ORIGINAL PAPER

Auditory temporal resolution of a wild white-beaked dolphin (*Lagenorhynchus albirostris*)

**T. Aran Mooney · Paul E. Nachtigall ·
Kristen A. Taylor · Marianne H. Rasmussen ·
Lee A. Miller**

Abstract Adequate temporal resolution is required across taxa to properly utilize amplitude modulated acoustic signals. Among mammals, odontocete marine mammals are considered to have relatively high temporal resolution, which is a selective advantage when processing fast traveling underwater sound. However, multiple methods used to estimate auditory temporal resolution have left comparisons among odontocetes and other mammals somewhat vague. Here we present the estimated auditory temporal resolution of an adult male white-beaked dolphin, (*Lagenorhynchus albirostris*), using auditory evoked potentials and click stimuli. Ours is the first of such studies performed on a wild dolphin in a capture-and-release scenario. The white-beaked dolphin followed rhythmic clicks up to a rate of approximately 1,125–1,250 Hz, after which the modulation rate transfer function (MRTF) cut-off steeply. However, 10% of the maximum response was still found at 1,450 Hz indicating high temporal resolution. The MRTF was similar in shape and bandwidth to that of other odontocetes. The estimated maximal temporal resolution of white-beaked dolphins and other odontocetes was approximately twice that of pinnipeds and manatees, and more than ten-times faster than humans and gerbils. The exceptionally high temporal resolution abilities of odontocetes are likely due primarily to echolocation capabilities that require rapid processing of acoustic cues.

Keywords Dolphin · Mammal · Temporal resolution · Auditory evoked potential · Modulation rate transfer function

Abbreviations

AEP	Auditory evoked potentials
AM	Amplitude modulated
EEG	Electro encephalogram
FFT	Fast Fourier transform
MRTF	Modulation rate transfer function
RFR	Rate following response
RMS	Root mean square
SAM	Sinusoidally amplitude modulated
SPL	Sound pressure level
V_{p-p}	Peak-to-peak voltage

T. A. Mooney (✉) · P. E. Nachtigall · K. A. Taylor
Department of Zoology and Hawaii Institute of Marine Biology,
University of Hawaii, P.O. Box 1106, Kailua, HI 96734, USA
e-mail: mooneyt@hawaii.edu

M. H. Rasmussen
Húsavik Research Center, University of Iceland,
Gardarsbraut 19, 640 Húsavik, Iceland

L. A. Miller
Institute of Biology, University of Southern Denmark-Odense,
Campusvej 55, 5230 Odense M, Denmark

Present Address:
T. A. Mooney
Department of Biology, Woods Hole Oceanographic Institution,
Marine Research Facility, MS #50, 266 Woods Hole Road,
Woods Hole, MA 02543, USA

Introduction

Proper temporal processing of sound can be crucial for acoustic signal recognition, examples of which have been demonstrated across taxa. In certain crickets, amplitude modulated (AM) signals play a role in predator recognition (Fullard et al. 2005). Mates and competitors may be recognized by temporal cues in frogs and reef fish (Rose et al. 1985; Myrberg 1986; 1997). Song recognition is enhanced

by proper acoustic temporal patterns in song birds (Dooling and Searcy 1981). Neurons in the auditory cortex of little brown bats (*Myotis lucifugus*) respond to simulated echoes that are AM with the wing beat frequencies of insect prey (Condon et al. 1997). In all cases where deciphering of temporally modulated signals is important, the prerequisite is that the animals have sufficient ability to process AM signals at functional rates.

Hearing is an important sensory modality for marine mammals and is perhaps the most important sense for cetaceans. Marine mammals provide an important case for auditory temporal processing studies because their auditory system must compensate for sound speed underwater, which is nearly five times as fast as sound in air (Urick 1983). Like bats, odontocetes (toothed whales) have also developed the ability to echolocate, processing short-duration clicks and subsequent rapid echoes, both of which are only tens to hundreds of µs in duration and only a few ms apart (Au 1993; Madsen et al. 2004). These echolocators must have sufficient temporal processing capabilities to follow individual clicks and echoes, and discern information from echoes by using short integration times (Au et al. 1988). Because of the compensations for sound speed underwater and echolocation abilities, odontocetes are often considered to have evolved the auditory processing abilities which follow AM sounds at high rates relative to many other animals (Fuzessery et al. 2003; Supin and Popov 2003).

One odontocete whose temporal resolution capabilities seem particularly intriguing is the white-beaked dolphin (*Lagenorhynchus albirostris*), a species that can hear relatively high frequency sounds (up to 180 kHz) (Nachtigall et al. 2008). High-frequency hearing and corresponding peripheral auditory filter bandwidths are theoretically associated with increased temporal resolution (Fay 1992; Supin et al. 2001). As a general rule, the wider the filter band, as is typical at higher frequencies, the greater is the auditory temporal resolution. It has been suggested that sensitive high-frequency hearing in some dolphins and porpoises is related to concurrent high auditory temporal resolution (Supin et al. 2001; Mulsow and Reichmuth 2007). This may also hold true for white-beaked dolphins.

However, comparisons of temporal resolution across taxa can be confusing because methods vary, constrained by the limits of experimental conditions; thus the scope of such evaluations is inherently limited. For example, human auditory temporal resolution speeds may be referenced from 30–500 Hz, depending on whether the response was determined behaviorally (Szymaszek et al. 2006), recorded from cortical potentials (Kuwada et al. 1986), or measured from brainstem evoked potentials (Purcell et al. 2004). In bottlenose dolphins, temporal resolution estimates have varied from 1,000 to 4,000 Hz (approximately 1–0.264 ms)

based on variation in stimulus type and physiological versus behavioral methodologies (Au et al. 1988; Dolphin et al. 1995; Supin and Popov 1995).

