ABR frequency tuning curves in dolphins

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Abstract. Tone-tone masking was used to determine auditory brain-stem response tuning curves in dolphins *(Tursiops truncatus)* in a simultaneous-masking paradigm. The Q_{10} of the curves was as large as 16–19 in the frequency range 64–128 kHz. In the range 45–16 kHz, Q_{10} decreased proportionally to the frequency with the bandwidth of the curves being constant, about 3.5–4 kHz at the 10-dB level. Tuning curves below 45 kHz are supposed to reflect broad spectral bandwidth of the probe's effective part which is no longer than 0.5 ms, irrespective of actual probe duration. Tuning curves above 64 kHz are supposed to reflect the real frequency tuning of the dolphin's auditory system.

Key words: Dolphin – Hearing – Auditory brain-stem response – Frequency tuning

Introduction

The auditory system of cetaceans, particularly dolphins, is of special interest since they are capable of underwater hearing and are adapted for echolocation. The great bulk of information on auditory perception of cetaceans has been obtained in behavioural conditioning studies (Popper 1980; Fobes and Smock 1981; Watkins and Wartzok 1985) as well as in electrophysiological experiments (Bullock et al. 1968; Ridgway et al. 1981; Popov et al. 1986; Popov and Supin 1990a, b). However, many properties of the cetacean auditory system, in particular its frequency tuning, remain unknown.

Attempts have been made to estimate the frequency tuning in dolphins by measurement of the critical ratio and critical bands (Johnson 1968; Johnson et al. 1989; Au and Moore 1990) and by tone-tone masking (Johnson 1971) using behavioural methods. However, the com-

plexity of the behavioural method limited accessible data.

An effective way to study frequency selectivity of hearing is the evoked potentials method in conjunction with tone-tone masking. Tuning curves were obtained in humans and some experimental animals using evoked potentials such as cochlear APs (Dallos and Cheatham 1976; Eggermont 1977; Harris 1978; Abbas and Gorga 1981; Harrison et al. 1981; Gorga and Abbas 1981) and ABRs (Mitchel and Fowler 1980; Salvi et al. 1982; Gorga et al. 1983; Brown and Abbas 1987).

In a preceding study we obtained tuning curves in dolphins using rather slow evoked potentials of cortical origin (Supin and Popov 1986, 1990). However, other investigators used mainly cochlear AP or ABR for this purpose. The difference in approaches made it difficult to compare the data obtained in that study with corresponding data on other animals and humans.

ABR can be recorded easily in dolphins from the head surface, without any surgical procedure and anaesthesia. Using ABR, it was possible to assess a number of the dolphin's hearing characteristics (Ridgway et al. 1981; Popov and Supin 1985a, b, 1987, 1990a, b). In this study ABR was used to obtain frequency-tuning curves in dolphins.

In deciding on a masking paradigm to obtain tuning curves, the following reasoning was used:

1) Tuning curves can be defined as the masker levels required to render a probe response either just detectable (near-complete masking criterion) or partially suppressed (partial masking criteria). There is some difficulty in judging the masker level required for near-complete masking due to recording noise comparable with a just-detectable response; therefore, some data were obtained using partial masking criteria (response amplitude reduction of 25–75%, in many cases 50%). In some studies a just-detectable masking effect was used (Pantev and Pantev 1982; Pantev et al. 1985; Salt and Garcia 1990). However, using the near-complete masking criterion results in sharper tuning curves than partial masking (Abbas and Gorga 1981; Gorga and Abbas 1981) and just-

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detectable masking (Salt and Garcia 1990). This indicates a better measure of hearing tuning abilities with the use of the near-complete masking criterion. This criterion is also preferable for comparing results with psychophysical and behavioural data. For these reasons we chose the near-complete masking criterion in the present study.

2) Either simultaneous or forward masking paradigm can be used to obtain tuning curves. However, it was difficult for us to use forward masking because of very short recovery time of the dolphin's ABR. When conditioning (masking) and probe stimuli are equal, complete suppression of the probe ABR lasts for about 0.2 ms, and 50% recovery requires about 0.7 ms (Popov and Supin 1985b, 1990a, b.) Presenting the probe so soon after the masker requires an abrupt fall of the masker which leads to broadening of its spectrum. Therefore, in the present study the simultaneous masking paradigm was used.

Even in the simultaneous masking paradigm the masker could either be presented continuously or appear shortly before the probe to minimize adaptation effects. However, frequent stimulus presentation during evoked potential collection makes it unreasonable to present the masker intermittently because the total time of the masker action would be prolonged enough and broadening of the masker spectrum would appear at each onset and offset; therefore, we used continuous maskers. As to the difference between action of continuous and intermittent maskers, we did not analyse this effect in detail in the first stage of our study.

Materials and methods

Experiments were carried out during the 1991 and 1992 summer seasons at the Utrish Sea Station of the Russian Academy of Sciences (Black Sea coast).

