Frequency resolving power of the dolphin's hearing measured by rippled noise

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Summary

Frequency resolving power (FRP) of hearing was studied in bottlenose dolphins in behavioral experiments (go/no-go paradigm) using rippled noise with a phase-reversal test. The rippled noise has a frequency spectrum with periodically alternating peaks and troughs (ripples) which is a convenient spectrum pattern to test frequency resolution. The principle of the phase-reversal test was to find the highest ripple density at which an interchange of peak and trough positions (the phase reversal) in the ripple spectrum is detectable. Measurements were made using narrow-band rippled noise stimuli with center frequencies varying from 2 to 128 kHz. The found FRP was frequency-dependent: it increased from 6.7–7.4 (mean 7.0) at 2 kHz to 33.2–62.8 (mean 48.3) at 128 kHz. At lower frequencies (2–16 kHz) the found FRP values are close to those of humans. At high frequencies (90–128 kHz) these values are several times higher which indicates very sharp frequency tuning.

Introduction

An important characteristic of the auditory system, significant for discrimination of complex sounds, is its frequency resolving power (FRP). It is the ability of the auditory system to discriminate fine spectral patterns of complex sounds. Investigation of the FRP of the auditory system in dolphins is of special interest because their hearing is adapted to higher sound frequencies than that of terrestrial mammals.

In the past years there were several attempts to measure frequency selectivity in dolphins by tone-tone and noise-tone masking behavioral experiments (Johnson, 1968: Au & Moore, 1990) and tone-tone masking evoked-potential experiments (Supin *et al.*, 1993). However, the results were contradictory and the true ability of the dolphin auditory system to resolve sound frequencies in complex sounds remains uncertain.

In this study the so called comb-filtered or rippled noise was used as a probe stimulus to measure the frequency selectivity. This sound is characterized by a rippled frequency spectrum with alternating maxima and minima of spectral power (Fig 1). The highest ripple density of the spectral ripples that could be resolved by the auditory system is a measure of FRP of the system.

To measure FRP using rippled noise, the phase-reversal test was proposed in previous studies (Supin & Popov, 1990: Supin *et al.*, 1994). The principle of the method is as follows (Fig. 1). Rippled noise of a certain ripple density is presented to a subject (spectrum 1). At some instance, this noise is replaced by another one of the same intensity, bandwidth, and ripple density but of the opposite position of spectral peaks and troughs at the frequency scale (spectrum 2). Thus, the phase reversal of spectral ripples occurs. A subject can detect this change only if it discriminates the fine spectrum structure. If the spectral ripples are spaced too densely to be discriminated, the change can not be detected because the noises before and after the change are identical in all respects (intensity, overall bandwidth, etc.) except the peak and trough positions. Thus the highest ripple density at which the phase reversal is detectable is a good measure of frequency resolution, i.e., FRP.

FRP measuring in such a way was used successfully to study the human auditory system in psychophysical experiments (Popov & Supin 1984, 1987: Supin *et al.*, 1994). In the present study, we measured the FRP of dolphin hearing in behavioral experiments. Some preliminary results of such measurements were published earlier (Supin *et al.*, 1992*a,b*). The task of the study was to measure FRP in several animals and in a wide frequency range, from rather low (2 kHz) to high (128 kHz) frequencies.

Material and methods

Experiments were carried out during 1992–1996 summer seasons in the Utrish Marine Station of the Russian Academy of Sciences (Black Sea coast). The care and use of the animals was conducted

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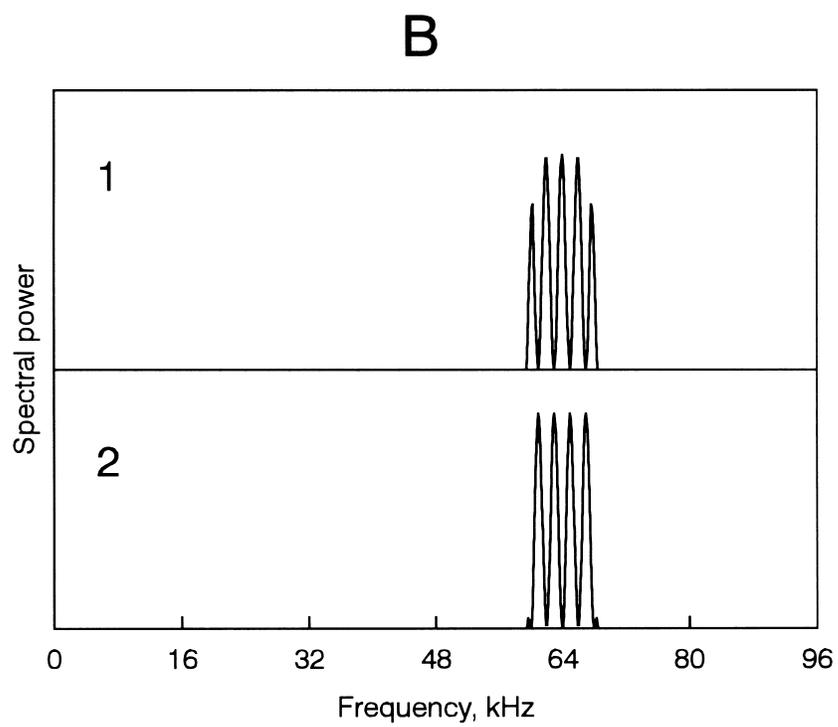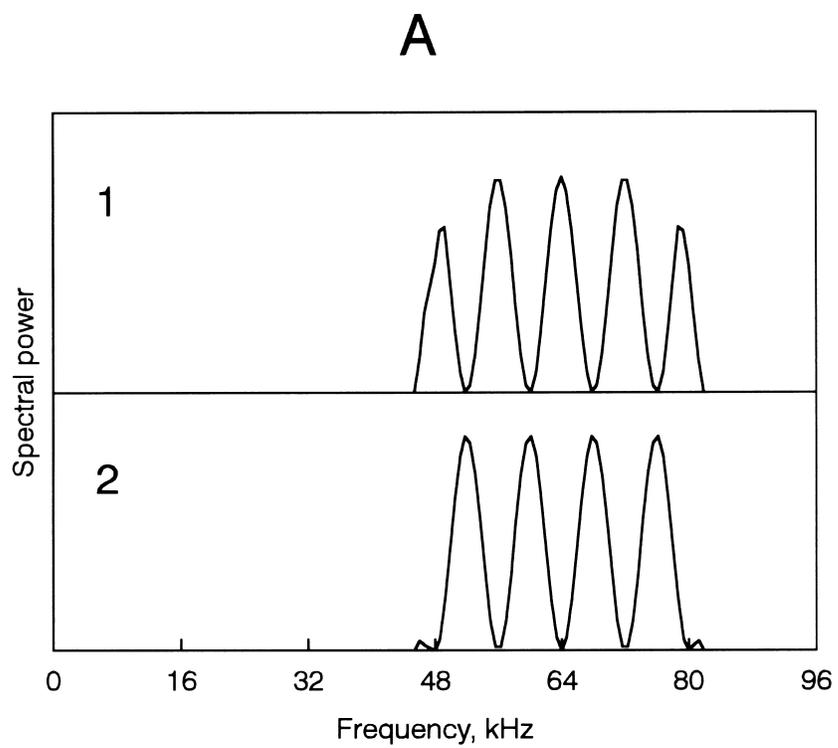
Figure 1. Diagrammatic presentation of rippled spectra with alternative peak and trough positions (1 and 2). A: center noise frequency 64 kHZ, ripple density 8. B: the same center frequency, ripple density 32.

