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# AUDITORY SENSITIVITY OF THE COMMON SEAL IN AIR AND WATER

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## INTRODUCTION

Knowledge of sensitivity of the mammalian ear to underwater sound is at present restricted to evidence from two species: Man, representing a terrestrial mammal with no adaptations for hearing in water, and the Bottlenosed Porpoise, a truly marine mammal. When examining the minimum sound energy required to reach threshold in water in the two species mentioned it is found that the porpoise is as sensitive as any terrestrial mammal in air (Johnson, 1966), while humans show a loss in sensitivity of about 30 db relative to the threshold in air (Ide, 1944; Reysenbach de Haan, 1957; Hamilton, 1957; Wainwright, 1958; Montague and Strickland, 1961). A loss of this magnitude is to be expected when a device like the human ear, adapted for reception of sound in air with a low specific acoustic resistance, has to work in a medium like water with specific acoustic resistance $3.7 \times 10^3$ times as high. For the same reason the sensitivity of the porpoise to airborne sounds presumably is as poor as the one found in submerged humans.

Reduced sensitivity in the foreign medium is hardly a disadvantage of any biological significance for the two species mentioned, but for amphibic mammals like the seals the problem of adaptation of hearing to the medium does not have a straightforward solution. Are seals water-adapted with a corresponding loss of sensitivity in air; are they air-adapted and consequently hard of hearing in water; or have they adopted more complicated solutions? One such would be a compromise between the two solutions already mentioned; another one would be separate tuning of the input characteristics of the ear to each medium in question.

In order to provide a base for discussion of these matters and to learn more about the mammalian underwater hearing, it was decided to measure the auditory sensitivity of a seal in air and in water.

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## METHODS

A male common seal *(Phoca vitulina vitulina)* of 40 kg, presumably 3 or 4 years old, was obtained from the Copenhagen Zoo, but prior to the experiment to be reported it worked on a pitch-discrimination problem in the same pen which is placed in an old harbour, at present closed to all traffic. The pen, 8m by 10m, mean depth 3m, was made of coarse mesh wire; a small raft within made it possible for the seal to rest out of water and dry its pelage.

The procedure for obtaining the audiograms was to produce pure-tone signals of various known sound pressures which the seal was required to indicate as audible or as inaudible by pressing levers.

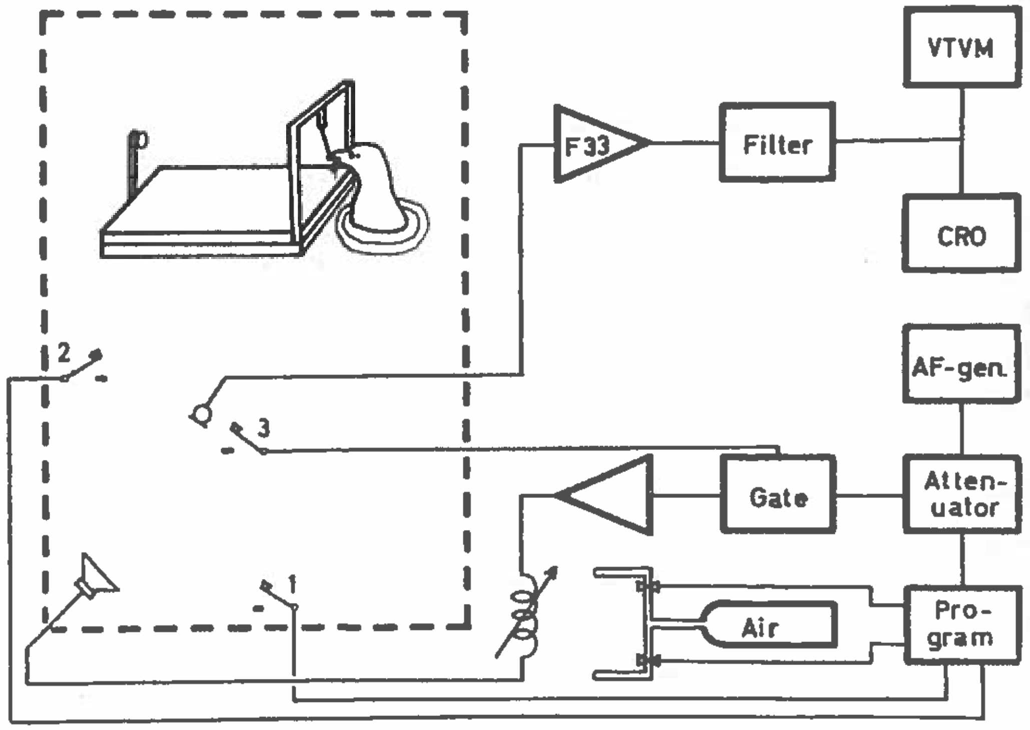

Fig. 1. The experimental set-up. Details in text.