One experimental method that provides temporal resolution estimates across taxa and allows for robust comparison is the use of AM stimuli and measurement of responses with auditory evoked potentials (AEPs) recorded from brainstem activity. The stimuli may be presented as either broadband clicks or sinusoidally amplitude modulated (SAM) tone-pips at varying rates (both stimuli produce comparable results; Supin et al. 2001). At lower presentation rates, AEP responses correspond with each stimulus modulation, forming an evoked potential rate following response (RFR; referred to as an envelope following response or EFR for SAM tones). This ability of the nervous system to follow various stimuli presentation rates is termed the modulation rate transfer function (MRTF). The maximum rate at which the auditory nervous system can follow the amplitude modulation of the stimulus can be used to estimate auditory temporal resolution (Supin and Popov 1995; Supin et al. 2001). This method has been applied to a variety of taxa, including odontocetes (Dolphin et al. 1995; Supin and Popov 1995), manatees (Mann et al. 2005), pinnipeds (Mulsow and Reichmuth 2007), humans (Purcell et al. 2004), and gerbils (Dolphin and Mountain 1992). The methodological similarities allow for comparisons of echolocating marine mammals (dolphins), non-echolocating marine mammals (manatees and pinnipeds), humans, and rodents.

The purpose of this study was twofold: (1) estimate the auditory temporal resolution of the white-beaked dolphin using broadband pulses and the RFR and (2) compare the determined auditory temporal resolution with other marine and terrestrial mammals. This research was part of a larger study to measure the hearing range and sensitivity of the white-beaked dolphin in a capture and release scenario.

Methods

Subject and experimental set-up

The study animal was a wild, white-beaked dolphin (*L. albirostris*) caught-and-released within Faxaflói Bay off the coast of Keflavík, Iceland. Groups of white-beaked dolphins frequent the bay during the summer months, and during our research period, 14 July to 11 August 2006, the animals often approached our 18-m modified fishing vessel, the *Hafborg*. The animals voluntarily bow-rode the vessel and twice during the expedition, when a dolphin surfaced in front of the boat, it was hoop-netted, maneuvered into a dolphin-stretcher, and lifted via a hydraulic winch on board the vessel (see Nachtigall et al. 2008). The dolphin was

placed into a $1 \times 1 \times 3.7$ m specially constructed plastic tank reinforced with a welded steel frame and filled with sea water. In this custom tank, the dolphin's temporal resolution was measured.

The subject was an adult male, 217 kg in mass, 224 cm in length, with a girth of 139 cm. Upon capture, the animal was placed into the tank and the vessel sailed to the nearby harbor of Garður for the hearing measurements. Conducting the experiment within this small harbor reduced water motion within the tank. The tank, lined with 3-cm-thick open cell mattress foam, was acoustically dampened; limiting reflections so that the subject's hearing could be measured under good acoustic and field conditions (Fig. 1).

Sound stimuli were projected from an ITC-1032 transducer (resonance frequency = 38 kHz) (Santa Barbara, CA, USA). The transducer was suspended from an overhead bar that stretched across the tank and secured at a position that was 80 cm from the animal's rostrum and 115 cm to the approximate location of the animal's ear, but near the foam tank wall. The transducer was hung 30 cm below the water surface and in line with the subject's head and lower jaw. The animal was positioned in the stretcher hanging from two mobile steel suspension bars over the box. A large flap in the front of the stretcher, near the animal's head, was unzipped in order to permit 'free' sound transmission to

Fig. 1 Experimental set-up picturing dolphin and acoustic tank. *1* projecting transducer, *2* active electrode (passive is on dorsal fin but hidden from view), *3* stretcher suspended from aluminum poles, note open flap around head and lower jaw, *4* acoustic tank lined with baffling open cell foam

the animal's head and lower jaw. The animal remained calm and still throughout the experiment, with very little head-movement. This reduced variability in the subject's received sound levels. The received stimuli were monitored using a CS12 miniature hydrophone (Derell Engineering, Virum, Denmark: sensitivity -210 dB re 1 V/μPa and 0 to -3 dB from 1 to 150 kHz) placed about 25 cm from the lower jaw of the animal. Received sounds were amplified by 70 dB (Etec, Frederiksværk, Denmark) (high pass 100 Hz) and sampled at 1 MHz (AD Link 12 bit, Taiwan, Formosa and Magma PCI expansion box) recorded to the hard disk of a laptop computer.

Acoustic measurements and stimuli

The tank was calibrated several days before the experiment. The projecting transducer was placed in position and a calibrated reference hydrophone, a Reson TC 4034 (sensitivity -218 dB re 1 V/μPa, ±3 dB up to 300 kHz, Slangerup, Denmark), was placed 1 m from the projector and at 30 cm depth. This position was determined to be the approximate location of the subject's head and there was little measurable variation in received levels within a few centimeters of the original hydrophone position. Stimuli were short pulses, 100 μs in duration with a peak frequency of 38 kHz, but with a spectrum that ranged from 1–60 kHz and consisted of approximately three full cycles (Fig. 2). Each of these pulses was transmitted in the tank and the received peak-to-peak voltage (V_{p-p}) was measured on the oscilloscope. The V_{p-p} measure was used to calculate the sound pressure levels (SPLs) of the brief pulses, as is typical of transient, short-duration signals (Au 1993; Madsen 2005). These SPLs were kept constant during the experiment at 128 dB re: 1 μPa (p–p). While some reflections were likely in the relatively small tank, they were not observed (see also Nachtigall et al. 2008). This is likely due to precautions taken to reduce acoustic interference including the extremely short duration of the clicks (100 μs) and click trains (19 ms), which reduced potential signal overlap, and good dampening material along the tank walls which baffled sound. Acoustic signals were also presented at relatively low p–p SPLs to ensure direct path stimuli were of the greatest amplitude, and likely masking attenuated reflections. As a precautionary measure the received signals were simultaneously recorded to determine the spectrum and ensure that no competing signals or reflections existed. Finally, while some multipath may have occurred, the actual effects on sound reception by the animal were likely to be minimal. This is because an odontocete receiver (its head and lower jaws) gathers sound not at a single point, where reflections would have greatest effects, but across the head at multiple locations (Møhl et al. 1999; Mooney et al. 2008). Interference certainly would not occur at all
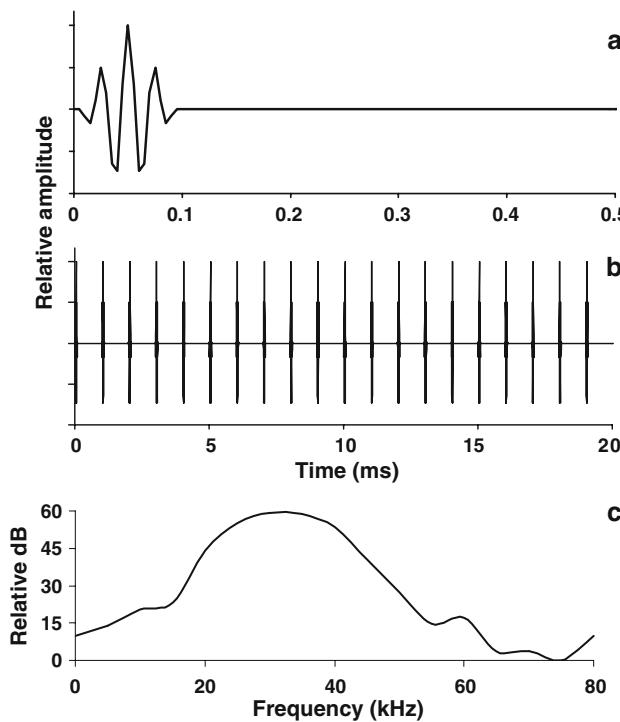
Fig. 2 a Waveform of single click stimulus. **b** Waveform of click train at 1,000 Hz presentation rate. Note the difference in time scale between **a** and **b**. **c** Spectrum of a click stimulus recorded in the tank during calibration

