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ORIGINAL PAPER

Modulation rate transfer functions from four species of stranded odontocete (*Stenella longirostris, Feresa attenuata, Globicephala melas, and Mesoplodon densirostris*)

Adam B. Smith[1,2] · **Aude F. Pacini**[1,2] · **Paul E. Nachtigall**[1,2]

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Abstract

Odontocete marine mammals explore the environment by rapidly producing echolocation signals and receiving the corresponding echoes, which likewise return at very rapid rates. Thus, it is important that the auditory system has a high temporal resolution to effectively process and extract relevant information from click echoes. This study used auditory evoked potential methods to investigate auditory temporal resolution of individuals from four different odontocete species, including a spinner dolphin (*Stenella longirostris*), pygmy killer whale (*Feresa attenuata*), long-finned pilot whale (*Globicephala melas*), and Blainville's beaked whale (*Mesoplodon densirostris*). Each individual had previously stranded and was undergoing rehabilitation. Auditory Brainstem Responses (ABRs) were elicited via acoustic stimuli consisting of a train of broadband tone pulses presented at rates between 300 and 2000 Hz. Similar to other studied species, modulation rate transfer functions (MRTFs) of the studied individuals followed the shape of a low-pass filter, with the ability to process acoustic stimuli at presentation rates up to and exceeding 1250 Hz. Auditory integration times estimated from the bandwidths of the MRTFs ranged between 250 and 333 μs. The results support the hypothesis that high temporal resolution is conserved throughout the diverse range of odontocete species.

Keywords Dolphin · Toothed whale hearing · Auditory evoked potentials · Modulation rate transfer function · Auditory temporal resolution

Abbreviations

ABR	Auditory brainstem response
EFR	Envelope following response
ERB	Equivalent rectangular bandwidth
ERD	Equivalent rectangular duration
FFT	Fast Fourier transform
MRTF	Modulation rate transfer function
RFR	Rate following response
SAM	Sinusoidally amplitude modulated

Introduction

Odontocetes (toothed whales and dolphins) possess highly developed echolocation systems, which require both the effective production of echolocation clicks and also the reception of click echoes. Echolocation clicks are short-duration acoustic signals that are produced at variable rates depending on the distance between the dolphin and an echolocation target (e.g., Au 1993; Au and Benoit-Bird 2003). Inter-click intervals can be as low as 1.5–3 ms, corresponding to click rates in some species as high as 300 to above 400 clicks per second (e.g., Lammers et al. 2004; Madsen et al. 2004; Verfuß et al. 2009), which are often associated with the final moments of prey capture. Echoes during such click trains can likewise return to the animal at similarly high rates. Temporal and spectral characteristics of target echoes contain important information about the target that are processed by the odontocete auditory system (Bullock et al. 1968; Au et al. 1988; Au 1993). Thus, it is important that the auditory system has a high temporal resolution to

✉ Adam B. Smith
adambsmi@hawaii.edu

[1] Department of Biology, University of Hawaiʻi at Mānoa, 2538 McCarthy Mall, Edmondson Hall Room 216, Honolulu, HI 96822, USA

[2] Hawaiʻi Institute of Marine Biology, 46-007 Lilipuna Road, Kāneʻohe, HI 96744, USA

effectively process and extract relevant information from such rapid acoustic signals.

Auditory Brainstem Responses (ABRs) have been increasingly used to investigate many aspects of the odontocete auditory system, including directional hearing (e.g., Popov and Supin 1988, 1990, 2009; Popov et al. 1992, 2006), hearing pathways (e.g., Møhl et al. 1999; Mooney et al. 2008, 2014, 2015; Popov et al. 2016), audiograms (e.g., Nachtigall et al. 2005, 2007; Yuen et al. 2005; Cook et al. 2006; Finneran et al. 2009), binaural hearing cues (Popov and Supin 1991), and temporal resolution (Supin and Popov 1995a, b; Dolphin et al. 1995; Mooney et al. 2006). Use of ABR methodology is advantageous by allowing research with subjects that have little behavioral training and has proven valuable for measuring auditory characteristics of previously unstudied odontocete species from the wild that have stranded or been rehabilitated (Nachtigall et al. 2005, 2007; Cook et al. 2006; Finneran et al. 2009; Mann et al. 2010; Pacini et al. 2010, 2011, 2016; Schlundt et al. 2011; Montie et al. 2011; Greenhow et al. 2014).

When trains of short, tone burst stimuli are presented to a test subject, the individual ABRs generated in response to the stimulus train merge together into a steady state wave called a envelope following response (EFR). If the stimulus train consists of broadband clicks, the steady-state evoked response is called a rate following response, or RFR (Supin et al. 2001). The magnitude of these following responses can be plotted as a function of the pulse presentation rate to generate a Modulation Rate Transfer Function, (MRTF) when the stimulus is a sinusoidally amplitude modulated (SAM) tone. When the stimulus is a broadband click, these functions have been termed an RFR amplitude-vs-rate curve (Supin et al. 2001). In mammals, including marine mammals, these functions are generally the shape of a low-pass filter, with response magnitudes decreasing and eventually ceasing above a certain modulation or presentation rate as the auditory system can no longer follow the rapid changes of the stimulus envelope. The upper limits of presentation rates that elicit ABR responses have been used as an estimation of the temporal resolution of test subjects (Supin and Popov 1995b; Popov and Supin 1998; Linnenschmidt et al. 2013). Although distinct by virtue of the stimulus type, MRTFs and amplitude-vs-rate curves can both be used to facilitate investigation of auditory temporal resolution, which has led to frequent use of the former term for both types of data in previous marine mammal studies. Following this convention, the term “MRTF” is used solely hereafter in this study.