Figure 1 shows the general plan of the set-up. A Wavetek oscillator Model 104 generated a sine wave of the proper frequency; its output was fed to an attenuator from which a series of 8 voltages in 6-db steps, and zero voltage for catch trials, was tapped. A programming unit made of 20 switches and a stepping relay selected the proper voltage level for each trial in turn and applied it to a photoresistor gate. The seal controlled this gate by means of Key 3; as long as the key was pressed the gate was open. Consequently, the seal controlled stimulus onset as well as stimulus duration which appeared to average half a second. The gate determined the stimulus rise- and fall-time, about 80 msec each. From the gate the signal was led via an emitterfollower and a tuning coil to the transmitters where driving voltage was measured by means of a vacuum tube voltmeter.

The transmitters used in water were Dyna Empire TR 127 and TR 129 ($BaTiO_3$). TR 127 was used from 1 to 16 kc/s, and TR 129 from 32 to 180 kc/s. Another pair of TR 127 and TR 129 served as receiving hydrophones. As a control of the calibration supplied with the transducers these were calibrated within 2 db by the reprocity method in the range 5 – 32 kc/s by the Danish Defence Research Board or checked against other transducers calibrated by this method; no serious deviations from manufacturer's calibration sheet were found. The 1, 2, and 180 kc/s measurements are based on extrapolations which for the two low frequencies are rather safe. At 180 kc/s the TR 129 was operated just beyond resonance; for several reasons the value given for the threshold of the seal at this frequency is only indicatory, the uncertainty being unknown.

The receiving hydrophone was placed close to the signal key (3 in Fig. 1) at a distance of 2 yards from the transmitter at a mean depth of 80 cm below the surface; care was taken to align the acoustic axes of the transducers in respect to each other.

In air, an ordinary moving coil, pressure chamber loudspeaker (Peerless MI 25) served as transmitter in the range from 1 to 16 kc/s; at 22.5 kc/s, a TR 129 was substituted. A Melodium Model 88 microphone, calibrated in the measuring position against a Bruel and Kjaer Model 2203 sound level meter, measured the sound level produced. At 22.5 kc/s measurements were based on extrapolation from calibrations made up to 20 kc/s. The loudspeaker and the signal key with the microphone were mounted at each end of and 30 cm above a 1-m long rockwool covered raft. In this way sound reflections from the water surface were avoided, resulting in a close approximation to a free field situation; this was shown by pulse technique.

A Radiometer Model F 33 measuring amplifier with a specified accuracy of ± 0.5 db up to 40 kc/s and calibrated to 200 kc/s by the Danish Defence Research Board, a Dawe Type 1471 filter, a Tektronix Model 502A oscilloscope and a Danbridge Model FR 31 vacuum tube voltmeter were used for the analysis of the signals received by the hydrophones and the microphone. No waveform distortion was traceable when using the oscilloscope as indicator; the tuning of the $BaTiO_3$-transmitter was important to achieve this result.

TABLE I
NOISE, SPECTRUM LEVELS

| Frequency kc/s | Air dB re 2 x $10^{-4}$ $\mu$B | Water dB re 1 $\mu$B |
|---|---|---|
| 1 | 10 | $\leq$-55 |
| 2 | 0 | -62 |
| 4 | -10 | -69 |
| 8 | -25 | -77 |
| 16 | -29 | $\leq$-82 |
| 32 | | -87 |

Noise (Table I) was measured in air with the sound level meter and a Model 1613 octave filter. In water a selective, calibrated amplifier (Danish Defence Research Board model) and a TR 127 hydrophone served this purpose. The self noise of the system did not allow measurements at all frequencies of the acoustic noise in the pen at ordinary, quiet conditions. Assuming the critical bandwidth of the seal to be 1/5 of the center frequency, a calculation showed that no masking effect would be present if the acoustical noise in the pen were below or equal to the values given in Table I. Masking during the actual experiments cannot be entirely excluded over the complete frequency range tested since the noise measurements were not performed simultaneously with the experiments and since the assumed critical bandwidth (based on measurements on humans below 16 kc/s (Feldtkeller and Zwicker, 1956)) could be inapplicable to the seal. Previously stated figures for the noise level at this facility (Møhl, 1964, 1967) are erroneous, representing electrical interference rather than acoustic noise.