Fig. 3 Noise spectrum level (dB re: 1 μPa^2/Hz) of the experimental tank. Ambient tank noise was sampled at 1 MHz and analyzed using a 1,024-point FFT using a 5-point moving average

locations on the head and the dolphins' auditory system seems to process sound received across its jaw (Norris and Harvey 1974).

Noise level measurements were also calibrated and recorded to determine the spectrum level of the background noise (Fig. 3). For this we used a Reson TC 4032 hydrophone (sensitivity −170 dB re 1 V/μPa, ±3 dB up to 120 kHz), Etec amplifier (HP at 100 Hz), an AD-Link (Taiwan) 12 bit digital-to-analog data acquisition card set at 1MSamples/s and a Magma PCI expansion box (San Diego, CA, USA). The noise level in the tank on board ship was 118 dB re 1 μPa RMS (BW = 100 Hz to 120 kHz, $\tau = 2.3$ s) or leveling off at approximately 60–80 dB re 1 μPa²/Hz noise spectral density (Nachtigall et al. 2008). The system noise was 102 dB re 1 μPa RMS (BW = 100 Hz to 120 kHz, $\tau = 881$ ms).

The acoustic stimuli were digitally generated using a custom LabView program. The signal was then converted from digital to an analog signal with a National Instruments-PCMCIA-6062E digital-to-analog data acquisition card (Austin, TX, USA) implemented into a laptop computer, using an update rate of 256 kHz. From the data acquisition card, the stimuli were sent to a custom-built signal-shaping box that allowed for the stimulus level to be increased or decreased in 1-dB steps and from this box the signal was sent directly to the ITC transducer. An EZ
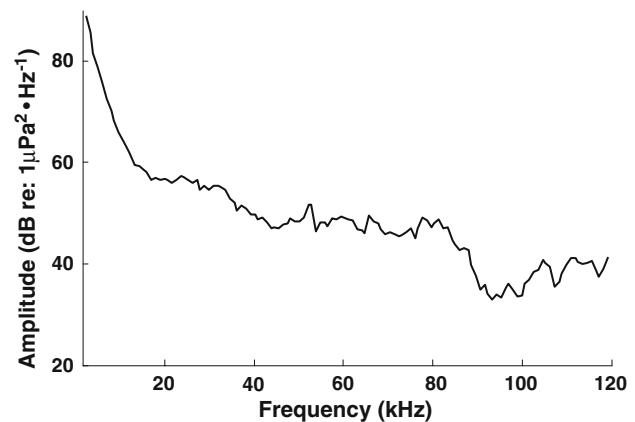
OS-310 M battery-powered digital oscilloscope (Puchonsi, Kyunggi-do, Republic of Korea) was used to monitor the outgoing stimuli from the signal-shaping box to the projecting transducer. Stimuli consisted of a series of pulses of varying modulation rates, but the total pulse-series was always 19 ms long followed by 30 ms of silence. This presentation sequence reduced adaptation by the animal's auditory system. A total of 1,000 pulse-series were presented for each modulation rate, which was varied from 125 to 3,000 Hz, providing 14 different rates.

Auditory evoked potential measurements

Hearing measurements were collected using AEP responses to the pulsed stimuli. For each stimulus of an appropriate SPL and rate, there was a corresponding AEP response. As a pulsed stimulus presentation was modulated from low to high rates a RFR could be measured, and maximum following rates could be used to estimate the animal's AEP temporal resolution. Responses were collected using two standard 10-mm gold electroencephalogram (EEG) electrodes, embedded in custom, latex suction cups and of the same electrode type used for human EEG collection. The two suction cups were placed on dorsal skin using standard conductive gel. The active electrode was attached 3–4 cm behind the blowhole but slightly off to the right. The second cup contained the reference electrode and was attached on the dorsal fin. This seemed to reduce background noise levels as there are few muscles and noise-producing nerves in that location. The system was grounded to the water in the holding tank. The animal rested in the stretcher at the water's surface with most of its head underwater to receive sound input through the major tissue routes to the ears (Møhl et al. 1999; Ketten 2000) while the suction cups remained in the air to maximize signal strength.

The measured responses from the electrodes were amplified 10,000 times using an Iso-Dam Biological Amplifier (WPI, Sarasota, FL, USA). Both the Iso-Dam and a Krohn-Hite Filter Model 3103 (Brockton, MA, USA) filtered the responses for anti-aliasing protection and noise reduction, using a bandpass of 300 to 3,000 Hz for stimulus rates of 375–3,000 Hz. The high-pass setting was set at 100 and 200 Hz when stimuli were presented at 125 and 250 Hz. The amplified and filtered responses were transferred to an analog input using the same data acquisition card in the same laptop computer and then digitized at 16 kHz using the same custom LabView program used for stimulus generation. Evoked potential records were recorded in 26-ms segments, beginning at the onset of the sound stimulus presentation. In order to extract the recorded AEP from noise, 1,000 samples were averaged per trial and each trial lasted 49 s.