MRTFs have been described for nine species of odontocete so far, including the Yangtze finless porpoise (*Neophocaena phocaenoides asiaeorientalis*; Mooney et al. 2011), harbor porpoise (*Phocoena phocoena*; Linnenschmidt et al. 2013), bottlenose dolphin (*Tursiops truncatus;* Supin and Popov 1995b; Dolphin et al. 1995; Popov and Supin 1998; Finneran et al. 2007), white beaked dolphin (*Lagenorhynchus albirostris*; Mooney et al. 2009), Risso’s dolphin (*Grampus griseus*; Mooney et al. 2006), beluga (*Delphinapterus leucas;* Dolphin et al. 1995; Klishin et al. 2000), false killer whale (*Pseudorca crassidens*; Dolphin et al. 1995), Gervais’ beaked whale (*Mesoplodon europaeus*; Cook et al. 2006; Finneran et al. 2009), and the killer whale (*Orcinus orca*; Szymanski et al. 1998). While there are some intra and inter-specific differences in MRTF characteristics, all species exhibited the ability to follow acoustic stimuli at presentation rates up to or exceeding 1.2 kHz. In studies using brief, pulsed acoustic stimuli, odontocetes exhibit an auditory temporal resolution that is many times greater than non-echolocating mammals, both marine and terrestrial (Mulsow and Reichmuth 2007). Similarly, high temporal processing abilities have been found in echolocating bats (Wiegrebe and Schmidt 1996), lending support to the hypothesis that such high temporal resolution is an adaptation for echolocation (Supin and Popov 1995b). Longer integration times of dozens of milliseconds were found in behavioral experimentation with a bottlenose dolphin when long-duration, pure tone stimuli were used (Johnson 1968), which may reflect different temporal resolutions between the auditory periphery and higher auditory levels. Thus, estimates of auditory temporal resolution have varied. It is still unclear to what extent temporal processing differs between odontocete species and how such differences may relate to other aspects of their acoustic biology such as hearing ranges, peripheral filter bandwidths, or echolocation characteristics. Data on temporal processing from additional odontocete species may prove valuable to uncovering these relationships. In the current study, electrophysiological methods were used to investigate auditory temporal resolution from four species of stranded odontocete; a Blainville’s beaked whale (*Mesoplodon densirostris*), long-finned pilot whale (*Globicephala melas*), pygmy killer whale (*Feresa attenuata*), and spinner dolphin (*Stenella longirostris*).

Methods

Test subjects

Hearing measurements were recorded from a single individual of four odontocete species (spinner dolphin, pygmy killer whale, pilot whale, and beaked whale) which stranded in four separate events from 2006 to 2014. On August 27th, 2006, a neonate male long-finned pilot whale stranded at a beach near Nazaré, Portugal. The animal was transferred to the Lisbon Zoo in November 2006 for treatment. The animal began to eat solid food after approximately a year of rehabilitation, and was subsequently trained to station horizontally at the surface of the water for auditory evoked potential hearing tests. The audiogram was previously measured and showed good hearing up to 64 kHz (Pacini et al. 2010).

An adult male pygmy killer whale was found stranded near Maalaea Harbor, Maui, on May 22, 2009. The animal weighted 285 kg and was 2.1 m in length. After the initial veterinary assessment, the animal was determined to be in poor health and exhibited a very low white blood cell count. Auditory evoked potential measurements were conducted at the stranding site as an additional diagnostic test.

A sub-adult male Blainville's beaked whale stranded near Kihei, Maui on the morning of August 16, 2010. The initial diagnostic tests suggested the animal was suffering from severe immune compromise and renal insufficiency. The animal was subsequently transferred to a rehabilitation pool in Hilo, on the Big Island of Hawai'i for treatment and rehabilitation. The whale weighed approximately 800 kg and measured 3.5 m in length. To assist in determining the animal's prospects for rehabilitation, auditory evoked potential hearing measurements were selected as an additional diagnostic test. The audiogram of this individual was previously published by Pacini et al. (2011).

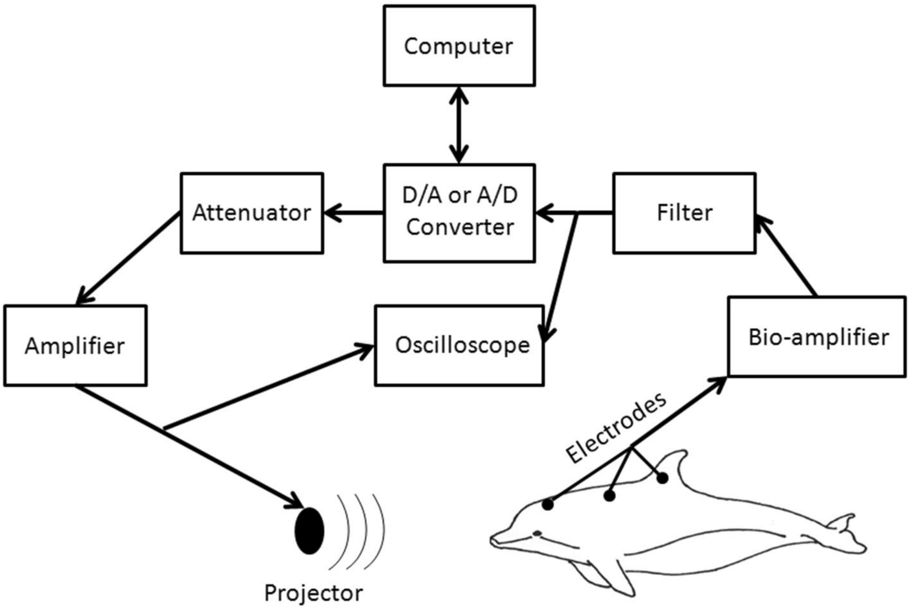
In 2014, a spinner dolphin stranded near Badoc municipality on the west coast of Ilocos Norte province in the Philippines. The animal was initially treated on site for 2 weeks before being transferred to Ocean Adventures Marine Park, in Subic Bay, the Philippines, for additional treatment and rehabilitation. The animal weighed 38.5 kg and was 1.7 m in length upon arrival at Ocean Adventures, and was treated with antibiotics, fluids, b-complex, vitamin E, and liver support. No ototoxic drugs were administered to the animal. An audiogram of this individual was previously published by Pacini et al. (2016). Auditory temporal resolution measurements were collected on October 8, 2015.