A factor introducing variance to the underwater sound level measurements was the interference between the direct and the surface-reflected radiation; reflections from other objects and from the bottom were of minor importance. The standard deviation of the mean of the level measurements from session to session at the same frequency averaged 3 db with the highest values at low frequencies, probably due to the inverse relationship between frequency and the vertical radiation angle of the transmitters. Since both receivers and transmitters were calibrated, the measured level could be checked against expected level; the mean difference from the expected level was -7 db, again with highest values at low frequencies ($\leq$8 kc/s). This discrepancy is also attributed to the deviations from the free field situation. The levels stated in Table II refer to measured level at the position of the head of the seal during listening, except for 180 kc/s where the level given is derived from the extrapolated transmitter-response curve (calibrated to 175 kc/s).

A session consisted of 20 trials, half of which were catch trials, i.e. no sound was emitted. The catch trials were irregularly interspersed with trials with sound levels around and above threshold, the pattern being varied from session to session. The catch trials and the subthreshold trials were by definition indistinguishable by the seal and it was trained to respond to them by pressing Key 2. Audible levels were responded to at Key 1. It was rewarded with small fishes or pieces of fish for all correct responses and was "punished" with a blast of air in its face from nozzles mounted just behind the response keys. The programming unit switched the response keys either to a reward indicator or to solenoid-valves which controlled the air flow to the nozzles. In this way no delay between a wrong response and its consequences occured.

It is relevant to note that the seal obviously took advantage of the fact that it controlled the signal: if the background noise for some reason, e.g. due to a passing aircraft, suddenly increased during a session the seal stopped working until conditions became favourable again. Low level signals and catch trial signals it usually repeated 1 or 2 times before making a response. Even then it sometimes stopped with the nose on the response key without activating it, turned away and made a resting trip in the pen before it switched on the signal again.

## RESULTS

The psychophysical procedure employed was that of constant stimuli. Thresholds and standard deviations have been computed according to the normal graphic process (Guilford, 1954) and listed in Table II. The 6-db

TABLE II

Water

| Frequency in kc/s | Threshold in db re 1 μBar | Standard deviation in db | Number of Catch Trials | % Correct Catch Trials |
|---|---|---|---|---|
| 1 | (−16) | 9 | 67 | 96 |
| 2 | (−25) | 5 | 78 | 96 |
| 4 | −27 | 7 | 63 | 100 |
| 8 | −33 | 4 | 60 | 98 |
| 16 | −36 | 5 | 68 | 94 |
| 32 | −37 | 5 | 76 | 95 |
| 45 | −28 | 3 | 66 | 98 |
| 64 | 6 | 5 | 82 | 96 |
| 90 | 20 | 4 | 50 | 100 |
| 128 | 25 | (4) | 66 | 100 |
| 180 | (33) | 2 | 74 | 97 |

Air

| Frequency in kc/s | Threshold in db re $2 \times 10^{-4}$ μBar | Standard deviation in db | Number of Catch Trials | % Correct Catch Trials |
|---|---|---|---|---|
| 1 | 36 | 4 | 61 | 97 |
| 1.42 | 34 | 5 | 47 | 100 |
| 2 | 19 | 3 | 64 | 94 |
| 2.83 | 22 | 5 | 57 | 98 |
| 4 | 26 | 4 | 50 | 96 |
| 8 | 19 | 4 | 52 | 100 |
| 11.25 | 16 | 5 | 48 | 100 |
| 16 | 26 | 2 | 70 | 100 |
| 22.5 | (58) | 4 | 39 | 87 |

difference used between two successive levels of stimulation was too large to yield a sufficient number of probabilities of detection between 0 and 1 for the exact requirements of the analysis. The standard deviation consequently depends somewhat (at 128 kc/s very much) on the tail assumptions made for the psychometric functions. Measurements were terminated when ten or a few more judgements of each 6-db level in the threshold region had been obtained, giving a mean of 2 db as standard error of the threshold estimates.

Sessions at the various frequencies were presented in an irregular manner in order to spread out possible learning effects over the whole range. Such effects were, however, not traceable in the results, except for a tendency towards a slightly lesser variation in responses for the last part of the experiment. Measurements in water were completed before measurements in air were taken.