under the guidelines established by the Russian Ministry of Higher Education on the use of animals in biomedical research.

Subjects

Four adult bottlenose dolphins (*Tursiops truncatus*), one female and three males were used in the experiments. The animals were caught 2–3 months before the study and were adapted to the keeping conditions and to the experimental procedure. The animals were kept in on-land pools 4 × 9 m in size, 1.5 m deep.

Stimulation

Rippled noises were used as stimuli to measure the FRP of hearing. The noise spectrum was narrowband with 4 ripples within the band (Fig,1A, B). The noises were produced by mixing a quasi-random binary sequence with a delayed version of itself (Narins *et al.*, 1979). This results in spectral ripples with frequency spacing of $\delta = 1/\tau$ where δ is the ripple spacing, kHz, and τ is the delay, ms.

Ripple density of narrow-band noise is characterized here by its relative measure which is the noise center frequency divided by the ripple spacing: $D = F/\delta = F\tau$, where D is the relative ripple density, δ is the ripple spacing, kHz, τ is the delay, ms, and F is the center frequency, kHz.

We used narrow-band noises with center frequencies varying in half-octave steps, namely, of 2, 2.8, 4, 5.6, 8, 11.2, 16, 22.5, 32, 45, 64, 90, and 128 kHz. Ripple densities were varied using the following steps: 4, 5, 6, 8, 10, 12, 16, 20, 24, 32, 40, 48 and 64 relative units; i.e., three steps per ripple density doubling. As to the noise bandwidth, it varied together with the ripple density in such a way as to hold the number of ripples constant, namely 4, i.e., two ripples above and two below the center frequency. This relation between ripple density and bandwidth is illustrated in Figure 1A and B showing examples of spectra with various ripple density. Both exemplified spectra are of 64 kHz center frequency. At the ripple density of 8 (ripple spacing 8 kHz), the total noise bandwidth is as wide as 4 × 8 kHz = 32 kHz (Fig 1A). At the ripple density of 32 (ripple spacing is 2 kHz), the bandwidth is as narrow as 4 × 2 kHz = 8 kHz (Fig. 1B). The variation of noise bandwidth together with ripple density was used to make the bandwidth as narrow as possible, which was necessary to attribute measurement results to a certain center frequency, but provide at least several spectral ripples within the bandwidth. It was shown (Supin *et al.*, 1994) that the number of four ripples is enough to avoid sound level change at phase-reversal switches.

Two signal types were used in our experiments. One signal type named 'constant' was a rippled noise of a certain ripple density that was presented to the animal without any changes during the presentation. The other type called 'alternating' was a rippled noise containing ripple phase reversals, i.e. the ripple peaks and troughs periodically interchanged their positions at the frequency scale. Phase reversal switches were made with a rate of 1/s, presenting two spectral patterns with opposite peak and trough positions for equal time; i.e., each spectral pattern replaced the other one every 500 ms.

Sounds were presented through a spherical piezoceramic transducer. At frequencies of 32 kHz and lower, a transducer of 6 cm in diameter was used; at frequencies of 45 kHz and higher, it was a transducer of 3 cm in diameter. The transducer was immersed in water at the depth of 0.5 m. Sound intensity at the animal start position was varied depending on the center frequency from 110–150 dB re 1 μPa keeping it 50–70 dB above the hearing threshold.

Procedure

During the preliminary training, dolphins were taught to discriminate between the constant and alternating signal types in the 'go/no-go' paradigm. Except the position of ripples at the frequency scale, all other parameters of the alternating signal remained unchanged during the phase reversals.

In the experiments with dolphin No. 1, the constant signal was presented continuously and from time to time it was replaced by the alternating signal for 20 s periods. Intervals between alternating stimuli varied randomly within a range of 30–210 s. The animal was required to touch a paddle not later than 20 s after the alternating signal onset and not touch the paddle in the absence of the alternating signal. The correct response (touching the paddle during the alternating stimulus presentation) was rewarded by fish.

In experiments with dolphins No. 2–No. 4, the animal was trained to stay at a start position (Fig. 2) touching the start paddle 2 and wait for the signal. The signal was presented for 20 s, either constant or alternating, in a random sequence. If the presented signal was the alternating one, the dolphin had to go to a response paddle 3 and touch it. The solving of this task was bordered by 20 s time. The correct response (correct detection) was rewarded by fish. If the signal was a constant one, the dolphin had to stay quiet at the start position for 20 s; the correct behavior (correct rejection) was rewarded by fish. Incorrect behavior (missing the alternating signal or false alarm to the constant one) was not rewarded.