Data analysis

To estimate the subject's response at each modulation rate, a 16-ms window of each average evoked response was fast Fourier transformed (FFT) for each modulation rate. The 256-point FFT provided a response frequency spectrum of the data, where a peak showed received energy, or the animal's physiological following response, at the respective modulation rate. Thus peaks were typically found in the FFT spectra at the rate at which the clicks were presented and higher amplitude peaks indicated a better AEP "following" of that rate. The FFT peak value at each modulation rate was plotted relative to the modulation frequency to estimate the MRTF. This MRTF was then taken as an estimate of the subject's auditory temporal resolution. A "weighted MRTF" was also estimated by taking the square-root of the sum of the squares of the fundamental and harmonic FFT peaks. An example of the AEP waveform spectrum was also provided for comparison to the MRTF. Due to the difficulties and limitations of working with wild cetacean species, AEP data were based upon one individual.

Results

The observed AEP waveform of the white-beaked dolphin was typical of odontocetes and other mammals and was comprised of several waves that reflected a series of neurological responses to acoustic stimuli (Fig. 4). We designated the negative and positive vertices of these waves N1–N4 and P1–P3. Although not precisely known in odontocetes, these waves were assumed to reflect the positive and negative polarizations of multiple auditory nerve bundles within the brainstem (Szymanski et al. 1998; Supin et al. 2001; Hall 2007). The early portions of each wave are usually

considered to be the initial depolarization of auditory nerves, thus labeled with an 'N' for negative, and we followed such protocol. An onset delay was found for each AEP record, reflecting a period of time, usually 3–6 ms, from the onset of the initial sound stimulus until the response was observed. When stimulus modulation rates were such that the subject's auditory system could follow individual clicks, similar delays were found between later stimuli and their concurrent AEP responses. Amplitudes of the AEP responses varied and were dependent upon whether they were responses to the first click stimulus, a response to a click later in the stimulus train, or even the rate at which the click train was presented. Typically, the onset response (the first several waves) was the largest, on the order of 1–2 μV. Subsequent responses to acoustic stimuli were usually less than 1 μV and on the order of 0.5–0.25 μV. Peak-to-peak amplitudes decreased exponentially as stimulus presentation rates increased ($r^2 = 0.93$; $P < 0.001$; $y = -0.97*\log(X) + 3.39$; $n = 13$).

The animal's auditory system generally followed individual click stimuli at lower presentation rates. For example at 250 Hz, or 1 click every 4 ms, the averaged AEP showed responses for each click in a train (Fig. 4a). As presentation rates were gradually increased, the individual waveforms to each click stimulus began to blend together and become more sinusoidal in the 'following' of the individual click stimuli, exhibiting the typical RFR shown in other odontocete auditory systems. This RFR could be seen in the AEP responses at 1,000 Hz (Fig. 4a) and until a rate of 1,250 Hz. At higher rates, the animal's AEP waveforms did not reflect following of individual clicks, but rather, simply an onset response to the click train as a whole, as if it were one continuous stimulus (e.g. 2,000 Hz). The onset is characterized by the initial series of vertices of positive and negative waves (Fig. 4b). The spectrum of the single AEP response demonstrates a similar cut-off rate to the RFR, at approximately 1,250 Hz (Fig. 4c).

Fast Fourier transforms of the RFRs provided similar indications of following responses. For example, the dolphin's system followed the 1,000-Hz click rate relatively well and showed a strong peak in the FFT at 1,000 Hz (Fig. 5). When lower-rate stimuli were used, the frequency spectrum revealed not only a peak at the fundamental click rate but also at harmonics of the fundamental. This was clear when using the 250-Hz click rate and peaks were evident at 500, 750, 1,000, and 1,250 Hz as well. At presentation rates of 1,500 Hz and above, the dolphin's auditory system did not follow individual clicks well, relative to lower click rates. This was reflected by a lack of dominant peaks in the frequency spectrum and the amplitude of the peak at the respective modulation rate being similar to the background noise level (e.g. Fig. 5; 2,000 Hz). The animal was not considered to follow click trains well at 2,000 Hz
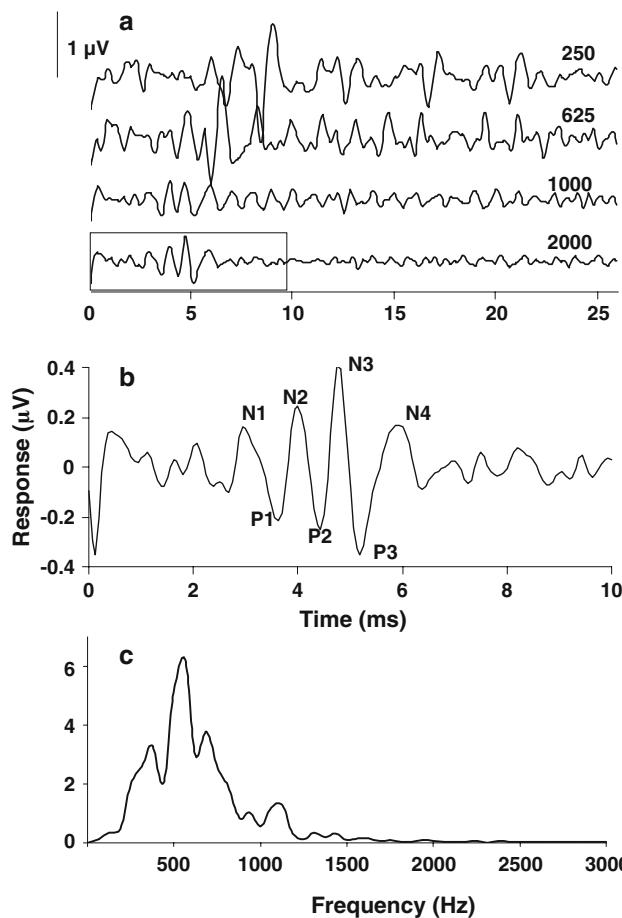
Fig. 4 a Rate following responses in μV generated using click pulses at four different modulation rates; 250, 625, 1,000, and 2,000 Hz, using a SPL of 128 dB re: 1 μPa (p–p). Responses are averages of 1,000 records. **b** 10 ms close-up of a selected white-beaked AEP waveform highlighted in **a**. The positive (P) and negative (N) waves of the AEP are shown where negative indicates the apparent initial neural depolarization response. **c** Spectrum of highlighted AEP response in **b**

fundamental response amplitude level used by Popov and Supin (1998) as an upper limit of temporal resolution, the limit of temporal resolution of the white-beaked dolphin was 1,450–1,500 Hz. The weighted MRTF had a similar shape with peaks near 500–600 and 1,000–1,125 Hz (Fig. 6a). However, it also reflected strong AEP response energy at lower frequencies (125–250 Hz), which was not as easily detected by simply plotting the amplitude of the peaks at the fundamental frequencies.

