

## Frequency-modulation sensitivity in bottlenose dolphins, *Tursiops truncatus*: evoked-potential study

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### Abstract

Evoked-potential responses to rhythmic frequency modulations at carrier frequencies from 32 to 128 kHz were recorded in two bottlenose dolphins. The envelope-following response appeared at modulation rates up to 2000 Hz, with the best responses appearing at rates of 600–650 Hz and around 1000 Hz. Frequency-modulation thresholds were measured at a modulation rate of 625 Hz. Thresholds decreased with increasing sound level up to 130–150 dB re 1  $\mu$ Pa. The lowest thresholds were found at carrier frequencies from 45 to 108 kHz: threshold modulation depths were from 0.025% to 0.2%, inter-individual means were approximately 0.05%, which corresponds to 0.1% of peak-to-peak frequency deviation. For comparison, amplitude-modulation thresholds were measured under the same conditions. At all carrier frequencies, amplitude-modulation thresholds (being expressed in terms of modulation depth) were about 10 times higher than frequency-modulation thresholds.

Key words: dolphins, frequency discrimination limen, frequency modulation, amplitude modulation.

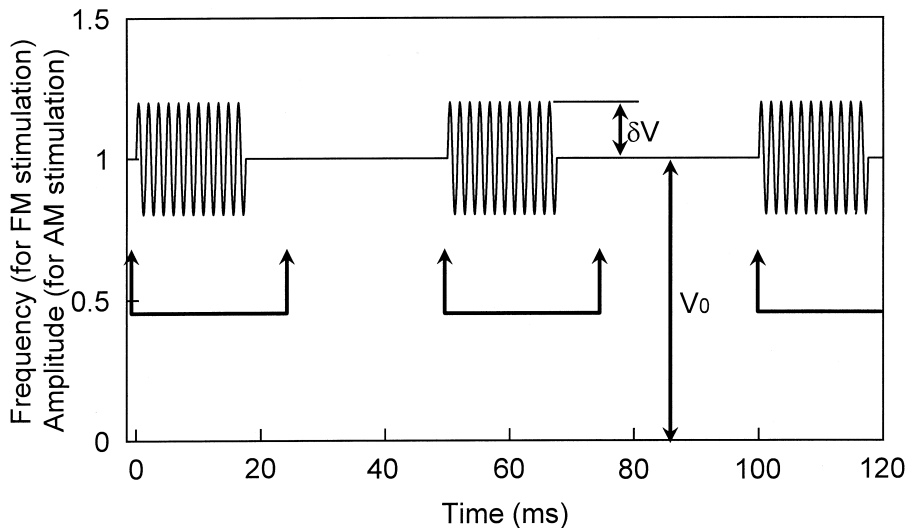
### Introduction

The unique abilities of the dolphin's auditory system have been the subject of many investigations; in particular, frequency selectivity at high frequencies (more than 100 kHz). Frequency tuning in dolphins was measured by a number of approaches: (i) behavioural experiments by use of the critical ratio and critical band paradigms (Johnson 1968; Johnson *et al.* 1989; Au & Moore 1990) as well as the tone-tone masking paradigm (Johnson, 1971), and (ii) in evoked-potential experiments in conjunction with the tone-tone masking (tuning-curve) and notch-noise masking paradigms (Supin *et al.*, 1993; Supin & Popov, 1955; Popov *et al.*, 1995, 1997).

Data obtained provided evidence for a high degree of frequency selectivity in dolphins, in particular, at high sound frequencies. However, the exact degree of frequency tuning in dolphins is still the subject of controversy. Estimates of frequency tuning obtained in evoked-potential studies were high enough:  $Q_{10\text{dB}}$  of 16 to 18,  $Q_{\text{ER}}$  (equivalent rectangular) of 35 to 40, whereas the behavioural experiments gave lower estimates. Thus, the problem is not yet fully clarified and calls for further investigation.

An additional estimate of frequency tuning is the frequency modulation sensitivity which is measured by the lowest detectable frequency shift of pure tone (frequency discrimination threshold). This measure does not coincide with the critical band or the peripheral auditory filter bandwidth. For example, the frequency discrimination thresholds in humans are mainly below 1%, depending on frequency, sound level, etc. (e.g., Weir *et al.*, 1976) whereas critical bands in a major part of the hearing frequency region are about 10% (Moore & Glasberg, 1983; Glasberg & Moore, 1990). Nevertheless, the frequency discrimination threshold is a valuable indicator of frequency discrimination abilities. Several attempts have been made to measure frequency discrimination thresholds behaviourally in dolphins (Herman & Arbeit, 1972; Thompson & Herman, 1975; Jacobs, 1972). These studies yielded moderated values of frequency discrimination thresholds: from fractions of a percent at frequencies of an order of a few kHz to about 1% at frequencies of around 100 kHz. However, threshold estimates obtained in those studies varied significantly. This is understandable given that each study was carried out on only one subject.

Thus, a need exists for further studies on frequency discrimination thresholds in dolphins. Apart from that, it would be of interest to compare data obtained by the behavioural and evoked-potential methods. The latter method has been efficiently employed to investigate a number of important features of the dolphin's hearing, in particular, frequency selectivity (see ref. above).



**Figure 1.** Stimulation and evoked-response technique. The diagram shows the time course of a modulated parameter (frequency for FM stimulation or amplitude for AM stimulation) and presents a short fragment of continuous stimulation. Double-headed arrows show the middle value of the parameter  $V_0$  and deviation  $\delta V$ . Upward-pointing arrows show instants of evoked-response data collection.

There are reasons to expect that the evoked-potential technique will be helpful in measuring frequency discrimination thresholds.