Subjects. The experimental subjects were two bottlenosed dolphins, *Tursiops truncatus*, females, 225 and 230 cm body length. The animals were caught 2–3 months before the study and were adapted to the holding conditions and to the experimental procedure.

Experimental conditions. During the experiments, a 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. Since no surgical procedures were used, the animal was neither anaesthetized nor curarized. After several experiments the animal became used to the bath and did not attempt to escape from the stretcher, thus allowing ABR recording. Each experiment lasted for 3–4 h, after which the animal was placed back into the pool where it was kept.

ABR recording. The recording of ABR was performed using needle-shaped electrodes (diameter 0.3 mm) inserted 3–5 mm into the skin. Since the dolphin's skin is relatively insensitive to small injuries, no pain responses to the procedures were observed. There was no reason to use local anaesthesia since the electrode insertion was less traumatic than intracutaneous anaesthetic injection. The active electrode was placed in the dorsal part of the head, the reference one in the back near the dorsal fin, both electrodes above the water surface. The recorded signals were amplified ($10^4 \times$) and were bandpass filtered between 100 and 10^4 Hz. One thousand responses were averaged to provide satisfactory evaluation of response parameters.
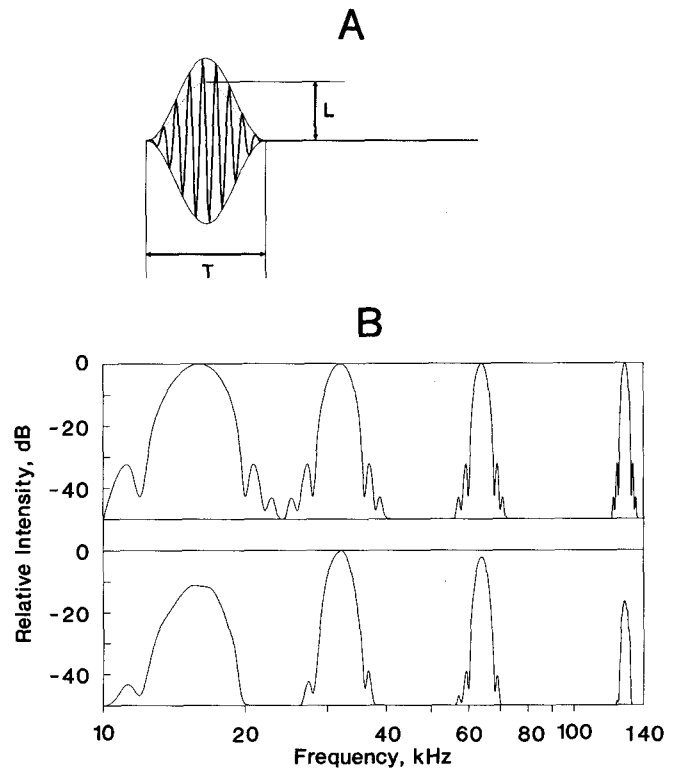

Fig. 1A, B. Probe stimulus characteristics. **A** Waveform of a cosine-enveloped tone burst. The *thin lines* show the envelope contours, the *dotted line* shows the effective signal level during the burst. *T* duration of the burst; *L* signal level designation (as maximal effective level). **B** Spectra of electrical cosine-enveloped bursts of 16, 32, 64, and 128 kHz central frequency *(upper part)* and their acoustical reproductions monitored by a hydrophone near the animal's head *(lower part)*; all bursts of 0.5 ms duration

Stimulation. Probe stimuli were 16–128 kHz tone bursts with a cosine-wave envelope, i.e. the envelope was one period of a function $1-\cos(t)$ (Fig. 1A). This form of signal provides a narrower spectral band (Fig. 1B) than triangular or rectangular signals of the same duration. Duration of the signals is indicated below as a period of its enveloping cosine function and their intensity is indicated as maximal effective sound pressure (Fig. 1A). Stimuli were presented at a rate of $25 \cdot s^{-1}$.

Masking signals were continuous tones of various frequency and level. Probe and masker were not coherent.

Probe and masker were mixed and emitted through a piezoceramic transducer of 3 or 6 cm in diameter. The transducer was immersed in water at a depth of 30 cm, 1 m 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 sound absorbing material (rubber). Acoustic properties of the transducers and the bath provided satisfactory reproduction of the stimulus spectra, as comparison of the two parts of Fig. 1B shows.

Intensity and frequency spectra of signals were monitored through a probe hydrophone with a band pass of 150 kHz, located near the animal's head. The relative level for sound intensity indication in decibels was taken to be 1 mPa because it is a reliable level, near auditory thresholds of aquatic mammals.

Results

ABR characteristics and masking manifestations

Figure 2 exemplifies ABR evoked by a probe without a masker and in the presence of various maskers. ABR

consisted of a series of peaks occurring mainly within the first 5–6 ms following acoustic stimulation.

