100-µS TIME INTERVAL OF THE BOTTLENOSE DOLPHIN AUDITORY SYSTEM

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1 INTRODUCTION

The bottlenose dolphin's auditory time resolution is believed to be limited by the auditory integration time of around 300 µs [1-3]. The 300-µs time interval is considered to be a fundamental constant of the bottlenose dolphin hearing, which determines the auditory analysis of brief signals. As long as time highlights in target echoes are separated by less than around 300 µs, dolphins are thought to discriminate the targets based on differences in the echo frequency spectra. There are several models of echo-processing in bottlenose dolphins based on the 300-µs critical interval of the dolphin hearing. The set of hierarchically organized, independent features defined by the different scale of a click energy spectrum variation was introduced [4, 5].

Contrary to this widely accepted view we found that a bottlenose dolphin was able to discriminate double clicks with different energy spectra (Fig. 1) only if interclick intervals were shorter than around 100 µs [6, 7]. At interclick interval longer than around 100 µs a pair of clicks appears to disintegrate for the dolphin into two separate acoustic events. However, this interval seems to be involved in brief signals auditory analysis in much more complicated way. Surprisingly, the dolphin was able to discriminate the double clicks even when interclick intervals and energy spectra of the double clicks varied during a trial. In this paper we discuss some differences in the dolphin's response to the double clicks with constant and variable interclick intervals.

2 METHODS

The subject were two the Black Sea bottlenose dolphins (*Tursiops truncatus*). Experiments were conducted in a 28 × 13 × 4 m concrete pool. The two-response forced-choice procedure was used. A vertical net partition between two transducers set a minimum distance of 5 m, from which the dolphin was forced to make his choice. Signals were transmitted simultaneously through transducers situated 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. 1.5-cm piezoelectric spheres were used as transducers. The maximum of the transducer transmitting response was at 110-120 kHz. Standard analog electronic equipment was used to produce stimuli. Masking noise was mixed with the stimuli and transmitted through the same transducers. Periodic stimuli were presented to a dolphin at a repetition rate of 2 to 5 stimuli per second.

Threshold measurements were made using a method of constant stimuli. Signals were presented in 10-trials blocks with the same signal parameters repeated in every following trial. A 2 to 3-dB decrement in difference between a standard and test signal, depending on experimental task, was used to move between the 10-trials blocks. The dolphins performed 250 to 400 trials per session. Threshold measurements were completed when over at least 3 consecutive sessions threshold values were within 3 dB of each other. The threshold values from those sessions were averaged for a threshold estimate at a 75% correct response level.

The dolphins in our experiments were usually allowed to choose a stimulus to be a positive (conditioned) stimulus. At the start of a session or after experimental conditions change, the dolphin would be rewarded for approach to any (left or right) transducers transmitting two different stimuli.

If the stimuli were different enough, the dolphin would reveal its preference in 2 – 3 trials. After that only approach to a chosen stimulus was reinforced. The freedom of the choice allowed the dolphin to maintain the same recognition pattern in different experimental conditions. The change of a positive stimulus that followed the change of interclick intervals discussed in this paper was an indication of a specific cue used by the dolphin to discriminate the double clicks.

3 RESULTS

3.1 Constant interclick intervals

Initially the double clicks with equal interclick intervals (Fig. 1) were used to determine a bottlenose dolphin's auditory frequency resolution [6, 7]. One double click was composed of two identical clicks, in the other one click was phase shifted by 180° (amplitude-inversed clicks) relative to the other (Fig. 1). During a trial, the interclick intervals were constant, so that there were regular differences in the double click frequency spectra. At equal interclick intervals, the amplitude spectra of the pairs are rippled with the same period however maxima of one spectrum correspond to minima of the other. It is clear that the frequency spectra differences could only be generated if the first and the second clicks interfere with each other in the dolphin's auditory filters. Short-time Fourier transforms (STFT) of the double clicks with 100-µs intervals, for example, are clearly different if they are generated using a 300-µs analysis window, whereas STFT-spectrograms generated with a 100- µs integration window are practically identical.