Discussion

White-beaked dolphin evoked potentials were clear and distinct from the background noise, despite the unique field situation for the data collection. Overall, the field methodology and consequent AEPs were similar to those used and found in laboratory studies of odontocete hearing and evoked potential recording (Nachtigall et al. 2007). The dolphin's auditory temporal resolution was high, up to at least 1,125–1,250 Hz and perhaps as high as 1450–1,500 Hz. The general characteristics of individual AEP waveforms and MRTF demonstrated results consistent with other species of odontocetes tested with similar methodologies (e.g., Supin and Popov 1995; Szymanski et al. 1998; Mooney et al. 2006; Finneran et al. 2007).

However, there were some minor differences in the AEP waveform of the white-beaked dolphin and that of other odontocetes (Fig. 4b). Odontocete AEP waveforms differ slightly in the number, relative amplitude and overall pattern of negative and positive peaks (Supin et al. 2001). These waves are a summation of neurological responses from the general region of the brainstem in response to acoustic stimuli. It is logical that this pattern of waves may vary among species, dependent upon subtle morphological or physiological differences in the auditory nerves and surrounding tissues. Unfortunately, precise reasons for this variation have yet to be thoroughly investigated in marine mammals. Therefore, differences at this point are simply noted as species variation.

The MRTF was low-pass in shape, indicating the following of individual clicks up until approximately 1,250–1,450 Hz (Fig. 6). This bandwidth exceeds the spectrum of a single AEP (Fig. 4c), indicating that the MRTF is not limited by the spectrum of the AEP waveform. At higher frequency modulation rates, the animal's AEPs did not follow clicks as individual stimuli but rather as continuous stimuli, 19 ms in duration. This is supported by the sharp cut-off in the MRTF above 1,250 Hz and the lack of the rate following waveforms after the initial onset response. While the inter-click-intervals of white-beaked dolphins may be as brief as 3 ms (about 333 Hz) (Rasmussen and Miller 2002),

and higher due to no visible RFR and an FFT peak difficult to discriminate from the noise. Further, note the ordinate axes of Fig. 5 are different scales. This emphasizes the response amplitudes for the respective click rates (peaks indicate a following of the stimulus although amplitude is influenced by AEP response spectrum), and reflects that relatively good following responses are well above the background noise and poor following of a click rate provides an FFT peak similar to the noise level.

The dolphin's MRTF was low-pass filter in shape with peaks at 500–600 and 1,000–1,125 Hz (Fig. 6). The MRTF was relatively broadband (1,250–1,500 Hz), with a rather steep high-frequency cut-off after 1,125–1,250 Hz, reflecting high auditory temporal resolution, up to 1,250 Hz. Minimum noise level values were not completely reached until beyond 2,000 Hz. Applying the 10% of maximum

Fig. 5 Spectra of the rate following responses at four different modulation rates, 250, 625, 1,000, and 2,000 Hz. Peaks at the fundamental frequency are indicated in by *large, black arrows*. At modulation rates of 250 and 625 Hz harmonics of the fundamental modulation rate are also visible (*small gray arrows*). At 2,000 Hz only a small response peak was found, of which the amplitude was similar to the noise level, indicating little to no following of such rapid stimuli. Note the different *y*-axis scales for the response amplitude
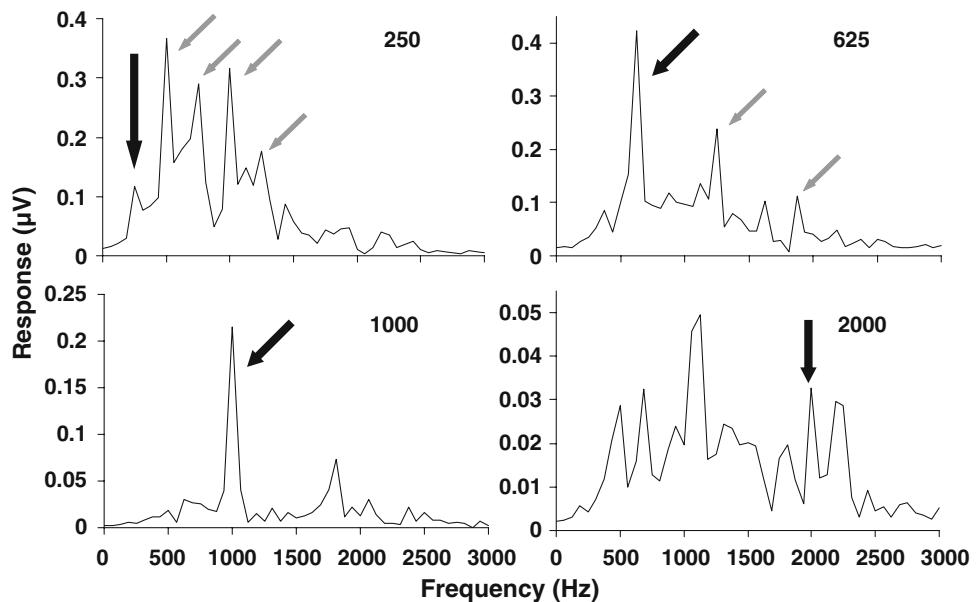
the RFRs presented here are sufficient to follow such rapid click rates and subsequent echoes (Mooney et al. 2006).

