The auditory time resolution in bottlenose dolphins: behavioral experiments versus auditory evoked potential methods

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Abstract: The bottlenose dolphin auditory time resolution of around 300 µs assessed using auditory evoked potentials (AEP) methods is generally believed to be in full agreement with behavioral measurements. In this paper we reassess some behavioral results which are believed to support AEP methods in light of numerous behavioral experiments indicative of the bottlenose dolphin time resolution as high as 20-30 µs. When behavioral results are evaluated according to the time resolution definition as a threshold interval between identical acoustic events, they all point to the bottlenose dolphin time resolution much higher than the AEP method limit of around 300 µs. Physiologically assessed modulation rate transfer functions (MTF) are compared to a bottlenose dolphin's perception of periodicity of a gated noise. The bottlenose dolphin appeared capable of perceiving periodicity of noise envelope as high as 15- 20 kHz. The auditory temporal analysis of brief signals in bottlenose dolphins seems to be inaccessible by AEP methods.

1   Introduction

In cetacean, fundamental physiological mechanisms common to all mammals appear to support much more extensive hearing capacity than that known for most terrestrial mammals [1, 2]. Auditory temporal resolution in bottlenose dolphins is believed to be around 300 µs, which is close the physiological limit imposed by the duration of a single nerve spike of hundreds microseconds. The bottlenose dolphin auditory 300-µs time resolution measured using AEP methods is claimed to be in full agreement with behavioral measurements [1, 2]. Results on auditory temporal summation, double clicks discrimination and temporal masking are taken to support the claim. A widely used physiological method to assess the dolphin's auditory time resolution is to measure ABR to a double click [1]. A rate of ABR recovery to a second click (test click) is believed to be a credible measure of the dolphin auditory time resolution. For the first click (conditioning click) and test clicks having equal intensity, complete recovery of ABR to the test click was observed for interclick interval of several ms, whereas just detectable ABR were recorded at intervals as short as 200-300 µs [1]. When the test click was smaller than the conditioning click, the ABR recovery time increased proportionally to the difference in intensities between the clicks.

Forward masking experiments [3] are frequently referred to as a basic proof of the bottlenose dolphin's time resolution of around obtained 300 µs in behavioral experiments. A signal and a backward masker were clicks similar to dolphin's echolocation clicks. Two dolphins discriminated between a single click and the pair comprised of a click and masker (Fig. 1A). Two different masking functions (Fig. 2, dolphin 1, dolphin 2) were obtained. From Fig. 2, Velmin and Dubrovskiy [3] chose a masker delay between 250 and 500 µs to be a measure of the temporal resolving power of the dolphin sonar. However, the masking functions do not have any irregularities between 100 and 500 µs and change gradually with the signal delay change. The backward masking functions produced a continuous sequence of the time resolution estimates as a function of the signal-to-noise ratio. The 300-µs estimate is only one of them, clearly not the best because it corresponds to a very low signal-to-noise ratio of around –36 dB (Fig. 2). For the signal-to-masker ratios of – 10 and –20 dB, for example, the time resolution estimates are 0.05 and 0.1 ms, respectively (Fig. 2, dolphin 2). By definition the time resolution is the shortest time interval between two acoustic events (two clicks) of equal amplitude and duration which could be perceived as separate acoustic events.
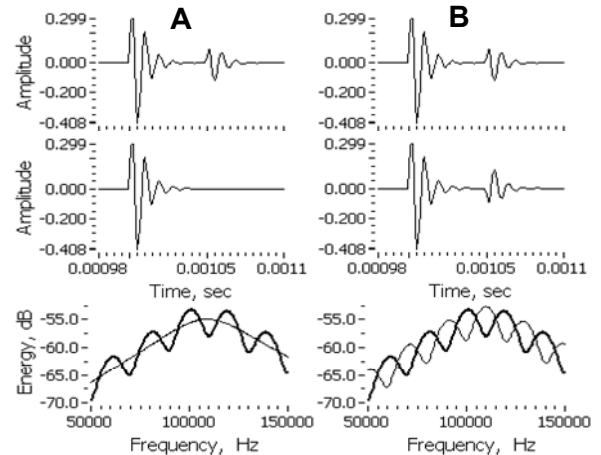

