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Frequency tuning curves of the dolphin's hearing: envelope-following response study

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Abstract Simultaneous tone-tone masking in conjunction with the envelope-following response (EFR) recording was used to obtain tuning curves in dolphins (*Tursiops truncatus*). The EFR was evoked by amplitude-modulated probes of various frequencies. A modulation rate of 600 Hz was found to fit the requirement to have a narrow spectrum and evoke EFR of large amplitude. Tuning curves were obtained within the frequency range from 11.2 to 110 kHz. The Q_{10} values of the obtained tuning curves varied from 12–14 at the 11.2 kHz center frequency to 17–20 at the 64–90 kHz frequencies.

Key words Dolphin · Hearing · Envelope-following response · Frequency tuning

Abbreviations *ABR* auditory brainstem response · *EFR* envelope following response · *ERB* equivalent rectangular bandwidth

Introduction

Unique capabilities of the dolphin's auditory system are a matter of special interest. Many properties of this system, however, remain uncertain, in particular its frequency tuning.

There were several attempts to estimate frequency tuning in dolphins using behavioral experiments. These studies were carried out using both the critical ratio and critical band masking paradigms (Johnson 1968; Johnson et al. 1989; Au and Moore 1990) as well as the tone-tone masking paradigm (Johnson 1971). However, the behavioral method limited accessible data, so the results were variable.

An effective way to study frequency selectivity of hearing is by recording evoked potentials in conditions of tone-tone masking. Such an approach makes it possible to obtain tuning curves of hearing. Based on this method, tuning curves have been measured in some experimental animals and humans (Dallos and Cheatham 1976; Eggermont 1977; Harris 1978; Mitchel and Fowler 1980; Abbas and Gorga 1981; Harrison et al. 1981; Gorga and Abbas 1981; Salvi et al. 1982; Gorga et al. 1983; Brown and Abbas 1987). In these studies both cochlear action potentials (APs) and auditory brainstem responses (ABRs) were used.

Our previous work (Supin et al. 1993) has demonstrated that this method is effective to investigate frequency tuning in dolphins. The ABR can be recorded easily from the dolphin's head surface, without any surgical procedure and anesthesia. By using ABR recording in conjunction with tone-tone masking, we have obtained tuning curves in dolphins within a frequency range of up to 128 kHz.

The frequency tuning in dolphins was measured by this method within a high-frequency range of 64–128 kHz. However, the method was shown to underestimate the frequency tuning at lower sound frequencies because the ABR is evoked by short, transient acoustic stimuli. Even with a slowly rising and falling tone burst, only its short initial part was able to evoke ABR, and the spectrum of this short part was as wide as 3.5–4 kHz. Therefore, in tone-tone masking experiments, the effective probe spectrum was found not to be narrower than 3.5–4 kHz. Such probe was satisfactory at frequencies above 64 kHz where tuning curves were wider than the stimulus bandwidth. It was not appropriate, however, at frequencies below 64 kHz where tuning curves were expected to be narrower (Supin et al. 1993).

Therefore we searched for a method to obtain tuning curves in dolphins which would be as effective as the ABR recording method but made it possible to use a narrow-band probe. The idea of this study was to use

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the so-called envelope-following response (EFR). This evoked response appears in conditions of amplitude-modulated acoustic stimulation and follows the rate of amplitude modulation. The EFR was demonstrated both in humans (Rodenburg et al. 1972; Hall 1979; Galambos et al. 1981; Rickards and Clark 1984; Kuwada et al. 1986; Rees et al. 1986) and in some animals (Dolphin and Mountain 1992). It was shown recently that EFR can be recorded in dolphins as well (Dolphin, 1995).

The expected advantage of this approach is that EFR can be recorded non-invasively from the head surface, similar to ABR. On the other hand, contrary to short tone bursts which evoke ABR, sinusoidally amplitude-modulated tones have a strictly limited spectral bandwidth which is either $2f$ or f depending on the modulation type, where f is the modulation rate. Since an EFR can be evoked by modulation rates of an order of dozens or hundreds Hz, we expected to evoke EFR by more narrow-band stimuli (up to hundreds Hz) than those evoking ABR (3.5–4 kHz). The narrow-band stimuli are more convenient probes to obtain tuning curves. Thus, the goal of this study was to obtain tuning curves in dolphins using narrow-band probe stimuli (sinusoidally amplitude-modulated tones) and tonal maskers.