The maximum rate of the white-beaked dolphin's auditory temporal processing is near 1,450 Hz which is relatively high for odontocetes. However, the MRTF did not reflect exceedingly rapid processing rates which might be predicted by the unusually high frequency components of their echolocation clicks or high frequency (180 kHz) hearing (Rasmussen and Miller 2002; Nachtigall et al. 2008). That is, auditory filter bandwidths typically increase as the frequency of hearing increases; the higher the frequency, the wider the filter bandwidth (Yost 1994; Supin et al. 2001). A wider auditory filter is associated with improved temporal resolution. While white-beaked dolphins produce sounds and hear at relatively high frequencies for odontocetes, these traits do not dramatically increase their temporal resolution capabilities, relative to other odontocetes.

Comparisons to other odontocetes

In fact, the white-beaked dolphin MRTF shape was similar to those of other odontocetes including that of the Risso's dolphin and killer whale (Szymanski et al. 1998; Mooney et al. 2006), although the white-beaked dolphin's MRTF is a bit higher in estimated processing frequency than these animals (Fig. 6b). The data in all three of these studies were collected using essentially the same AEP method. However, the utilization of relatively low frequency clicks in this study may have underestimated the auditory temporal resolution of the white-beaked dolphin (based upon their high frequency traits).

Thus, for comparison of temporal processing within odontocetes, the white-beaked dolphin MRTF was plotted relative to a mean odontocete MRTF (Fig. 6c). The mean odontocete MRTF was generated from the averages of seven odontocete MRTFs collected using SAM tones or clicks and similar AEP techniques (Supin and Popov 1995; Szymanski et al. 1998; Klishin et al. 2000; Cook et al. 2006; Mooney et al. 2006; this study; *Pseudorca crassidens* (unpublished). All MRTF amplitudes were normalized to a linear scale of 0–1, where 1 was the maximum response provided in the original research. Based on the rather similar shape and bandwidth of the MRTF among odontocetes (Fig. 6b and c), it appears that temporal processing capabilities are comparable and conserved. This is further supported by the notion that, neither hearing range nor stimulus frequency, appears to affect temporal resolution patterns, at least within odontocetes (Supin and Popov 1995; Finneran et al. 2007).

One odontocete worth testing for its MRTF is the harbor porpoise. Porpoises are echolocators that, unlike most dolphins, use a narrow-band high frequency (130–150 kHz) signal (Au et al. 1999). Interestingly, they have narrow critical bands overlapping the frequency of their pulse (Popov et al. 2006). This suggests high frequency resolution, but reduced temporal resolution for the harbor porpoise.

Comparisons to other marine and terrestrial mammals

Relative to pinnipeds and manatees, the mean odontocete MRTF is broader in bandwidth with a maximum response at higher frequencies indicating increased temporal resolution (Fig. 7) (Mann et al. 2005; Mulsow and Reichmuth 2007). When temporal resolution bandwidth was estimated as the rate at which the response amplitude was 10% of the maximum response (Popov and Supin 1998), odontocetes,
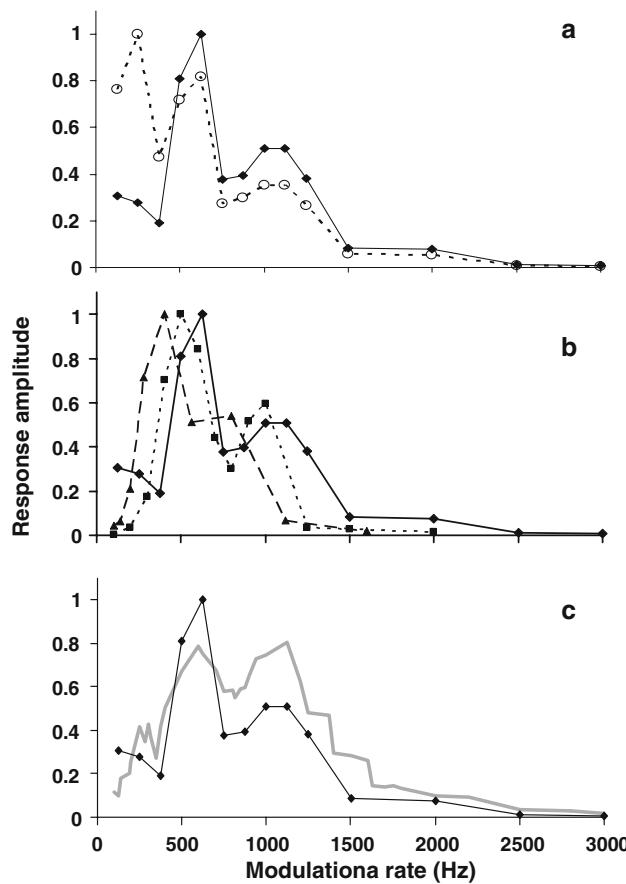
Fig. 6 **a** The MRTF of a male white-beaked dolphin determined in this experiment plotted based on the peak value of the FFT at the respective modulation rate (*solid line*, *diamonds*) and a weighted-MRTF estimated by the square root of the sum power of the fundamental and harmonics (*dotted line*, *open circles*). **b** Comparative standard MRTFs of the white-beaked dolphin (*solid line*, *diamonds*), the Risso's dolphin (*dotted line*, *squares*; Mooney et al. 2006) and the killer whale (*dashed line*, *triangles*; Szymanski et al. 1998) on a normalized amplitude scale. **c** Modulation rate transfer functions of a white-beaked dolphin (*black line*, *diamonds*) and a mean of seven odontocete species measured to date (*gray line*)

Fig. 7 Comparison of the mean odontocete MRTF (*solid gray line*) with that of the mean pinniped MRTF (*dotted line*, *asterisk's*; Mulsow and Reichmuth 2007), the manatee MRTF (*solid line*, *circles*; Mann et al. 2005), the gerbil (*dotted line*, *triangles*; Dolphin and Mountain 1992) and human (*solid line*, *squares*; Purcell et al. 2004) on a normalized amplitude scale. The comparisons of marine and terrestrial mammal MRTFs must be interpreted cautiously since the terrestrial mammal AEPs reflect cortical as well as brainstem recordings