The sound level variations in water due to surface interference and the behaviour of the seal in making several judgments of weak or absent sound levels imply that not the mean sound level at the listening position, but a somewhat higher value was the one to which the seal reacted. However, the amount of "sampling" made by the seal was too small to allow for peak values being listened to but very infrequently. In relation to the sound level variation pattern observed, the influence of this effect can be assumed to be within a few db (the noise problem has been dealt with in Methods, above).

The number of catch trials (being approximately equal to the number of trials with sound) and the response to catch trials are also given in Table II in order to show that the seal used a stable and high criterion of detection. This is attributed to the consistent pattern of coding the sessions (50% catch trials, and 15% probable subthreshold trials) together with the combined use of reward and "punishment". Furthermore, the unrestrained situation on the experimental animal may have played a role; the seal was never forced to do anything or to avoid something, and if it was in doubt about the outcome of a response it simply refused to make it.

In order to compare the two audiograms from the seal with each other as well as with audiograms of other animals the thresholds given in Table II have been plotted in db re 1 $\mu W/cm^2$ (Fig. 2). In this dimension, thresholds obtained in the two media are directly comparable (Wainwright, 1958; Wodinsky and Tavolga, 1964).

Ignoring for the present the 2 kc/s region, the general trend is seen to be qualitatively alike for the seal's two audiograms, showing a slope of about 5 db/octave from the lowest frequency explored (1 kc/s) to the area of maximum sensitivity (best frequency). At frequencies above this area the thresholds increase at about 65 db/octave; still higher, between 64 and 90 kc/s, the water-audiogram levels off at a threshold-increase of only 12 db/octave up to 180 kc/s, the highest frequency investigated.

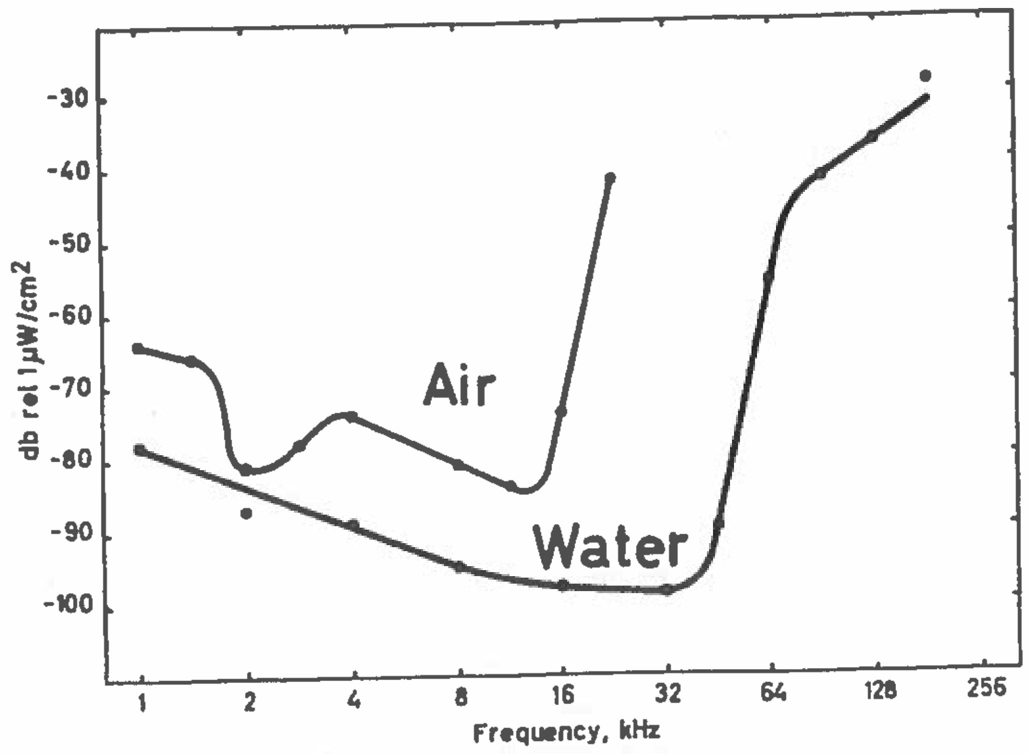

Fig. 2. Sound intensity at the threshold of the seal.

Because of the moderate slope of the audiogram at the highest frequencies, response from the seal at frequencies still higher than 180 kc/s could probably have been obtained with appropriate instrumentation. Thus no upper hearing limit in the conventional meaning of this term (Wever, 1949, p.330) can be established for the seal from the present data; and yet 180 kc/s is, to my knowledge, the highest frequency to which response has been reported from any species in a behavioural, minimum audible field experiment.

