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Temporal resolution of the Risso's dolphin, *Grampus griseus*, auditory system

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Abstract Toothed whales and dolphins (Odontocetes) are known to echolocate, producing short, broadband clicks and receiving the corresponding echoes, at extremely rapid rates. Auditory evoked potentials (AEP) and broadband click stimuli were used to determine the modulation rate transfer function (MRTF) of a neonate Risso's dolphin, *Grampus griseus*, thus estimating the dolphin's temporal resolution, and quantifying its physiological delay to sound stimuli. The Risso's dolphin followed sound stimuli up to 1,000 Hz with a second peak response at 500 Hz. A weighted MRTF reflected that the animal followed a broad range of rates from 100 to 1,000 Hz, but beyond 1,250 Hz the animal's hearing response was simply an onset/offset response. Similar to other mammals, the dolphin's AEP response to a single stimulus was a series of waves. The delay of the first wave, PI, was 2.76 ms and the duration of the multi-peaked response was 4.13 ms. The MRTF was similar in shape to other marine mammals except that the response delay was among the fastest measured. Results predicted that the Risso's dolphin should have the ability to follow clicks and echoes while foraging at close range.

Keywords Risso's dolphin · *Grampus griseus* · Modulation rate transfer function (MRTF) · Auditory evoked potential (AEP) · Envelope following response (EFR)

Abbreviations ABR: Auditory brainstem response · AEP: Auditory evoked potential · DAQ: Data acquisition · EEG: Electroencephalogram · EFR: Envelope following response · FFT: Fast Fourier transform · ICI: Inter click interval · MRTF: Modulation rate transfer function · RFR: Rate following response · SAM: Sinusoidal amplitude modulated · SPL: Sound pressure level

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Introduction

Odontocetes, or toothed whales and dolphins, are known for their exceptional auditory sensory systems. In adapting to an aquatic life, odontocetes have evolved unique capabilities including broadband hearing, high frequency sensitivities, rapid neurophysiological responses, and short temporal resolutions. It is presumed that these capabilities have developed to survive in an underwater world where sound travels five times faster than in air, and where light is quickly attenuated and often limited at depth or at night. All of the odontocetes tested to date have demonstrated the ability to echolocate.

Toothed whales have demonstrated the ability to make at least two types of sounds, echolocation clicks and burst pulses. Marine mammal echolocation clicks typically consist of short, broadband pulses of sound, as short as 40 μs (Au 1993) and temporally spaced between 5 and 500 ms (Madsen et al. 2004a; Penner 1988). Echoes from targets such as fish prey will return to the animal in a similarly rapid fashion. Field recordings have demonstrated that odontocetes, including sperm whales, beaked whales, and delphinids, vary the echolocation inter click interval (ICI) and decrease the ICI when approaching prey (Johnson et al. 2004; Lammers et al. 2004; Zimmer et al. 2005). Just before prey capture, clicks are produced at their most rapid rates with minimum ICI of 5–20 ms, which is referred to as the terminal buzz. It is yet to be investigated whether the auditory system of odontocetes may be able to individually follow these outgoing clicks and received echoes of this terminal buzz without the masking of either sound. To do so, the auditory neurophysiological responses and temporal resolution of toothed whales must be fast and highly derived.

Burst pulses are similar to echolocation clicks in the individual pulse, but are typically spaced with extremely short ICIs of approximately 1–10 ms (Lammers et al. 2004). These are often produced in a social context (Herzing 1996). Because of the rapid click rate of burst pulses, it is also uncertain whether the producing animal follows the click, the echo or both.

Although there have been a number of studies of the auditory system of cetaceans, there are only ten published audiograms (Nachtigall et al. 2000) out of 83 species (Rice 1998). Further, the temporal resolution of the odontocete family has only been investigated in six species (Dolphin et al. 1995; Popov and Supin 1990; Supin and Popov 1995; Szymanski et al. 1998). In order to better comprehend the physiological abilities of odontocetes, it is necessary to measure the hearing capabilities and temporal resolution of those uninvestigated species. One method to measure the temporal resolution of the auditory system is to estimate the modulation rate transfer function (MRTF) using auditory evoked potentials (AEPs). The AEP technique is a noninvasive and rapid method to measure the hearing range and temporal resolution of animals. It is a method that requires no training of the subject and is used also to assess hearing responses in human infants (Hecox and Galambos 1974).

In humans, the AEP response to a single click or tone pip is actually the summation of neurological responses from multiple sources (Kuwada et al. 2002). For this reason, AEP responses consist of several waves, PI, NII, PII, NIII, PIII and NIV and are often termed an auditory brainstem response (ABR). These waves are all visible at the onset of an envelope following response (EFR), but if a stimulus is played at a rapid enough rate, most of the waves blend together in a sinusoidal fashion. In dolphins, a similar blending seems to occur (Supin and Popov 1995).