During the measurement, noise ripple density varied according to the adaptive (staircase) procedure (one-down two-up): when the animal detected alternating stimuli and responded correctly
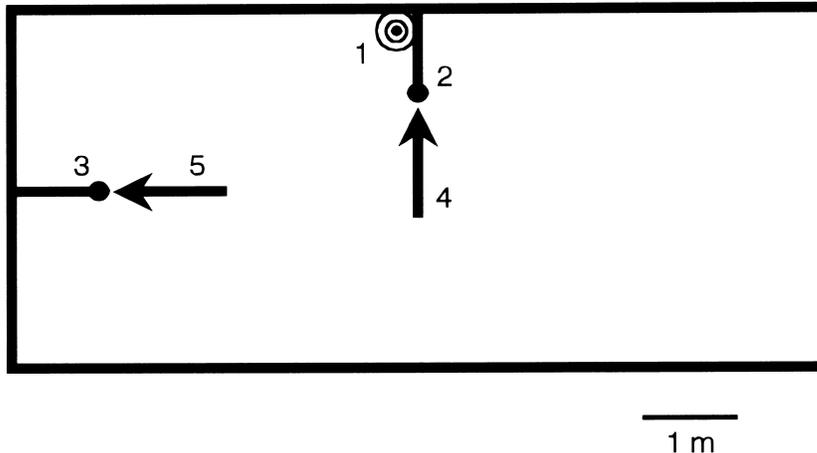
Figure 2. Layout of the experiment environment. The rectangular pool is shown schematically. 1—hydrophone, 2—start paddle, 3—response paddle, 4—animal start and correct rejection position, 5—animal correct detection position.

twice, the ripple density of the next stimulus (either alternating or constant) was increased by one step, i.e., was made more difficult to detect. When the animal missed an alternating stimulus once, the ripple density of the next stimulus was decreased by one step, i.e., it was made more easy to detect. Responses to constant stimuli did not influence the next stimulus parameters: these served only as training stimuli. This adaptive procedure resulted in the ripple density valued close to that providing 70.7% correct responses (Levitt, 1971). For every animal and every center noise frequency 4 measurements were made, each of 50 to 130 trials; about a half of these trials were presentation of alternating signals.

To find the resolvable ripple density limit, the probability of correct detections and false alarms was counted for several ripple density values. For experiments with the dolphin No. 1 (constant non-alternating stimulus presentation), the probability of false alarms was calculated as being referred to the 20 s time period, i.e. $p = n \times 20/T$, where p is the false alarm probability, n is the number of false alarms during the period between two presentations of alternative stimuli, and T is the duration of this period. The correct detection and false alarm probabilities thus found were presented in the receiver-operating-characteristic (ROC) format: correct detection vs. false alarm probability at several ripple densities. The ROC-line, meeting the point of 0.75 correct detection probability and 0.25 false alarm probability, was adopted as the resolution limit criterion. Intersection of the experimental plot with this line was adopted as the resolution limit. The resolvable ripple density was calculated by

interpolation between the values which provided the correct-detection to false-alarm combinations just above and below the criterion ROC-line.

Results

Figure 3 exemplifies a typical measurement course using the adaptive procedure and shows how ripple density resolution limits were determined. The noise center frequency in this experiment was 128 kHz. The figure shows a sequence of presented ripple densities that varied according to the animal's responses.

The experiment started with a series of stimuli of low ripple density, below the anticipated limit. These presentations played a part of a training sequence. At these low ripple densities, all alternating stimuli resulted in correct detections and almost all constant stimuli resulted in correct rejections (initial 20 trials). Then the adaptive procedure brought the ripple density to a range around the resolution limit. The plot shows typical fluctuations of presented ripple densities, depending on the detection or missing of the alternative stimuli by the animal. Correct detection probability decreased and false alarm probability increased at these ripple densities as compared with the start training sequence. In this experiment, the highest ripple density achieved using the adaptive procedure was 64 relative units, but most of presented stimuli were of ripple densities of 32–48 units.

Combinations of correct detection to false alarm probabilities obtained in this experiment were 0.93–0.22, 0.70–0.43, and 0.71–0.46 for ripple-density valves of 32, 40, and 48 units respectively. Figure 4
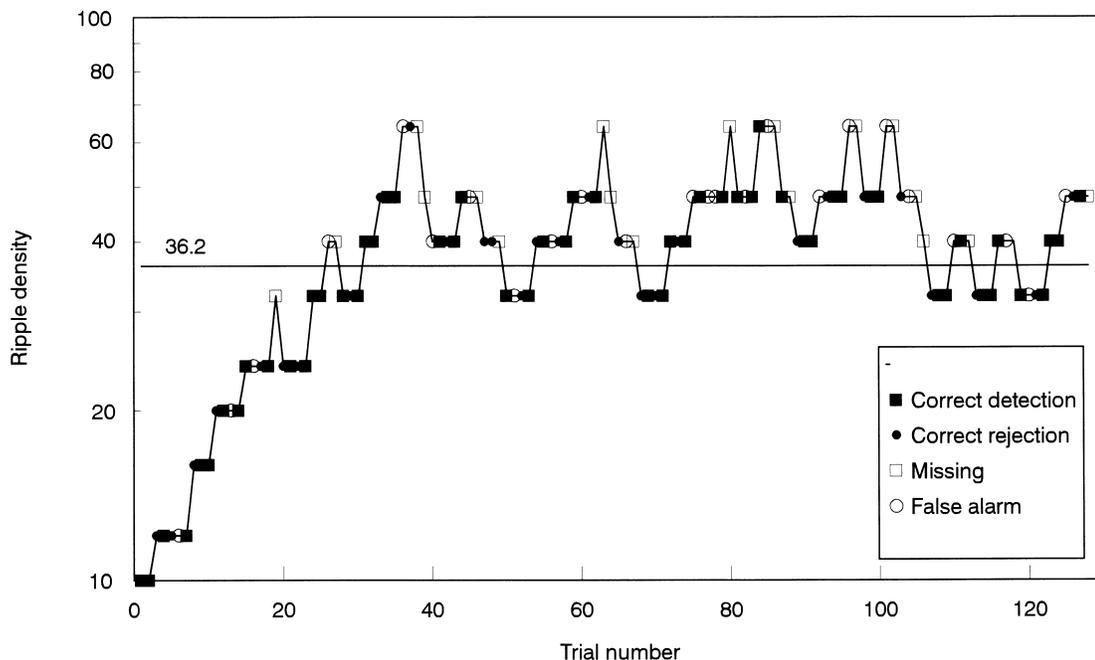
Figure 3. An example of measurement at a center frequency of 128 kHz: presented ripple density *vs* trial number. Ripple density was established according to the adaptive procedure. The horizontal straight line at the level of 36.2 shows the estimation of ripple-density resolution limit.