A probe stimulus of a moderate intensity (40–50 dB re. 1 mPa) evoked a response of about 3 µV amplitude when measured between the largest positive and negative peaks (Fig. 2A). The same stimulus in a masker background evoked a smaller response. As the masker level increased, the ABR diminished until it disappeared in the noise.

The masking was the most effective when the probe and masker frequencies were equal (90 kHz in Fig. 2B). In this case the complete masking required the masker level of about 10 dB above the probe level (60 dB re. 1 mPa). When the masker and probe frequencies were different the masking was less effective: in Fig. 2C the masker frequency was 80 kHz while that of the probe was 90 kHz, and the masking required masker levels 25–30 dB higher than in the preceding case. In particular, the near-complete masking required the masker level of 85 dB (35 dB above the probe level).
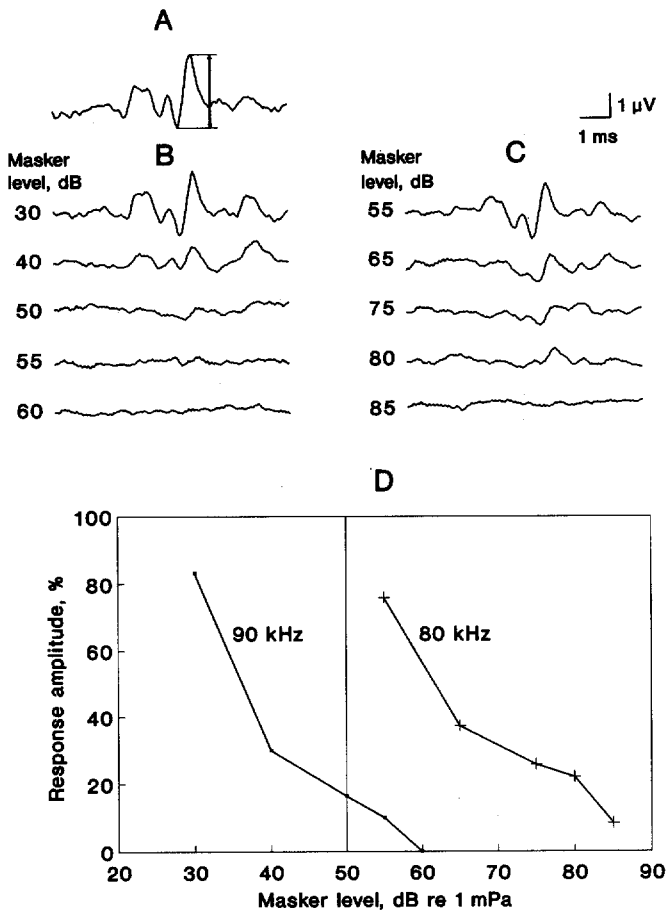
Figure 2D plots response amplitude versus masker level at two of the masker frequencies. The amplitude dependence on masker intensity is steep. The masker level required for near-complete masking (response amplitude of 5–7%, i.e. 0.15–0.2 µV) can be identified with an accuracy of 2–3 dB (we used a step of 2.5 dB). The figure shows a shift between the plots reflecting frequency dependence of masking. The shift was 27–30 dB at a response amplitude of less than 30%.

A response of 0.15–0.2 µV amplitude (5–7% of the unmasked response) was considered as just-detectable, and this masking criterion was used to generate tuning curves.

Tuning curves in various frequency ranges

For obtaining a tuning curve, the probe frequency and intensity were fixed and masker frequencies and intensities were varied. For each masker frequency, the level
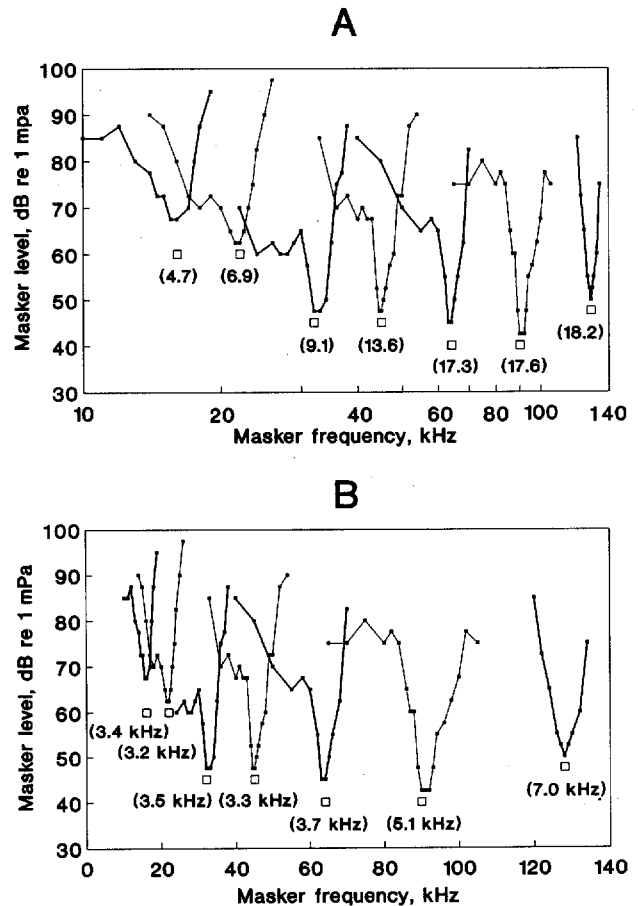