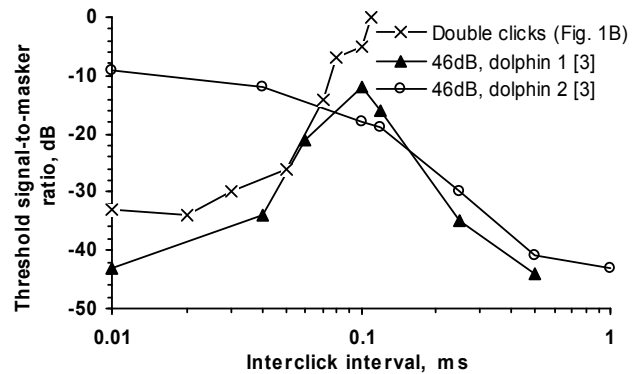Fig.1. Waveforms and energy spectra of the forward masking stimuli (A) and the double clicks (B).

Fig. 2. Forward masking as a function of the signal delay. The masker sensation level was 46 dB [3]. For the double clicks discrimination, Y-axis denotes threshold small-to-large click ratios.

The forward masking stimuli shown in Fig. 1A were readily discriminated by bottlenose dolphins [3-5]. Obviously, it would be impossible to detect any difference between ABR recordings to these stimuli simply because interclick intervals are much smaller than 300 µs and no ABR to a second click could be recorded. In fact, for a click-to-masker ratio of -36 dB [3] corresponding to a 300-µs time resolution estimate, no ABR to a second click could be recorded for delays shorter than 1- 2 ms [1] and it would be impossible to tell whether the dolphin discriminated the forward masking stimuli at all. Behaviorally assessed time resolution for a signal-to-masker ratio of -36 dB [3] or even -50 dB [6] is misleadingly compared with the time resolution estimate produced by ABR recording to a double click with the first and test clicks having equal amplitudes.

Furthermore, dolphin 1 (Fig. 2, dolphin 1) appeared to indicate auditory time resolution of about 100 µs quite

explicitly. For delays shorter than around 100 μs the amount of masking for dolphin 1 decreased with the delay decrease up to 10 μs. Sudden improvement in the dolphin's performance is a clear indication that the cues used by the dolphin to discriminate between a pair masker-signal and a masker before and after 100-μs delay were different. The negative slope above 100 μs is a typical for temporal masking, whereas the positive slope below 100 μs could indicate frequency discrimination. The smaller the delay, the larger the ripple separation in the energy spectrum of the pair masker-click and the easier to discriminate it from the flat spectrum of a masker (Fig. 1A) using a constant bank of auditory frequency filters.

A bottlenose dolphin discrimination of the double clicks with different interclick intervals [6] could hardly produce unambiguous indication of the discrimination cue because the stimuli differed in frequency spectra as well. To eliminate or at least to reduce time-frequency ambiguity for the dolphin we used the double clicks with equal interclick intervals but opposite polarity of second clicks shown in Fig.1B [5, 7]. At equal interclick intervals, the energy spectra of the double clicks are rippled with the same period however maxima of one spectrum correspond to minima of the other. The threshold small-to-large click ratio was measured as a function of interclick interval. The threshold small-to-large click amplitude ratio was found to be in inverse proportion to the interclick interval (Fig. 2, double clicks). Two other bottlenose dolphins tested in our experiments were able to discriminate the double clicks (Fig. 1B) with the first and second clicks having equal amplitudes only if interclick intervals were shorter than 100-110 μs. At intervals larger than around 100 μs a pair of clicks appears to disintegrate for the dolphins in two separate acoustic events. The 100-μs delay could be a measure of the time resolution of the bottlenose dolphin's narrow band auditory filters.