shows these probabilities presented in ROC-format (data for the ripple density of 64 were ignored because of the small number of presentations). It was only the 32 unit ripple density that resulted in the correct-detection to false-alarm combination above the resolution criterion. Ripple densities of both 40 and 48 units resulted in the combinations below the resolution criterion. The line connecting the points of ripple densities of 32 and 40 intersects the criterion line at a point of 0.81 detection probability and 0.33 false-alarm probability (the intersection point is shown by an arrow). Linear interpolation between the ripple-density values of 32 and 40 resulted in the ripple density of 36.2 corresponding to this intersection point. This value was adopted as the ripple-density resolution limit in this experiment. It is indicated by the horizontal straight line in Figure 3.

Similar measurements were made at various noise center frequencies. All the measurements gave results which were qualitatively similar in that increasing ripple density diminished the probability of correct detections and enlarged the probability of false alarms. A few examples of results obtained at various center frequencies are presented in Figure 5. Contrary to Figure 4 which shows data of one particular experiment, Figure 5 shows combined data obtained in all experiments with the animal at
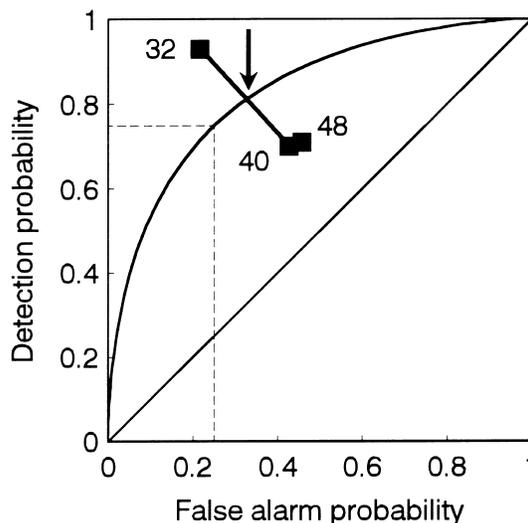

Figure 4. Correct detection *vs* false alarm probability presented in ROC format (the same experiments as in Fig. 3). Dashed straight thin lines show the point of 0.75 correct detection probability and 0.25 false alarm probability; the curve meeting this point is the criterion ROC-curve. The polygonal plot shows experimental data; ripple densities are indicated near the experimental points. The arrow shows intersection of the experimental point with the criterion ROC-curve.

each of the presented frequencies. The examples show that ripple-density resolutions are different at different center frequencies. At the frequency of 2 kHz, the plot presenting experimental data crosses the criterion line between points of ripple densities 8 and 10 (estimate of the resolution limit was 9.0); at the frequency of 16 kHz, this crossing is between points 8 and 12 (estimate of the resolution limit was 10.2); at the frequency of 64 kHz, the crossing is between points 20 and 24 (estimate of the resolution limit was 23.3).

Overall results of ripple-density resolution limits found as described above are presented in Figure 6 and Table 1. The figure and the table cover the results obtained in four animals at frequencies from 2–128 kHz. The animals No. 1 and No. 2 were tested throughout all this frequency range by varying center frequencies with half-octave steps. Animal No. 3 was tested with center frequencies varying with octave steps; more detailed investigation of this animal was not available. Animal No. 4 expressed a distinctive aversion to the discrimination task when the noise center frequencies were below 16 kHz: it refused to come to the start position and did not respond to stimuli in any way; therefore, this animal was tested with satisfactory precision only within the frequency range of 22.5–128 kHz.

The individual results obtained in four tested animals are presented in Figure 6A. The plots show significant inter-individual variability of ripple-density resolution limits of up to 2–2.5 times. Nevertheless, the general trend is obvious: the higher center frequency, the higher resolution limit. A result of inter-individual averaging of the data is presented in Figure 6B (means ± SD). The mean resolution limit changed from 7.0 relative units at 2 kHz to 48.3 at 128 kHz. Being presented in the double logarithmic scale, this dependence could be satisfactorily approximated by a straight line with a slope of 0.44.