pinnipeds and manatees demonstrated bandwidths of 1450, 750 and 1,400 Hz, respectively. This indicates that odontocetes process AM sounds twice as fast as pinnipeds and similar to manatees. However, this method likely overestimates manatee temporal resolution as their AEP responses are generally in the noise level at 700 Hz (Mann et al. 2005) and the 10% level may be too high a criterion. If a 50% criterion is used, the average odontocete follows sounds at 1,400 Hz, the pinniped at 300 Hz, and the manatee at 425–650 Hz. Similar trends are found at 90% of the maximum response (odontocete, 1,150 Hz; pinniped, 220 Hz; manatee, 160 Hz) indicating that odontocetes have very good temporal resolution capabilities relative to other marine mammals. While, manatees, another fully aquatic marine mammal, seem to show temporal processing at surprisingly high rates and an unusual peak in their MRTF at
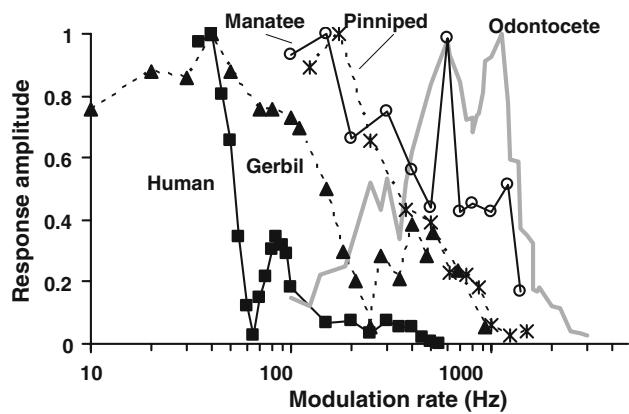
600 Hz (Mann et al. 2005) it is safe to say that at least odontocete temporal resolution appears considerably higher than other marine mammals tested.

To place these high temporal resolution estimates in perspective with those of terrestrial mammals, we compared the mean odontocete MRTF to that of the gerbil and the human (Fig. 7). Unlike odontocetes, the gerbil and human AEPs were considered to have a cortical component in addition to the brainstem evoked potentials (Dolphin and Mountain 1992; Purcell et al. 2004). Thus, the summated responses provided in the human and gerbil MRTFs are only cautiously compared to the brainstem evoked potentials of marine mammals. There was approximately an order of magnitude difference in maximum temporal response, with the 10% decrease for the gerbils and humans being 200 and 60 Hz, and 90% at 48 and 42 Hz, respectively (Dolphin and Mountain 1992; Purcell et al. 2004). While this is a limited comparison due to the differences in AEPs measured, it generally reflects that odontocetes, as well as manatees and pinnipeds, likely have higher temporal resolution rates than some terrestrial mammals.

The relatively high temporal resolution of odontocetes is likely a function of three non-mutually exclusive reasons: (a) adaptation to a fully aquatic environment (Supin and Popov 1995; Mann et al. 2005), (b) their wide auditory filters at high frequencies (Mulsow and Reichmuth 2007), and (c) echolocation abilities requiring discrimination of rapid clicks and echoes (Mooney et al. 2006). Adaptation to an aquatic environment likely plays a role but is probably not the primary reason for high odontocete MRTF values because the manatee is also exclusively marine with a lower temporal resolution. High frequency hearing capabilities

may also contribute to greater temporal resolution but are likely not the principal driving force. Gerbils hear well at higher frequencies but their temporal resolution is similar to humans (Ryan 1976; Dolphin and Mountain 1992; Purcell et al. 2004), and reduced hearing ranges in odontocetes do not affect temporal resolution (Finneran et al. 2007).

However, echolocation is consistent with high temporal resolution, as shown in micro bats, as well as odontocetes. These bats demonstrate short integration times (Surlykke and Bojesen 1996; Wiegrebe and Schmidt 1996) and medial superior olive neurons follow AM stimuli up to rates of 500 Hz (Grothe et al. 1997). Thus, it seems that natural selection put odontocetes and micro bats on unique evolutionary paths and the evolution of echolocation has likely played a significant role in the appearance of high temporal processing abilities.

In conclusion, the white-beaked dolphin demonstrates high temporal resolution similar to other odontocete species. Odontocete temporal resolution is well conserved and typically of higher rates than non-echolocating terrestrial mammals, pinnipeds, and manatees. More extensive studies of auditory temporal resolution in more species of mammals would certainly broaden our understanding. For example, knowledge of the mysticete MRTF and temporal resolution would help fill out this picture in marine mammals. High frequency hearing alone is not a predictor for fast temporal resolution. Rather, we propose that selective pressures giving rise to the evolution of echolocation in odontocetes and micro bats also favored high temporal resolution to better detect and follow brief AM sounds.

References

Au WWL (1993) The sonar of dolphins. Springer, New York

Au WWL, Moore PWB, Pawloski DA (1988) Detection of complex echoes in noise by an echolocating dolphin. J Acoust Soc Am 83:662–668

Au WWL, Kastelein RA, Rippe HT, Schooneman NM (1999) Transmission beam pattern and echolocation signals of a harbor porpoise (*Phocoena phocoena*). J Acoust Soc Am 106:3699–3705

Condon CJ, Galazyuk A, White KR, Feng AS (1997) Neurons in the auditory cortex of the little brown bat exhibit selectivity for complex amplitude-modulated signals that mimic echoes from fluttering insects. Audit Neurosci 3:269–287

Cook MLH, Verela RA, Goldstein JD, McCulloch SD, Bossart GD, Finneran JJ, Houser DS, Mann DA (2006) Beaked whale auditory evoked potential hearing measurements. J Comp Physiol A 192:489–495

Dolphin WF, Mountain DC (1992) The envelope following response: scalp potentials elicited in the mongolian gerbil using sinusoidally AM acoustic signals. Hear Res 58:70–78

Dolphin WF, Au WWL, Nachtigall PE, Pawloski JL (1995) Modulation rate transfer functions to low frequency carriers by three species of cetaceans. J Comp Physiol A 177:235–245

Dooling RJ, Searcy MH (1981) Amplitude modulation thresholds for the parakeet, *Melopsittacus undulatus*. J Comp Physiol A 143:383–388

Fay RR (1992) Structure and function in sound discrimination among vertebrates. In: Fay RR, Popper AN (eds) The evolutionary biology of hearing. Springer, New York, pp 229–263

Finneran JJ, London HR, Houser DS (2007) Modulation rate transfer functions in bottlenose dolphins (*Tursiops truncatus*) with normal hearing and high-frequency hearing loss. J Comp Physiol A 193:835–843