The threshold small-to-large click ratio as a function of the interclick interval was proved to be very similar to the forward masking function for signal delays shorter than 100 μs obtained for dolphin 1 [3] (Fig. 2). The differences between the energy spectra of the double clicks with identical interclick intervals (Fig. 1B) are larger, for corresponding interclick intervals and small-to-large click ratio, than between spectra of a pair click-masker and a single masker (Fig. 1A). Therefore, the threshold 100 μs interclick interval is also a threshold interval for frequency discrimination of the temporal masking stimuli (Fig. 1A). At the signal delays longer than around 100 μs, dolphin 1 (and of course dolphin 2) definitely discriminated the forward masking stimuli in the time domain. However, dolphin 2 appeared to continue discriminating the stimuli in time domain even at interclick intervals smaller than 100 μs. For any masker sensation level, the threshold delay is a function of the signal-to-noise ratio [5] and it can be as small as 20-30 μs.

Backward masking experiment by Johnson et al. [8] is also widely believed to support the 300-μs auditory time resolution. An Atlantic bottlenose dolphin detected a water-filled aluminium cylinder masked with wideband 1000-μs long noise pulse delayed by 100 to 700 μs relative to the target echo (backward masking experiment). The noise masker level was set so the target was just masked from the dolphin when the target echo was centered in the noise. This noise level corresponded to signal-to-noise ratio of -17 dB (noise above signal) which seems to contradict with other threshold measurements [9, 10]. The threshold signal-to-noise ratio for the bottlenose dolphin was found to be at least 6-8 dB (signal above the noise). The confusion might be partly because the authors did not specify which parameters of the echo and masker were compared. The dolphin detected the cylinder only if the noise masker was delayed by more than around 300 μs. But again for a higher signal-to-noise ratio a threshold delay should be smaller. This experiment produced the auditory time resolution for a specific signal-to-noise ratio as well as for the noise masker much longer than the target echo. In similar target detection experiments a bottlenose dolphin was able to detect a 4.0-cm solid steel sphere masked with a backward short click-masker delayed by less than 200 μs at signal-to-noise ratio as small as -50 dB [6]. For a noise temporal masker having the same duration as a click signal, the threshold delays could be as small as 40-60 μs even for a signal-to-noise ratio as small as -25 - -30 dB [5].

Thus, the behavioral data, which are claimed to support the 300-μs time resolution, actually indicate much higher time resolution. Furthermore, there are numerous behavioral data on the bottlenose dolphin discrimination of brief signals indicative of the auditory time resolution as high as 20-30 [4, 5, 7, 11-15], which are usually ignored whenever comparison between behavioral and physiological data is made.

Physiologically assessed 300-μs bottlenose dolphin's auditory time resolution is usually compared to a single gap of 3-5 ms in noise detectable by human listeners to emphasize more than tenfold difference. However, there is an abundance of evidence that the auditory time resolution in humans can be as high as around 500 μs [17-23], or even 250 μs [19]. The difference in the time resolution estimates appears due to differences in a stimulus duration used in experiments; the shorter the stimulus, the higher the time resolution [22].

Envelope following response (EFR) to sinusoidal amplitude modulated (SAM) tones is now widely accepted as a true measure of the dolphins' auditory time resolution assessed using AEP methods [24-26]. Modulation rate transfer function (MTF) was determined with AEP technique in several species of dolphins however no attempts have been made to compare physiological MTF with behavioral results. MTF measurements in bottlenose dolphins are also believed to produce the 300-μs auditory time resolution. In this paper, we discuss how physiologically assessed MTFs are compared to a bottlenose dolphin's perception of amplitude modulation in gated noise.

