TEMPORAL ORDER DISCRIMINATION IN THE DOLPHIN

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1. ABSTRACT

The dolphin's discrimination between the mirror image double-clicks comprised of a small and a large click was studied. Threshold differences in the click amplitudes were measured as a function of the interclick interval. The dolphin was also able to discriminate between a forward and a reverse order of a small and a large noise pulse at the pulse separation as small as 20μs.

KEY WORDS: discrimination; temporal order; identical energy spectra; time resolution

2. INTRODUCTION

The Black Sea bottlenose dolphin was able to distinguish the double-click comprised of a small and a large click from its time-reversed replica [1]. Despite differences in the waveform, the mirror image double-clicks had identical energy spectra. A minimum interclick interval of around 3 ms, at which humans were able to discriminate between the double-clicks, can be associated with the time resolution of the auditory system [2]. The dolphin, however, discriminated between the double clicks at an interclick interval as small as 5 μs. For interclick intervals smaller than 200 μs, the difference in the first and second click amplitudes had to be at least 14 dB for the dolphin to discriminate between the double-clicks. For greater interclick intervals, there was a noticeable drop in the threshold amplitude difference between the first and second clicks of the mirror image double-clicks [3]. It was concluded that at intervals greater than a critical interval of around 300 μs, the dolphin discriminated the stimuli by a difference in the order of the small and large pulses.

The Atlantic bottlenose dolphin also discriminated between the mirror image double-clicks although its performance was just slightly above the 75% correct response level [4]. Johnson *et al.* [4] assumed that the dolphin could not temporally separate the clicks at the tested 200 μs interclick interval and chose to concentrate on the frequency domain cues. Windowed FFT analysis was used to demonstrate the difference in a short-time spectrum of a direct and a time-reversed double click. A chi-square function with 90 % decay by 300 μs was used for the analysis. For a 200-μs interval and a 10-dB difference in the click amplitude, the 300-μs chi-square window strongly enlarged the actual ripples for one double-click and diminished the rippling in the reverse double-click. After the second click entered the window, the differences in the short-time spectra became similar to the differences in a flat energy spectrum of a single click and rippled spectrum of the double-click comprised of equal clicks.

The order of the small and the large clicks is an obvious time domain cue for the double-click discrimination at long interclick intervals. However, for interclick intervals smaller than the auditory time resolution of around 25 μs, [7, 8], the time domain differences between the double-clicks cannot be described in such simple terms. Theoretically, the mirror image double-clicks could easily be identified by their phase spectra.

We found it necessary to replicate the threshold measurements made by Dubrovskiy et al. [1]. The smallest and the biggest differences in the amplitude of the first and the second clicks at which the dolphin was able to discriminate between the double-clicks were measured. We also examined whether the dolphin would be able to distinguish the double-pulse comprised of a small noise pulse followed by a large noise pulse from its time-reversed counterpart. The noise double-pulses were not mirror image signals because the first and the second noise pulses were uncorrelated. In contrast to the mirror image double-clicks, the noise double-pulses have random amplitude and phase spectra. It appeared that the only way to discriminate between the noise double-pulses was the auditory analysis of the pulses in the time domain.

3. MATERIALS AND METHODS

The subjects were three the Black Sea bottlenose dolphins (*Tursiops truncatus*). The experiments were conducted in a 28 × 13 × 4 m concrete pool. A two-response forced-choice procedure was used. A vertical net partition set a minimum distance of 5 m from which the dolphin was forced to make its choice. The transducers were situated on either side of the partition at 1m depth and 3 m from each other. Prior to stimuli presentation, the dolphin positioned itself at the far (from the transducers) end of the partition. Having made its choice, the dolphin approached the transducer, which was transmitting a standard signal.

Spherical transducers of 1.2 cm in diameter were used. The maximum of the transducer transmitting response to voltage was at 110-120 kHz. The transducers transformed pairs of electrical 2-μs pulses (figure 1) into pairs of 25-μs acoustic clicks. The double-clicks were transmitted simultaneously through both transducers. The sensation level of the signals was 30 to 60 dB. The stimuli repetition rate was 3 – 5 per second. Threshold values were measured with the method of constant stimuli at a 75% correct response level. The animals performed 250-350 trials per session. The experimental results from the last 3 – 4 sessions were averaged for each threshold estimate.