It was expected that dolphin would be able to discriminate the double clicks as long as interclick interval was shorter than some threshold interval determined by the auditory frequency resolution. For interclick intervals longer than a threshold interval, the double click should disintegrate for the dolphin into two separate and identical acoustic events.

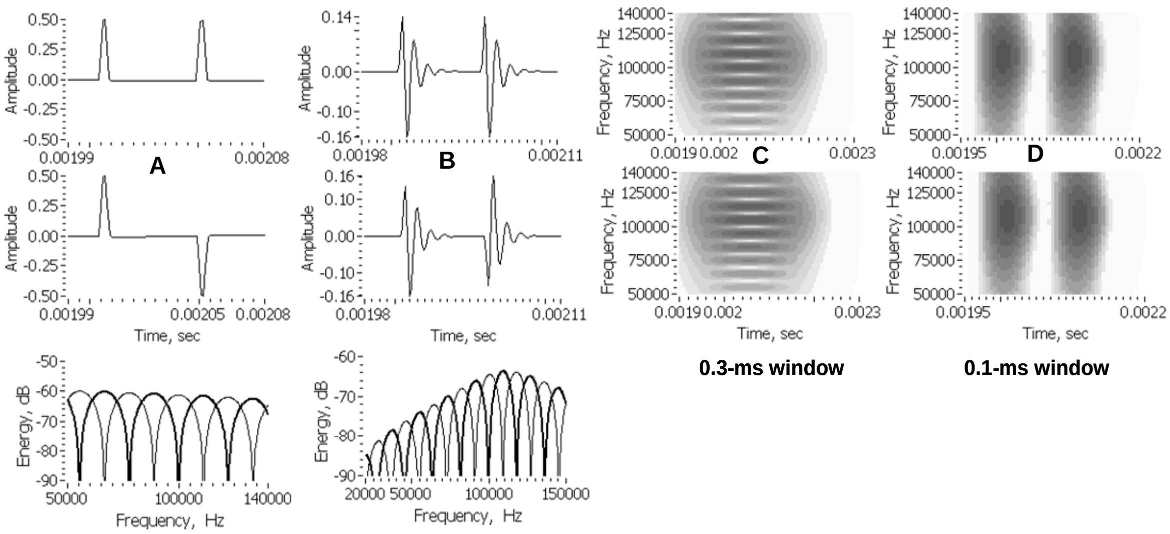

Figure. 1. Computer simulated waveforms of double clicks with identical intervals but different frequency spectra at the electrical (A) and the acoustical (B) side of the transducers. Y-axes are in volts. (C) and (D) – STFT spectrograms generated for the double clicks with 100- µs interclick intervals using a 300 and 100- µs Hanning analysis window and 2-µs time increment. Darker areas correspond to higher energy. Bottom frames are superimposed energy spectra of the double clicks.

The largest interclick interval for which the dolphins were able to discriminate the double clicks with constant interclick intervals (Fig. 1) was found to be 100-110 µs (Fig. 2). A 10-kHz ripple separation in the double click energy spectrum corresponding to the threshold interclick interval represents the frequency resolution of the bottlenose dolphin auditory system for brief signals. This frequency resolution estimate agrees well with the auditory filter bandwidths at high frequency of the bottlenose dolphin hearing range [3].