Stimulus presentation and evoked response recording

While the general equipment and hardware setup used to conduct the experiments was the same between the separate subjects, different models of instruments were sometimes used. A diagram of the general equipment setup can be seen in Fig. 1. Acoustic stimuli were digitally generated from a laptop computer using a custom LabView program and sent to a National Instruments PCMCIA-6062E or USB-6251 data acquisition card (Austin, TX, USA). The stimulus level was controlled in 1 dB steps via an attenuator before being amplified by 20 dB and projected to the animal from a Reson 4013 or 4040 underwater transducer (Slangerup, Denmark). Projected signals were monitored in real time during the experiments on a Tektronix TPS 2014 oscilloscope (Beaverton, OR, USA). During experimentation, the test subjects were in a stationary position with the tops of their heads and backs above the surface of the water. In the case of the beaked whale, pygmy killer whale, and spinner dolphin, the animals were lightly held and supported in the proper position for the tests by training or veterinary staff, while the pilot whale was trained to station in position on its own. The projecting hydrophone was placed 1 m directly in front of the rostrum of each of the animals at a depth of 30 cm.

Acoustic stimuli consisted of trains of individual broadband tone pulses (0.1 ms duration) presented within a maximum 20 ms time window (Fig. 2) at presentation rates ranging from 300 to 2000 Hz. Peak spectral power of the stimuli was 45, 50, 32, and 50 kHz for the spinner dolphin,

Fig. 1 General diagram of the equipment used to collect electrophysiological data from the four test subjects



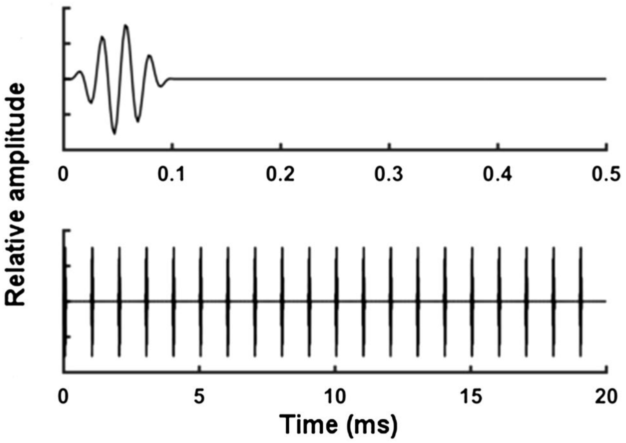


Fig. 2 Example of the electric stimulus waveforms of a single 45 kHz pulse (top panel) and 20 ms train of pulses presented at a rate of 1000 Hz (bottom panel)

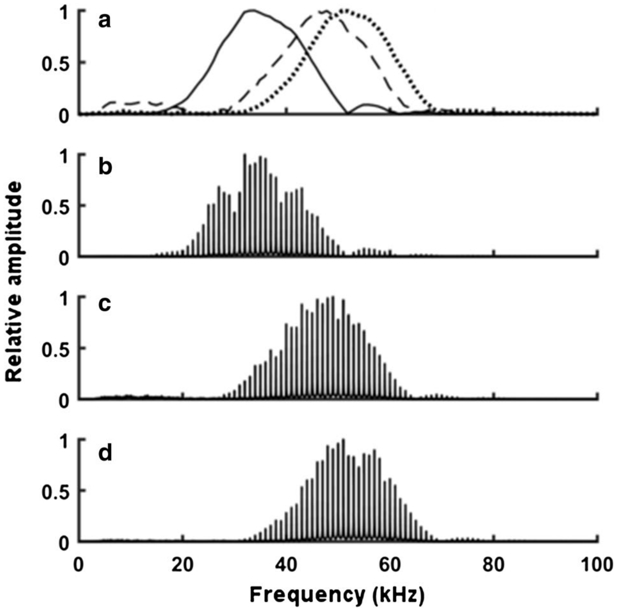


Fig. 3 Frequency spectra of acoustic stimuli after transformation by the transducer, including: **a** individual stimulus pulses with peak frequencies of 32 (solid line), 45 (dashed line), and 50 kHz (dotted line), **b** a 32 kHz pulse train, **c** a 45 kHz pulse train, and **d** a 50 kHz pulse train. For **b**–**d**, pulse trains were presented at a rate of 1000 Hz

pygmy killer whale, pilot whale, and beaked whale, respectively (Fig. 3). The number and frequency of pulse presentation rates that were tested differed between the animals. Evoked responses were collected at 11 different presentation rates for the spinner dolphin and pilot whale, while the pygmy killer whale and beaked whale were tested at 7 and 8 different rates, respectively. The difference in tested rates was due to the different experimental circumstances between each species. In the case of the pygmy killer whale and beaked whale, the animals had stranded only a few days prior and were under ongoing veterinary care and treatment. At the time of the data collection, the primary purpose of the MRTF tests was to determine suitable modulation frequencies for audiogram measurements. Thus modulation rate tests were conducted opportunistically around the timeline of the more essential veterinary care requirements of the animals. Conversely, the pilot whale and spinner dolphin had already been successfully rehabilitated prior to the MRTF measurements and were in good health and were more available for a greater number of hearing measurements.

Gold plated, 10 mm electrodes (GRASS, West Warwick, RI, USA) embedded in silicon suction cups were used to record evoked potentials. The active electrode was placed behind the blowhole and the reference electrode was placed on the back towards the dorsal fin. A third, ground electrode was placed on the side of the dorsal fin. Evoked responses were amplified 10,000 times and bandpass filtered from 0.1 to 3 kHz by a Grass CP511 bioamplifier. The responses were further filtered from 0.1 to 3 kHz with a Krohn–Hite 3384 bandpass filter (Brockton, MA, USA) before being sent to the data acquisition card and recorded on the same computer that produced the stimulus signal. The evoked responses were recorded at a sample rate of 16 kHz over successive 26 ms time windows that were synchronized with the onset generation of the stimulus signal. Between 800 and 1000 ABR recordings were averaged for each stimulus level to extract the evoked response from noise and were saved on the computer for offline analysis using MatLab software (Mathworks, Natick, MA, USA).