Fig. 2A–D. ABR waveform and suppression by maskers. **A** Unmasked ABR evoked by a probe stimulus of 90 kHz frequency, 0.5 ms duration, 50 dB re. 1 mPa level. The *double-headed arrow* shows the response amplitude measurement used in this paper. **B** Responses to the same probe in the background of the 90-kHz masker. **C** The same with the 80-kHz masker. Masker levels (dB re. 1 mPa) are shown near the curves. **D** Normalized response amplitude as a function of masker level with masker frequency as the parameter

Fig. 3A, B. Tuning curves obtained at various probe frequencies. Probe frequencies (for curves from left to right) are 16, 22, 32, 45, 64, 90, and 128 kHz. Probe duration is 0.5 ms, the *square symbols* represent probe frequency and level (40 dB above the ABR thresholds). **A** Data are presented using standard logarithmic frequency scale; the value of Q_{10} for each tuning curve is shown in parentheses. **B** The same data presented using linear frequency scale; the value of B_{10} (bandwidth 10 dB above the tip) for each tuning curve is shown in parentheses

required for near-complete masking of the probe response was determined with a 2.5-dB step. This procedure was repeated at each frequency of the masker to yield a complete tuning curve.

A family of ABR tuning curves obtained for one animal is shown in Fig. 3. These tuning curves possess the same features as the well-known curves in other mammals. There is a relatively sharp tip segment, an elongated low-frequency tail, and steep rise at high frequencies. All the curves peaked at or near the probe frequency. At this frequency the near-complete masking required a masker level of 2.5–7.5 dB above the probe level.

The curves demonstrated graduation of tuning depending on frequency. Tuning was sharper at higher frequencies and less sharp at lower frequencies. When presented in the standard logarithmic frequency scale (Fig. 3A), tuning was little dependent on frequency in the high frequency range 64–128 kHz. The Q_{10} values (the centre frequency divided by the bandwidth at a level 10 dB above the tip of the curve) are a convenient measure of the sharpness of tuning. For curves with probe frequencies of 64–128 kHz the Q_{10} values were virtually constant at 17.3–18.2. At lower frequencies Q_{10} diminished and was as low as 4.7 at the 16 kHz probe frequency. In this case the tuning was so broad that the tip and tail segments could not be separated.

Using the linear frequency scale (Fig. 3B) shows that the tip segments of the tuning curves are of virtually constant width in the low-frequency range of 16–45 kHz. Bandwidth 10 dB above the tip may be a convenient measure of the curves' width; hereafter designated as B_{10}. The B_{10} values were 3.2–3.5 kHz for curves obtained with probe frequencies 16–45 kHz. From this it immediately follows that Q_{10} is proportional to frequency. At higher frequencies (64–128 kHz) B_{10} enlarged proportionally to the frequency, which resulted in constant Q_{10}.

The other animal studied gave similar results. The Q_{10} values were 16.0–19.1 within the range 64–128 kHz, and the B_{10} values were 3.5–3.8 within the range 16–45 kHz.

Both B_{10} and Q_{10} dependencies on the probe frequency for both of the animals are plotted in Fig. 4. The plots demonstrate a virtually constant value of B_{10} in the low-frequency range (16–45 kHz) and a virtually con-
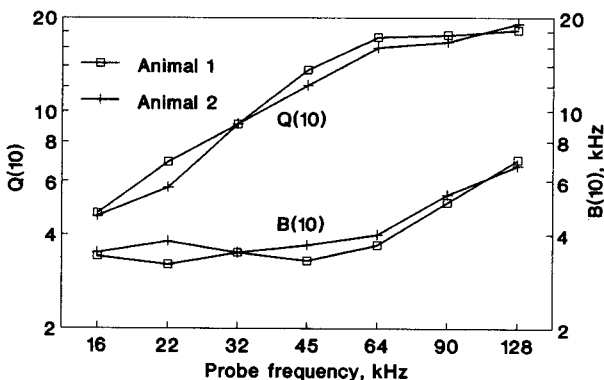
stant value of Q_{10} in the high-frequency range (64–128 kHz). The mean Q_{10} value ($\pm$ SD) over both of the animals and over frequencies of 64–128 kHz was 17.5 $\pm$ 1.1; the mean B_{10} value over frequencies of 16–45 kHz was 3.5 $\pm$ 0.2 kHz.