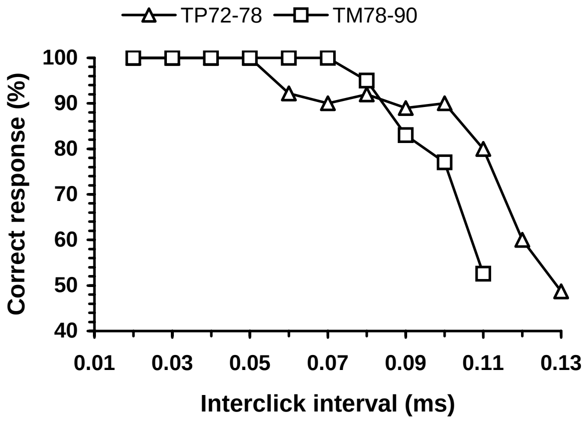

Figure. 2. Discrimination of the double clicks with constant interclick intervals and different frequency spectra as a function of the interclick interval by two bottlenose dolphins.

A double click appears to disintegrate for the dolphin into two separate acoustic events at interclick interval longer than around 100 µs. In this respect, the 100- µs threshold interval can also be the estimate of the time resolution of the bottlenose dolphin’s auditory filters.

Furthermore, as long as the first and second clicks interfere in the auditory filters producing different energy spectra, the waveforms of a single filter reaction to the comparison double clicks are also different. It appears that the dolphin indeed discriminated the waveforms of an auditory filter reactions, because he was able to discriminate the double clicks masked with bandpass noise from 10 to 100 kHz and narrow band noise with center frequency of 130 kHz (Fig. 3D). Despite that most of the hearing frequency range was masked with the noise, the threshold interclick interval was found to be around 100 µs which is the same as that for the double click discrimination in quiet.

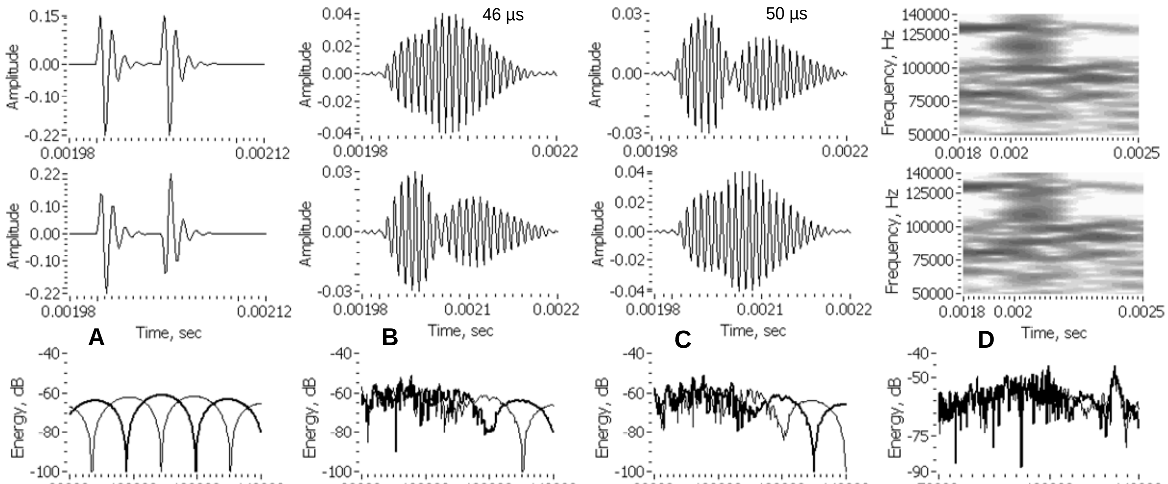

Figure. 3. Bandpass filter (125-135 kHz, 2-order, Butterworth) reactions to the double clicks (A) with interclick intervals 46 µs (B) and 50 µs (C). Double clicks in (B) and (C) were masked with bandpass noise 10-100 kHz. (D) - STFT spectrograms generated the double clicks masked with bandpass noise 10-100 kHz and narrow band noise with a center frequency of 130 kHz using a 300 µs analysis window and 2-µs time increment. Bottom frames are superimposed energy spectra of the stimuli in top frames.