Just as in our preceding work (Supin et al. 1993), we used in this study the simultaneous masking paradigm and choose the near-complete masking criterion to obtain tuning curves. Since long amplitude-modulated sound bursts must be used to evoke EFR and recovery time of evoked potentials in the dolphin's auditory system is as short as a few milliseconds or less (Popov and Supin 1990), no significant forward masking of such long probes might be expected. Thus, it was impossible to use the forward masking paradigm in conjunction with EFR recording.

As to the masking criterion, the near-complete criterion was shown to yield sharper tuning curves than partial masking criteria (Abbas and Gorga 1981; Gorga and Abbas 1981). This indicates a better measure of tuning abilities with the use of the near-complete criterion. Apart from that, using the same criterion and the same masking paradigm as in the preceding work made it possible to compare directly the results obtain by ABR and EFR recordings in dolphins.

Material and methods

Experiments were carried out during the 1994 summer season at the Utrish Marine Station of the Russian Academy of Sciences (Black Sea coast). The care and use of the animals were made under regulation of guidelines established by the Russian Ministry of Higher Education on the use of animals in biomedical research.

Subjects

The experimental subjects were two bottlenose dolphins, *Tursiops truncatus*, males. The animals were caught 2–3 months before the study and were adapted to the keeping conditions and to the experimental procedure.

Experimental conditions

During the experiments, a dolphin was placed in a bath 4 × 0.6 × 0.6 m filled with sea water. The animal was supported by a stretcher so that the dorsal surface of its body and the blowhole were above the water surface. The animal was neither anaesthetized nor curarized. Each experiment lasted 3–4 h, after which the animal was returned to the home pool.

Evoked response recording

The recording of evoked responses was performed using surface cup electrodes secured at the head surface by adhesive electric-conductive gel. The active electrode was placed in the dorsal part of the head, at the midline, 6–8 cm behind the blowhole, above the water surface. This site was shown to be the best for ABR recording, and the used electrode position made it possible to compare recorded responses with those described earlier using the same recording technique (Popov and Supin 1990; Supin et al. 1993). The reference electrode was in the back near the dorsal fin, also above the water surface. The recorded signals were amplified and bandpass filtered between 200 and 5000 Hz. Averaging of 512 responses was used to measure response parameters with satisfactory precision. The averager contained an artifact-rejection system, however the number of rejected trials was negligible.

Stimuli

In the main experiments, probe stimuli were amplitude-modulated tone bursts. The burst duration was 12 ms plus time to complete the last modulation cycle. The bursts were produced by analogous multiplying the tone carrier by a modulating signal. Tone carriers were not coherent with the starting point of evoked-response collection. Carrier frequencies varied from 2 to 128 kHz by half-octave steps. Modulation signals always started from a zero phase in coherence with evoked-response collection. The probe bursts were presented at a rate of 10/s.

In preliminary experiments, modulation rates from 250 to 2000 Hz in approximately 1/4 octave increments were tested. Then only the rate of 600 Hz evoking the best EFR was used. Modulation depth was 100%. In several experiments, short tone bursts with a cosine-wave envelope were used as probes for comparison. Their duration measured as a period of the envelope cosine function was 0.5 ms.

Masking signals were continuous tones of various frequency and level. Probe and masker were produced by different generators and were not coherent.

Probe and masker were mixed and emitted through a piezoceramic transducer of 3 or 6 cm in diameter, depending on the carrier frequency. The transducer was immersed in water at a depth of 30 cm, 75 cm in front of the animal's head. To increase regularity of the acoustic field, the bath walls and free water surface in front of the animal were covered with a sound absorbing material which provided echo reduction of −15 to −25 dB within the frequency range of 5 to 100 kHZ.

Emitted signals were monitored through a probe hydrophone with a band pass of 150 kHz, located near the animal's head. In the presence of the animal in the bath, acoustic field irregularity measured near the head surface within a region from the lower jaw to the auditory meatus did not exceed ±3 dB. A mean of 3 to 5 measurements in a few points near the head surface was used to characterize probe and masker levels.

Results

EFR waveform and dependence on stimulus parameters

To provide high response-to-noise ratio in masking measurements, a higher response amplitude is desirable. Therefore, at the first stage of the study we investigated EFR dependence on amplitude-modulated stimulus parameters to find out the stimulus type which evokes EFR of the highest amplitude.