Dependence of tuning curves on masking criterion

The data presented above were obtained using the near-complete masking criterion. A special investigation was carried out to test the dependence of tuning curves on masking degree. For this purpose, the masker level was varied in a 5-dB step from minimal masking (10–20% decrement of the probe ABR) to near-complete masking (85–95% decrement). Masker levels required to obtain a specified response decrement were calculated by interpolation between the nearest higher and lower levels. Using these data, tuning curves for various response amplitude were obtained (Fig. 5). These tuning curves
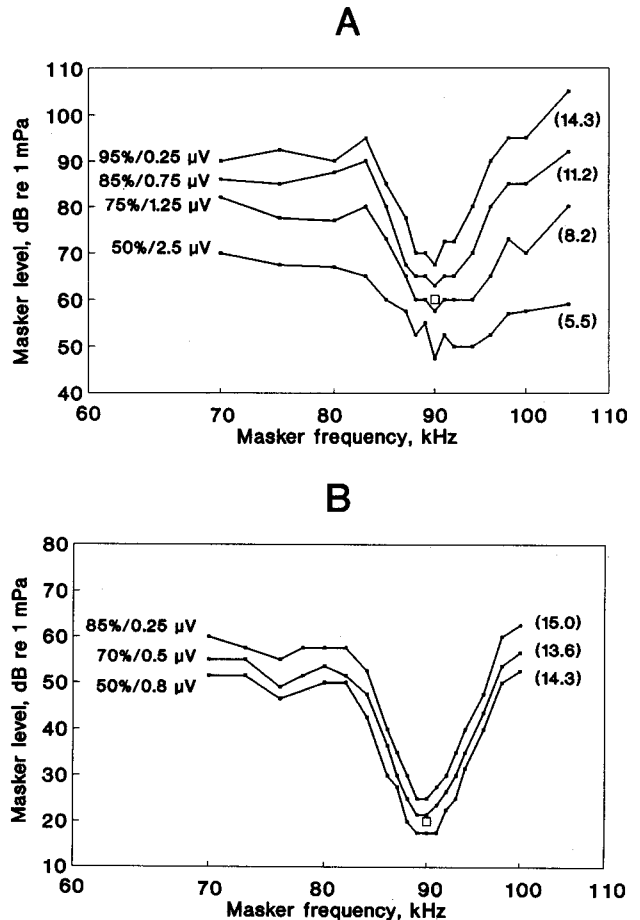
Fig. 5A, B. Tuning curves obtained using various values of response decrement. Masking criterion is indicated near each curve (on the *left*) as the response decrement, %, and as the remainder response amplitude, μV. The value of Q_{10} for each curve is shown in parentheses (on the *right*). The *square symbol* represents the probe frequency (90 kHz) and level. **A** The probe level is 60 dB re. 1 mPa (the response threshold is 0 dB), the unmasked response amplitude is 5 μV. **B** The probe level is 20 dB re. 1 mPa, the unmasked response amplitude is 1.6 μV

Fig. 4. Dependence of Q_{10} *(left ordinate scale)* and B_{10} *(right ordinate scale)* on probe frequency (data for the two animals)

were dependent on the masking criterion. Apart from the self-evident shift of the curves (the deeper masking, the higher masker level was required), their tuning sharpness depended on the criterion as well.

When a high-level probe was used, which evoked a large response, the tuning depended significantly on the masking criterion (Fig. 5A). The tuning was most sharp for the near-complete masking ($Q_{10} = 14.3$ for the 95% response decrement) and became broader with diminishing masking criterion ($Q_{10} = 5.5$ for the 50% response decrement).

Another dependence was observed when a low-level probe was used which evoked a low-amplitude response. In this case curve characteristics were little dependent on the masking criterion (Fig. 5B). All the curves demonstrated sharp tuning without systematical dependence of Q_{10} on the response decrement criterion.

However, there is no distinct difference between results obtained with high- and low-level probes if the masking criterion is expressed as remainder absolute response amplitude (in μV) instead of amplitude decrement percentage. Independently of the decrement percentage, the curves demonstrate sharp tuning when the criterial response amplitude is low (less than 1 μV in our recording conditions). It was observed both in conditions of deep masking of a high-level probe and in deep or light masking of a low-level probe. The tuning became broader when the response amplitude became higher, in conditions of light masking of a high-level probe.

Influence of probe level on tuning curves

When the near-complete masking criterion was chosen, shape and bandwidth of tuning curves were little dependent on the probe level (Fig. 6). The curves obtained at probe levels of 20–60 dB had a similar tuning degree corresponding to a Q_{10} of 15–17.3. Only the curve obtained at the 80 dB probe level was broader with a Q_{10} of 10.8.