Evoked potentials are used to measure hearing capabilities by modulating the amplitude of a tone at a specific rate. As the subject's auditory system responds to the tone, it may follow the envelope of the loud–soft modulation of the tone by a corresponding EFR. Determining the amplitudes of the EFR at various modulation rates provides the MRTF. A typical MRTF is low pass in shape, and the corner frequency of that MRTF can be inferred as the temporal resolution of the subject (Supin et al. 2001).

Auditory evoked potentials have been used to estimate MRTFs and thus temporal resolution in several species of mammals. Human maximum MRTF responses were measured at 10–50 Hz (Kuwada et al. 1986; Rees et al. 1986). Gerbils may be the fastest measured auditory system of terrestrial mammals, with responses measured at 100–150 Hz (Dolphin and Mountain 1993). The highly specialized auditory system of odontocetes has a much faster temporal resolution with the killer whale at 800 Hz (Szymanski et al. 1998), the false killer whale at 1,000 Hz (Dolphin et al. 1995), and the bottlenose dolphin at 1,200 Hz (Supin and Popov 1995). These rates are 20–40 times that of previously measured land mammals.

Recent work has explored the acoustic capabilities of the Risso's dolphin, *Grampus griseus*, a pelagic species of squid-eating odontocetes whose offshore habitat often limits the species' sightings and interactions with humans. This includes the first audiogram of this species using behavioral psychoacoustic methodology (Nachtigall et al. 1996), as well as a recent redefining of the species' audiogram using AEP techniques (Nachtigall et al. 2005). Further investigations have demonstrated the Risso's dolphin's echolocation capabilities and signal characteristics (Madsen et al. 2004b; Philips et al. 2003). The goal of this study was to measure the temporal resolution from the maximum rate following response (RFR) rate of a Risso's dolphin using AEP measurements. The MRTF of the Risso's dolphin as well as the physiological time lag of the animal's auditory response was measured.

Methods

Subject and facility

The study animal was an infant male Risso's dolphin *G. griseus* that stranded off the southwest coast of Portugal in May 2004 and thus its exact age was unknown. However, due to its small size and the presence of fetal fold markings on the animal's body, it was determined to be a neonate. For assessment and care, the animal was brought to a rehabilitation facility at ZooMarine in Guia, Albufeira, Portugal. During the experiment, the animal measured 147 cm long, weighed 47 kg, ate well and gained weight. The study was conducted for four consecutive days in late May, 2 weeks after the stranding. Two weeks following the experiment, the animal died of pneumonia and possibly a secondary viral infection, both of which were unrelated to this work.

The animal was housed in an open-air, covered, concrete rehabilitation pool, 3 m deep and 5 m diameter. The artificial sea water depth was kept at a constant level of 1.1 m and 19°C (Fig. 1). Pumps and filters recycling the water in the tank were turned off 15 min before the beginning and during the experiment to reduce bubbles in the water and background noise. A desk adjacent to the tank served as the observation and data collection center, where the equipment was housed and where the experiment operators were seated.

Experimental design and stimuli presentation

During the experiment, the animal was moved toward the middle of the tank and held in position by the experimenter. The animal became relaxed in that resting position, decreasing its breathing rate and relaxing its muscles. During a sound presentation, the dolphin was stationed 0.5 m from the center of the tank, on axis of

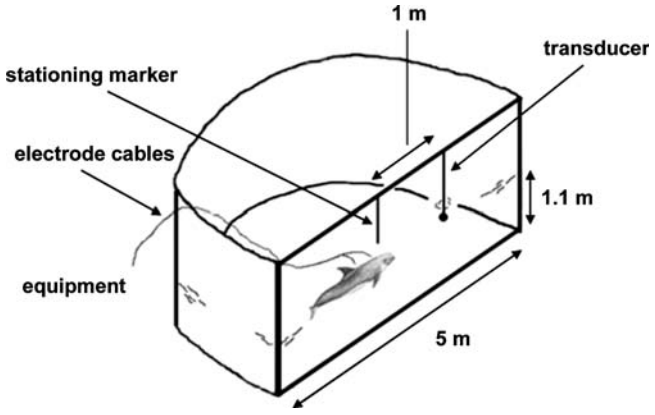

Fig. 1 Experimental setup shown in a cross-section of the research tank. The subject was stationed by the researcher 1 m from the transducer so that melon and lower jaw were below the surface of the water. Water depth was 1.1 m and diameter of tank was 5 m. The animal was always stationed in the same position, the blowhole directly under the hanging weight. A rope was strung across the tank, from which the transducer and stationing marker were hung. Sides of the tank were lined with sound baffling cushions (not pictured)

the diameter of the tank. The transducer used to produce the stimuli was positioned 0.5 m from the center of the pool (which was 1 m from the subject), at a depth of 30 cm, and also on axis to cross-section the tank.