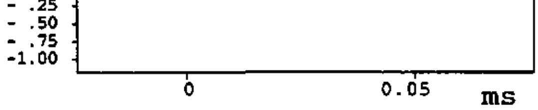

Figure 1. A double-pulse and its mirror image counterpart (on the electrical side of a transducer).

In the first series of experiments, the maximum and minimum threshold differences in amplitude of the first and second clicks were determined as functions of the interclick interval. The dolphin was trained to approach the transducer transmitting the double-click comprised of a small click followed by a large click (a standard double-click).

In the second series of experiments, a threshold signal-to-noise ratio in a band-pass noise 10-100 kHz (figure 2) was measured for the double-clicks as a function of the interclick interval.

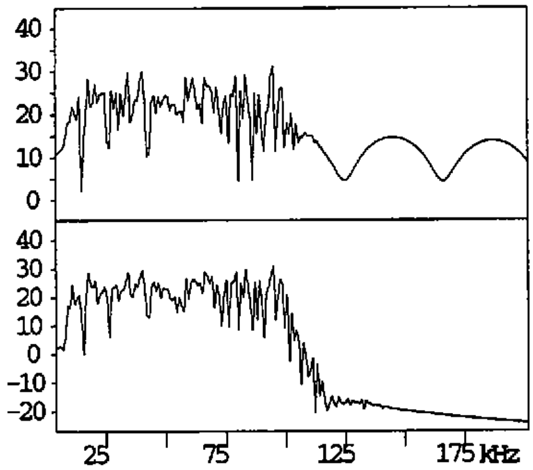

Figure 2. Energy spectra of the double-click mixed with band-pass noise 10-100 kHz (upper block) and the noise alone (bottom block). The interclick interval in the "plus-minus" double-click was 25 μs. The noise level was 6 dB lower than the threshold one. Computer simulation for a 256-μs block size. Y-axis is in dB.

In the presence of the noise, the dolphin was forced to use frequencies of the double-clicks in between 100 kHz and its upper hearing limit of around 130 kHz. As the interclick interval changes, one minimum of the double-click energy spectrum leaves the unmasked frequency range and others enter it. Two types of the mirror image double-clicks were used. The first type, which we named "plus-plus" double-click, was produced by the transducer in response to the pair of electrical square pulses of the same polarity (figure 1). The double-clicks of this type were used by Dubrovskiy et al. [1]. The other type was the transducer response to the pair of square pulses of opposite polarity ("plus-minus" double-click). The frequency spectrum of the double-clicks of the two types differed in the position of the minima and maxima. For equal interclick intervals, the maxima of the energy spectra of the "plus-plus" double-clicks corresponded to the minima of the energy spectra of the "plus-minus" double-clicks (figure 3). If the dolphin analyzed the frequency spectra around the spectrum minimum, the signal-to-noise ratio should be a function of the interclick interval and different for the two types of the double-clicks.

Using simultaneous masking with the band-pass noise 10-100 kHz and a narrow band noise, we then determined the auditory frequency response during the dolphin discrimination between the double-clicks. The narrow band noise was produced by filtering the broadband noise through a second-order LCR resonator with adjustable center frequency. The frequency response of the resonator dropped by 40 dB per octave from the center frequency. The "plus-minus" double-clicks of a 25-μs interclick interval with the third minimum in the frequency spectra at 120 kHz were used. The difference in the click amplitude of the double-clicks was 6 dB. The level of the band-pass noise was constant and high enough to prevent the dolphin from using the frequencies below 100 kHz. The auditory frequency response was measured in terms of the threshold signal-to-noise ratio as a function of the center frequency of the narrow band noise.