The frequency range from around 110 to 125 kHz free of noise is narrow enough to be associated with a bandwidth of the bottlenose dolphin's auditory filter at high frequencies [3]. Computer simulation shows that reactions of a bandpass filter (125-135 kHz, 2-order, Butterworth) to the first and second click interfere with each other producing differences in the filter reactions to the comparison double clicks (Fig. 3B and 3C). A low and high fragment in the filter reaction to the comparison double clicks comes in reversed order. Clearly, amplitude difference between the first and second fragments (Fig. 3B and 3C) in the filter response is only generated if interclick intervals are shorter than the filter impulse response. For interclick intervals longer than around 100 µs the filter responses to the double clicks are almost identical because the reactions to the first and second click no longer interfere with each other.

When the dolphin's choice of an auditory filter for the double click analysis was restricted by the masking noise to a narrow frequency range, the dolphin sometimes changed a positive stimulus when interclick intervals were altered between, for example 46 and 50 µs (Fig. 3B and 3C). Due to interclick interval change, the waveform of the filter reactions to the double clicks also changed. The dolphin always chose the double click, to which the filter reaction apparently consisted of a low amplitude fragment followed by a high amplitude fragment, for example top reaction in Fig. 3B and bottom reaction in Fig. 3C.

In the absence of the bandpass noise, the dolphins also often chose different double clicks to be a positive for different interclick intervals. Giving the very broad frequency range of the dolphin's hearing, the dolphin could change the position of an auditory filter to be used to compare the filter reactions to the double clicks. Therefore, the waveform of a single filter reaction to the double click could change as a result of both the change of interclick interval and position of the auditory filter.

3.2 Variable interclick intervals

To further verify suggestion that the dolphins discriminated the frequency spectra of the double clicks, the dolphins were presented with the double clicks having interclick interval randomly and independently changed during a trial (Fig. 4). It appeared that if the dolphin discriminated frequency spectra of the double clicks or the double click waveforms at the output of a single auditory filter, the interval variation during a trial would make the discrimination impossible because, as a result of the interval variation, the frequency spectrum also considerable varied (Fig. 4B).

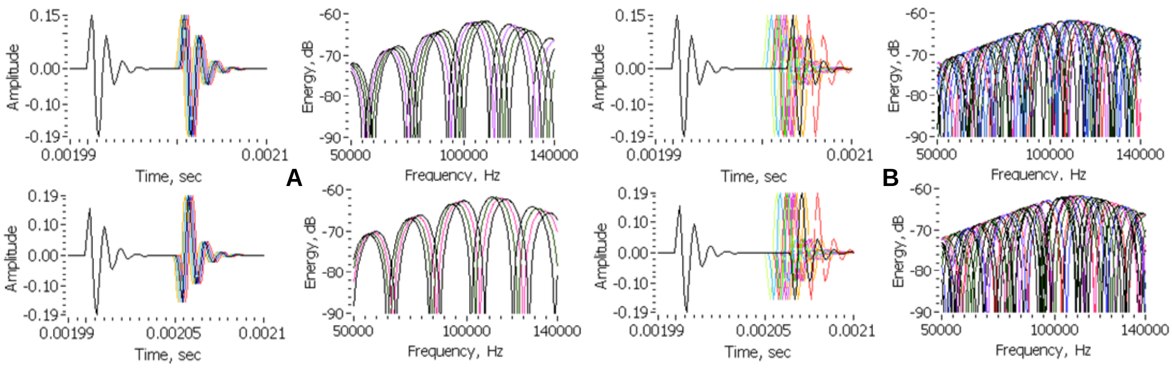

Figure. 4. Superimposed waveforms and energy spectra of 10 consecutive double clicks for interclick interval variation of around 4 µs (A) and 30 µs (B). Y-axes are in volts but proportional to acoustic pressure.