Thus, probe levels up to 60 dB are preferable for revealing frequency tuning. However, low probe levels
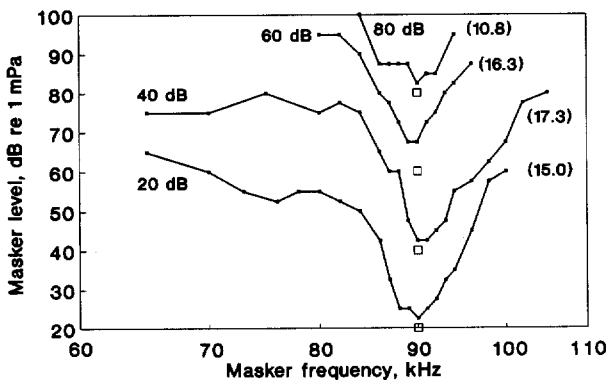
(20–30 dB) evoked ABR of low amplitude which made it difficult to measure their amplitude precisely enough. Therefore, in the present study the probe levels of 40–50 dB re. 1 mPa were the most used.

Influence of probe duration on tuning curves

Influence of probe duration on tuning curves was studied in the duration range 0.125–1 ms. Cosine-enveloped stimuli longer than 1 ms evoked ABR of low amplitude which made it difficult to measure the degree of their masking.

A family of tuning curves obtained with probes of various durations is presented in Fig. 7. The figure shows that there was a region of probe duration (0.5–1 ms in the presented example) in which the curve shape and width were constant (their Q_{10} was 17.3–17.4). At the 0.25 ms probe the curve was less sharp ($Q_{10} = 12.5$), and it became significantly broader when the probe duration was as short as 0.125 ms ($Q_{10} = 3.5$).

Curve bandwidth dependency on probe duration was measured at various probe frequencies, from 32 to 128 kHz. For this purpose only the tip segments of the
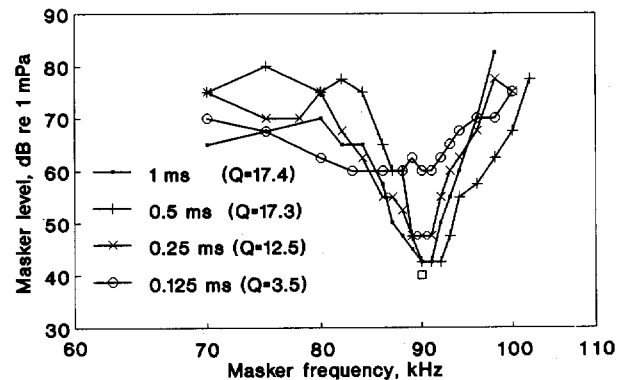

Fig. 7. Tuning curves at various probe duration (0.125–1 ms). The values of Q_{10} are shown in parentheses in the legend. The *square symbol* represents the probe frequency (90 kHz) and level (40 dB re. 1 mPa; the response threshold is 0 dB)

Fig. 6. Tuning curves at various probe levels, 20–80 dB (indicated near the curves in dB re. 1 mPa; the response threshold is 0 dB). Probe duration is 0.5 ms. The values of Q_{10} are shown in parentheses (on the *right*). The *square symbols* represent the probe frequency (90 kHz) and levels
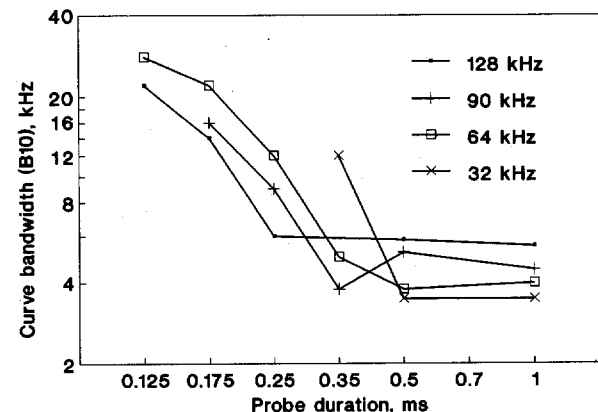

Fig. 8. Tuning curve bandwidth (B_{10}) dependence on probe duration with probe frequency as the parameter

curves, which are necessary to measure their bandwidth 10 dB above the tip, were obtained for every probe frequency and duration.

Figure 8 plots the curve bandwidth (B_{10}) as a function of the probe duration at various probe frequencies. The common feature of all the plots is that they consist of two segments: the horizontal one (bandwidth was constant) and the inclined one (bandwidth increased with shortening probe duration). Position of the inflection point was dependent on the probe frequency: the higher the frequency the less the critical probe duration at the inflection point. It was 0.25 ms for the 128 kHz probe frequency, 0.35 ms for 90 kHz, and 0.5 ms for 64 and 32 kHz. At all probe frequencies, duration enlargement from 0.5 to 1 ms did not influence the curve bandwidth. Thus, at all probe frequencies, the 0.5 ms probe duration was long enough to avoid broadening of the curves. This probe duration was the most used in this study.