It may also be of interest to express the obtained data in terms of absolute ripple density; i.e., how many spectral ripples per frequency unit, say 1 kHz, are resolvable by the auditory system. Such a presentation is shown in Figure 7. The absolute ripple density resolution decreased with increasing frequency. Inter-individual averaging resulted in ripple-density resolution limits from 3.5/kHz at 2 kHz center frequency to 0.38/kHz at 128 kHz center frequency.
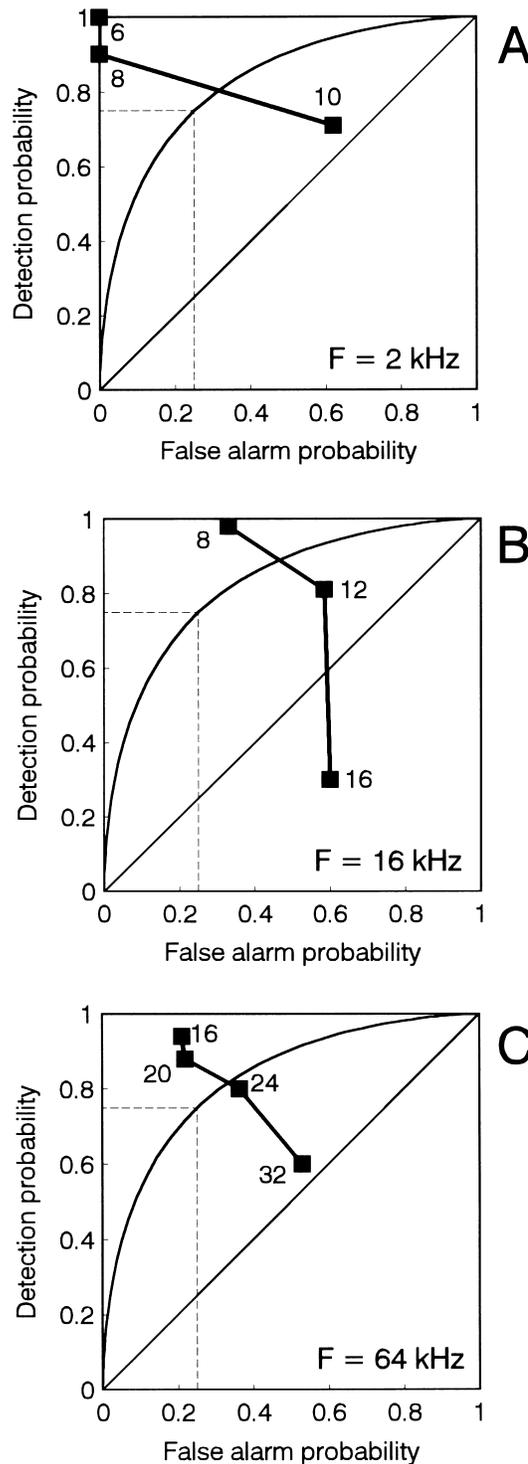
Figure 5. Experimental data obtained at three center frequencies presented in ROC-format. A: 2 kHz center frequency, B: 16 kHz; C: 64 kHz. Designations are the same as in Figure 4.

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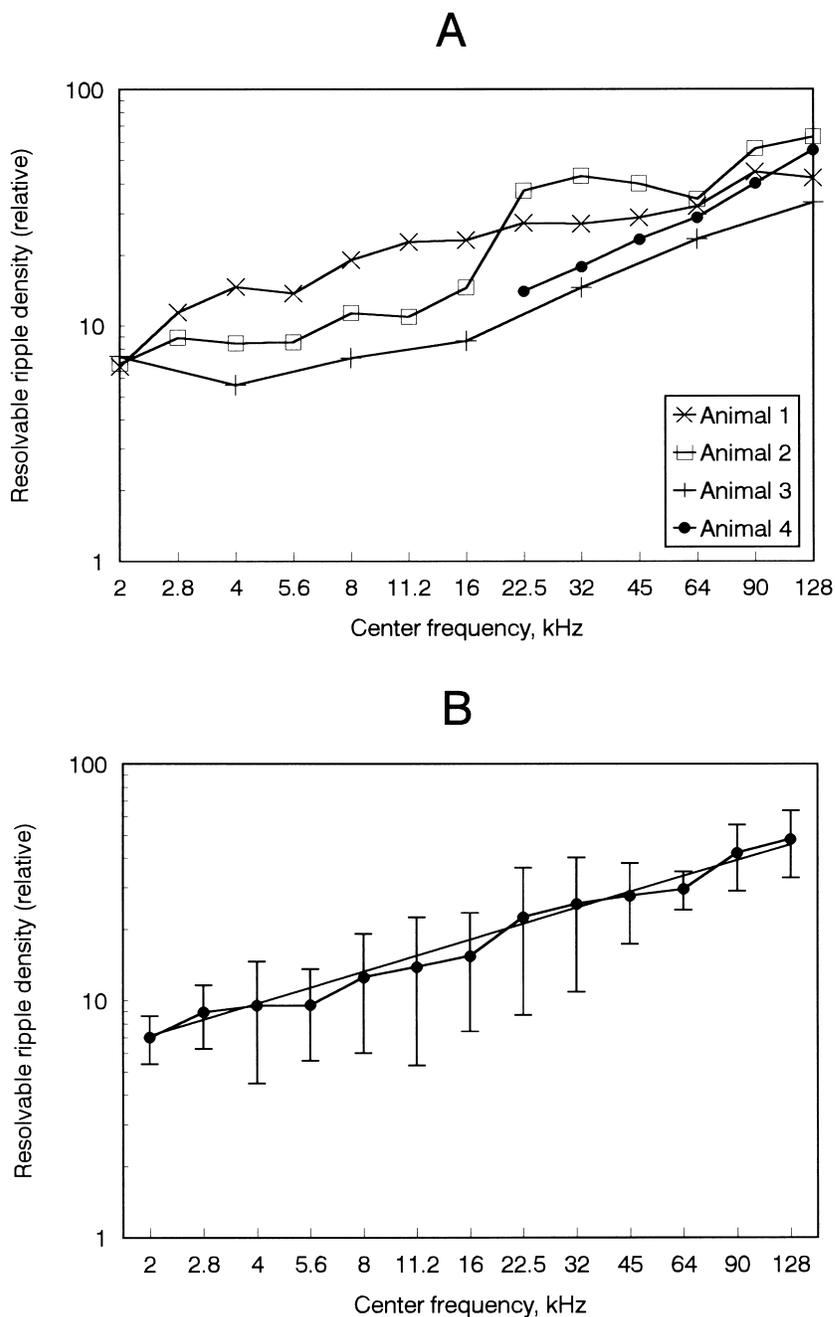
Figure 6. Resolvable ripple density (relative values) *vs* noise center frequency. A: individual data for four animals. B: averaged data, means ± SD. Oblique straight line shows approximation of the averaged data.

Discussion

The data presented herein show the ripple density limits resolvable by the dolphin's auditory system. These limits may be considered as FRP measures at various sound frequencies, from 2–128 kHz.