2   Methods

The ability of listeners to resolve the spectral components of SAM tone limits the usefulness of a tone carrier for determining MTF in humans. Instead a noise is used as a carrier because the long-term power spectrum of SAM or gated noise is uniform and invariant with changes in modulation frequency [18, 21]. There is common agreement that the noise carrier does not produce spectral cue for human listeners and time periodicity is perceived at frequency modulation as high as at least 2 kHz. Gated white noise which has envelope periodicity was used to measure temporal resolution in humans [17, 18].

In our experiments the dolphins discriminated between white gated noise and continuous noise (Fig. 3). A threshold on-time fraction of the gated noise (also called a duty factor) was determined as a function of the gate repetition rate.
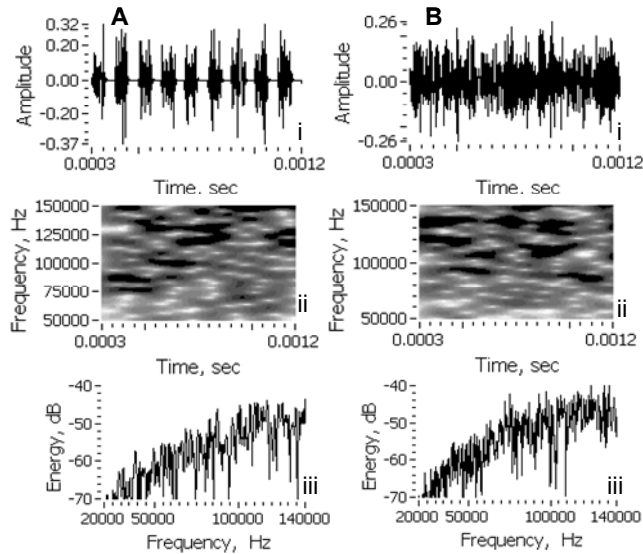

Fig. 3. Waveforms (i), STFT-spectrograms (ii) and energy spectra (iii) of gated noise (A) and continuous noise (B). STFT-spectrograms were generated using 300-μs Henning window and time increment of 5 μs. Gate repetition rate for this picture was 10 kHz, on-time fraction was 0.5. Computer simulation.

At a set gate repetition rate, the on-time fraction of noise was gradually increased until the discrimination dropped to 50 % correct response. Repetition rate than was changed to a new value and a threshold on-time fraction was again determined. In order to eliminate intensity cue for the dolphin, the intensity of both stimuli was randomly and independently varied by 6 to 10 dB. In fact, using this procedure we measured the minimum detectable by the dolphin gap in noise as function of the gap (or noise pulse) repetition rate.

The noise stimuli were produced using standard analog equipments. Electronic switch was carefully balanced to eliminate switching transients which is known could be heard and employed by human listeners. The level of the switch transients was so low that the dolphin simply could not detect the gated signal in the absence of noise carrier.

Because the stimuli were transmitted simultaneously, they apparently interfered with each other at the dolphin start position. Although directionality of the dolphin's hearing should considerably reduce this interference for the dolphin, the modulation depth of the gated noise was apparently less than 100%. The pool reverberation also added to reduction of the gated noise modulation depth which of course made the discrimination more difficult.

The subjects were three adult Black Sea bottlenose dolphins (*Tursiops truncatus*). Experiments were conducted in a 28 x 13 x 4 m concrete pool. A two-response forced-choice procedure was used. A vertical net partition between two transducers set the minimum distance of 5 m, from which the dolphin made its choice. The transducers were placed at 1m depth and at 30° azimuth separation. Prior to stimuli presentation, a dolphin positioned itself at the far (away from the transducers) end of the partition. The dolphin was required to approach a transducer transmitting a gated noise

on any particular trial. Stimuli were transmitted simultaneously through the left and right transducers. The choice of the transducer to transmit a standard signal for a given trial was randomized. Spherical transducers of 1.2 cm in diameter were used. The transducers transmitting response had maximum at 110-130 kHz and rolled off by 12 dB per octave toward lower frequencies (Fig. 1iii). The method of constant stimuli was used to determine discrimination thresholds at 75% correct response level.