Data analysis

A Fast Fourier transform (FFT) was performed on a 16 ms section of the recording which contained the evoked response. The magnitude of the response was measured as the value of the spectral peak corresponding to the presentation rate, which was then corrected for the frequency response of the filters. Corrected response magnitudes were plotted according to the presentation rate to visualize the modulation rate transfer function. Keeping the 20 ms stimulus duration constant for all tested modulation rates resulted in a different number of individual pulses and overall stimulus energy being presented at each rate. To account for this, weighted MRTFs were also generated using two different methods. First, the magnitude of responses for each modulation rate was summed for the fundamental response peak and its harmonics, and second, the response magnitude was calculated from the square root of the sum of squares for the fundamental response peak and its harmonics.

Results

Envelope following responses were elicited and detected from all four of the test subjects, and could be seen across a broad range of modulations rates. RFR response waveforms of the spinner dolphin and beaked whale can be seen in Fig. 4. Small onset responses can be seen at higher modulation rates in these individuals, although offset responses were not visible. The magnitude of the RFR response was quantitatively determined by calculating an FFT over a 16 ms window of the waveform corresponding to the RFR and the magnitude of the spectral peak was measured at each modulation frequency (Fig. 5). Harmonics were clearly observed in FFTs of the RFR waveforms at modulation rates below 1000 Hz. As has been noted in the previous studies, the harmonics result from deviations in the response waveform from a sine wave (Mooney et al. 2006).

The MRTFs for each animal all showed a low-pass filter shape with clear peaks and notches (Fig. 6). The subjects followed modulation rates up to and above 1250 Hz, which was the peak following response for both the spinner dolphin and the pilot whale. Peak following responses for the beaked and pygmy killer whale were found slightly lower at 1000 Hz. Response magnitudes dropped off rapidly above the peak response frequency in all subjects except the beaked whale. In that individual, response magnitudes appeared to decrease more gradually up to 1500 Hz before falling into the noise floor of the ABR system at 1750 Hz.

Weighted MRTFs for each species showed a slightly different shape from non-weighted functions. Differences primarily occurred at lower frequencies, with some weighted response magnitudes even exceeding the non-weighted peak modulation rate magnitudes. As has been documented in other odontocete MRTFs, this difference is due to the fact that harmonics are more present at modulation rates below 1000 Hz, and thereby increased the weighted magnitude at those rates (Mooney et al. 2011; Linnenschmidt et al. 2013).

A clear notch was observed between 600 and 900 Hz in the pilot whale before response magnitudes rose to a secondary peak at 500 Hz. A faint notch was observed in the spinner dolphin MRTF from 700 to 900 Hz due to a small secondary peak at 600 Hz. In both the spinner dolphin and pilot whale, responses dropped off gradually below the secondary peaks. Modulation rates were not tested below 500 Hz for the beaked and pygmy killer whale, making determination of a secondary peak inconclusive. There was a clear notch

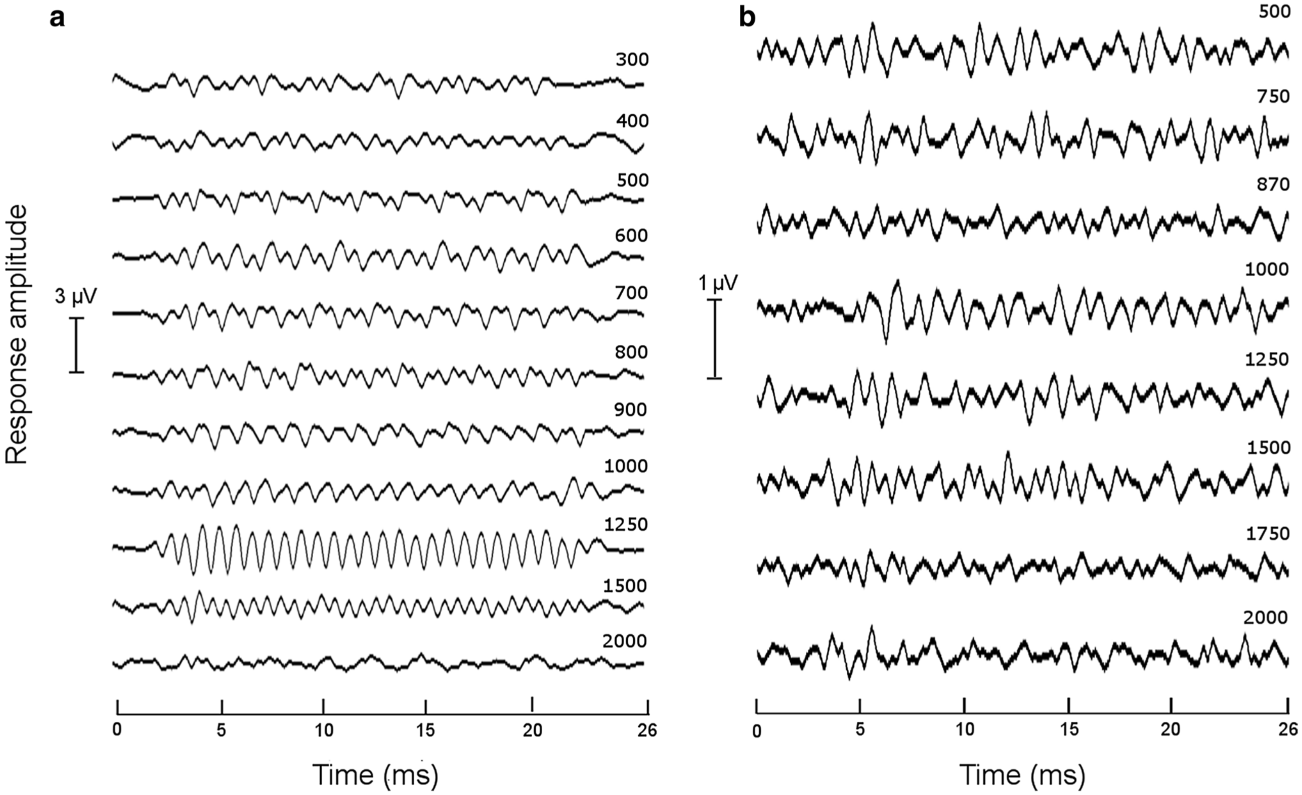


Fig. 4 Rate following response waveforms to different stimulus presentation rates recorded from the spinner dolphin (**a**) and Blainville's beaked whale (**b**)