From a variety of evoked potential techniques described in dolphins, we chose an evoked response to rhythmic sound modulation. This envelope-following response (EFR) was recorded in dolphins to rhythmic amplitude modulated (AM) sounds (Dolphin, 1995; Dolphin *et al.*, 1995; Supin & Popov, 1995). It was reasonable to expect that similar responses could be recorded to rhythmic frequency modulated (FM) stimuli. An advantage of this technique is that even at low amplitudes responses can be easily quantified using Fourier analysis. We supposed that this response could be used for measuring FM thresholds.

Thus, the goal of the present study was to measure the frequency-discrimination thresholds in bottlenose dolphins using an evoked-potential technique, namely EFR recording to rhythmic FM. In addition, responses to AM stimuli were recorded under the same experimental conditions.

### Materials and Methods

#### Subjects

The experimental subjects were two adult bottlenose dolphins, *Tursiops truncatus*, a male and a female. Preliminary pilot data were obtained on the male in the 1995 summer season. The main body of data were collected on the female in the 1998

summer season. Each animal was caught 2 months before the study and kept at the Utrish Marine Station of the Russian Academy of Sciences (Black Sea coast). At the time of experimentation, the animals were adapted to the holding and experimental conditions.

#### Experimental conditions

During the experiments, the dolphin was placed in a bath ( $4 \times 0.6 \times 0.6$  m) filled with sea water. The animal was supported by a stretcher so that the dorsal part of its body was above the water surface. No surgical procedure, anaesthesia or muscle relaxants were used. Each experiment lasted 3–4 h, after which the animal was returned to the home pool.

#### Stimuli

Both FM and AM signals were produced by hardware (an AM-FM sine-wave generator). During evoked-response collection, a carrier tone was presented continuously, and short sinusoidal modulation bursts were applied onto the carrier (Fig. 1). The burst duration was 16 to 20 ms; within this range, the duration varied depending on the modulation rate since the burst always contained a whole number of cycles. Bursts were presented at a rate of 20/s. Each burst began and ended at the zero phase of the sinusoid. When necessary, small AM was added to FM stimuli in such a way as to compensate the irregularity of the transducer frequency response around the carrier frequency.

Both the FM and AM values are specified below as fractional modulation depth (Fig. 1) i.e., as ratios

$$m_A = \delta A / A_0$$

$$m_f = \delta f / f_0$$

where,  $m_A$  and  $m_f$  are modulation depths for amplitude and frequency modulation respectively,  $\delta A$  and  $\delta f$  are deviation from the mean value amplitude and frequency respectively, and  $A_0$  and  $f_0$  are the mean levels of these parameters. It should be noted that a common way to express FM changes is the modulation index  $\beta = \delta f / f_m$  where,  $f_m$  is the modulation rate. However, the task of the present study was to find frequency discrimination limits, i.e., the lowest detectable fractional deviation of frequency. For this purpose, it is more proper to express FM in terms of  $\delta f / f_0$ . The used modulation depth was from 0.01% to 10% for the FM stimuli and from 0.1% to 100% for the AM stimuli.

Stimuli were attenuated and played through a B & K 8104 transducer placed in the bath at a depth of 30 cm and at a distance of 1 m from the jaw tip in front of the dolphin's head. Intensity and spectra of signals were monitored through a hydrophone with a passband of 150 kHz, located near the dolphin's head.

#### Evoked response collection

ABR was recorded using plate electrodes 1 cm in dia. They were attached to the body surface by adhesive gel. The active electrode was placed on the dorsal part of the head, 6 to 8 cm behind the blowhole and the reference electrode on the back near the dorsal fin; both electrodes were above the water surface. The recorded signals were amplified by  $5 \times 10^4$  within a passband of 200 to 5000 Hz, digitized (sampling rate 20 kHz), averaged, and stored in computer memory for subsequent analysis. The average sweeps were triggered at instants of burst onsets (see Fig. 1). Each record was obtained by averaging 512 sweeps.

## Results

#### EFR waveform and dependence on FM rate

At moderate modulation depths (on order of a few percent), FM stimuli evoked robust EFR i.e., a rhythmic sequence of potential waves which reproduced the modulation rate. Figure 2 exemplifies EFR at a few modulation rates and shows that EFR amplitude was rate-dependent: it was low at rates both below 400–500 Hz and above 1500–1800 Hz. The most prominent responses were observed at modulation rates of 600–650 Hz (625 Hz in Fig. 2) and around 1000 Hz.

In more detail, the EFR amplitude dependence on modulation rate for FM stimuli is plotted in

Figure 3. This amplitude-vs-rate function was similar to those obtained in dolphins for AM stimuli (Dolphin, 1995; Supin & Popov, 1995); it peaked at rates of 600–650 Hz and 1000–1200 Hz and above 1600–1700 Hz the response amplitude fell steeply.

Since modulation rates of 600–650 Hz and 1000–1200 Hz evoked the most prominent EFR, these rates were considered preferable for threshold measurements based on EFR recording. To minimize the stimulus bandwidth, we preferred to use the low of these two regions. Therefore, for detailed measurements described below the modulation rate of 625 Hz was used.