3   Results

All three dolphins were able to discriminate continuous noise from gated noise with a 0.5 duty factor for the gate repetition rate as high as 15000 s^{-1} (Fig. 4). For one of the dolphins (Dolphin TL77-79), a threshold duty factor was found to be more than 0.65-0.7 even at the gate repetition rates of 10000-15000 s^{-1}. At a repetition rate of 10000 s^{-1}, the minimum detectable gap by this dolphin was around 30 μs. The dolphin detected a 30-μs gap between periodic 70 μs broadband noise pulses. The minimum audible gap in broadband noise was found decrease from around 160 μs for repetition rate of 100 s^{-1} to 25-30 μs for repetition rate of 15000-20000 s^{-1}.
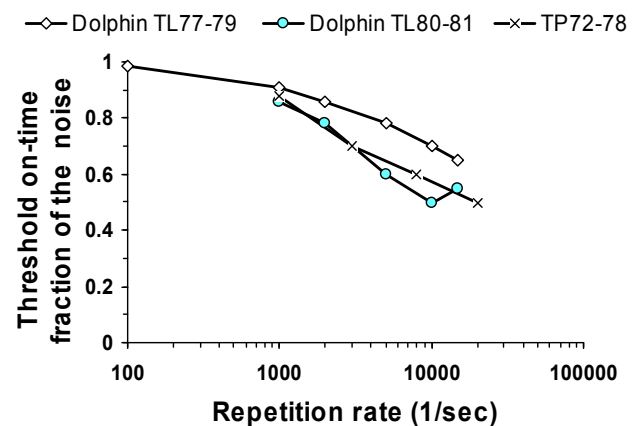

Fig. 4. Threshold on-time fraction of the gated noise as a function of the gate repetition rate.

In humans, a minimum detectable gap in noise is also depends on the gap repetition rate. At threshold repetition rate of gated noise of 2000 s^{-1} [18], at which humans were still capable of detecting envelope periodicity, the threshold gap was just 250 μs compare to a 2-3 ms minimum single detectable gap in long noise pulse.

The bottlenose dolphins appear to be capable of following noise envelope periodicity as high as 20 kHz. Behavioural measurements indicate the auditory time resolution in the bottlenose dolphin almost 10 times better than estimates based on ABR recordings.

In normal hearing human listeners, the behavioral MTF for SAM noise or gated white noise can be modelled as a low-pass filter with a 3-dB cut-off near 20 Hz [21] or 50 Hz [20] with very slow roll-off of 3-4 dB per octave, which is even less than 6-dB roll-off known for an energy integrator (Fig. 5). The rate of decline is slow enough for listeners to detect a just 25% amplitude modulation up to about 500 Hz. At amplitude modulation of around 50 % human listeners were able to detect amplitude modulation in noise at frequency modulation as high as 2 kHz [18-19]. The highest frequency at which a subject could discriminate 100%

amplitude modulation was approximately 2.5 kHz. The frequency at which EFR in humans was no longer measurable was significantly correlated with the maximum perceptible modulation frequency in behavioral experiments [21]. For some human subjects EFR were still detectable at amplitude modulation frequency of at least 600 Hz (for a just 25% amplitude modulation depth). These subjects could perceive noise periodicity at modulation frequency as high as 750 Hz.
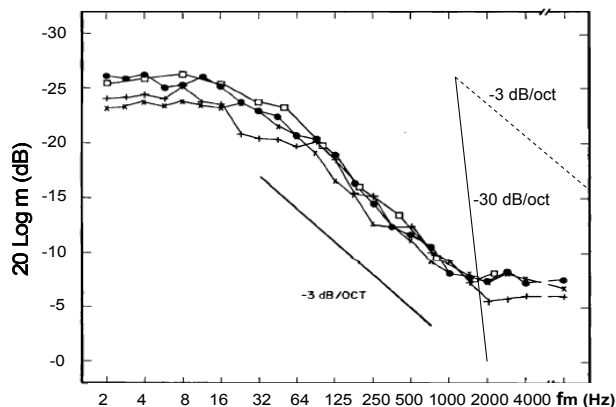