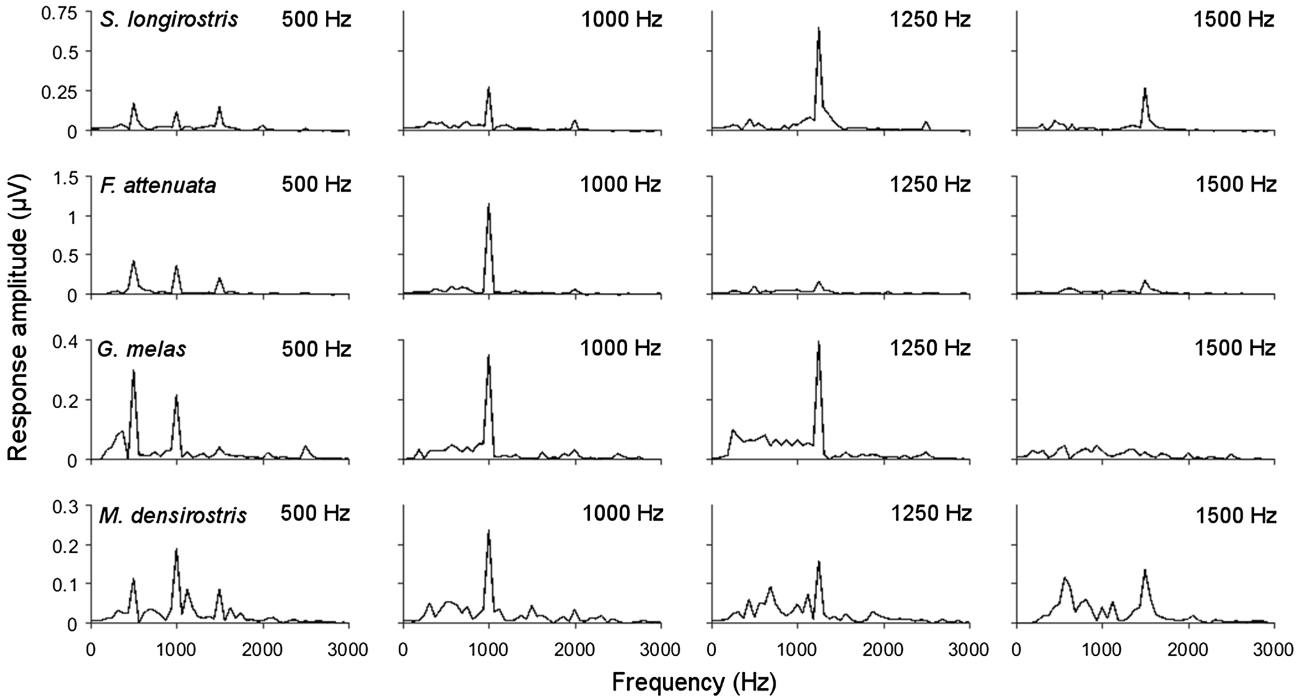


Fig. 5 Fast Fourier transform spectra of RFRs at varying modulation rates in the four subject animals. Response magnitudes were determined as the spectral peak corresponding to the stimulus presentation rate

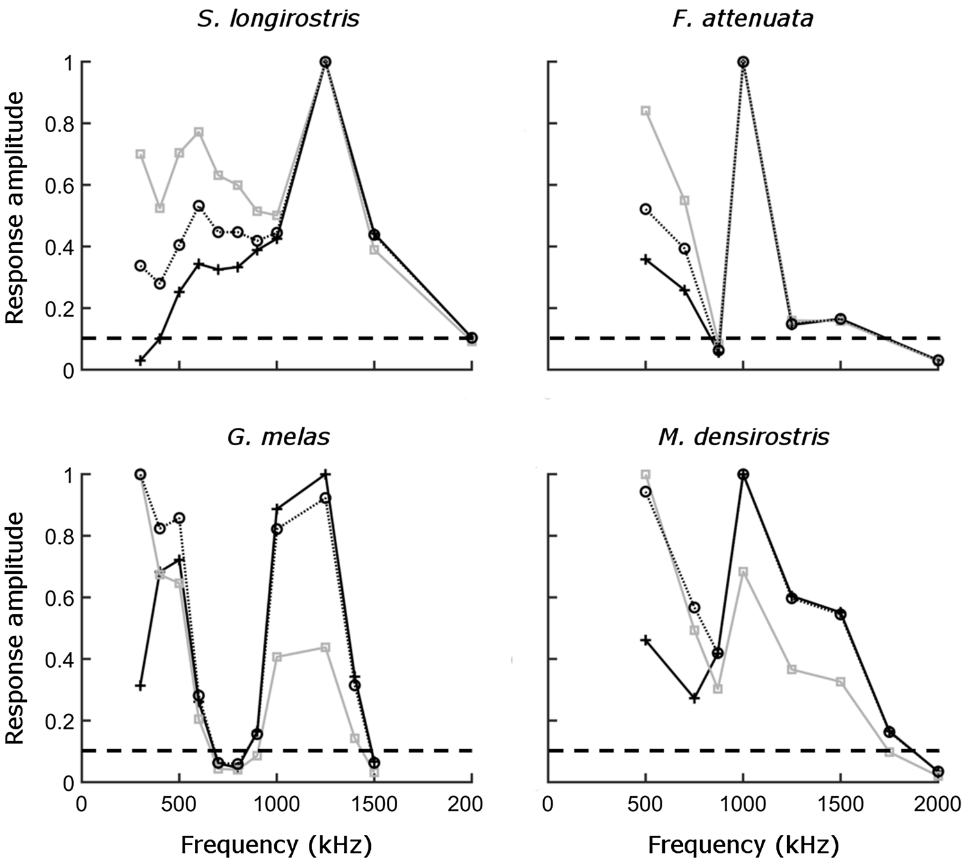


Fig. 6 Normalized fundamental (black lines) and weighted modulation rate transfer functions for the four studied odontocetes. Weighted MRTFs were calculated by taking either the summed magnitude of the fundamental response and its harmonics (dotted lines) or the square root of the sum of squares of the fundamental response ad its harmonics (grey lines). Weighted response magnitudes are larger at lower frequencies due to the increased presence of harmonics in the response spectra. The horizontal dashed line denotes 10% of the peak response magnitude

below the primary peak in the MRTF for the beaked and pygmy killer whales before the response magnitude began to increase again up to 500 Hz.