The stimulus was a broadband click from 1 to 40 kHz designed as a rectangle function that was 50 μs in duration. The rate at which the click was played varied from 100 to 2,000 Hz (Table 1). This broadband nature of the stimulus ensured that the animal's presumed hearing range and the click bandwidth would overlap. Clicks were digitally generated with a computer that contained a custom LabVIEW data acquisition program that was created with a National Instruments PCI-MIO-16E-1 DAQ card. The DAQ card converted the signal from digital to analog, using an update rate of 200 kHz. The signal was then played through a custom built signal shaping box that could attenuate the click bursts in 1 dB steps. The outgoing stimulus from the signal shaping box was sent to the projecting hydrophone and was monitored using a Techtronix TDS 1002 oscilloscope. The signal was played through an ITC-1032 transducer with a resonance frequency of 38 kHz. The amplitudes of the stimuli were calibrated before data collection by placing a calibrated hydrophone, a Biomon 8261, near the dolphin's head while the dolphin was in the correct position. The received peak-to-peak level (V) of the click stimuli were measured with the calibrated hydrophone. This Vp–p was converted to peak-equivalent rms voltage (peRMS) by subtracting 9 dB. The peRMS was taken as the RMS voltage and used to calculate the SPL by referring to the hydrophone sensitivity. These values were taken as the received level of the click.

Table 1 Fourier transform and peak-to-peak averages of Risso's dolphin AEP when stimuli were played at varying rates (from 100 to 2,000 Hz)

Click rate (Hz)	Fourier transformed AEP (μV)	Weighted pk–pk AEP (μV)
100	0.02	2.35
200	0.14	2.77
300	0.69	3.01
400	2.80	4.60
500	3.99	5.37
600	3.35	4.27
700	1.76	1.87
800	1.21	1.37
900	2.05	2.13
1,000	2.37	2.35
1,250	0.15	0.54
1,500	0.12	0.48
2,000	0.06	0.37

Note the decline in the AEP between click rates of 1,000 and 1,250 Hz

AEP recording and measurement

The animal's ABR was recorded using two standard 10 mm gold EEG electrode sensors placed on the surface of the subject's skin, attached by two latex suction cups. Passive conductivity of the animal's AEPs from the skin surface to the electrode was enhanced by standard human EEG gel. One suction cup was embedded with the recording electrode, and was placed 3–4 cm behind the dolphin's blowhole and off to the right, i.e., over the animal's brain. The second suction cup contained the reference electrode, and was placed on the back of the animal near its dorsal fin. The animal rested at the surface with most of its head and lower jaw underwater to receive sound input through the major tissue routes to the ears (Ketten 2000; Mohl et al. 1999; Norris 1968) but with the suction cups in the air.

The received signal was then amplified 10,000× using an Iso-Dam Isolated Biological Amplifier. The Iso-Dam as well as a Krohn-Hite Filter Model 3103, with a bandpass of 100–3,000 Hz, filtered the responses for anti-aliasing protection. The amplified and filtered responses were transferred to an analog input of the same DAQ card in the same desktop computer. The received signal was digitized at a rate of 16 kHz. In order to extract the recorded AEP from noise, the entire trial was extended to about 1 min by averaging 1,000 samples of the stimuli that were presented at a rate of 20/s.

The optimal stimulus amplitude that would result in a suitable EFR from the animal was initially unknown for this species. Therefore, the initial sound was low in amplitude and was slowly increased until a clear record was established (Fig. 2). The first stimulus was played at 77 dB re: 1 μPa sound pressure level (SPL), the second at 91 dB, the third at 96 dB and the fourth and final stimulus level was 101 dB, the level at which all of the following experimental stimuli were presented. An MRTF had not previously been determined for the Risso's dolphin, and therefore the rate at which to first

present the clicks was based on prior published data of other odontocete species such as the bottlenose dolphin and false killer whale. These species follow a stimulus presentation rate of 1,000 Hz relatively well (Dolphin et al. 1995; Supin and Popov 1995), and hence the initial stimulus was presented at that rate.

The modulation, or click presentation, rate was then varied, presenting clicks to the animal at rates from 100 to 2,000 Hz at the above the SPL (Table 1). During the data collection, the AEP of the animal was monitored and a 30 ms window starting at the onset of the stimulus presentation was recorded by the same custom LabVIEW program mentioned above. Each window was successively averaged during collection and simultaneously viewed as the data was being collected in order to ensure good data signals, and then saved for offline data analysis.