Two types of amplitude-modulated stimuli are widely used: those containing three and two harmonic components in their spectra (Fig. 1A–D). We compared their effectiveness in evoking EFR. The result was that both stimulus types were equally effective to evoke EFR.

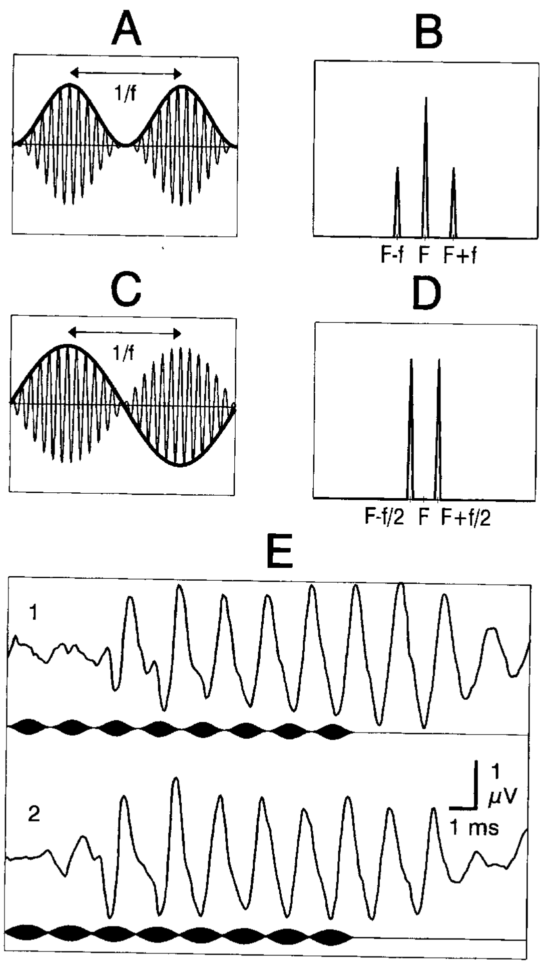

Fig. 1A–D Probe stimulus characteristics. **A** and **B** Three component signal, **C** and **D** two component one. **A** and **C** Stimulus waveforms (*thick lines* show the modulation waveform), **B** and **D** stimulus spectra (*F* carrier frequency; *f* modulation rate). **E** EFR evoked by the three-component stimulus (*1*) and two-component stimulus (*2*); carrier tone of 90 kHz, 120 dB re 1 μPa. Stimulus envelopes are shown *under the records*

This result is illustrated by Fig. 1E. Amplitude-modulated tone bursts of the both modulation types evoked robust rhythmic response which followed the modulation rate, i.e., EFR. The bursts onset evoked a small transient on-response which after a few milliseconds was replaced by the quasi-sustained EFR. Both the start and the end of the response appeared with a few ms lag relative to the stimulus. This lag presented a good opportunity to check artifact contamination of records. The response-free initial part of records showed clearly that they were not contaminated with electromagnetic artifacts, as well as the response existence until about 4.5 ms after the stimulus end showed the physiological nature of the response.

The responses were virtually the same in amplitude for both stimulus types when the modulation depth was equal, i.e., 100%. It is noteworthy that the two-component stimulus with separation *f* between the components evoked EFR with wave rate equal to *f* (Fig. 1E, 2) i.e., with the rate of the stimulus envelope, although the actual modulation frequency of this signal is half as much, i.e. *f*/2, as Fig. 1C shows.

Although the two-component and three-component signals were equally effective in provoking EFR, the two-component one, is preferable as a probe for tuning measurements since its bandwidth is narrower by a half. Therefore, in the subsequent measurements the two-component amplitude-modulated sounds were used.

Then the effect of modulation rate on EFR amplitude was tested. Figure 2 shows representative EFR examples at various modulation rates. EFR amplitude depended markedly on modulation rate. Higher response amplitude appeared at modulation rates of 500–600 and 1000–1250 Hz. At rates less than 500 Hz, the response amplitude fell steeply, and the response waveform became far from a sinusoid (i.e., the weight of the fundamental became little). At modulation rates of 1000 Hz and higher, the response waveform was closer to a sinusoid; however, response amplitude fell steeply at rates above 1250 Hz.