The upper cut-off frequency of the MRTF has been defined in the previous studies as the presentation rate that produces a response magnitude −20 dB (or 10%) relative to the peak response magnitude (Popov and Supin 1998; Mulsow and Reichmuth 2007). Using the same metric here, upper cut-off frequencies were 2000 Hz for the spinner dolphin and 1750 Hz for the beaked whale. The response of the pygmy killer whale at 1500 Hz was slightly above the −20 dB magnitude, suggesting a cut-off frequency of around 1600 Hz. For the pilot whale, the upper cutoff was slightly below 1500 Hz. Although an RFR was not detected above the background noise at this rate, the response magnitude at 1400 Hz represented only an 8 dB decrease in relation to the MRTF peak. Thus, a 1500 Hz cutoff was deemed the most accurate in relation to the −20 dB criteria.

Discussion

Comparison of MRTF characteristics

The MRTFs of the four individuals presented here are very similar to other odontocete species, showing a low-pass filter shape and detectable RFRs to high modulation rates up to and exceeding 1250 Hz, followed by decreasing response magnitudes at higher rates. It should be noted that due to the differing experimental circumstances in this study that resulted from some of the animals undergoing medical and rehabilitation efforts, the data collected here are somewhat limited in the range and number of modulation frequencies tested, resulting in differences in resolution of the MRTFs at both the higher and lower modulation frequencies. Nonetheless, some comparisons can be made. Corner frequencies (i.e., the upper rate where responses' amplitudes begin to drop off steeply) between 1000 and 1250 Hz are generally similar to most other odontocetes, although a corner frequency of 1250 Hz in the spinner dolphin and pilot whale is slightly higher than most other toothed whales (800 Hz: *O. orca*; Szymanski et al. 1998; 1,000 Hz: *G. griseus*; Mooney et al. 2006, 2009; 1000 Hz: *D. leucas*; Klishin et al. 2000; 1,125 Hz: *L. albirostris*). The exception to this is the harbor porpoise (*P. phocoena*) which showed a corner frequency of 1400 Hz (Linnenschmidt et al. 2013). The location and magnitudes of peaks and notches in the functions vary somewhat between the species, which is not unexpected given the inter- and intra-specific variation found in other odontocetes. The relative magnitude of these features in the MRTF likely results from response latencies from different locations of anatomical generators of the ABR response (Supin and Popov 1995b; Popov and Supin 1998).

Estimation of auditory integration time

It has previously been adopted that marine mammal temporal resolution of the auditory system can be characterized from the MRTF bandwidth (Popov and Supin 1998; Mulsow and Reichmuth 2007; Linnenschmidt et al. 2013); a correspondence that has been previously illustrated in humans (Viemeister 1979; Kuwada et al. 1986; Rees et al. 1986; Eddins 1993). Estimates of the auditory integration time have been calculated using the equation ERD = 1/(2 × ERB), where ERB is the bandwidth of the MRTF converted to an equivalent rectangular bandwidth, and ERD is the temporal integration function converted to an equivalent rectangular duration (Supin and Popov 1995b). A wider MRTF bandwidth would yield a lower estimated integration time and thus a better temporal resolution. MRTF bandwidths for the pilot whale, pygmy killer whale, Blainville's beaked whale, and spinner dolphin result in estimated temporal integration times of 333, 313, 294, and 250 µs, respectively. Resolution differences between species at the higher frequencies of the MRTFs result in some uncertainty in these estimates, yet even conservative ERB estimates indicate that these individuals exhibit very high auditory temporal resolution that is comparable with other studied odontocetes. It also further supports the notion that acute temporal resolution is likely conserved across the diversity of odonocete species.

Comparison between odontocete species

Despite the increased number of odontocete species for which data are available, it is still difficult to tease apart the extent to which specific biological characteristics may be related to, or influence, auditory temporal processing capabilities. It is notable that temporal resolution is comparably high between the similar sized porpoise species (*P. phocoena* and *N. phocaenoides*), which use long-duration, narrow-band high-frequency clicks (Møhl and Andersen 1973, Kamminga 1988), and the spinner dolphin, which produces shorter, broadband clicks (Schotten et al. 2004). This similarity may suggest that auditory temporal processing abilities of different odontocete species are not related to the specific temporal or spectral characteristics of their outgoing echolocation signals.

Temporal resolution as estimated by MRTFs from a harbor porpoise (Linnenschmidt et al. 2013), bottlenose dolphin (Finneran et al. 2007), and killer whale (Szymanski et al. 1998) appear to be correlated with animal size (Linnenschmidt et al. 2013). Smaller animals exhibit a broader MRTF bandwidth, shorter estimated integration times, and thus a more acute temporal resolution. Despite having published MRTFs, estimated integration times were not stated for six other previously studied species, but can be estimated from either reported MRTF bandwidths (2000 Hz for *N.*

phocaenoides, 1475 Hz for *L. albirostris*, 1400 Hz for *D. leucas*; Klishin et al. 2000; Mooney et al. 2009, 2011) or approximated via visual inspection of the MRTFs themselves (1150 Hz for *G. griseus*, 1800 Hz for *M. europeus*, 1500 Hz for *P. crassidens*) (Dolphin et al. 1995; Cook et al. 2006; Mooney et al. 2006; Finneran et al. 2009). Using studies where the body length of individual subjects is available, the trend between body size and auditory temporal resolution appears to be generally corroborated (Fig. 7), including when mean body lengths of the species are compared to the MRTF data (Table 1).