Data analysis

To quantitatively determine the EFR magnitude, the 20-ms portion of the record that contained the response cycles were fast Fourier transformed (FFT). This provided frequency response spectra and allowed the weight of the modulation-rate fundamental to be determined. The amplitude of the FFT peak was calculated as the AEP response amplitude of the animal to the click stimulus at the corresponding modulation rate. A higher peak reflected a greater response to the corresponding click presentation rate.

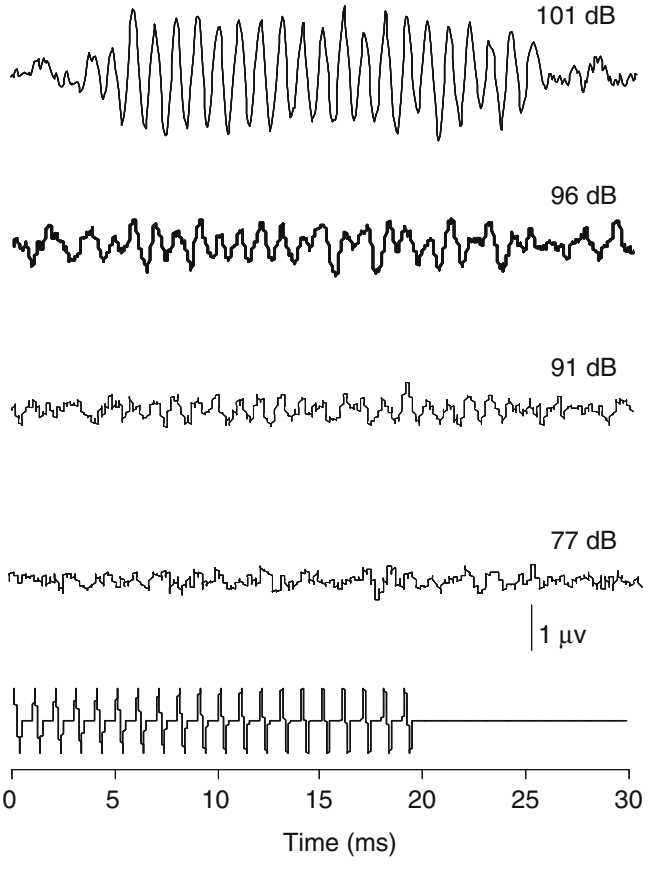

Fig. 2 Click stimulus (*bottom trace*) and rate following responses recorded using four different stimulus amplitudes (101, 96, 91, and 77 dB re: 1 μPa). All AEPs are relative to 1 μV. Each stimulus was played for 20 ms, and AEPs were recorded during a 30 ms window, beginning at the onset of stimulus presentation

Although Fourier transforming the EFR provides a rapid assessment of the animal's response at a certain frequency, it does not weigh the number of stimulus presentations per unit time. Within a 20 ms stimulus, a 100 Hz click would be presented only twice, whereas a 1,000 Hz click would be presented 20 times. Thus within the recording, the subject may only have two AEP responses at 100 Hz, but 20 responses at 1,000 Hz. The Fourier transform does not account for this bias, but rather will reflect the greater energy at 1,000 Hz. To adjust for this, a weighted response amplitude was derived using a custom MATLAB program that would average the peak-to-peak amplitude of the physiological responses to the click at each presentation rate. The response amplitudes determined by both methods were then plotted against frequency of click presentation to determine the MRTF and estimate the temporal resolution of the Risso's dolphin. Further analysis was conducted using EXCEL and MINITAB software.

The time lag of the subject's auditory responses was measured using the multiple waves of an auditory brainstem response (ABR), a type of AEP involving a series of 5–7 "waves" evoked by clicks or short tone bursts of acoustic stimuli. It was possible to capture the entire ABR of a single click by using the initial response to a low rate click. In order to measure response delay, the time at which a response reached its maximum or minimum value was conservatively determined to be the onset latency of the response peak. In order to determine response duration, the point where the response wave started and stopped had to be defined as well. Within the 30 ms measured window, the onset of the signal was then defined as the point at which the first peak (PI) of the wave was 10% larger than the average noise level, and the offset was defined as the point when the declining slope of the last null wave (NIV) was 10% greater than the average noise level. The duration of a single AEP response was measured as the time separation from waves PI to NIV. Delay mean values were measured from the first click in each of the thirteen stimuli presentations and adjusted for the system delay, 40 µs from the start of A/D conversion to activation of the loudspeaker, and transmission delay for 1 m (670 µs, $c = 1{,}490$ m/s).