In first two sessions the interclick interval variation larger than 3-4 µs indeed disrupted the dolphin's discrimination of the double clicks. As long as the variation was small enough, there were regular differences in the energy spectra between the double clicks (Fig. 4 A). However, by the end of the second session the dolphin readily discriminated the double clicks when interclick interval variation was as large as 30-50 µs (Fig. 4B). Another tested bottlenose dolphin was also able to discriminate the double clicks with randomly changed interclick intervals.

The largest interclick interval for which dolphins were able to discriminate the double clicks with variable intervals was found to be the same as that for the double clicks with constant interclick intervals. Dolphins discriminated the double clicks as long as during a trial at least some of variable intervals were shorter than around 100 µs.

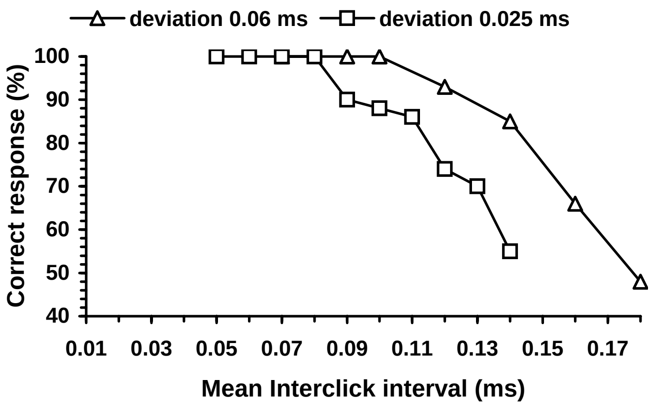

Figure 5. Discrimination of the double clicks with variable interclick intervals as a function of the mean interclick interval. The interval deviation from a mean interval was ± 25 µs and ± 60 µs. Bottlenose dolphin (TM78-90).

The larger was the interclick interval deviation from a mean interval, the larger was the threshold mean interval. For a ±25-µs interval deviation the threshold mean interval was about 120 µs. For a ±60-µs interval deviation, the threshold median interval was almost 150 µs (Fig. 5). At the stimuli repetition rate of 3-5 per second and trial duration of 5 to 10 seconds, some of randomly changed from 90 to 210 µs interclick intervals were smaller than 100 µs.

Parity of the threshold interclick intervals suggests that the cue used by dolphins to discriminate the double clicks with variable intervals was the same as that to discriminate the double clicks with constant intervals. However, how could the dolphin discriminate the double clicks with randomly changed interclick intervals and energy spectra?

Although the threshold intervals were the same, there were some differences in the dolphin response to the double clicks with constant and variable interclick intervals. Contrary to the double clicks with constant intervals, when discriminating the double clicks with variable intervals, the dolphin always chose the double click consisted of identical clicks (Fig. 1A and 1B, top frames) to be a positive stimulus.

Perhaps more important difference was that, in order for the dolphin to discriminate the double clicks with variable intervals, the frequency range available for double clicks analysis had to be as wide as 70-80 kHz (Fig. 6C and 6D) compared to only 15-20 kHz range (Fig. 6A and 6B) that the same dolphin needed to discriminate the double clicks with constant intervals. The dolphin was able to discriminate the double clicks with variable intervals as long as the masking bandpass noise was limited to the frequencies below 40-50 kHz (Fig. 6C and 6D). Further broadening of the noise above 50 kHz disrupted discrimination of the double clicks.

It does not seem possible to discriminate either the energy spectra or reactions of a single auditory filter to the double clicks having variable interclick intervals. We couldn't find a better suggestion than that the dolphin somehow was able to perceive the first and second clicks separately in time so that discrimination cue was not a product of the clicks interference with each other but rather belonged to each of the clicks. There are many facts obtained in behavioral experiments which indicate that the bottlenose dolphin's auditory time resolution is as high as around 20 µs [7-12], so they are capable of perceiving the first and second clicks (Fig. 1) as two independent acoustic events. The wide frequency range required for the dolphin to be able to discriminate the double clicks (Fig. 6C and 6D) also suggested that the dolphin perceived the first and second clicks as two separate acoustic events. Clearly, to reach the auditory time resolution as high as 20-µs, the bandwidth of an auditory filter should be as large as at least 50 kHz.