To quantitatively evaluate EFR magnitude, a whole number of response cycles in the last 12-ms part of the response were Fourier transformed to find the weight of the component at the modulation frequency. Figure 3 shows the EFR amplitude found in such a way, as a function of modulation rate. The dependence was a multipeak function with peaks at modulation rates of 600 and 1000 Hz, a trough at 850 Hz and steep decays below 500 Hz and above 1750 Hz. Modulation rates of 600 and 1000 Hz were almost equally effective to evoke high-amplitude EFR. However, the modulation rate of 600 Hz is preferable for a probe in tuning measurements since the probe bandwidth is narrower in this case. Of course, modulation rates

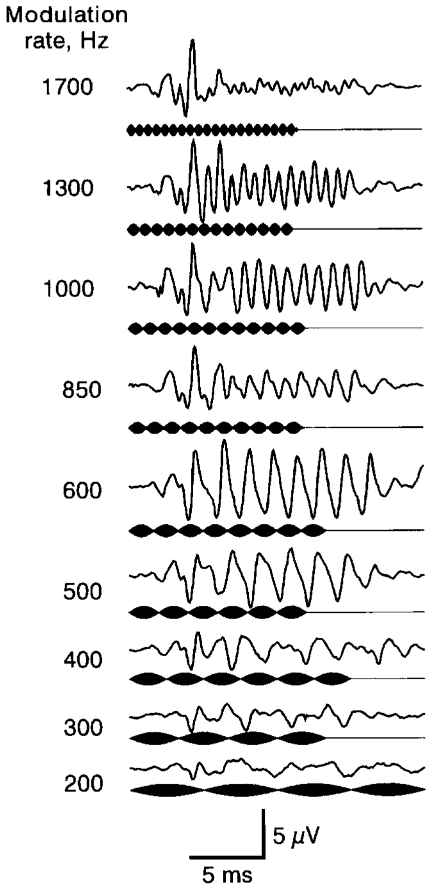

Fig. 2 EFR at various modulation rates (indicated *near the records*). Carrier tone of 90 kHz, 120 dB re 1 μPa. Stimulus envelopes are shown *under the records*

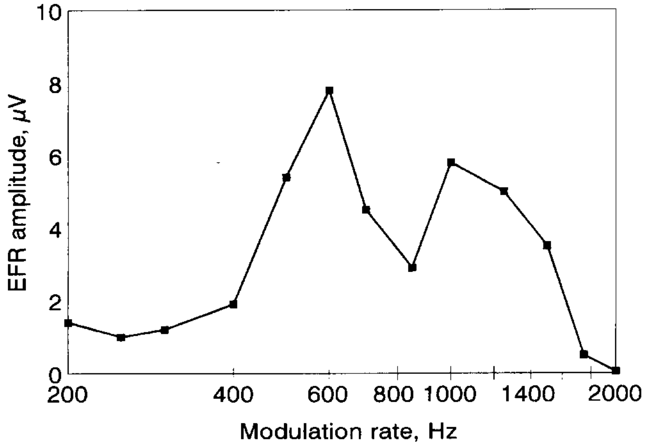

Fig. 3 EFR fundamental amplitude dependence on modulation rate. The same stimulus conditions as those shown in Fig. 2

lower than 600 Hz result in an even narrower bandwidth, but EFR amplitude was rather low at these rates. Therefore, in subsequent measurements the modulation rate of 600 Hz was used.

EFR masking manifestation

Figure 4 exemplifies EFR evoked by an amplitude-modulated probe without a masker and in the presence of various maskers. The records were made with the probe stimulus of a moderate intensity of 100 dB re 1 μPa, i.e., about 40 dB above the response threshold. Such a stimulus evoked a response of less than 1 μV peak-to-peak amplitude (Fig. 4A). The same stimulus in a masker background evoked a smaller response. As the masker level increased, the EFR diminished until it disappeared in the noise.

The masking was the most effective when the probe carrier frequency and masker frequency were equal (90 kHz in Fig. 4B). In this case, the complete masking required the masker level of about 15 dB above the probe level (i.e., 115 dB re 1 μPa). When the masker and probe carrier frequency were different, the masking was less effective: in Fig. 4C, the masking frequency was 85 kHz while the probe carrier frequency was 90 kHz, and the masking required the masker levels which were 25 dB higher than in the preceding case. In particular, the near-complete masking required the masker level of 40 dB above the probe level (140 dB re 1 μPa).