Results

The plotted functions of the subject's response to stimuli of increasing SPL are shown in Fig. 2 Stimulus intensity was increased from 77, 91, 96 and finally to 101 dB re: 1 μPa, where the AEP was clear, level, and distinct from

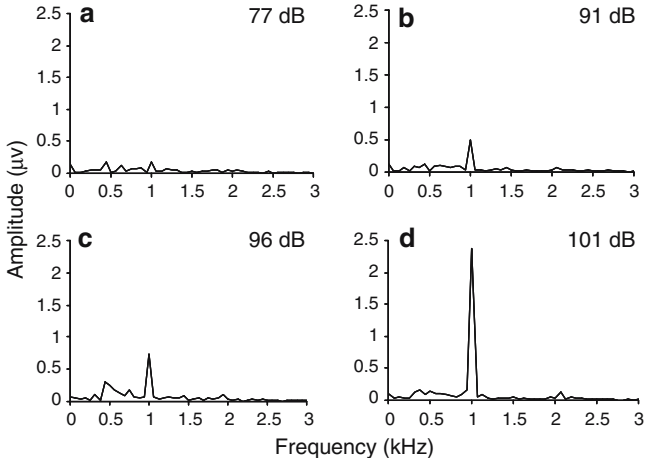

Fig. 3 Fourier spectra using a click repeated at 1.0 kHz varying the SPL. Sound intensity of the click stimuli series for each respective graph is labeled on the graph. A SPL of 101 dB re: 1 μPa was determined as the amplitude of stimulus presentation level for all modulation rates when quantifying the MRTF

the background noise. The response here was a sinusoidal AEP, as is typical for higher frequency modulation rates.

A portion of each AEP was fast Fourier transformed and viewed in the frequency spectrum (Fig. 3). The corresponding peak at the modulation frequency was taken as the amplitude of the response. As SPL increased, the peak at 1,000 Hz increased, thereby reflecting the same trend as the AEP. Again, at 101 dB, there was a very clear peak, distinct from the background noise.

The Risso's dolphin MRTF using the FFT data was low-pass in shape, similar to that of other odontocete MRTFs (Fig. 4; Table 1). This animal showed obvious following of click rates up to 1,000–1,200 Hz. There was a lower frequency peak at 500 Hz and a higher frequency peak at 1,000 Hz. The MRTF was relatively broadband, spanning from 200 to 1,200 Hz, with a clear notch at 800 Hz. Beyond 1,000 Hz there was a steep, high-frequency cut-off. The function decline was more gradual at the lower frequencies, declining after 300–400 Hz. Using the weighted pk–pk results (Table 1), the responses to lower frequency click rates were of higher amplitude (Fig. 5). Above the lower frequencies, the Risso's MRTF was still the same general shape, regardless of methodology in data analysis.

When lower rate stimuli were used, the frequency spectrum of the EFR revealed harmonics present in the EFR (Fig. 6). These harmonics were multiple peaks of the fundamental frequency and separated by amounts equal to the fundamental frequency. For example, when

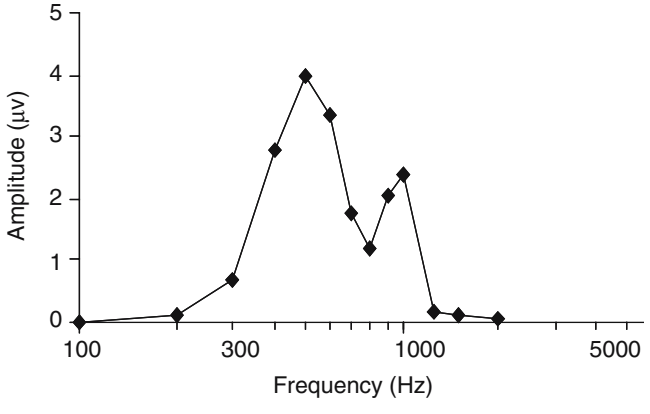

Fig. 4 Modulation rate transfer function based on peak values of Fourier transforms of the Risso's dolphin's AEP. Peaks typically occurred at the modulation frequency of the click presentation

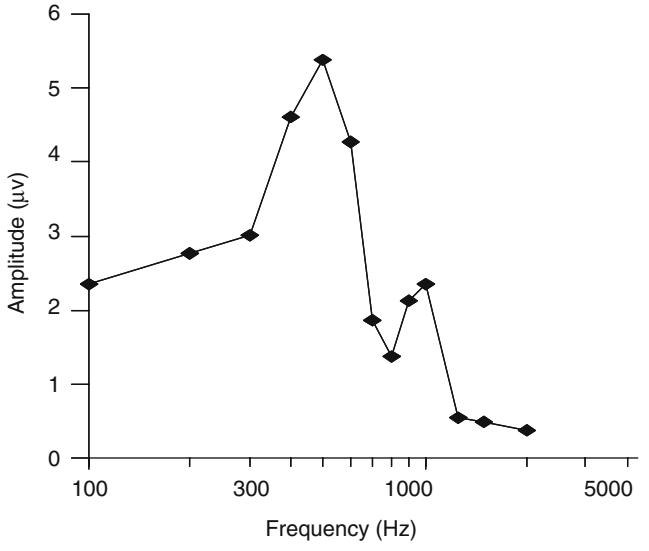

Fig. 5 Weighted modulation rate transfer function based on the average of the peak-to-peak values of the Risso's dolphin's AEP at each respective response