#### FM and AM thresholds

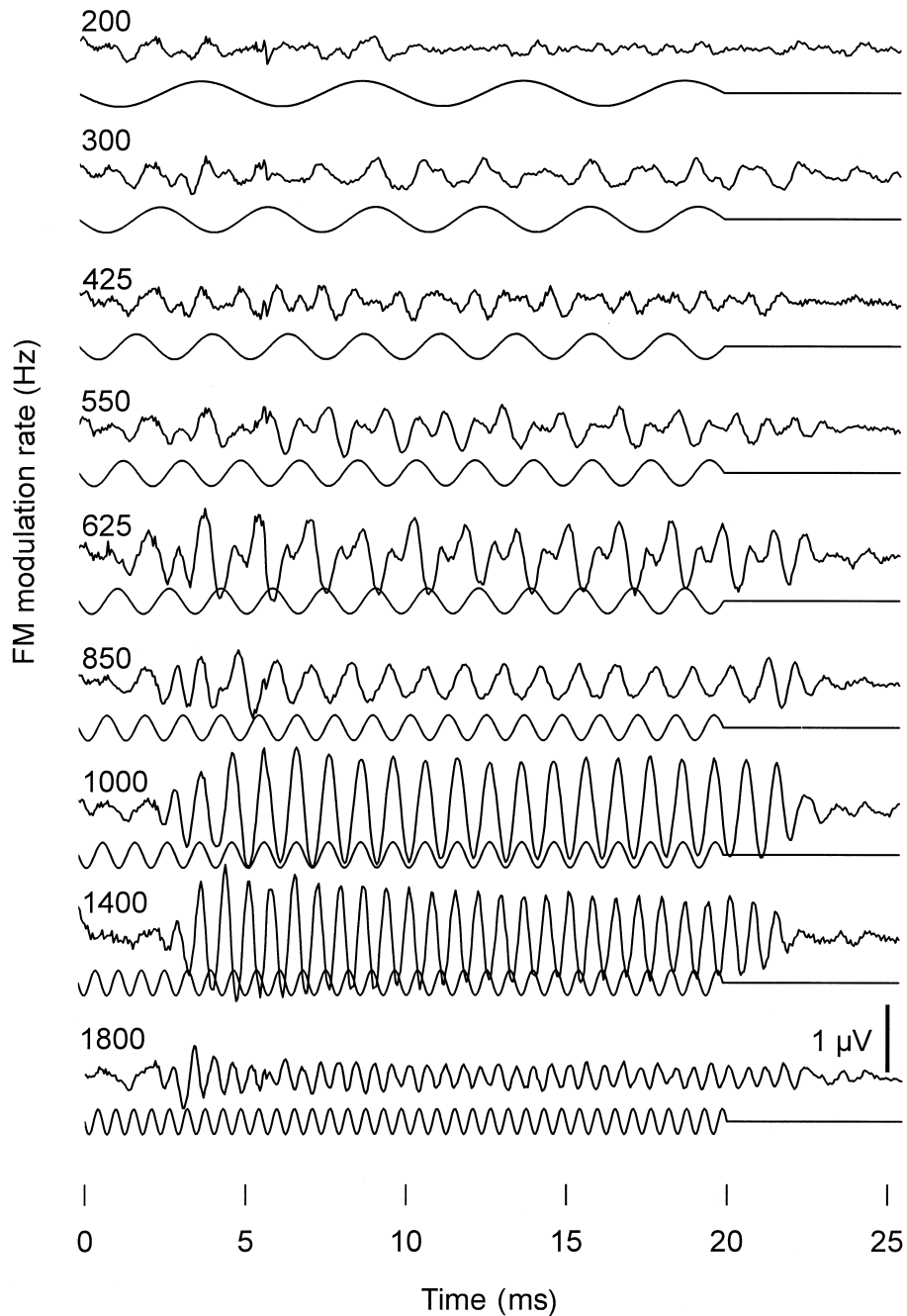
EFR amplitude was dependent on modulation depth; the lower the depth, the less amplitude of the response (Fig. 4). Nevertheless, noticeable responses were observed at modulation depths far below 1%. These responses were used for measuring FM thresholds.

To quantify EFR amplitude and find its threshold, a part of EFR record was Fourier transformed. The temporal window taken for the transform was 16-ms long, starting at 5.5 to 21.5 ms after the record began. This window covered a major part of EFR (which appeared with a lag of about 3 ms relative to the stimulus) but did not include the initial transient part of the response. Note that the window duration was equal to a whole number of stimulus cycles—a condition desirable for Fourier transform.

The Fourier analysis of records are presented in Fig. 5. All the spectra had prominent peaks at the rate fundamental (625 Hz) and harmonics. At high FM depths, harmonics were significant; at low depths, they became negligible. Figure 5 illustrates a significant fundamental peak (0.11  $\mu\text{V}$ ) at a modulation depth as low as 0.1%.

Spectrum levels between the fundamental and harmonics were low. At low response amplitudes (modulation depth below 1%), they were a magnitude of 0.03–0.05  $\mu\text{V}$  around the fundamental frequency of 625 Hz. In this background, a spectral peak magnitude of 0.07  $\mu\text{V}$  could be identified confidently. Thus, the 0.07  $\mu\text{V}$  level was chosen as an arbitrary criterion for threshold estimation. To find a threshold, the EFR was recorded when the modulation depth varied in 5-dB steps i.e., 10% 5.6%, 3.2%, 1.8%, 1% etc. The threshold was calculated by linear interpolation between modulation depths evoking EFR fundamental magnitudes just above and just below the 0.07  $\mu\text{V}$  criterion level.

For comparison, EFR to AM stimuli were recorded under the same conditions and analyzed in the same manner, using the same threshold criterion. Figures 6 and 7 exemplify the EFR to AM stimuli of various modulation depths and their



**Figure 2.** EFR of the female dolphin to FM stimuli at various modulation rates. The stimulus carrier was 90 kHz, at 120 dB *re* 1  $\mu$ Pa, with a modulation depth 5.6%. In each pair of records, the upper one is the EFR record, the lower one is the modulating function (frequency deviation) record. Modulation rates (Hz) are indicated near the curves.