To evaluate EFR magnitude at a given masking condition, a whole number of response cycles in the last 12-ms part of the response were Fourier transformed to find the weight of the component at the modulation

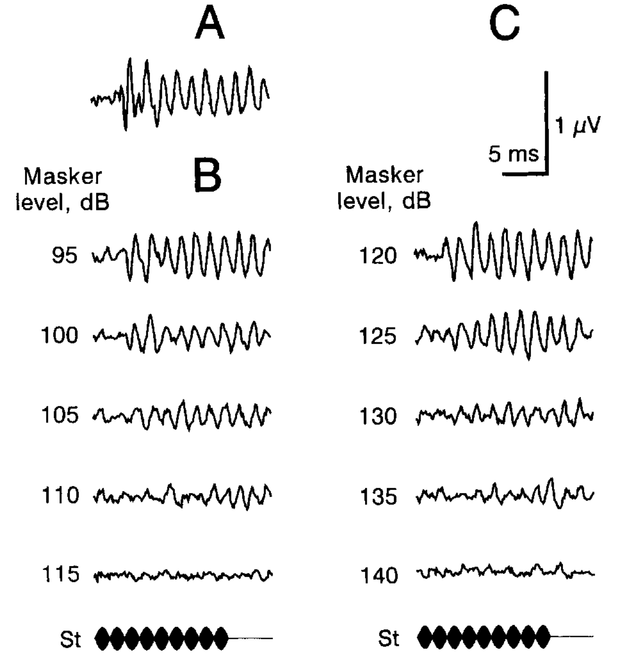

Fig. 4A–C EFR suppression by maskers. **A** Unmasked EFR evoked by a probe stimulus of 90 kHz carrier frequency, 600 Hz modulation rate, 100 dB re 1 μPa level. **B** Responses to the same probe in the background of the 90-kHz masker. **C** The same with the 85-kHz masker. Masker levels (dB re 1 μPa) are shown near the curves. The stimulus envelope is shown at the *bottom of the panels*

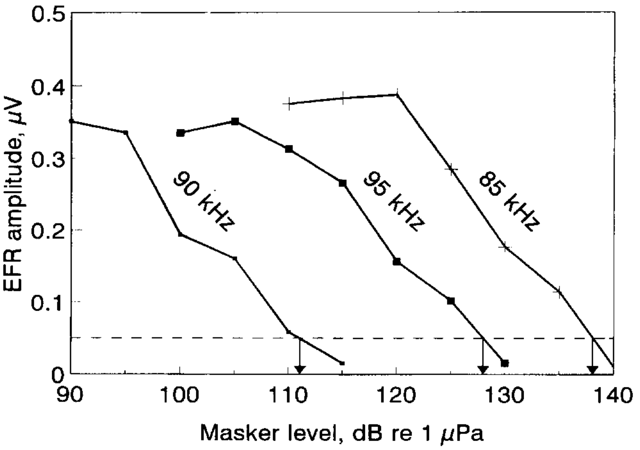

Fig. 5 EFR amplitude as a function of masker level with masker frequency as the parameter. The 90 kHz probe had a level of 100 dB re 1 µPa. *Dashed straight line* shows the 10% amplitude level adopted as a near-complete masking. *Arrows* show estimations of masker levels at 85, 90, and 95 kHz masker frequencies

frequency. The peak-to-peak amplitude of this component was taken as the EFR magnitude measure (at the modulation rate of 600 Hz it was close to the peak-to-peak amplitude of the native record). Figure 5 plots EFR amplitude found in such a way versus the masker level at three of the masker frequencies: coinciding with the probe frequency (90 kHz), higher (95 kHz) and lower (85 kHz) than the probe frequency.

A response magnitude of 0.05–0.07 µV (about 10% of the unmasked response and obviously above the background noise) was adopted in this study as the masking criterion, and the masking up to this level was considered as near-complete. The masker level required for the near-complete masking could be identified with an accuracy of 2–3 dB (we used a step of 2.5 dB to vary masker level). Figure 5 shows a shift between the plots reflecting frequency dependence of masking. In the presented case, the shift was about 25 dB when masker frequency changed from 90 to 85 kHz and about 15 dB for the change from 90 to 95 kHz.

EFR tuning curves in various frequency ranges

For obtaining tuning curves, the probe carrier frequency and intensity were fixed and masker frequencies and intensities were varied. For each masker frequency, the level required for near-complete masking of the probe response was determined with 2.5-dB steps. This procedure was repeated at each frequency of the masker to yield a complete tuning curve.

