward masking also depends on the duration of the noise masker. The threshold delay increases from approximately 80 to 400 μs as the masker duration increases from 20 to 4000 μs (Fig. 5, 38dB, TM78-90, click)

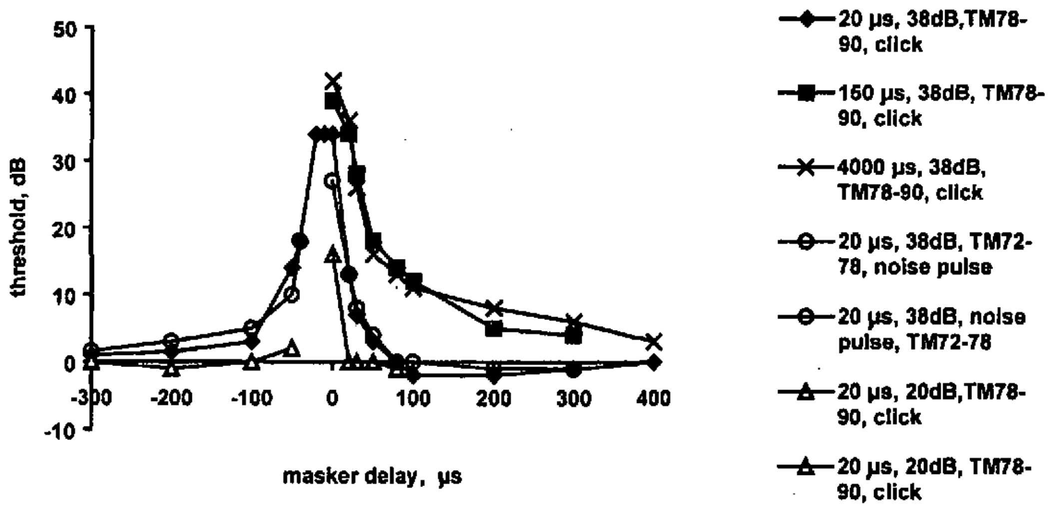

Figure 5. Threshold level of the signal versus delay of the noise masker. Positive delay: backward masking, negative delay: forward masking. Noise masker duration, masker level, dolphin's nickname, type of the signal (click or noise pulse of 20 µs) are shown in the legend.

At low masker levels of 20 dB, forward masking did not affect signal detection for delays greater than - 40 µs (Fig. 5). Even at a moderate level of 38dB the forward masking almost vanished beyond delays of -100 µs.

4. DISCUSSION

Velmin and Dubrovskiy [1] found that a backward masker of 46 dB (above absolute threshold) did not affect the detection of a click if the delay was greater than approximately 500 µs. The authors concluded that the "strong interaction" of the signal and masker in the dolphin auditory system occurred at delays shorter than 300 µs. However, our results show that the masking threshold strongly depends on the masker level. The lower masker level the shorter threshold delay. At a 20 dB masker level, for instance, there is no masking effect at all for delays as short as 20 µs.

Actually it is not clear at which point on the backward masking function the time resolution estimate should be made. For a signal-to-noise ratio of -36 dB (ratio from Velmin & Dubrovskiy [1]) the threshold delays from Fig. 6 are close to 20 and 150 µs (for masker levels of 36 and 47 dB respectively). At a -17 dB signal-to-noise ratio (from Moore et al. [6]), threshold delays of 20 and 60 µs correspond to 20 and 4000 µs masker duration (Fig. 5). It seems more definite to choose an absolute (0dB) threshold as a reference point for estimating of the time resolution. The threshold delay at this threshold level defines a time limit for interaction between signal and masker in the auditory system. Yet again, this delay depends on the masker level and ranges from 20 to 300 µs. By definition the time resolution is a time interval between two acoustic events of equal amplitude. For a signal-to-noise ratio close to 0 dB the threshold delay was about 20 µs at all tested masker levels.

Moore et al. [6], using a noise phantom masker of 1000 μs, found their backward masking results to be consistent with the critical interval concept. They arrived to the same threshold delay of 265 μs at a signal-to-noise ratio 20 dB lower than that of Velmin and Dubrovskiy [1], which is likely the result of a difference in the masker duration (Fig. 5). A long noise masker produced the same amount of masking as a short masker because the latter was much more intense. Therefore, the coincidence of the two threshold delays is incidental. The critical interval as it was determined from the backward masking results is likely to be just one point from an infinite set of threshold delays, corresponding to different combinations of intensity and duration of a masker.

No indication of the critical interval was found at the dolphin's discrimination of the noise double pulses. The dolphin TP72-78, that had previously shown irregularity at double click discrimination, attributed to the critical interval phenomenon, Velmin & Dubrovskiy [1], Zanin & Zaslavskiy [3], produced a continuous discrimination function (Fig. 1, TP72-78, t = 85 μs) for the noise double pulses, Zaslavskiy & Ryabov [8]. The DLI jump at 100μs for the noise double pulses was found to be the result of dolphin's transition from interpulse intervals to double pulse durations discrimination (from onset of the first pulse to offset of the second). There is a probability that in our previous experiments with correlated pulses, Zanin & Zaslavskiy [3], the dolphin had also switched between the two temporal discrimination cues. Therefore, the irregularity in the dolphin's performance can not identify the critical interval as the time resolution of its sonar.

There is divergence of DLI between noise double pulses from that of between correlated double clicks at interpulse intervals shorter than 40 - 50 μs (Fig. 2, TM78-90, double clicks). We suggest that at short intervals, dolphin TM78-90 distinguished the correlated double clicks in the frequency domain, whereas the time domain cues were used for discrimination of the noise double pulses (see "Double click representation in the dolphin auditory system" by Zaslavskiy, this volume). This does not signify that the dolphin was incapable of distinguishing the correlated double clicks in the time domain. He probably chose between the two and selected the more suitable domain for the specific conditions. Because there was no such option for the noise stimuli, the dolphin was compelled to use the time domain cues, which resulted in the DLI increase at short interpulse intervals (Fig. 2, TM78-90, noise double pulse, t = 10 μs).

Although DLD was approximately twice as much as DLI, both grow abruptly below 20 - 30 μs. The increase of the two indicates an approach to the time resolution of the dolphin auditory system.

The increase of amount of backward masking with masker duration is likely to be the result of an integration process in the dolphin's auditory system. What might seem strange is that the integration time proved to be shorter than 150 μs (Fig. 5). The amount of the backward masking remained practically the same after the masker duration had been further increased up to 4000 μs. There are two more estimates of the integration time of the dolphin hearing, about 500 μs, Zanin at el. [7], and 264 μs, Au et al. [8], acquired with similar behavioral procedures and stimuli. The 150 μs estimate can indicate that the dolphin integration time depends on the hearing task.

The auditory system time resolution of 20 - 30 μs proved to be very close to the theoretical time resolution of dolphin sonar clicks of 12 to 15 μs, Au [9]. The two values match up perfectly with the broad frequency range of the dolphin hearing. The dolphin shows remarkable performance in the time domain analysis of very short noise pulses. Its ability to measure interpulse interval and pulse duration remains high at amplitude difference between stimuli as high as 30 - 40 dB. The dolphin is capable of ignoring the envelope's shape of a noise stimulus at measuring interpulse interval or pulse duration. This signifies that the dolphin pays no attention to amplitude spectra of the noise stimuli.

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