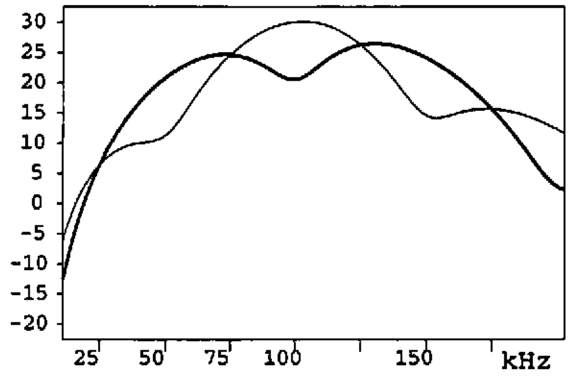

Figure 3. The amplitude spectra of the "plus-plus" (thin line) and "plus-minus" (thick line) double-clicks of 10-μs interpulse interval. Difference in the amplitude of the first and second clicks is 6 dB. Corrections were made for the transducers transmitting response. Y-axis is logarithmic, displayed in dB.

In the last series of experiments, the dolphin's discrimination between the noise double-pulses with reverse order of the small and large noise pulses was studied (figure 4). The broadband 15-μs noise pulses (at the electrical side of the transducer) were used. The difference in amplitude between the first and the second pulses was 6 dB. Even for the same interpulse interval, the noise double-clicks were no longer mirror image signals. In contrast to the mirror image double-clicks, the noise double-clicks had random amplitude and phase spectra. It appeared that the only way to discriminate between the noise double-clicks was the time domain analysis by measuring amplitude of the pulses.

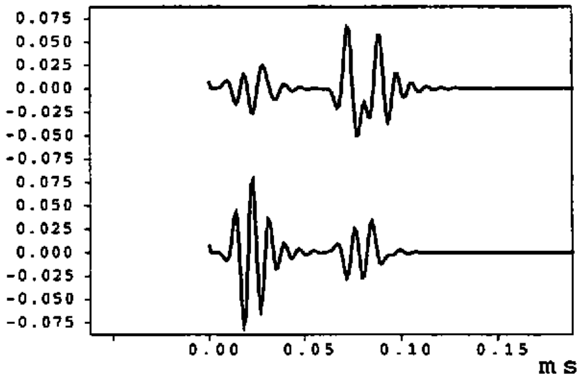

Figure 4. One of the realizations of the noise double-pulses with reversed temporal order of the small and large pulses (at the acoustical side of the transducers).

The dolphin discrimination performance as a function of the interpulse interval was studied. The minimum interpulse interval at which the dolphin was able to discriminate between the noise double-pulses was measured. The interpulse interval was gradually decreased until the discrimination dropped to the 50% correct response.

4. RESULTS AND DISCUSSION

4.1 Threshold difference in the click amplitudes

A minimum (MinD) and a maximum (MaxD) threshold difference in amplitude between the first and second clicks of the double-click are presented in figure 5 as functions of the interclick interval.

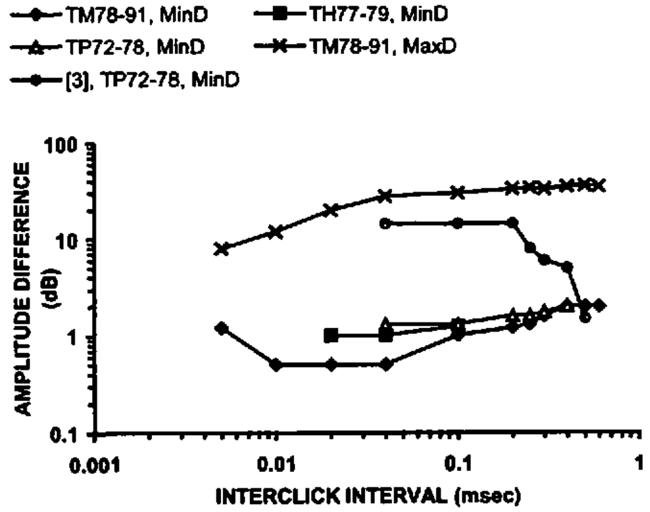

Figure 5. Minimum and maximum threshold amplitude differences between the first and second clicks of the double-click versus interclick interval. The sensation level of a large click was 40 dB.

Within the range of the amplitude differences limited by the top and bottom curves, the double-clicks were distinguishable for the dolphins. The MinD ranged between 0.5 and 1.5 dB, which is much smaller than was previously measured by Dubrovskiy (figure 5, [3], TP72-78, MinAD).