A family of tuning curves obtained in such a way for one animal is shown in Fig. 6. These tuning curves possessed many features similar to those of the curves in other mammals. They had a relatively sharp tip segment, steep rise at high frequencies and similar or less steep rise at low frequencies. All the curves peaked at or near the probe carrier frequency. At this frequency, the near-complete masking required a masker level of 5 to 15 dB above the probe level.

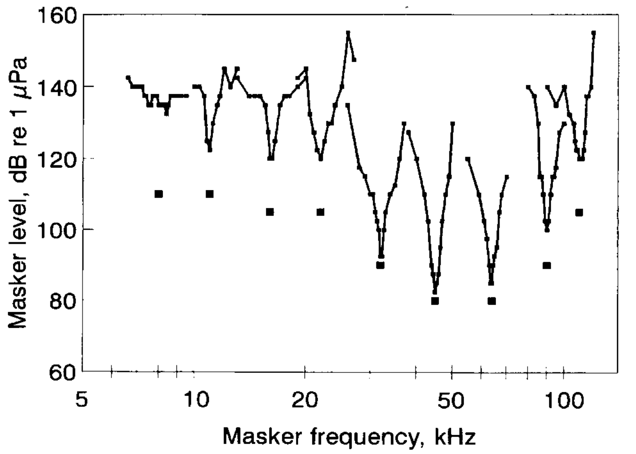

Fig. 6 Tuning curves obtained at various probe frequencies. Probe frequencies (for curves from left to right) are 8, 11.2, 16, 22.5, 32, 45, 64, 90, and 110 kHz. The *square symbols* represent probe frequencies and levels (30 dB above the EFR thresholds)

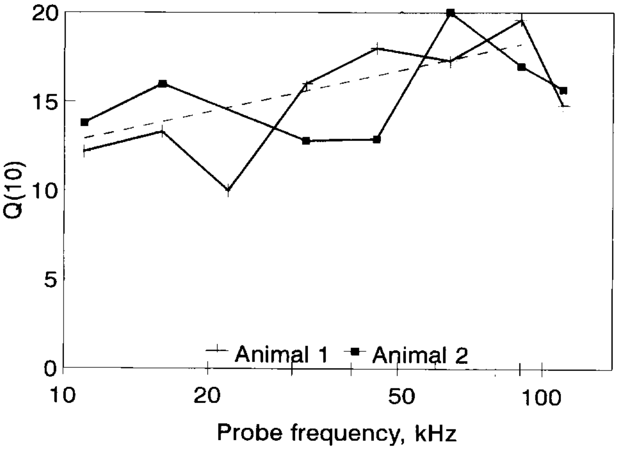

Fig. 7 Dependence of Q_{10} on probe frequency (data for the two animals). *Dashed straight line* is the regression line for data within the range of 11.2 to 90 kHz

The Q_{10} values (the center frequency divided by the bandwidth at the level 10 dB above the tip of the curve) are a convenient measure of tuning. For the curves presented in Fig. 6, the Q_{10} values varied within a range from 10 (at the 22.5 kHz probe frequency) to 19.6 (at the 90 kHz frequency), with a slight trend within the frequency range from 11.2 to 90 kHz. The other animal studied gave similar results: the Q_{10} values were from 14 to 20 depending on frequency. At probe frequencies 8 kHz and lower, masking was much little dependent on the masker frequency (8 kHz probe in Fig. 6), so it was impossible to obtain real tuning curves and evaluate their Q_{10} at such probe frequencies.

Figure 7 presents Q_{10} as a function of central frequency for both of the animals studied. The plots

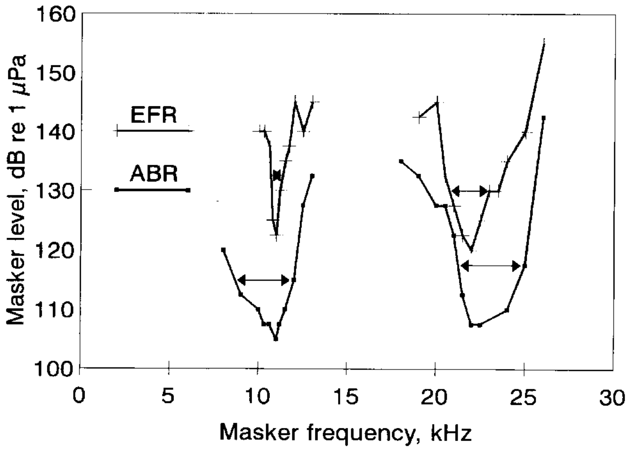

Fig. 8 Tuning curves obtained at 11 and 22 kHz probe frequencies using EFR and ABR recording. *Horizontal double-headed arrows* show the curve bandwidths at the level 10 dB above the tip

demonstrate slight increase with frequency within a range of 11.2 to 90 kHz; at 110 kHz, the Q_{10} values were a little lower again. Averaging all the data by a regression line (dashed line in Fig. 7) resulted in a Q_{10} rise from 13.0 at 11.2 kHz to 18.3 at 90 kHz.