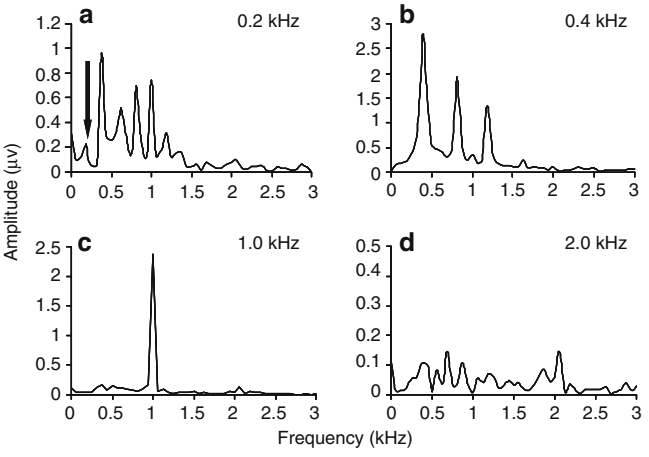

Fig. 6 Fourier spectra of records at click modulation frequencies of 0.2, 0.4, 1.0, and 2.0 kHz. Response amplitudes are on the *y*-axis and in μV (note the different scales). The *x*-axis is in kHz. At 0.2 and 0.4 kHz the peaks at higher frequencies are harmonics in the AEP found at lower stimuli modulation rates. An *arrow* points to the fundamental response at 0.2 kHz

using a 400 Hz click rate, as in Fig. 6, there was a clear peak at the fundamental frequency of 400 Hz, as well as peaks at the harmonic frequencies of 800 and 1,200 Hz. The harmonics resulted from an AEP that deviates in shape from a normal sine wave (Fig. 7).

An ABR from a single click was taken out of the series of clicks in the animal's rate following response (RFR) (Fig. 7b). The compaction of these multiple ABRs in the RFR resulted in the deviation from a "normal" sine wave response as in an EFR in Fig. 7. Thus, harmonic components as seen in Fig. 6 were a result.

The Risso's response was also measured at click stimulus rates of 1,250, 1,500, and 2,000 Hz. At these rates that were greater than 1,000 Hz, the Risso's dolphin did not follow the sound as an EFR but rather only as an onset and offset response to the click stimuli (Fig. 8).

The peaks of these various waves were used to measure the onset response time of the Risso's dolphin's initial response to an auditory stimulus. Mean response time for the Risso's dolphin was 2.76 ms for PI, 3.29 ms for NII, 3.78 ms for PII, 4.18 ms for NIII 4.56 ms for PIII, and 5.17 ms for NIV (Table 2). The total duration of the multi-peaked response was also measured at 4.13 ms.

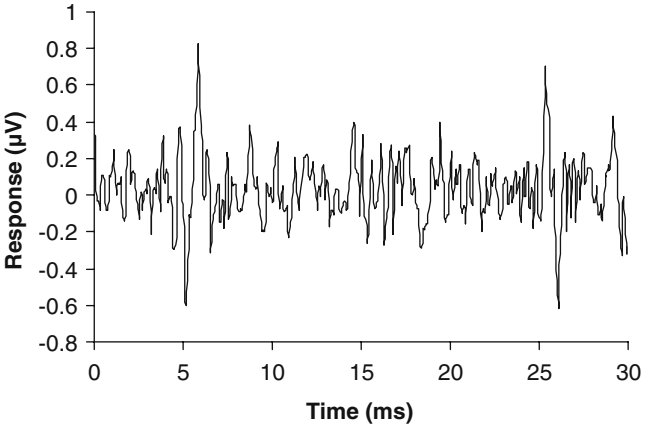

Fig. 8 Onset and offset response to click stimuli at a rate of 2,000 Hz. Peaks at 5–6 and 25–26 ms are likely the onset and offset responses to the click stimuli