Discussion

A remarkable feature of the tuning curves obtained in this study is their sharpness. The Q_{10} values were as large as 16–19 (mean 17.5) in the high-frequency range. For comparison, in the majority of studies in terrestrial mammals and humans, the maximal obtained Q_{10} values were 4–6 for both cochlear AP and ABR tuning curves (Dallos and Cheatham 1976; Mitchell and Folwer 1980; Harrison et al. 1981), and in rare cases values greater than 10 were reported (Brown and Abbas 1987).

The tuning curves reported here are sharper than in a preceding study based on recording of cortical-evoked potentials in dolphins (Supin and Popov 1986, 1990). In that study the tuning curves had the mean slope of the low-frequency branch 55 dB per octave, and of the high-frequency branch 97 dB per octave. It is easy to compute that these slope values correspond to a Q_{10} of 5.2, i.e. several times less than in the present study. Perhaps the auditory cortex realizes some more complex functions than simple frequency analysis, and therefore cortical responses do not manifest the frequency tuning in full measure. ABR manifests the activity of the auditory periphery and may better reflect its frequency selectivity.

As to tuning curves obtained in a dolphin by the behavioural method (Johnson 1971), it is difficult to estimate their sharpness because of a characteristic dip in sensitivity when the masker and the probe were of the same frequency. This well-known effect is assigned to beats arising when the tonal probe and masker are superimposed. Tuning curves obtained by the evoked potential method never displayed such effect, apparently because of the broader spectra of short probes. The same was observed in dolphins in the present study.

Behavioural measurements of the dolphin's frequency tuning carried out with the use of the so-called comb-filtered noise as the test stimulus gave the frequency tuning at the −3 dB level (Q_3) of about 40 (Supin et al. 1992), and our recent measurements gave the value of about 50 (unpublished observation). Taking into account that for the standard resonance curve $Q_3 \approx 3\,Q_{10}$, these data correspond to a Q_{10} of about 17. This value is close to that found in the present study.

The question arises whether the difference between frequency tuning in dolphins and terrestrial mammals reflects peculiarities of the dolphin's auditory system or a difference in methods. In the present study we used the near-complete masking of evoked potentials instead of the 50% masking criterion as applied in many other studies. Masking criterion can influence the tuning curve sharpness to some extent (Abbas and Gorga 1981; Gorga and Abbas 1981). However, our results show that this influence is insignificant when a low-level probe, about 20 dB above the ABR threshold, is used. It is this range of the probe level (10–20 dB above the response threshold) that was used in the majority of studies (Dallos and Cheatham 1976; Eggermont 1977; Abbas and Gorga 1981; Gorga and Abbas 1981; Harrison et al. 1981). Using such low-level probe, Dallos and Cheatham (1976) observed little influence of masking criterion on the curve sharpness. Thus, it is unlikely that tuning sharpness in terrestrial mammals was underestimated due to inadequate masking criteria. Therefore, we suppose that sharper frequency tuning in dolphins, as compared with terrestrial mammals, reflects peculiarities of their auditory system.

Moreover, we cannot exclude underestimation of frequency tuning in dolphins due to the use of the simultaneous masking paradigm in our experiments. Simultaneous masking may result in broader tuning curves than forward masking because of complex interaction between simultaneously presented probe and masker, in particular, two-tone inhibition. Thus, frequency tuning in dolphins may be even sharper than our data show.

It is remarkable that very sharp tuning was observed only in a high-frequency range, above 64 kHz. On lowering the probe frequency the curves became broader, and below 20 kHz (i.e. the same frequency range which was tested in terrestrial mammals) we found the same tuning degree as in terrestrial mammals with Q_{10} values of about 4–5. These data would provide a basis for determining the relationship between frequency range and frequency tuning in the auditory system, if it were not for the possibility of underestimation of frequency tuning in the low-frequency range.

Indeed, the main difficulty associated with using the evoked potentials in frequency-tuning measurements arises from the fact that these responses are evoked by transient acoustic stimuli, e.g. a short sound burst, or sound onset, or offset, or quick change. Transient stimuli feature broader frequency spectra than long duration, slowly rising and falling stimuli. This limits their use as probes for measuring the frequency selectivity. The problem is that we do not know exactly which part of a stimulus is actually effective in eliciting the evoked response. Hence, we do not know how broad the effective spectrum of the stimulus actually is. Even with a slowly rising and falling stimulus, only the initial part may be effective enough to evoke the response, and the spectrum of this initial part is broader than the spectrum of the whole burst, as the scheme in Fig. 9 shows.
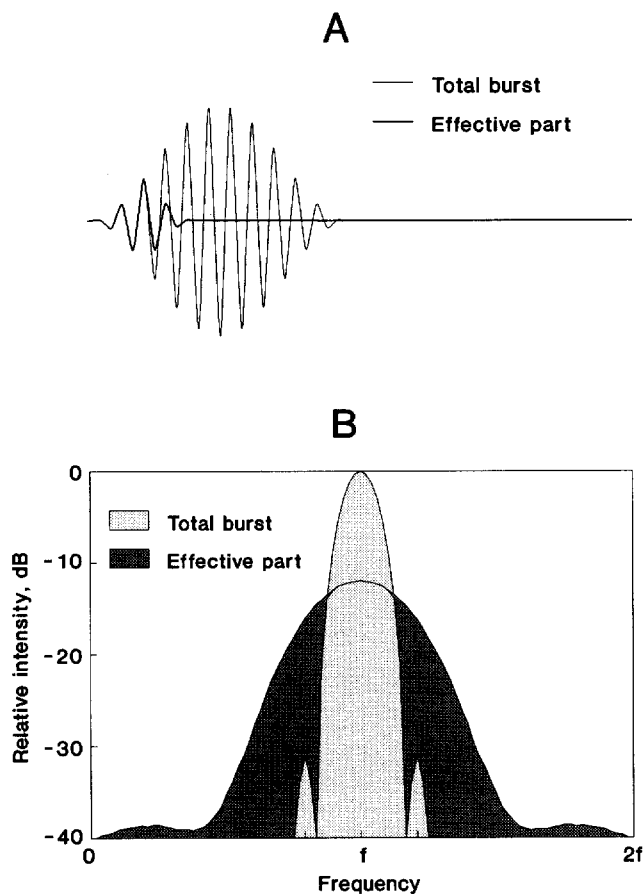
A