The estimated temporal resolution of the small neonate Risso's dolphin (Mooney et al. 2006) appears as an interesting outlier compared the data from other species. When data from this individual are removed from the analysis, linear regressions fit to the data in Fig. 7 are generally improved. While the animal was a stranded individual and its exact age was unknown, its small size and the presence of fetal folds indicate that it was likely no more than a few months old. This dolphin was of a similar size (1.47 m) to the spinner dolphin (1.7 m), harbor porpoise (1.43 m), and Yangtze finless porpoise (1.44), yet showed an upper cut-off frequency at 1100 Hz, lower than the similar sized odontocetes by 900 Hz and lower than much larger individuals and species such as the killer whale and false killer whale (Table 1). The relatively poor temporal resolution of that Risso's individual thus cannot be attributed to size differences. Since the neonate Risso's is the only individual of the species and the only neonate cetacean for which these data are currently available, it is difficult to conclude if the comparatively poor temporal resolution is characteristic of the species, or perhaps is influenced by the animal's young age. Auditory temporal acuity in humans and rats is comparably poor during infancy, and improves into adulthood (Dean et al. 1990; Werner et al. 1992; Trehub et al. 1995; Trehub and Henderson 1996; Friedman et al. 2004). It is possible that auditory temporal resolution in odontocetes could show similar ontogenetic improvements. The first ontogenetic measurements of ABRs of an odontocete have recently been described in harbor porpoise calves, which exhibit fully developed hearing within a day after birth (Wahlberg et al. 2017). Due to the importance of hearing for odontocete survival, it is likely that other odontocete species likewise exhibit precocial hearing development (Wahlberg et al. 2017). Furthermore, similar relative latencies between individual ABR waves in the neonate (Mooney et al. 2006) and an adult Risso's dolphin suggest that the neonate Risso's also had fully functional hearing (Wahlberg et al. 2017). However, since there are no MRTF measurements across life stages, the ontogeny of odontocete auditory temporal resolution requires additional exploration. It remains an open question if the comparably poor auditory temporal resolution of the neonate Risso's dolphin is characteristic of the species.

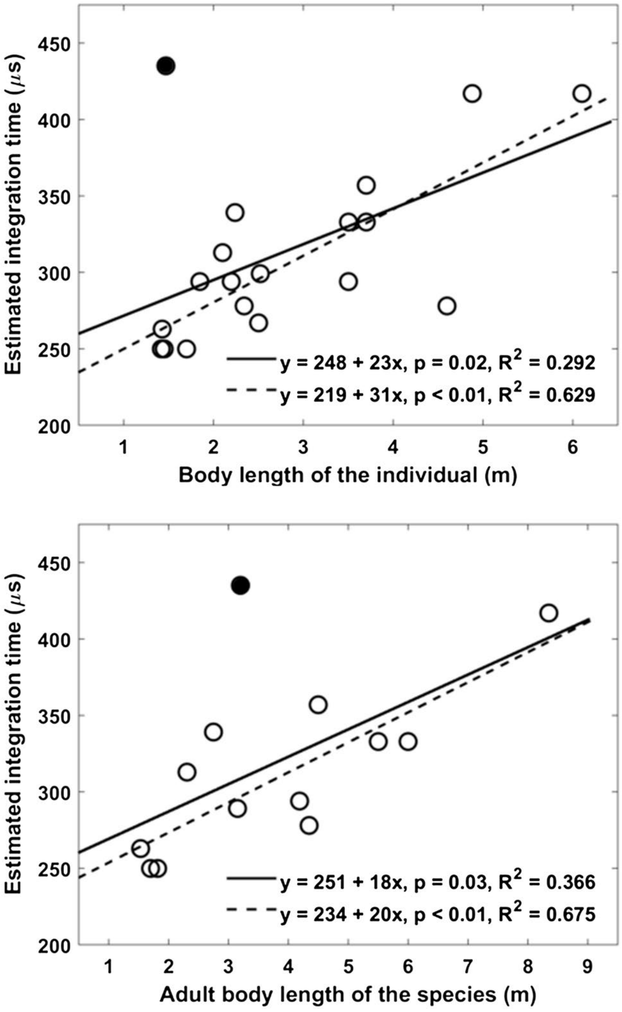


Fig. 7 Comparison of MRTF estimated auditory integration times to the body lengths of the studied individuals (top panel) and adult lengths of each species (bottom panel). In the bottom panel, estimated integration times were averaged for species with more than one tested individual. Linear regressions were fitted to data which included all subjects and species (solid line) and also excluded data from the Risso's dolphin (dotted line), which appeared as a noticeable outlier (filled circles) from the trend found with other species

One notable variation between odontocete studies is the acoustic stimulus, which includes SAM tones at varying frequencies (Supin and Popov 1995b; Dolphin et al. 1995; Klishin et al. 2000; Cook et al. 2006; Finneran et al. 2007, 2009; Linnenschmidt et al. 2013) as well as broadband clicks or pulses with varied spectral bandwidths (Szymanski et al. 1998; Klishin et al. 2000; Mooney et al. 2006, 2009, 2011). Investigation by Supin and Popov (1995b) and Finneran et al. (2007) found no substantial differences in MRTF characteristics of the same individual across a range of stimulus carrier frequencies, which included individuals with normal hearing and high-frequency hearing loss in the latter study. Therefore, it seems unlikely that differences

Table 1 List of MRTF cut-off frequencies, estimated integration times, individual body lengths, and adult body lengths for each subject and species

Species	MRTF BW (Hz)	Est. IT (μs)	Subject length (m)	Species length (m)
P. phocoena	1900[a]	263	1.43[a]	1.53[b§]
N. phocaenoides asiaeorientalis	2000[c]	250	1.45[c]	1.7[d]
N. phocaenoides asiaeorientalis	2000[c]	250	1.42[c]	1.7[d]
*G. griseus**	1150[e]	435	1.47[e]	3.2[f‡]
S. longirostris	2000	250	1.7	1.82[g‡]
F. attenuata	1600	313	2.1	2.31[h†]
L. albirostris	1475[i]	339	2.24[i]	2.75[j‡]
T. truncatus	1670[k]	299	2.52	3.15[l‡]
T. truncatus	1870[k]	267	2.5 [m]	3.15[l‡]
T. truncatus	1700[n]	294	2.2[n]	3.15[l‡]
T. truncatus	1700[n]	294	1.85[n]	3.15[l‡]
M. europaeus	1800[o]	278	2.34[p]	4.35[p†]
*M. europaeus**	1800[q]	278	4.6[q]	4.35[p†]
G. melas	1500	333	3.5	6[r†]
M. densirostris	1700	294	3.5	4.19[o†]
*P. crassidens**	1500[s]	333	3.7[t]	5.5[u§]
D. leucas	1400[v]	357	3.7[v]	4.5[w‡]
*O. orca**	1200[x]	417	4.88	8.35[y§]
*O. orca**	1200[x]	417	6.1[z]	8.35[y§]