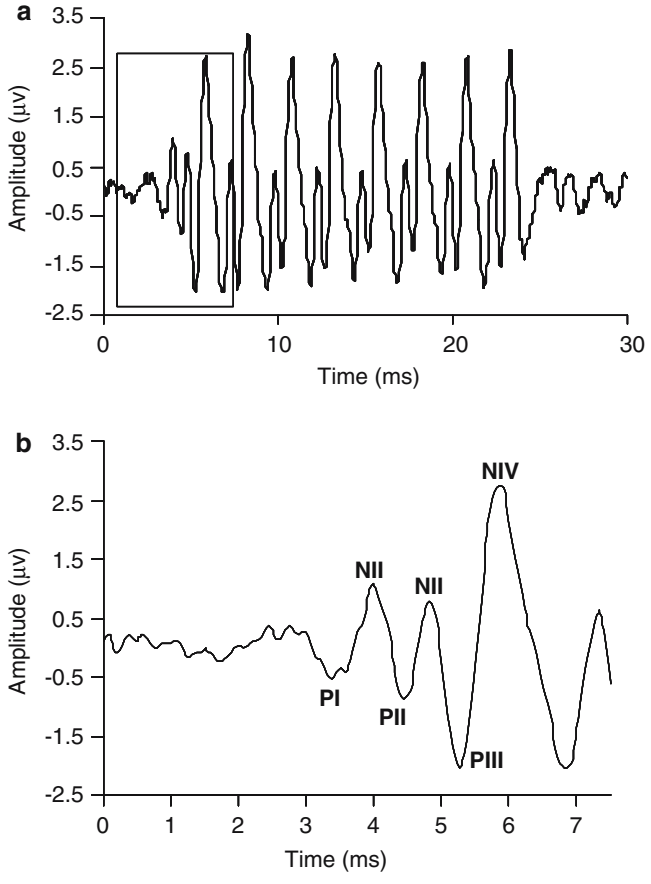

Fig. 7 **a** Rate following response of 400 Hz click stimuli. **b** Series of AEP waves (PI–NIV) from a single click stimuli. b is a close-up section of the AEP highlighted in (**a**), and shows the physiological delay as well as the series of response waves

Discussion

The MRTF of the Risso's dolphin presented here revealed a similar shape and temporal range to that of other odontocete cetaceans. The animal's capability to follow stimuli presented at a rate over 1,000 Hz indicated that the animal has a very high temporal resolution, beyond that of most mammals and similar to other echolocating odontocetes.

The particular shape of the MRTF revealed several peaks and notches, including the largest response peak at 500 Hz and a second, corner peak at 1,000 Hz. The corner frequency of 1,000 Hz is important for two reasons: (1) it is the modulation frequency used for sinusoidal amplitude modulated (SAM) waves in AEP audiograms for the species, and (2) it is the predicted temporal resolution of the subject. For this Risso's dolphin, the AEP audiogram was conducted soon after the MRTF, and the corner frequency of 1,000 Hz was

Table 2 Measured response delay to click stimuli

Wave	Response delay (ms)	SD
PI	2.76	0.157
NII	3.29	0.099
PII	3.78	0.050
NIII	4.18	0.101
PIII	4.56	0.101
NIV	5.17	0.094

Delay mean value measured from the first click in each of the thirteen stimuli presentations, adjusted for a 710 μs system and travel time delay. Units are ms. SD is the standard deviation from the mean of the delay of each wave

used as the SAM rate in the presented tones (Nachtigall et al. 2005).

This high temporal resolution presumably evolved as an adaptation to the physical consequence that sound travels about five times faster in water than in air, and as part of the animal's echolocation ability. The echolocation click of an odontocete is very short in duration, and has been measured from a Risso's dolphin to be from 30 to 50 μs, with the inter-click interval (ICI) at a consistent 20 ms (Madsen et al. 2004b). However, in other odontocetes such as bottlenose dolphins or beaked whales, the ICIs will often vary, ranging from 5 to 500 ms (Madsen et al. 2004a; Penner 1988). Presumed burst pulses of Hawaiian spinner dolphins (*Stenella longirostris*) have an ICI as low as 1.5–2 ms (Lammers et al. 2004). Although variations in Risso's dolphins ICIs have not been published, many odontocetes vary the inter click interval with target range and it is reasonable to at least compare these other odontocete results with what a Risso's dolphin is likely to be capable of using. This Risso's dolphin MRTF reflected that the animal's auditory neurophysiology could follow sounds at a rate of at least 1,000 Hz, or on the order of one per millisecond. Based on the MRTF, the animal measured here should easily be able follow echolocation click trains including burst pulse trains.

The AEP of the Risso's dolphin was made up of several peaks. This was visible at the onset of the SAM stimuli. As in other terrestrial mammals, the various peaks and valleys of the response most likely stemmed from different sources (Kuwada et al. 2002). In addition, the auditory physiological response delay of the subject was measured by the latency of these peaks. The response delay of this animal was extremely rapid, between 2.76 and 5.17 ms, for the various response waves of PI-NIV (Table 2). This time delay takes into account the 710 μs system and travel time delay. These results compared favorably to those of a bottlenose dolphin *Tursiops truncatus*, for which delays were measured between 2.0 and 4.5 ms (Supin and Popov 1995). Considering our conservative method of determining a peak's onset, the response of the Risso's dolphin was quite fast.