If the dolphin perceived the clicks separately, it could discriminate the double clicks based on differences between the first and second clicks. In one double click the first and second click were identical; in the other they were amplitude-inversed (Fig. 1). Although the bottlenose dolphins are capable of discriminating the clicks with identical energy spectra but different waveforms [6-9], they are known to be unable to discriminate a single click from its amplitude-inversed replica [5]. However, the dolphin appeared capable of discriminating such clicks when they are presented in pairs at interclick intervals smaller than around 100 µs.

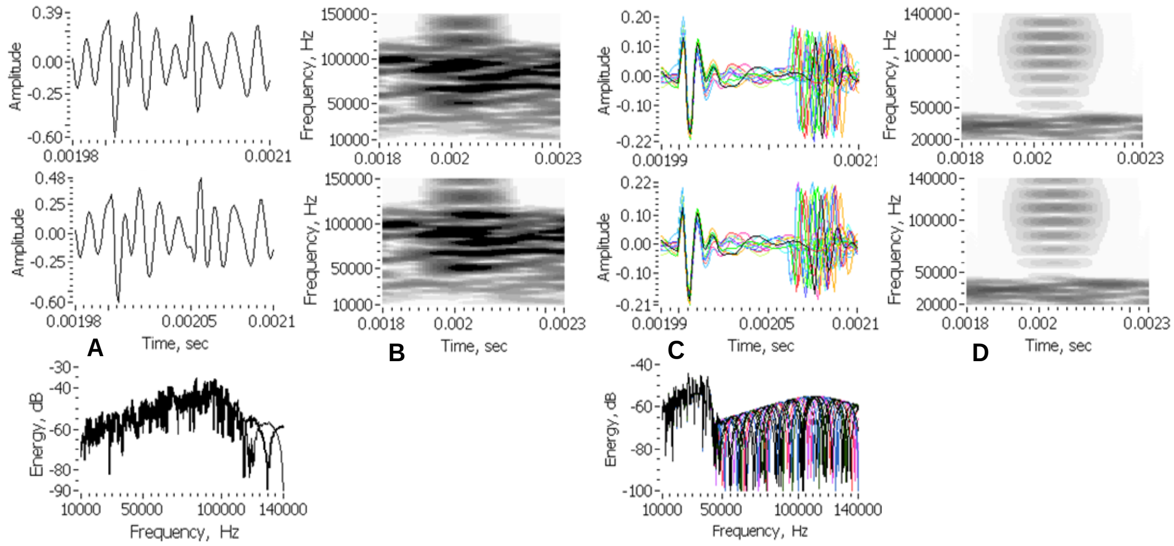

Figure 6. Double clicks with constant (A and B) and variable (C and D) interclick intervals masked with bandpass noise 10-100 kHz (A and B) and 5-40 kHz (C and D). (C)- Superimposed waveforms of 10 consecutive double clicks. Signal-to-noise ratio was about 3-dB above the threshold. (B) and (D) – STFT spectrograms generated for the double clicks masked with the bandpass noise using 300-µs analysis window and 2-µs time increment. Bottom frames are superimposed energy spectra of the stimuli in top frames.

A straightforward suggestion could be that the dolphins somehow perceived difference in the initial phase of the first and second clicks. In one double click the clicks had had the same initial phase, in the other the first and second clicks were phase shifted by 180° (Fig. 1B). To test this suggestion, one more pulse was added to each double click as shown in Fig. 7B.