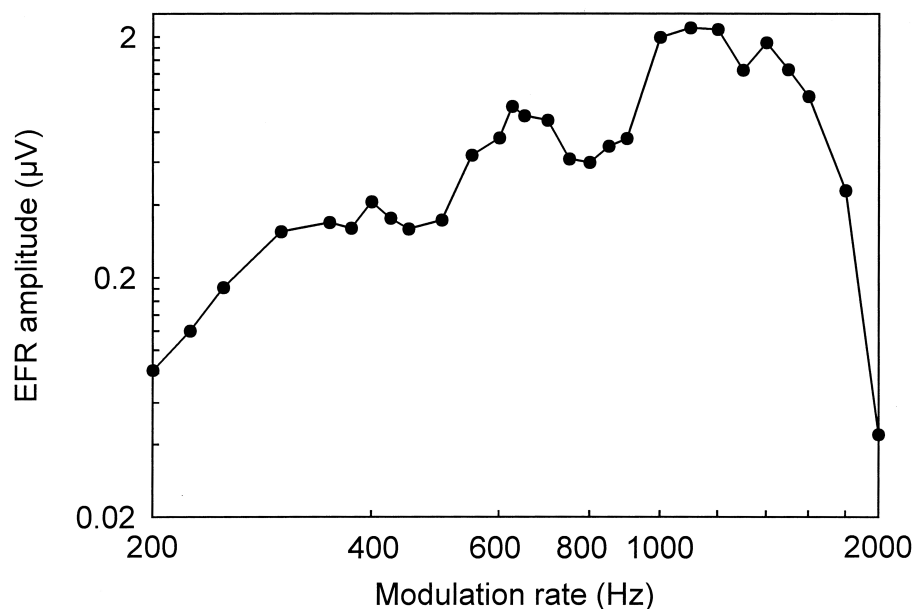


Figure 3. EFR amplitude dependence on modulation rate plotted on a logarithmic scale. The same data are presented in Figure 2.

frequency spectra. Apparently, the EFR waveforms to AM stimuli were similar to those obtained for FM stimuli. Their amplitudes also depended on modulation depth. However, contrary to FM stimuli, AM stimuli required modulation depths of about an order of magnitude higher; robust responses appeared at modulation depths of tens of percents and just detectable responses at depths of about 1%.

Using this technique of threshold estimation, FM and AM thresholds were measured as a function of sound level at a variety of carrier frequencies, from 32 kHz to 128 kHz. Results obtained in the female dolphin are presented in Figure 8. Both the FM and AM thresholds decreased with increasing the stimulus level. At high levels (130–150 dB *re* 1 µPa), FM thresholds were less than 0.1% at carrier frequencies between 54 and 108 kHz (Fig. 8A). The lowest AM thresholds were about 1% (Fig. 8B).

All data obtained on the two animals are summarized in Figure 9 as the lowest FM and AM thresholds found at each of the tested frequencies. The plot shows low FM thresholds (modulation depth about 0.05%) within a rather wide high-frequency range, from 45 to 108 kHz. Outside this range, FM thresholds increased although remained rather low within the frequency range under study (mean 0.5% at 32 kHz). The male displayed thresholds a little below this level, the female—a little above. Minimal AM thresholds were found in almost the same range; however, being expressed in

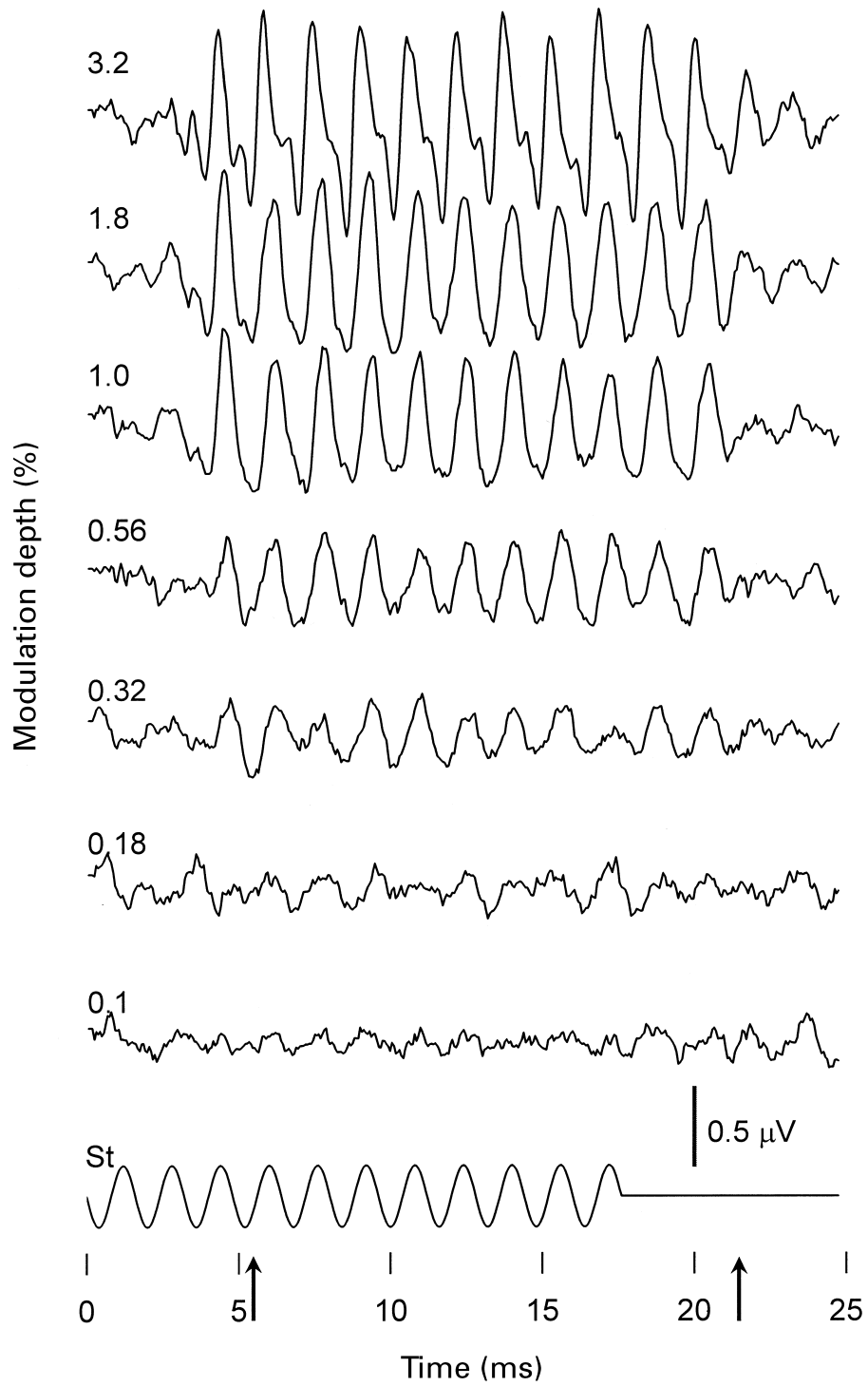
terms of modulation depth, these thresholds were about 10 times higher than FM thresholds (the lowest mean value was 0.5% at 64 kHz).