ABR tuning curves

The tuning curves obtained in this study differed significantly from those obtained in the previous work (Supin et al. 1993) using short tone burst as a probe and ABR as a response. This difference was remarkable in the low-frequency region (below 64 kHz). However, because of the limited number of accessible animals for the study, individual variability of their hearing could not be excluded as a reason for this difference. Therefore, in order to make a direct comparison with previous data obtained by the same method, a few tuning curves were obtained using short tone burst as a probe and ABR as a response. The curves were obtained based on the same masking criterion as in the previous work, i.e., 5–7% of the unmasked response.

These tuning curves for the probe frequencies of 11.2 and 22 kHz are shown in Fig. 8, together with the curves obtained by EFR recording. There was an obvious difference between the ABR and EFR curves. The bandwidth of ABR tuning curves was rather large: 3.3–4 kHz at 10 dB above the tip, resulting in the Q_{10} value as low as 3.4 at the 11.2 kHz probe frequency. This is very similar to values obtained in the preceding study.

Discussion

A remarkable feature of the curves obtained using sinusoidally amplitude-modulated probes and EFR as the masked response is their sharp tuning. The Q_{10} values obtained in this study were 18 to 20 in the high frequency range (64–90 kHz). It is close to the values obtained in the preceding study (Supin et al. 1993) using short tone bursts as probes and ABR as the masked response.

At lower frequencies, the Q_{10} values were somewhat less, although still high: more than 12 at the probe frequency as low as 11.2 kHz. Thus, their bandwidth 10 dB above the tip was less than 1 kHz. These bandwidths are much less and Q_{10} values much higher than those obtained with short tone bursts as probes and ABR as the masked response (the bandwidth of about 3.4 kHz which corresponds to Q_{10} of 4.7 at the 16 kHz probe frequency).

These results agree well with the proposal that the rather high bandwidths of the tuning curves obtained by ABR recording reflect the bandwidth of a short ABR-eliciting part of the probe. The results also confirm that sinusoidally amplitude-modulated tones can serve as convenient narrow-band probes to obtain tuning curves by EFR recording.

However, this probe type can only be used when the tested filter bandwidth is wider than the probe spectrum. This limitation explains why we could not obtain tuning curves at frequencies of 8 kHz and lower. Indeed, at the probe frequency of 11.2 kHz, the Q_{10} value of 12–14 corresponds to the filter bandwidth of less than 1 kHz at the 10-dB level: it is still wider than the probe spectrum. However, at the 8 kHz frequency, a filter bandwidth of only 550–650 Hz at the 10-dB level may be anticipated based on the Q_{10} trend (Fig. 7). This bandwidth is comparable to the width of the probe spectrum.

It is of interest to compare the data presented herein with tuning curves obtained in behavioral tone-tone masking experiments on dolphins (Johnson 1971). The behavioral curves had a characteristic dip when the masker and the probe were of a similar frequency. This well-known effect arises because of beats when the tonal probe and masker are superimposed, and this effect does not allow one to measure behaviorally masking levels just around the probe frequency. It is noteworthy that beats between the probe and masker arise in EFR-recording experiments as well, and these beats superimpose with the probe amplitude modulation. However, contrary to behavioral experiments, averaging procedure during EFR recording reveals only responses to sound modulations which are coherent with the evoked potential collection. Modulations of other origin are ignored since they are not coherent with the response collection. Therefore, our records never demonstrated any rhythmic response with a rate of beats between the probe and masker. Apparently, this is the reason why we had no problem in obtaining the tip segments of the tuning curves.