Table 1. Number of measurement trials and FRP values obtained in four experimental animals

| Centre frequency kHz	Animal No.							
	1 (Male)		2 (Male)		3 (Male)			4 (Female)
	Number of trials	FRP	Number of trials	FRP	Number of trials	FRP	Number of trials	FRP
2	222	6.7	275	6.9	188	7.4		
2.8	186	11.4	296	8.9				
4	232	14.6	259	8.4	120	5.6		
5.6	190	13.7	266	8.5				
8	161	19.0	291	11.3	84	7.3		
11.2	183	22.7	255	10.9				
16	161	23.1	244	14.5	95	8.6		
22.5	146	27.2	214	37.3			209	14.0
32	152	27.0	197	42.9	87	14.5	184	17.8
45	156	28.7	222	40.0			315	23.3
64	294	32.0	240	34.3	115	23.3	244	28.8
90	169	44.6	252	56.0			297	40.0
128	255	42.0	281	62.8	155	33.2	122	55.3

Note: the number of trials is the number of alternative stimulus presentations only.

FRP values obtained for dolphins in this study are much higher than those obtained earlier by the evoked-potential method (Supin & Popov 1988, 1990). Being expressed in its absolute measure (ripples per kHz), the resolvable ripple density found in this study reached the value as high as 3.5/kHz, whereas in evoked-potential studies it was not higher than 0.5/kHz. This difference may be attributed to a limitation of the effective stimulus duration in evoked-potential studies. Evoked potentials are rapid transient phenomena. These responses are evoked by transient acoustic stimuli, e.g. a short sound burst or quick sound change. Even with the use of a slowly rising and falling stimulus, only its short initial part may be effective enough to evoke the response. Transient stimuli feature a broad splatter of their frequency spectra; therefore, they can not have very fine spectrum structure. Perhaps, this is the reason why evoked-potential measurements did not reveal the true FRP in dolphins. Behavioral responses have no such limits of the effective stimulus duration. Therefore it seems that the true FRP of the dolphin's hearing is better reflected by the data of the present study than the earlier ones.

The FRP data make it possible to compute the bandwidth of peripheral bandpass filters of the auditory system and thus compare these data with other estimations of frequency tuning. Let us approximate a filter transfer function by its equivalent rectangular bandwidth (ERB); i.e., assume that the filter has a rectangular bandpass function (function 1 in Fig. 8A, B). Let us assume further that the input signal has rippled spectrum 2, which at ripple-phase reversal is replaced by spectrum 3. The output signals of the filter are proportional to the areas under the curves 2 and 3 within the bandpass 1. If the ripple density is low (A), the two output signals differ to a large extent; thus the phase reversal results in a large response at the filter output. At a higher ripple density (B), the difference between output signals becomes small or lacking; i.e., the filter response is weak or absent. Figure 8C shows the dependence of the filter output on ripple density when the ripple peak is centred on the filter (1) and when the trough is centred on the filter (2). The difference between the two outputs is the highest at zero ripple density, and the two outputs become equal when the ripple density is equal to F/B, where F is the center frequency and B is ERB of the filter. Consequently, the change of the input signal from spectrum 2 to spectrum 3 becomes unrecognizable (i.e., phase reversal becomes undetectable) when the ripple density approaches F/B. More precise computation taking into account an actual filter transfer function showed that this limit may be around $0.7F/B$ (Supin *et al.*, 1994). Hence $B \approx 0.7F/D$, where D is the ripple density. Thus, FRP of 50 indicates filter ERB of 0.014. It is a very sharp frequency tuning.

These data are in satisfactory agreement with frequency tuning estimations as obtained by tone-tone masking measurements in bottlenose dolphins (Supin *et al.*, 1993). These measurements provided frequency tuning estimates in terms of Q_{10} index: this index is a filter center frequency divided by its bandwidth at the -10-dB level. ERB to Q_{10} ratio can be easily calculated for a

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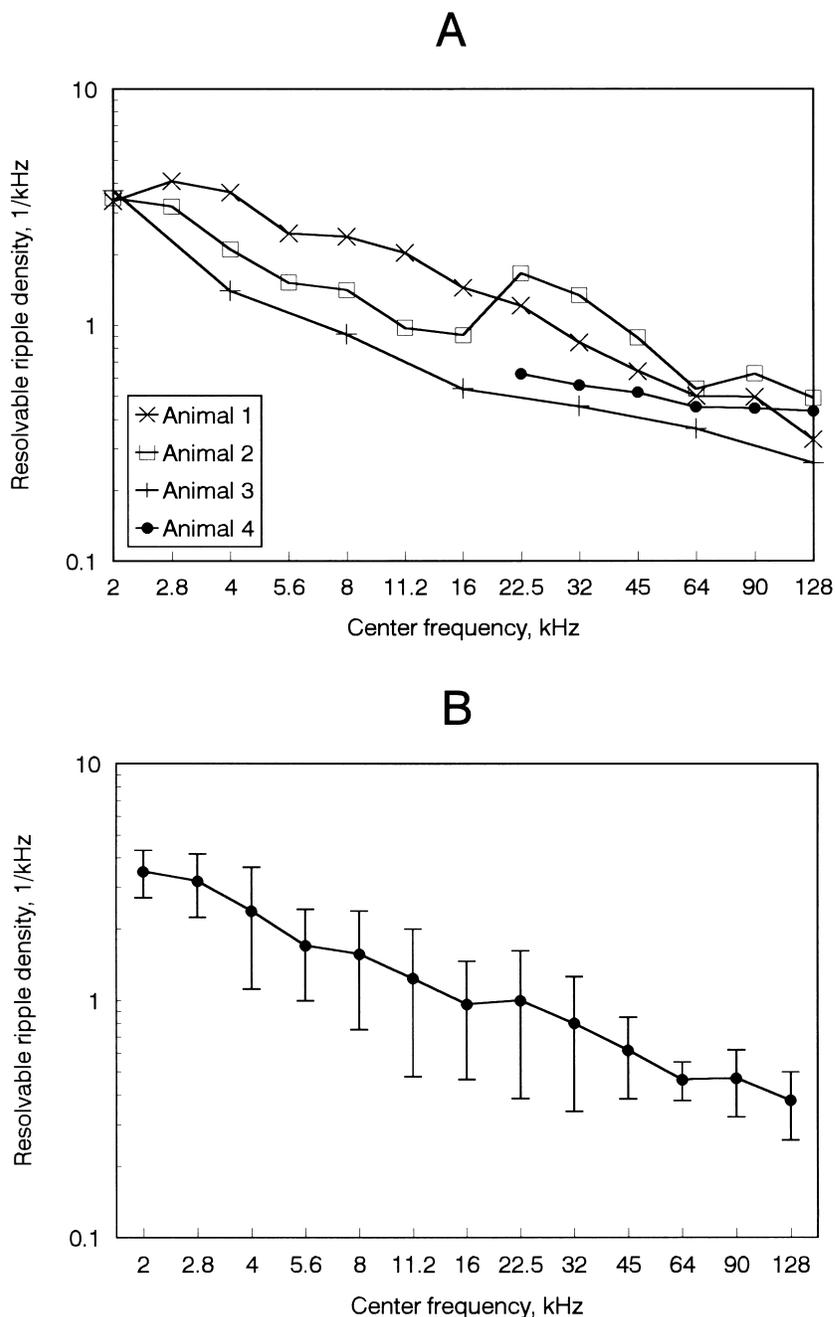
Figure 7. The same data as in Figure 6, ripple density is presented in its absolute measure (ripples/kHz).