BW is bandwidth of the MRTF and IT is the estimated integration time

*MRTF upper cut-off frequencies visually approximated from published data

[†] Mean adult length

[‡] Median of adult length range

[§] Median of adult male/female length maximums

[a] Linnenschmidt et al. 2012

[b] Bjørge and Tolley 2009

[c] Mooney et al. 2011

[d] Amano 2009

[e] Mooney et al. 2006

[f] Chen et al. 2011

[g] Perrin 2009

[h] Donahue and Perryman 2009

[i] Mooney et al. 2009

[j] Kinze 2009

[k] Finneran et al. 2007

[l] Wells and Scott 2009

[m] Ridgway et al. 2006

[n] Popov and Supin 1998

[o] Cook et al. 2006

[p] NMFS 2016

[q] Finneran et al. 2009

[r] Olson 2009

[s] Dolphin et al. 1995

[t] Au et al. 1995

[u] Baird 2009

[v] Klishin et al. 2000

[w] O'Corry-Crowe 2009

[x] Szymanski et al. 1998

[y] Ford 2009

[z] Walsh 1997

in stimulus characteristics would substantially influence comparison between species or be causing the trend seen in Fig. 7. Nonetheless, fine-scale comparison should be made with caution due to the limited number of individuals tested for most species, and thus, it is difficult to draw conclusions about the possible causes or biological significance of the trend between body size and temporal resolution from the current data. It should first be considered that the trend is possibly a byproduct of the electrophysiological methodology. Non-invasive ABR signal amplitudes are influenced by the distances between electrodes and the responding auditory centers of the brain; the distance being greater in larger species and resulting in a lower amplitude ABR response (Supin et al. 2001). While the relatively narrow MRTF of the neonate Risso's dolphin compared to the similar sized spinner dolphin and porpoise species suggests that MRTFs may detect poor temporal resolution in small subjects, temporal resolution in larger subjects could still be underestimated due to increased attenuation of the ABR signal. In addition, although MRTF estimates of integration times in the bottlenose dolphin (300 µs: Popov and Supin 1998) closely resemble those determined from behavioral experiments (250–300 µs: Moore et al. 1984; Au et al. 1988; Au 1990; Dubrovsky 1990), behavioral estimates of integration times have not been done with additional odontocete species. Therefore, it should not be assumed that the same correspondence would necessarily occur. It would be valuable to compare temporal resolution as measured by behavioral and electrophysiological methods between additional odontocete species, as well as pinnipeds, another group of marine mammals.

High temporal resolution in odontocetes is likely related in part to broad peripheral auditory filters which result from a wide range of hearing up to and above 140 kHz in some species (Popov et al. 2005; Houser et al. 2008; Nachtigall et al. 2008). Since the upper limits of sensitive hearing tend to occur at higher frequencies in smaller odontocete species, it could be speculated that the trend in Fig. 7 is driven by smaller species generally possessing wider filter bandwidths due to a broader hearing range. However, auditory filter bandwidths in multiple species appear to be generally constant above 40 kHz (Popov et al. 2006a; Lemonds et al. 2011, 2012) and also wide (>3 kHz), negating any improvement in temporal resolution that would result from differences in hearing range. The generally consistent MRTF bandwidths found across a range of frequency-specific tone pips within individual subjects in the previous studies further suggests temporal resolution is limited primarily by a central integration process (Supin and Popov 1995b).Therefore, it seems unlikely that potentially improved auditory temporal resolution in the smaller species could simply be attributed to hearing range or broader peripheral filter bandwidth.

Improved auditory temporal resolution could possibly provide some benefit for smaller species. Mammalian auditory systems utilize binaural cues to help determine the direction and location of a sound in the horizontal plane, including resolution of differences in time of arrival and intensity differences of a sound between the two ears (Heffner and Heffner 1992). While the mechanisms of sound localization are not well studied in odontocetes, the bottenose dolphin has been shown to possess an acute ability to resolve inter-aural time delays and inter-aural level differences (Moore et al. 1995) between the two ears. Since the availability of such cues is largely dependent on head size (Heffner and Heffner 1992), perhaps differences in auditory temporal acuity could be related to binaural resolution requirements of the differing head sizes between species. Alternatively, the temporal and spectral characteristics of biosonar echoes contain important information for the detection and discrimination between desired prey targets (Bullock et al. 1968; Au et al. 1988; Au 1993). Echoes originating from small-bodied prey items would contain increased fine-scale variation in echo structure that would need to be identified by a foraging animal that preferred such prey. Perhaps, different auditory temporal resolutions across species are instead related to prey selection and the need to adequately resolve temporal variation in echo structure of preferred prey types and sizes. However, such hypotheses are purely speculative. Both behavioral and electrophysiological data on auditory temporal resolution in additional odontocete species would be valuable towards further investigation of these possibilities.

Conclusion

Modulation rate transfer functions were measured from four stranded odontocetes by recording auditory evoked potentials in response to temporally modulated stimuli. The individuals all showed the ability to process acoustic stimuli at high presentation rates, indicating auditory temporal resolution similar to other studied odontocetes and supporting the idea that high temporal resolution is conserved throughout the diverse range of odontocete species. Comparison of the MRTFs between species of different echolocation characteristics suggests that auditory temporal resolution is not largely related to echolocation signal type. MRTF estimates of temporal resolution were found to be correlated with animal body size, although further experimentation is required to elucidate the possible causes and significance of this relationship in terms of each species' biology and auditory processing.

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