Frequency tuning in dolphins appears much sharper than in many other mammals. For comparison, in the

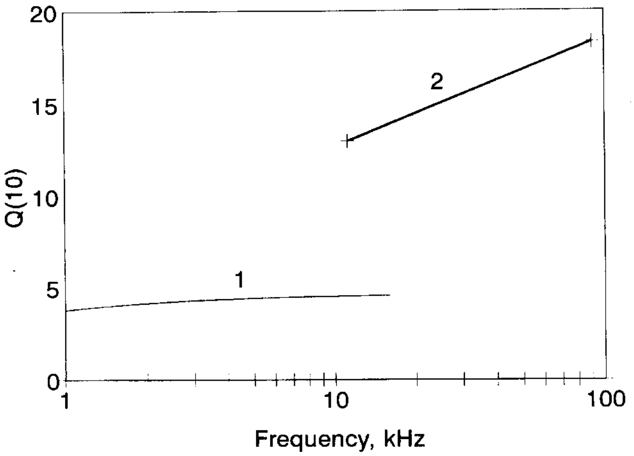

Fig. 9 Comparison of frequency tuning in humans and dolphins. *1* humans (formula by Glasberg and Moore (1990) converted to Q_{10} dependence on frequency). *2* dolphins (regression line for Q_{10} dependence on frequency, see Fig. 7)

majority of studies in terrestrial mammals and humans, the maximal Q_{10} values of evoked-potential tuning curves were 4–6 (Dallos and Cheatham 1976; Mitchel and Fowler 1980; Harrison et al. 1981); in rare cases values greater than 10 were reported (Brown and Abbas 1987).

In the case of humans, there is a large amount of psychophysical data on frequency tuning of hearing obtained in various experimental paradigms. To summarize these data, several analytical expressions have been proposed which describe the equivalent rectangular bandwidth (ERB) of the auditory filters as a function of frequency. For example, a simple equation given by Glasberg and Moore (1990) may be used:

$$ERB = 24.7(4.37F + 1), \qquad (1)$$

where *ERB* is in Hz, and *F* is the center frequency in kHz. Our data on frequency tuning in dolphins are given not in ERB but in Q_{10} terms. However, the ERB to Q_{10} ratio can be easily calculated for a given filter shape. In particular, for the rounded exponential function (*roex*) (Patterson et al. 1982) which is widely used to approximate the auditory filter shape, this ratio is: $Q_{10} \approx 0.51\ F/ERB$; thus, it follows from Eq. (1):

$$Q_{10} = 1/(0.212 + 0.048/F), \qquad (2)$$

where *F* is the center frequency in kHz. This function does not exceed the 4.72 limit (at $F \rightarrow \infty$). This value also is much less than the Q_{10} values in dolphins (Fig. 9).

Moreover, there may be some underestimation of frequency tuning in dolphins due to the use of simultaneous masking paradigm in our experiments. This paradigm may result in broader tuning curves than forward masking because of the two-tone inhibition. Thus, frequency tuning in dolphins may be even sharper than the present data show. This possibility is confirmed by behavioral measurements of the dolphin's frequency tuning with the use of the so-called rippled noise (Supin et al. 1992). The resolvable limit of relative ripple density was from 20–22 at the frequency of 11 kHz to about 40 at the frequencies of 64–128 kHz. The resolvable ripple density *D* to ERB ratio for the *roex* filter was shown to be: $ERB = 0.71\ F/D$ (Supin et al. 1994). Conversion of ERB to Q_{10} as described above gives: $Q_{10} = 0.72\ D$. Thus, *D* values from 22 to 40 correspond to Q_{10} values from 16 to 29, i.e., a little higher than the Q_{10} values obtained herein (12 to 20). This agrees with the possibility that the frequency tuning of the dolphin's hearing may be even higher than the present data show.

The acute frequency tuning in dolphins may be associated with the frequency range of their hearing which is as wide as 100–150 kHz. Indeed, both frequency tuning and temporal resolution in the auditory system are limited by passbands of peripheral auditory filters. Higher frequency tuning requires narrower passbands whereas temporal resolution requires wider passbands. This contradiction becomes less important at high frequencies because the filter center frequency *F*, passband *B* and tuning *Q* are related as: $Q = F/B$. Thus, at high frequency *F*, auditory filters can combine high tuning *Q* with wide passband *B* which renders transfer of rapid sound modulations. For example, at the 90 kHz frequency, the Q_{10} value as high as 20 corresponds to the bandwidth as wide as 4.5 kHz at the 10-dB level. This filter passband transfers amplitude modulations of the same rate, i.e., it combines high frequency tuning with high temporal resolution.

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