given filter shape. In particular, for the rounded exponential function (*roex*) which is widely used to approximate the auditory filter shape, this ratio is: $B \approx 0.5$ F/Q_{10}. At higher frequencies (90–128 kHz), the Q_{10} index was found to be as high as 17–18. Thus, it corresponds to ERB of about 0.03. This ERB estimation differs about twice from that obtained from FRP data (0.014).
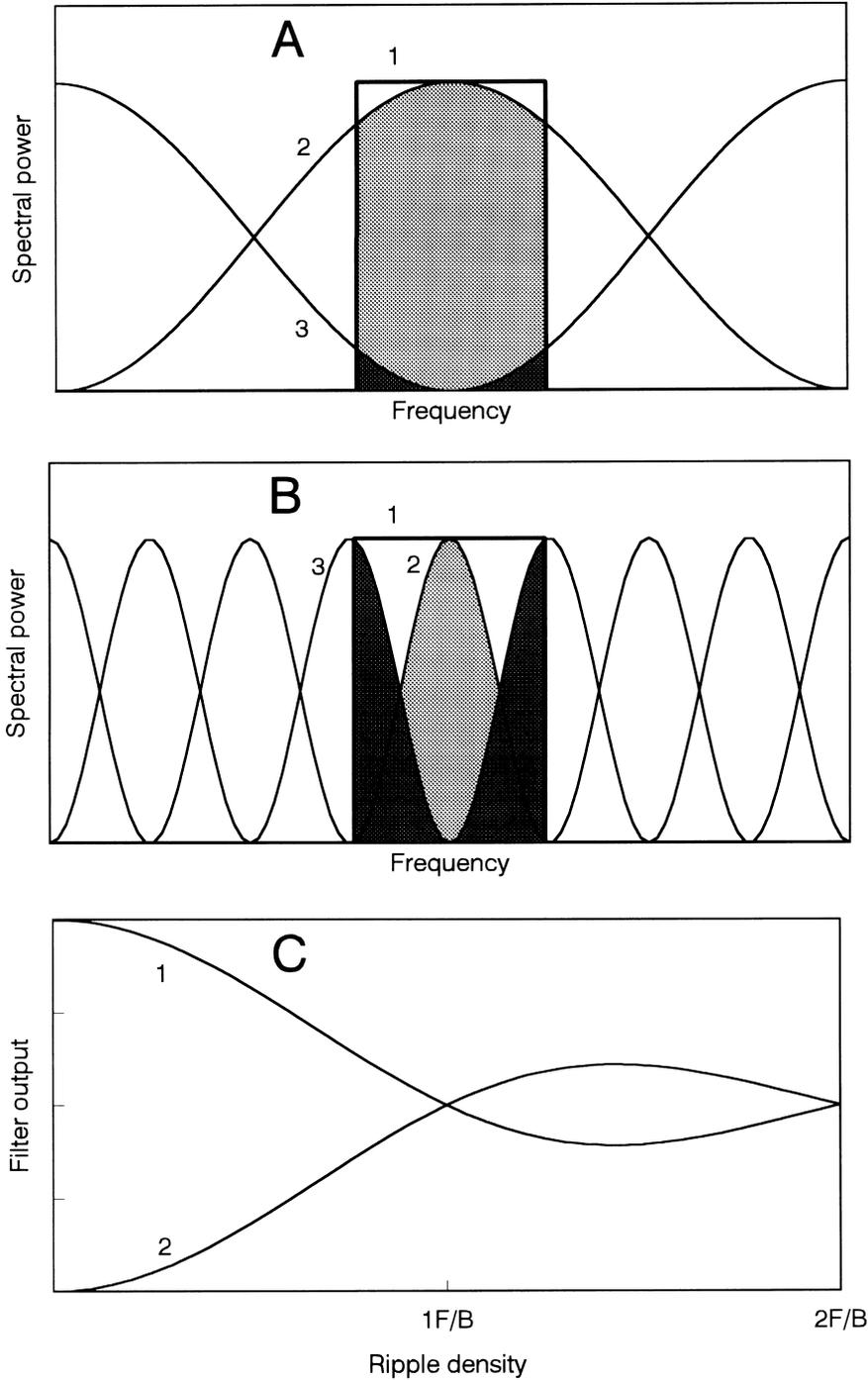
Figure 8. Relationship between bandpass of a frequency filter and FRP. A: filter ERB (1) and spectra with ripple peak (2) and trough (3) centered on the filter. B: the same at higher ripple density. C: dependence of filter outputs on ripple density when ripple peak (1) and trough (2) centered on the filter.