Fig. 5. MTFs obtained for human listeners using continuous wideband noise. The ordinate is the threshold modulation index for 70% correct response (From [20], reprinted with permission). A -30 dB/octave line indicates the roll-off of the MTF obtained in bottlenose dolphins by AEP recording in response to amplitude modulated tones (for example, [24, 25]).

There is an important difference between behaviourally obtained MTFs in humans and physiologically measured MTFs in dolphins. Although MTF cut-off frequency of 1-1.5 kHz (3-dB level) in dolphins' is much higher than MTF cut-off frequency in humans, it rolls-off above this frequency as fast as 30-40 dB per octave (Fig. 5, -30 dB/octave line) so that above 3-4 kHz even for 100% modulation depth, EFR could not be recorded [24].

It means that MTF in dolphins could not be associated with a first order low pass filter for which the filter time constant related to a cut-off frequency f_o as $T=1/2\pi f_o$, as it approximately holds for humans. For a first order low pass filter with a 1.5 kHz cut-off frequency, the time constant would be around 0.1 ms. If the dolphins' MTF obtained using AEP have described the same physiological mechanisms indicated by behavioural MTF in humans, the roll-off of dolphins MTF would not have been more than 6 dB/oct. With the 3-4 dB/oct roll-off above the 1.5 kHz (as indicated by dotted line -3 dB/oct in Fig 5), the MTF attenuation at modulation frequency of 15 kHz would have been only around -15 dB (below maximum).

Although the bottlenose dolphins are able to perceive periodicity of amplitude modulated noise at frequency modulation as high as 15-20 kHz (Fig. 4), EFR can not be evoked above 3-4 kHz. It appears that ABRs are not fast enough to follow periodicity of amplitude modulation at frequency modulation higher than 2-3 kHz.

Comparison of around 20-50 Hz cut-off frequency in humans' MTFs to around 1 kHz cut-off frequency of MTFs obtained in dolphins based on EFRs [24, 25] does not characterize at all the difference in the auditory ability to follow sound envelope periodicity between humans and dolphins. The 20-50 kHz cut-off frequency in humans approximately corresponds to around 3-5 ms time constant

of the low pass filter (or an auditory integrator). However, with this auditory integration time, humans are capable of perceiving a sound envelope periodicity of 2-2.5 kHz indicating the auditory time resolution as high as 400-500 µs [17, 20 and 21].

It appears to be even more misleading when physiologically obtained dolphins' MTFs and behavioural MTFs in humans are compared using different levels for cut-off frequencies (-20 dB from maximum for dolphins and -3 dB for humans) [1, 24]. If compared at the same -20 dB level from maximum, the humans (Fig. 5) and dolphins MTFs (indicated by -30-dB line) have practically the same bandwidth of 1.5 – 2.0 kHz (for the same 100% amplitude modulation). In fact, the dolphin's auditory time resolution, as obtained by AEP methods, is practically the same as the auditory time resolution in humans.

4   Conclusion

The claim that the physiologically assessed bottlenose dolphin auditory time resolution is in full agreement with behavioural results appears to be incorrect. When behavioral results are evaluated according to the time resolution definition, as a threshold interval between identical acoustic events, they all point to the bottlenose dolphin time resolution much higher than AEP methods limit of around 300 µs. There are numerous behavioral results indicative of the bottlenose dolphin time resolution as high as 20-30 µs. The bottlenose dolphins appear to be capable of following noise envelope periodicity as high as 15-20 kHz. The auditory temporal analysis of brief signals in bottlenose dolphins seems to be inaccessible by AEP methods.

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