The MinDs were close to the dolphin's intensity discrimination threshold. In fact, for dolphin TM78-91, they were even smaller than the intensity threshold. Each time when we switched from double-click discrimination to the discrimination of single clicks of different amplitude, the threshold amplitude difference increased by 1-1.5 dB. It seemed easier for the dolphin to determine an amplitude difference between the first and second clicks of the double-click, than between single clicks, coming from two different directions (from a left side and a right side transducer).

The MaxD increased by 20 dB with an interclick interval increase from 5 µs to 40 µs and only by another 10 dB further up to 800 µs (figure 5). The steep threshold change may indicate the approach of the interclick interval to the auditory time resolution, or even passing this time limit. For interpulse intervals greater than 30 µs, the amplitude of a small click of the double-click was as low as the absolute threshold for a single pulse, even for threshold amplitude differences greater than 30 dB. This suggests that the dolphin simply detected a small click before the large one. High auditory time resolution appears to allow such detection for interclick intervals as small as 20-30 µs. Such a auditory time resolution, however, is clearly not sufficiently high to allow recognition of the double-clicks for shorter interclick intervals.

4.2 Masked thresholds

The dolphin discriminated between the double-clicks as long as within frequency range of its hearing there was at least one spectrum minimum unmasked by a band-pass noise. In the presence of the band-pass noise from 10 to 100 kHz (figure 2), the masking noise level changed with the interclick interval as shown in figure 6.

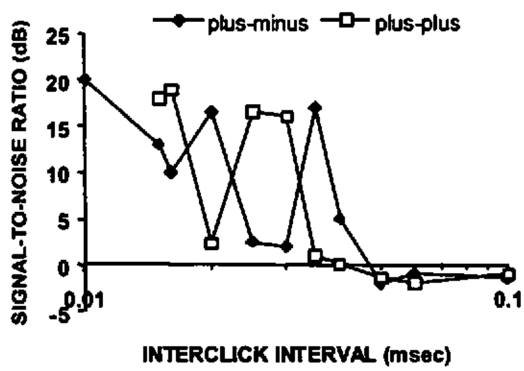

Figure 6. Threshold signal-to-noise ratio versus interclick interval. The difference in amplitude between the first and second clicks in the double-click is 14 dB. The peak amplitude of a small click is compared with the root-mean-square amplitude of masking broadband (10 - 100 kHz) noise.

A strong masking occurred each time the energy spectrum minimum was covered by the noise. Otherwise, when the minimum was above 110 kHz and below the dolphin's upper frequency limit of around 137 kHz, the masking was considerably weaker. Where strong masking occurred for the "plus-plus" double-clicks, there was weak masking for the "plus-minus" double-clicks and vice versa. It was only to be expected because the minima of the energy spectra of the plus-plus double-click corresponded to the maxima of the "plus-minus" double-click and vice versa. For interclick intervals greater than 40 µs, the masking was weak for both types of double-clicks because there always was at least one unmasked minimum within the dolphin hearing range above 100 kHz.

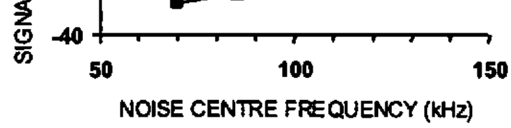

Figure 7. Threshold signal-to-noise ratio versus central frequency of the narrow band noise. The interclick interval was 25 µs. The amplitude difference between the first and second clicks was 6 dB. The peak amplitude of a small click was compared with the root-mean-square amplitude of the noise.

The results of simultaneous masking of the double-pulses with the band-pass noise (figure 2) and the narrow band noise are presented in figure 7. The masking of the double-clicks with the narrow band noise was strongest at frequencies of 120-130 kHz. The masking curve is narrow enough (around 15 kHz at 3-dB level) to be associated with a single auditory filter. Au and Moore [5] found the critical ratio and critical bandwidth at 120 kHz to be around 17 kHz and 45 kHz respectively. A slightly smaller critical ratio of around 10 kHz was measured at 100 kHz [6, 5]. Even if two auditory filters cover the frequency range used by the dolphin, it is apparently not enough to analyze the double-click phase spectra. On the other hand, the double-clicks can be recognized in the time domain using a single auditory filter. If the filter passband covers a minimum of the amplitude spectra of the double-clicks, the waveforms of the filter reaction to the direct and reversed double-clicks are different (figure 8).