However, the same relation was noticed for humans (Supin *et al.*, 1994): FRP data revealed much better frequency tuning than that obtained by masking methods. Perhaps it is due to non-linear interaction in the auditory system when broad-band signals serve as stimuli.

Another point for discussion is the comparison of data on the dolphin's frequency tuning with those of humans. Comparing these data we have to take into account a significant difference between the hearing frequency ranges in humans and dolphins. However, a comparison of relative FRP values seems to be reasonable even in different frequency ranges. The comparison shows that in the frequency range which is common for both human and dolphin hearing (2–16 kHz), the FRP of dolphins is rather close to that of humans. In dolphins, these values were 6.7–7.4 (mean 7.0) at 2 kHz and 8.6–23.1 (mean 15.4) at 16 kHz. In humans, mean FRP in a high-frequency range (2.8–11.2 kHz) was about 22 units (Supin *et al.*, 1994). This is within the same range that was observed in dolphins. However, at higher frequencies, the dolphin's FRP is several times higher. At 128 kHz, the highest observed FRP was 62.8, the mean value among all the animals was 48.3. Thus, at high frequencies, frequency tuning in dolphins is much more precise than that of humans.

There may be several explanations of the acute frequency tuning of the dolphin's hearing at high frequencies. In particular, it may be associated with interaction between frequency and temporal resolutions of hearing. Indeed, both frequency and temporal resolutions are dictated by bandpasses of peripheral auditory filters: the narrower bandpass the better the frequency tuning and the worse temporal resolution. Thus, there is a contradiction between filter properties required by frequency and temporal resolutions: good frequency tuning requires a narrower bandpass, whereas good temporal resolution requires a wider bandpass. This contradiction, however, becomes less important at high frequencies. Indeed, the filter center frequency F, bandpass B and tuning Q are related as: $Q=F/B$. Thus, at high frequency F, auditory filters can combine high tuning Q with wide bandpass B; wide bandpass renders transfer or rapid sound modulations possible. For example, at 128 kHz frequency, filter tuning of about 50 corresponds to a bandpass of $128/50=2.56$ kHz. Filters of such bandpass are capable of transferring temporal modulations of the equally high rate. Indeed, it was shown that temporal resolution in dolphins is very high at high sound frequencies (Supin & Popov, 1995*a, b*). At a frequency of 2 kHz, filters of the same tuning would only be capable of transferring temporal modulations as low as $2/50=0.04$ kHz; this is a rather poor

temporal resolution. Actual frequency tuning at 2 kHz is about 10 both in humans and in dolphins, which renders transfer of temporal modulations as high as $2/10=0.2$ kHz. Thus, lower frequency tuning at a lower center frequency may be a result of a compromise between frequency and temporal resolutions.

References

Au, W. W. L. & Moore, P. W. B. (1990) Critical ratio and critical band width for the Atlantic bottlenose dolphin. *J. Acoust. Soc. Am.* **88,** 1635-1638.

Johnson, C. S. (1968) Masked tonal thresholds in the bottlenose porpoise. *J. Acoust. Soc. Am.* **44,** 965–967.

Levitt, H (1971) Transformed up-down methods in psychoacoustics. *J. Acoust. Soc. Am.* **49,** 467–477.

Narins, P. M., Evans, E. F., Pick, G. F. & Wilson, J. P. (1979) A combfiltered noise generator for use in auditory neurophysiological and psychophysical experiments. *IEEE Trans. Biomed. Eng.* **BME-26**, 43–47.

Popov, V. V. & Supin, A. Ya. (1984) Measurements of frequency resolving power of human's hearing (in Russian). *Dolk. Akad. Nauk SSSR* (Proc. USSR Acad. Sci.) **278**, 1012–1016.

Popov, V. V. & Supin, A. Ya. (1987) Frequency resolving power of human hearing in various parts of the frequency region (in Russian). *Sensorniye Sistemy* (Sensory Systems) **1**, 191–198.

Supin, A. Ya., Pletenko, M. G. & Tarakanov, M. N. (1992*a*) Frequency resolving power of the dolphin's hearing (in Russian). *Dolk. Akad. Nauk* (Proc. Acad. Sci) **323**, 794–797.

Supin, A. Ya., Pletenko, M. G. & Tarakanov, M. N. (1992*b*) Frequency resolving power of the auditory system in a bottlenose dolphin (*Tursiops truncatus*). In *Marine Mammal Sensory Systems*. (eds. R. A. Kastelein, J. A. Thomas & A. Ya. Supin) pp. 287–293. Plenum Press: New York.

Supin, A. Ya. & Popov, V. V. (1988) Frequency resolving power of the dolphin's hearing (in Russian). *Dolk. Akad. Nauk SSSR* (Proc. USSR Acad. Sci.) **300**, 1013–1016.

Supin, A. Ya. & Popov, V. V. (1990) Frequency-selectivity of the auditory system in the bottlenose dolphin, *Turisiops truncatus*. In *Sensory Abilities of Cetaceans.* (eds. J. A. Thomas & R. A. Kastelein) pp. 385–393. Plenum Press: New York.

Supin, A. Ya. & Popov, V. V. (1995*a*) Frequency tuning and temporal resolution in dolphins. In *Sensory Systems of Aquatic Mammals*. (eds. R. A. Kastelein, J. A. Thomas & P. E. Nachtigall) pp. 95–110. De Spill Publishers, Woerden, The Netherlands.

Supin, A. Ya. & Popov, V. V. (1995*b*) Temporal resolution in the dolphin's auditory system revealed by double-click evoked potential study. *J. Acoust. Soc. Am.* **97**, 2586–2593.

Supin, A. Ya., Popov, V. V. & Klishin, V. O. (1993) ABR frequency tuning curves in dolphins. *J. Comp. Physiol. A.* **173**, 649–656.

Supin, A. Ya., Popov, V. V., Milekhina, O. N. & Tarakanov, M. B. (1994) Frequency resolving power measured by rippled noise. *Hearing Res.* **78**, 31–40.