### Discussion

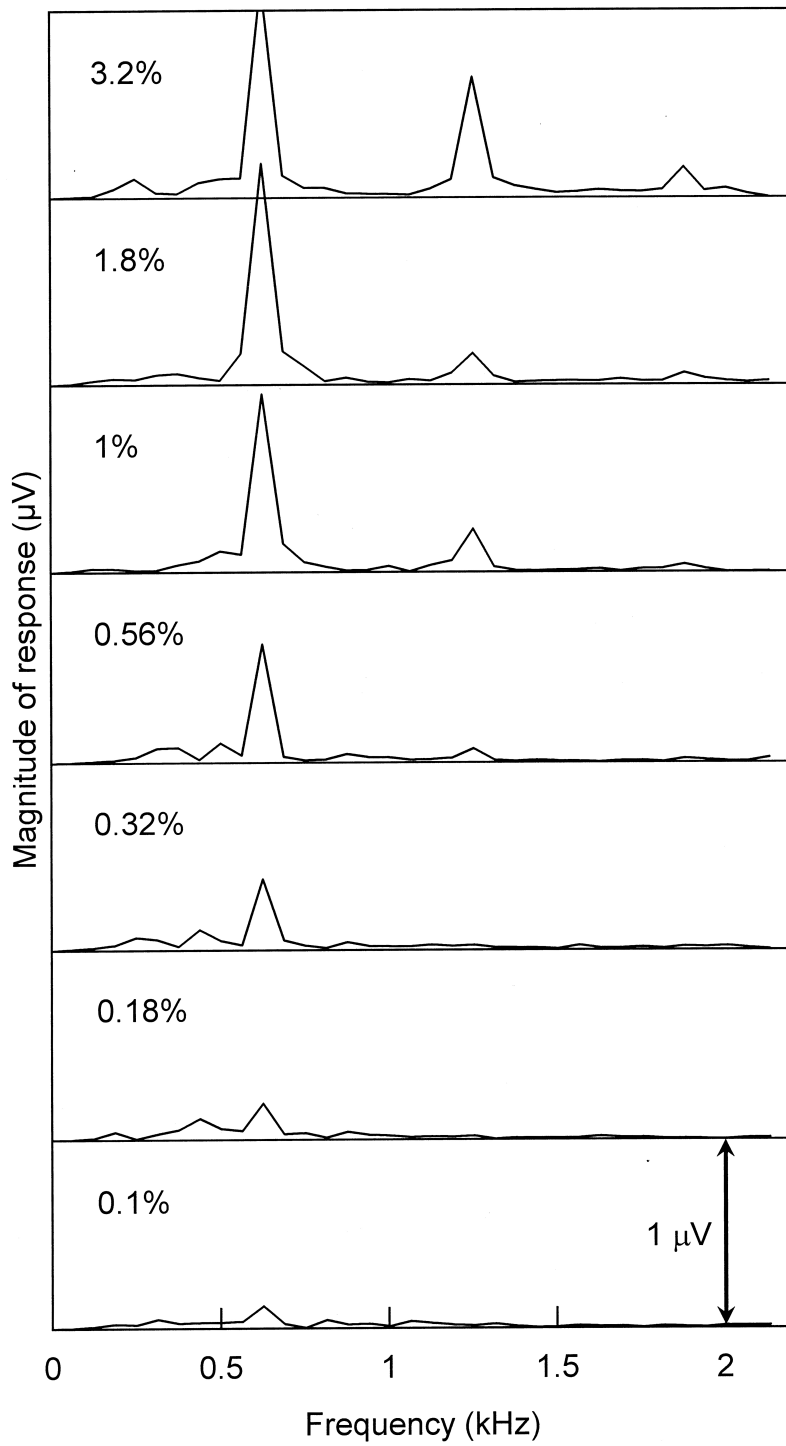
#### *Was EFR really FM-evoked?*

The first issue for discussion is: were the obtained responses to FM stimuli really evoked by frequency modulation? Indeed, any frequency change could produce an accompanying amplitude modulation because of irregularities of frequency responses of both the transferring and receiving system. As to the transducer, its frequency response was known and was compensated by corresponding amplitude modulation applied to the FM signal. However, it is difficult to quantify and compensate frequency-responses irregularities of sound-conducting pathways and of receiving structures of the dolphin. To some extent, it can be done based on the animal's audiogram; however, there is no assurance that at supra-threshold sound levels these irregularities reproduce the audiogram.