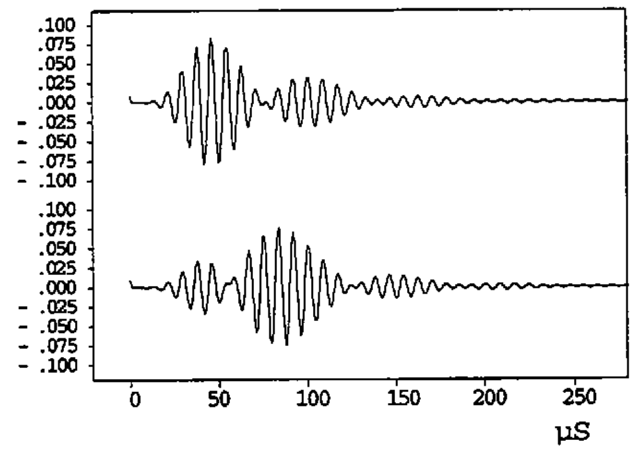

Figure 8. Computer simulated reactions of the filter, described by the masking curve presented in figure 7, to the "plus-minus" double-clicks. The interclick interval was 25 µs.

4.3 Noise double-pulses

After the correlated mirror image double-clicks were suddenly replaced with the noise pulses, the dolphin TM78-91 continued to readily discriminate between the noise double-pulses (figure 4). It chose the double-pulse with a small pulse followed by a large pulse to be a positive stimulus, i.e. the temporal order of the pulses identical to that of the clicks in the standard double-click. It looked like the dolphin continued to use the same discrimination cue, which it previously used for the mirror image double-clicks. The dolphin was able to discriminate between the noise double-pulses at interpulse intervals as small as 20 µs (figure 9), which is practically equal to the estimate of the dolphin auditory time resolution, [7, 8].

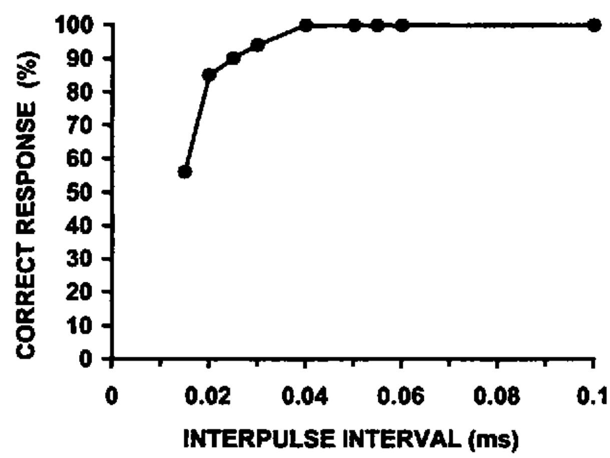

Figure 9. Dolphin discrimination between the noise double-clicks as a function of the interpulse interval. Dolphin TM78-91.

5. CONCLUSIONS

The time domain analysis appears to explain the dolphin's ability to discriminate between the mirror image double-clicks. The dolphin analyzed the double-clicks within a frequency band of at least 15 kHz around the minimum of the double-click energy spectrum, at the frequencies of characteristic differences in the phase spectra. The frequency band was narrow enough to be associated with a single dolphin auditory filter. The dolphin was able to discriminate between the noise double-pulses with reversed temporal order of the small and large pulses at interpulse interval as small as 20 μs. This threshold interval appears to be an estimate of the time resolution of the dolphin's auditory system. The results suggest that the dolphin discriminated between the time domain waveforms of the auditory filter reaction to the direct and reversed double-clicks. The dolphin's ability to discriminate between the mirror image double-clicks at very small interclick intervals might result from even more precise time domain analysis than can be described by the time resolution constant.

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