—— Total burst

—— Effective part

B

Fig. 9A, B. Schematic presentation of difference between spectra of a total sound burst and its effective part. **A** Waveforms of a cosine-enveloped burst and its arbitrary isolated initial part. **B** Frequency spectra of the burst and its initial part; f burst frequency

When the effective stimulus duration is constant, its absolute frequency bandwidth (kHz) is also constant, and its relative bandwidth is inversely proportional to the central frequency (see spectra of 0.5-ms tone bursts in Fig. 1 as an example). Correspondingly, its Q_{10} value is proportional to the central frequency. It is just this type of dependence that was observed for tuning curves in the range 16–45 kHz. This suggests that tuning curves in this frequency range may reflect the spectrum of the probe (or an effective part of the probe) rather than real tuning of the auditory system. If so, the bandwidth of the probe part eliciting the dolphin's ABR is close to a B_{10} of about 3.5 kHz (see Fig. 4).

Within the high-frequency range (64–128 kHz), the tuning curves were broader than the supposed probe spectrum (their B_{10} was more than 3.5–4 kHz). Hence, we consider these curves as reflecting the real frequency tuning of the dolphin's auditory system. This interpretation is supported by data on the influence of the probe duration on the tuning curves (Fig. 8). The curvre bandwidth was constant as long as the probe duration exceeded a critical value. It is reasonable to suppose that in this duration range the probe spectrum is narrower than the auditory tuning and thus does not influence the tuning curve. When the probe duration becomes shorter

than the critical value, the probe spectrum becomes broader than the auditory tuning, thus tuning curves reflect the probe spectrum and become broader with shortening of the probe. The lower the probe frequency, the longer the probe's critical duration (from 0.25 ms at 128 kHz to 0.5 ms at 64 kHz) because the tuning curve bandwidth (kHz) becomes narrower (see Fig. 3B). However, in none of the cases was the probe's critical duration longer than 0.5 ms (both at the 64 and 32 kHz probe frequencies). This suggests that irrespective of the actual probe duration, the effective duration which elicits the ABR in dolphins is no longer than 0.5 ms.

This conclusion is in good agreement with data on temporal summation of the dolphin's ABR. The summation time was about 0.5 ms at the near-threshold stimulus intensity and decreased at higher intensities (Popov and Supin 1990a). A near-completely masked response can be considered as a near-threshold one when the threshold is elevated by the masker. Correspondingly, the effective probe duration dictated by the summation time is about 0.5 ms in these conditions. A partially masked high-amplitude response can be considered as the supra-threshold response. Its summation time is shorter and the spectrum of the effective part of the stimulus is broader, which results in broadening of the tuning curves in such conditions (see Fig. 6).

It is easy to compute the B_{10} value for the 0.5-ms cosine-enveloped stimulus: it is equal to 5.0 kHz. This value is rather close to the bandwidth of the tuning curves in the low-frequency range (about 3.5 kHz). Thus, it is possible that our tuning curves underestimate the auditory tuning at frequencies below 64 kHz because of the broad spectrum of the probe's effective part.

The decrease of tuning with decreasing frequency, similar to that seen in our study, was found in most preceding studies based on the evoked potential technique. However, we have not found any detailed discussion as to thow the probe's effective duration and spectrum may influence the tuning curve bandwidth. However, tuning decrease with decreasing frequency was found not only with the use of evoked potentials, but in psychophysical and single-unit studies which do not require short transient stimuli (Evans 1974; Zwicker 1974; Fay 1992). It suggests that a tuning decrease on lowering the frequency does exist in the auditory system. However, this decrease is not as steep in proportion to the frequency (i.e. with constant bandwidth).

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