Fullard JH, Ratcliffe JM, Guignion C (2005) Sensory ecology of predator-prey interactions: responses of the AN2 interneuron in the field cricket, *Teleogryllus oceanicus*, to the echolocation calls of sympatric bats. J Comp Physiol A 191:605–618

Fuzessery ZM, Feng AS, Supin AY (2003) Central auditory processing of temporal information in bats and dolphins. In: Thomas JA, Moss CF, Vater M (eds) Echolocation in bats and dolphin. University of Chicago Press, Chicago, pp 115–122

Grothe B, Park TJ, Schuller G (1997) Medial superior olive in the free-tailed bat: response to pure tones and amplitude-modulated tones. J Neurophysiol 77:1553–1565

Hall JW (2007) The new handbook of auditory evoked potentials. Pearson Education, Boston

Ketten DR (2000) Structure of cetacean ears. In: Au WWL, Fay RJ, Popper AN (eds) Hearing by whales and dolphins. Springer, New York, pp 43–108

Klishin VO, Popov VV, Supin AY (2000) Hearing capabilities of a beluga whale, *Delphinapterus leucas*. Aquat Mamm 26:212–228

Kuwada S, Batra R, Maher VL (1986) Scalp potentials of normal and hearing impaired subjects in response to sinusoidally amplitude-modulated tones. Hear Res 21:179–192

Madsen PT (2005) Marine mammals and noise: Problems with root mean square sound pressure levels for transients. J Acoust Soc Am 117:3957–3962

Madsen PT, Kerr I, Payne R (2004) Echolocation clicks of two free-ranging, oceanic delphinids with different food preferences: false killer whales *Pseudorca crassidens* and Risso's dolphins *Grampus griseus*. J Exp Biol 207:1811–1823

Mann DA, Colbert DE, Gaspard JC, Casper BM, Cook MLH, Reep RL, Bauer GB (2005) Temporal resolution of the Florida manatee (*Trichechus manatus*) auditory system. J Comp Physiol A 191:903–908

Møhl B, Au WWL, Pawloski JL, Nachtigall PE (1999) Dolphin hearing: relative sensitivity as a function of point of application of a contact sound source in the jaw and head region. J Acoust Soc Am 105:3421–3424

Mooney TA, Nachtigall PE, Yuen MML (2006) Temporal resolution of the Risso's dolphin, *Grampus griseus*, auditory system. J Comp Physiol A 192:373–380

Mooney TA, Nachtigall PE, Castellote M, Taylor KA, Pacini AF, Esteban J-A (2008) Hearing pathways and directional sensitivity of the beluga whale, *Delphinapterus leucas*. J Exp Mar Biol Ecol 362:108–116

Mulsow J, Reichmuth CJ (2007) Electrophysiological assessment of temporal resolution in pinnipeds. Aquat Mamm 33:122–131

Myrberg AA (1986) Sound producing by males of a coral reef fish (*Pomacentrus partitus*): its significance to females. Anim Behav 34:913–923

Myrberg AA Jr (1997) Sound production by a coral reef fish (*Pomacentrus partitus*): Evidence for a vocal, territorial "keep-out" signal. Bull Mar Sci 60:1017–1025

Nachtigall PE, Mooney TA, Taylor KA, Yuen MML (2007) Hearing and auditory evoked potential methods applied to odontocete cetaceans. Aquat Mamm 33:6–13

Nachtigall PE, Mooney TA, Taylor KA, Miller LA, Rasmussen M, Akamatsu T, Teilmann J, Linnenschidt M, Vikingsson GA (2008) Shipboard measurements of the hearing of the white-beaked dolphin, *Lagenorynchus albirostris*. J Exp Biol 211:642–647

Norris KS, Harvey GW (1974) Sound transmission in the porpoise head. J Acoust Soc Am 56:659–664

Popov VV, Supin AY (1998) Auditory evoked responses to rhythmic sound pulses in dolphins. J Comp Physiol A 183:519–524

Popov VV, Supin AY, Wang D, Wang K (2006) Nonconstant quality of auditory filters in the porpoises, *Phocoena phocoena*, and *Neophocaena phocaenoides* (Cetacea, Phocoenidae). J Acoust Soc Am 119:3173–3180

Purcell DW, John SM, Schneider BA, Picton TW (2004) Human temporal auditory acuity as assessed by envelope following responses. J Acoust Soc Am 116:3581–3593

Rasmussen M, Miller LA (2002) Whistles and clicks from white-beaked dolphins, *Lagenorynchus albirostris*, recorded in Faxaflói Bay, Iceland. Aquat Mamm 28.1:78–89

Rose GJ, Brenowitz EA, Capranica RR (1985) Species specificity and temperature dependence of temporal processing by the auditory midbrain of two species of treefrogs. J Comp Physiol A 157:763–769

Ryan A (1976) Hearing sensitivity of the Mongolian gerbil, *Meriones unguiculatis*. J Acoust Soc Am 59:1222–1226

Supin AY, Popov VV (1995) Envelope-following response and modulation rate transfer function in the dolphin's auditory system. Hear Res 92:38–45

Supin AY, Popov VV (2003) Temporal processing of rapidly following sounds: Evoked potential study. In: Thomas JA, Moss CF, Vater M (eds) Echolocation in bats and dolphins. University of Chicago Press, Chicago, pp 153–160

Supin AY, Popov VV, Mass AM (2001) The sensory physiology of aquatic mammals. Kluwer, Boston

Surlykke A, Bojesen O (1996) Integration time for short broad band clicks in echolocating FM-bats (*Eptesicus fuscus*). J Comp Physiol A 178:235–241

Szymanski MD, Supin AY, Bain DE, Henry KR (1998) Killer whale auditory evoked potentials to rhythmic clicks. Mar Mamm Sci 14:676–691

Szymaszek A, Szelag E, Sliwowska M (2006) Auditory perception of temporal order in humans: The effect of age, gender, listener practice and stimulus presentation. Neurosci Lett 403:190–194

Urick RJ (1983) Principles of underwater sound. Mc-Graw-Hill, New York

Wiegrebe L, Schmidt S (1996) Temporal integration in the echolocating bat, *Meagderma lyra*. Hear Res 102:35–42

Yost WA (1994) Fundamentals of hearing: an introduction. Academic, New York