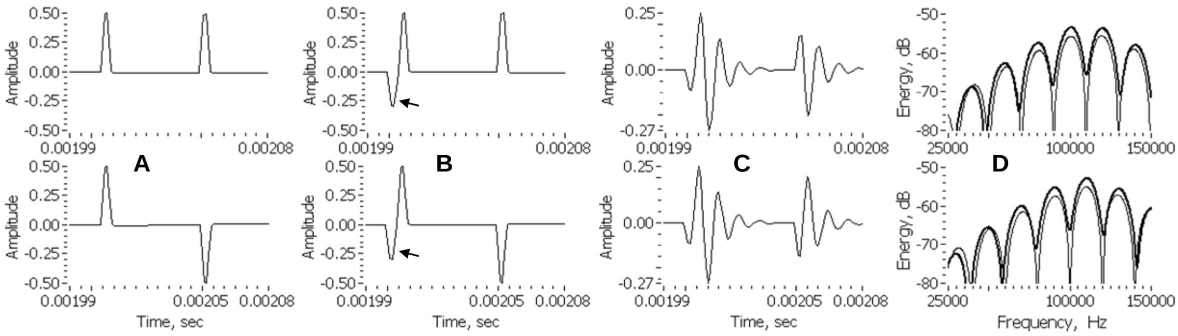

Figure 7. The pairs of electrical pulses (A), the same pairs with additional negative pulses (B, indicated by arrows) at the electrical and acoustical side (C) of transducers. (D)- Superimposed energy spectra of the double clicks A (thin lines) and triplets B (hard lines) at the acoustical side of transducers.

In the absence of the additional pulses, the dolphin always chose the top pair of pulses in Fig. 7A to be a positive stimulus. As the amplitude of additional negative pulses (Fig. 7B, indicated by arrows) was increased to more than around half amplitude of the adjacent positive pulses, the dolphin chose the bottom triplet to be positive stimulus (Fig. 7B and 7C). The additional pulses practically did not change energy spectra of the double clicks (Fig. 7D); at least there were no obvious changes which could reverse the dolphin's choice. Keep in mind that the double clicks in Fig. 7 are only for illustration because they are randomly taken out of sequence of the double clicks with variable interclick intervals (for example Fig. 4B). The interval variation during a trial should eliminate any regular differences in the energy spectra.

On the other hand, the additional pulses transformed the double click in which the first and second clicks had the same initial phase (Fig.7A, top double click) into the double click with the first and second clicks having opposite initial phase (Fig. 7B and 7C, top double click). In the other double click the first and second clicks with opposite initial phase were transformed into the clicks with the same initial phase. If the initial phase of the clicks was the cue for discrimination, the dolphin apparently had to change positive stimulus at certain amplitudes of the additional pulses. However, the additional pulses changed not only the initial phase of the clicks but also the waveform of the clicks. Our other experiments (not discussed here) indicate that the waveform of a single click play more important role than the click initial phase [8-13]. In any case, the dolphins consistently appeared to discriminate the double clicks based on differences between the first and second clicks perceived as two separate acoustic events. The reason why this kind of auditory analysis of the double clicks is restricted to interclick interval shorter than around 100 µs is unknown.

CONCLUSION

A 100-µs time interval appears to be important attribute of the bottlenose dolphin's auditory analysis, at least as far as brief signals are concerned. Threshold time interval of 100 µs corresponds to the 10-kHz threshold ripple separation in the double click energy spectra. The 10-kHz ripple separation in the double click energy spectrum represents the frequency resolution of the bottlenose dolphin auditory system for brief signals. At an interclick interval longer than around 100 µs a pair of clicks appears to disintegrate for the dolphin into two separate acoustic events. However, this interval seems to be involved in brief signals auditory analysis in a much more complicated way. The dolphins were able to discriminate the double clicks with different frequency spectra even when interclick intervals randomly and independently varied during a trial. And again, the discrimination was possible only if at least some of the interclick intervals were shorter than around 100 µs. Some significant differences in the dolphins discrimination of the double clicks with constant intervals and the double clicks with variable interclick intervals suggest different cues being used for discrimination.

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