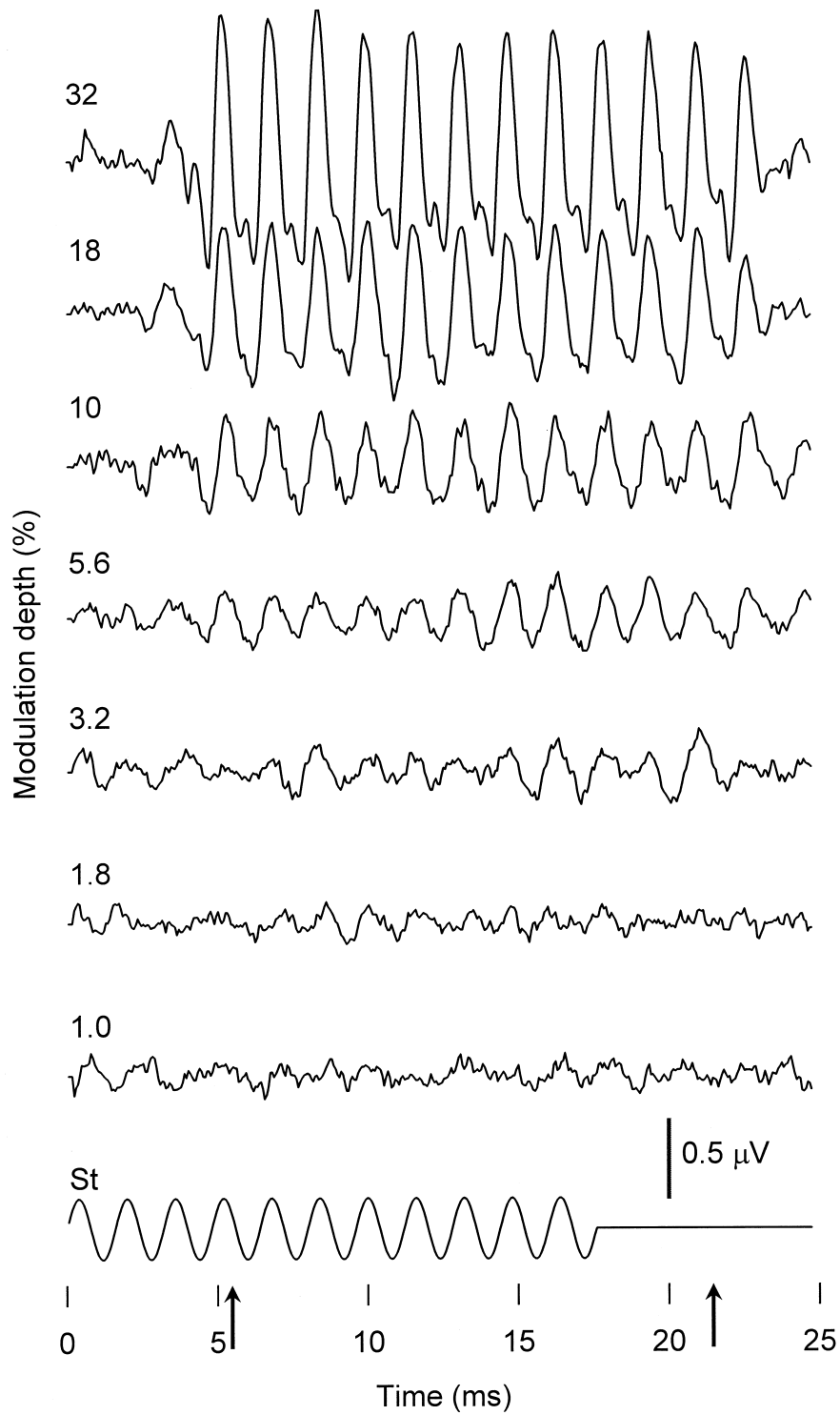
We believe that this problem can be solved by comparing the FM and AM thresholds. This was the main reason for recording AM-induced responses in the present study. AM thresholds expressed in terms of modulation depth were about 10 times higher than FM thresholds. Almost the same relation between the FM and AM thresholds reported in humans (rev. Kay, 1982). If responses to



**Figure 4.** EFR of the female dolphin to FM stimuli at various modulation depths. The stimulus carrier was 76 kHz, at 150 dB *re* 1  $\mu\text{Pa}$ , with a modulation rate 625 Hz. Modulation depth (%) is indicated near the curve, St (stimulus) is the modulating function (frequency deviation) record. Upward pointing arrows on the time scale delimit a window for Fourier transform.