However, the response delay of the Risso's dolphin was shorter by several metersecond than what was previously measured for a killer whale, *Orcinus orca* (Szymanski et al. 1998). It has been suggested that the longer delay was a result of the longer neural pathways of the larger killer whale's auditory system. This was likely to be a factor in determining response lag times. However, a comparison of the time lag of the infant Risso's dolphin in this study (weighing 76 kg), to that of adult bottlenose dolphin (upwards of 170 kg), showed that the size of the animal does not necessarily indicate the speed of the auditory response. This was especially true if marine and terrestrial mammals are compared. Cat AEP latencies have been measured on the order of 10–50 ms in their delay, considerably longer than that of odontocetes measured (Farley and Starr 1983). Human AEP latency at the NI wave is approximately 60–90 ms or more than an order of magnitude greater than the Risso's dolphin measured here (Yost 1994).

Although size may be of less importance, the evolution of the auditory system played a key role in evoked potential response latency. Cetaceans have evolved in an underwater environment where sound travels five times faster than in air, and evolution favored adaptation for short echolocation clicks, short echo delays, and rapid neural processing.

The duration of a single AEP response, measured from the onset of the initial wave to the offset of the last wave in a single ABR, corresponded well with the echolocation click patterns of odontocetes. This response duration of the Risso's dolphin was measured to be approximately 4.13 ms. With a minimum echolocation click rate of 5 ms (Madsen et al. 2004a), the animal may click and follow the response, as the stimulus (the click) is occurring at a rate of 200 Hz, well with this animal's measured MRTF. However, echolocating animals are usually receiving an echo as a result of the click returning from the target. Field recordings have shown that foraging odontocetes in their final approach phase click up until they are 1 m from the target (Madsen et al. 2004a). Therefore, the click and echo additively traveled a distance of 2 m, which would take 1.34 ms considering the two-way travel time of sound in water and assuming a speed of 1,490 m s^{-1}. At this range, the echolocating animal would hear a click and then the echo 1.34 ms, or 746 Hz, apart. Sounds presented at a rate of 746 Hz are well within the 1,000 Hz, Risso's dolphin MRTF predicted temporal resolution. Judging from the MRTF, the Risso's dolphin should also be able to follow the clicks of these final foraging phase clicks if they are produced at a rate consistent with the published Hawaiian spinner dolphin burst pulses (Lammers et al. 2004). However, the animal may not have the ability to follow both the click and the returning echo within a burst pulse because here the clicks are being sent out faster than 1:1 processing allows.

The recovery time of the animal was of certain interest as well. This duration of the Risso's dolphin's single AEP response (Fig. 7) was measured at 4.13 ms. However, the AEP consisted of a series of waves, each lasting 1–1.5 ms. Thus it seemed that the animal's auditory system may be able to recover from a single, short duration pulse of sound in 1–1.5 ms, or a series of pulses stimulating the auditory systems up to 1,000 Hz rate, corresponding very well with the animal's maximum MRTF values. This result is in accordance with the fact that AEP responses are measurements of compound neural activity (Kuwada et al. 2002). As stimuli presentation rates approach 1,000 Hz, our measurement of the multi-wave response blends to reflect only the most prominent waves. However, this is likely an accurate estimation of the animal's maximum auditory temporal processing because EFRs fall off at rates beyond 1,000 Hz. Sounds modulating at a rate beyond 1,000 Hz rate may only have an onset and offset response (Fig. 8), i.e., a re-

sponse to the sound stimulus turning on, and the sound stimulus turning off, and the click stimulus may not be followed. This indicated that if the animal were to produce sounds, such as echolocation clicks, at a rate less than 1,000 Hz, it could easily follow the clicks.

If the animal were to click at a rate higher than 1,000 Hz, which may occur in burst pulses, the animal may not follow individual clicks but rather the series of clicks as a single event. Sounds produced at a temporal rate greater than 1,000 Hz would most likely reflect a response more like the one depicted in Fig. 8 rather than the one in Fig. 2. Furthermore, the individual echoes from these types of events, where clicks are produced in an extremely rapid manner, may be physically masked by the initial click series event. Because burst pulse and terminal buzz clicks have not been measured at a rate of more than 1 per 1.5 ms, it seems that in these extremely rapid sound producing cases, the clicks themselves should be followed reasonably, but the echoes returning may overlap and thus be masked. Thus, at least in some cases, the animal may not need to detect the individual echoes of the click produced.

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