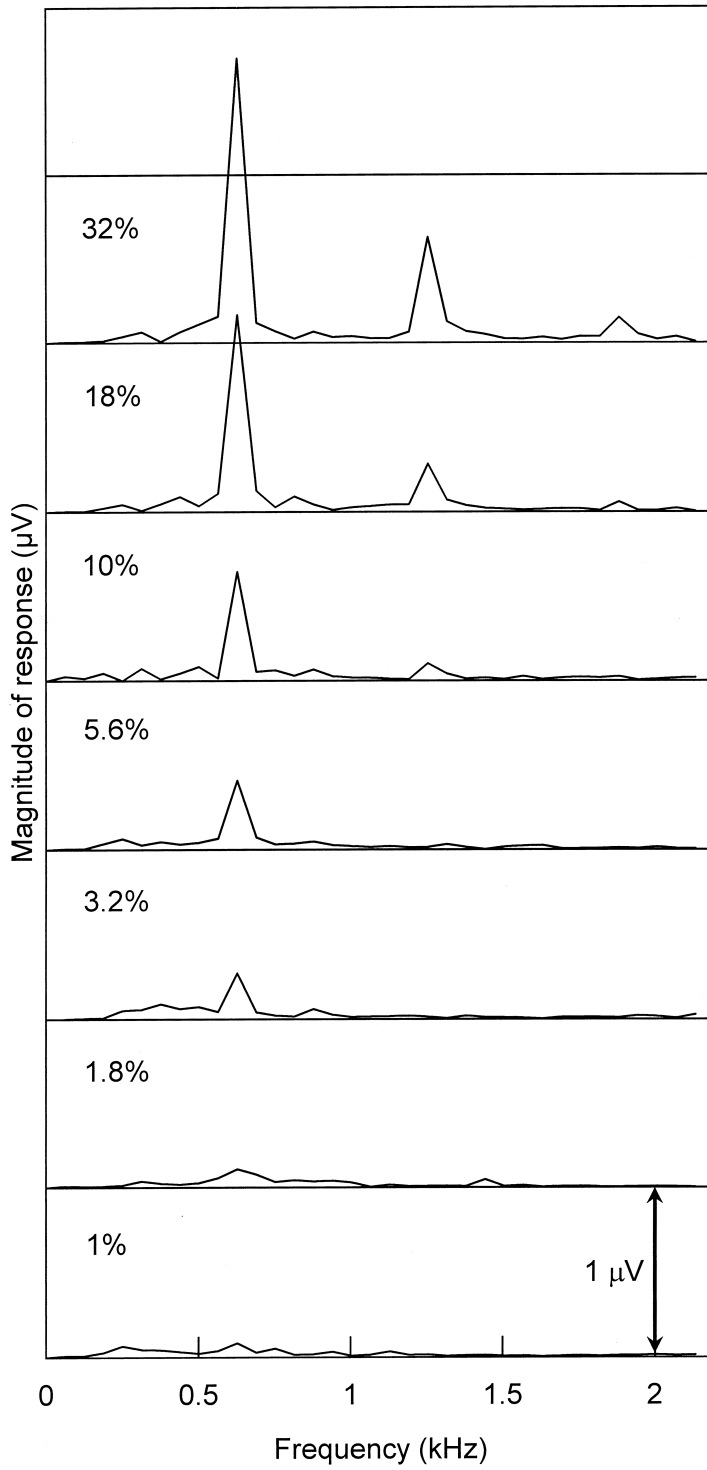


**Figure 5.** Fourier transforms of records presented in Figure 4. Modulation depth (%) is indicated near the spectra.

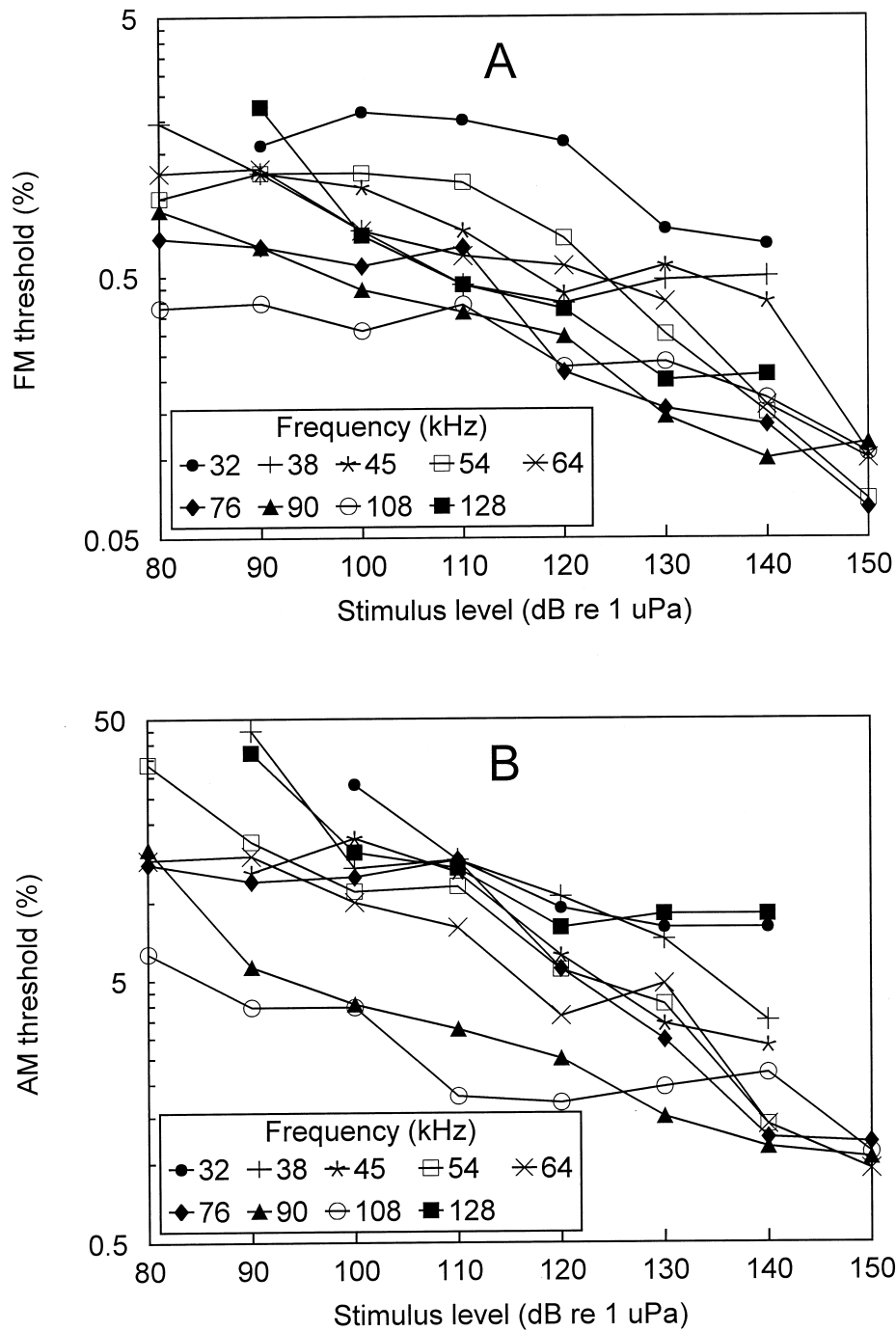


**Figure 6.** The same as Figure 4 for AM stimuli; St is the amplitude deviation record.

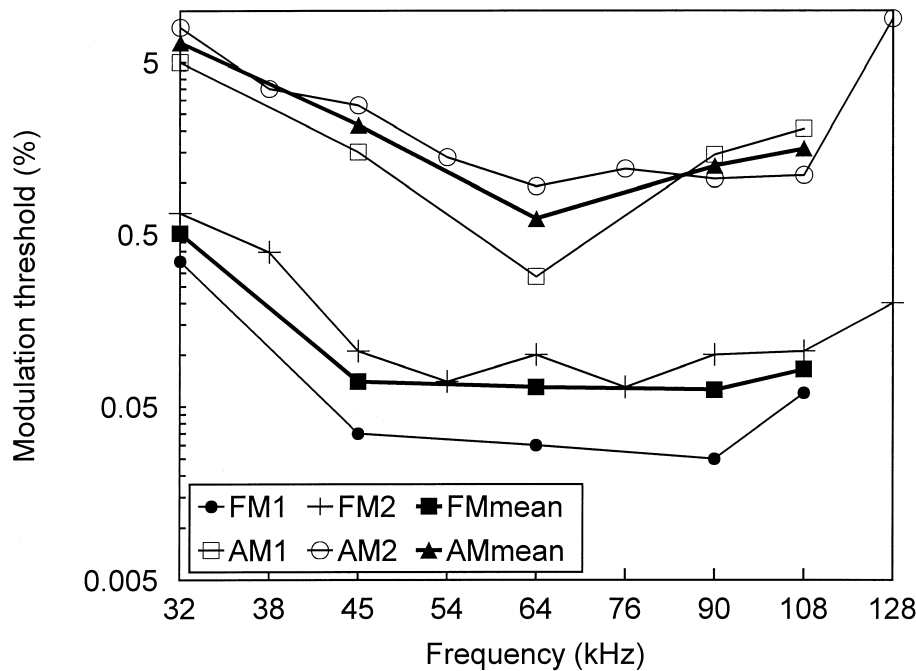




**Figure 7.** Fourier transforms of records presented in Figure 6. Modulation depth (%) is indicated near the spectra.



**Figure 8.** FM and AM thresholds for the female dolphin as a function of stimulus level with carrier frequency as a parameter. A—FM thresholds, B—AM thresholds.



**Figure 9.** Lowest threshold dependence on carrier frequency. FM1 and FM2 are FM thresholds for male and female respectively, AM1 and AM2 and AM thresholds for male and female, FMmean and AMmean are inter-individual means of FM and AM threshold, respectively.

FM stimuli were evoked not by the FM proper, but rather by AM, this would mean that small frequency shifts resulted in 10 times larger amplitude shifts (expressing both in relative measures):

$$\delta A/A_0 \approx 10 \delta f/f_0,$$

where,  $A_0$  and  $f_0$  are the mean amplitude and frequency and  $\delta A$  and  $\delta f$  are the amplitude and frequency shifts, respectively. Note that at  $\delta \ll 1$ ,  $(1+d1)^n \approx 1+n\delta$ , thus:

$$1 + \delta A/A_0 \approx (1 + \delta f/f_0)^{10}$$

i.e., to explain FM thresholds by accompanying amplitude modulations, one must assume that signal amplitude is approximately the 10-th power of frequency (60 dB/octave). Such steep dependence seems unrealistic; at least, there is no indication that such a degree of dependence can be expected. Thus, there is good reason to believe that the responses to FM stimuli were evoked by frequency shifts proper. Based on this conclusion, data presented herein can be used for estimation of frequency discrimination thresholds.

*FM thresholds*

Data presented herein show that at high stimulus levels, the threshold modulation depth was as low

as about 0.05% at frequencies between 45 kHz and 108 kHz. However, the modulation depth is the frequency deviation from the middle frequency value; the peak-to-peak frequency deviation is twice as large:

$$\text{from } f_0 - \delta f \text{ to } f_0 + \delta f,$$

where,  $f_0$  and  $\delta f$  are the middle frequency and frequency shift, respectively. Thus, the lowest frequency discrimination thresholds can be estimated as 0.1%. These values are close to the lowest estimates obtained in behaviour experiments (Herman & Arbeit, 1972). It is noteworthy that these lowest thresholds were found in a frequency region of the best hearing sensitivity (Johnson, 1967).

It should be stressed, however, that our threshold estimates were obtained using an arbitrary threshold criterion which was limited by response detection in noise. With the threshold detection technique used in this study, results depend on the response-to-noise ratio. This dependence could be a cause of threshold dependence on stimulus level (the higher level, the higher response amplitude and better response detection in noise) and a possible explanation for a significant (several times) threshold difference between the two dolphins

(Fig. 9). Thus, the results obtained can be considered as very approximate estimates of FM thresholds. We cannot exclude the possibility that at lower noise levels, threshold estimates would be even lower.

Additionally, we used a modulation rate as high as a few hundred Hz (specifically, 625 Hz) since lower rates did not evoke robust EFR. It is known, however, that in humans the frequency discrimination deteriorates at modulation rates higher than 2–3 Hz (rev. Kay, 1982). Although the dolphin's auditory system is capable of reproducing high-rate modulations (Dolphin, 1995; Dolphin *et al.*, 1995; Supin & Popov, 1995; Popov & Supin, 1998; the present data—Fig. 3), it cannot be excluded that at lower modulation rates the dolphin's frequency-discrimination ability is better. Therefore, we are inclined to consider our data as conservative threshold estimates; i.e., the frequency discrimination thresholds in dolphins are *at least* as low as those found in the present study. Even such conservative estimates show a very acute frequency selectivity in dolphins.

#### Acknowledgments

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