The response to high frequencies is consistent with an earlier experiment (Møhl, 1964) where another Common seal reacted to sound of 160 kc/s. The sound intensity in this earlier study was estimated to be -10 db rel. 1 μBar, but this estimate was of a very rough nature and does not justify considerations of the difference observed between the two experimental results. At low frequencies where instrumental difficulties are less severe the two experiments agree reasonably well.

Very conspicuous is a dip in the air-audiogram at 2 kc/s. Extensive examination of the sound field with the sound level meter failed to indicate any possibility of this dip being an instrumental artifact; I believe it is a real property of the seal's hearing in air. Possibly, this dip is caused by quarter-wave resonance in the long and narrow meatus. Wiener and Ross (1946) demonstrated this effect in humans and found a close agreement between the physical length of the meatus and the resonance frequency. In the seal it is difficult to estimate the effective length of the peculiar shaped meatus in the live animal; resin casts of the meatus of two cadaver specimens of young Common Seals revealed a length of 50 to 60 mm. If air temperature in the meatus is taken as 30°C the speed of sound will approximate 350 m/sec and the required length of a tube resonating at 2 kc/s will be 43 mm. This is somewhat shorter than the physical length of the meatus casts, but it is questionable whether a better correspondance can be expected because of the difficulties in estimating the effective length of the meatus as well as the peak frequency of the resonnance dip.

## DISCUSSION

The sensitivity at best frequency in water differs by only 1 db from the ASA standard for sound power based on the human threshold in air; sensitivity in air of this order of magnitude is found in most other mammals. Therefore, it seems reasonable to state that the seal's ear is water-adapted. (The term "Water-adapted" is used in a somewhat inexact manner. Strictly speaking, adaptation should describe the impedance match of the ear to the specific acoustic resistance of the medium. Only relative adaptation to the two media can be inferred from this experiment.)

Except for the 2 kc/s region, the air-audiogram shows a sensitivity reduced by about 15 db relative to the water-audiogram in the range below 12 kc/s. This difference contains the sum of errors in the experiment. However, such errors are unlikely to account for but a minor part of the observed difference, whence the lesser sensitivity for air-borne sound is considered real; it is significant because it is based on an intra-subject comparison.

If the sensitivity of a water-adapted ear to air-borne sound is predicted from the formula relating transmission of sound from one medium with a specific acoustic resistance $Z_1$ to another medium with a specific acoustic resistance $Z_2$:

$$T = \frac{4\,(Z_1 / Z_2)}{(1 + Z_1 / Z_2)^2}$$

where T is the transmitted fraction of the sound energy, the expected difference between thresholds in water and in air comes out as 30 db. As mentioned in the introduction this is the approximate loss of sensitivity found in submerged humans, the only species thus far measured in both media. The seal is doing 15 db better than expected from the formula and can thus be said to have an accomodation power of 15 db which allows for serviceable hearing in air without sacrificing sensitivity in water.

The nature of this accomodation is not known, but the fact that the best frequency in air differs considerably from the one in water is another indication that the seal is using mechanisms of different acoustical specifications for transmission of sound from the respective media to the cochlea (in which case the prediction from the formula given above, of performance in one medium based on knowledge of performance in the other medium, cannot be expected to hold).

The decrease in slope of the audibility function (water) at the highest frequencies has not been reported from other minimum audible field experiments and is in marked contrast with Johnson's (1966) finding in the Bottlenosed Porpoise, the only other marine mammal yet investigated. The porpoise shows in the upper part of its audible range (from 140 – 150 kc/s) a 70-db decrease of sensitivity (corresponding to a slope of 700 db/octave). Rather, the threshold curve for the seal resembles the one for boneconducted tones in the upper sonic- and ultrasonic region in human subjects which show a rise between 10 and 20 kc/s with a slope of approximately 50 db/octave and a slope of 15 db/octave between 20 and 100 kc/s (Corso, 1963). Furthermore, the upper limit of pitch in humans (Pumphrey, 1950) is located in the middle region of the steep part of the boneconduction audibility function; in the seal the pitch limit is at 60 kc/s (Møhl, 1967), again in the middle region of the steep part of the audibility function. This may suggest that the auditory processes in submerged seals and in humans stimulated by boneconduction are alike in certain respects. Obvious quantitative differences are that the seal's sensitivity is about 100 db better and that the steep slope is found at much higher frequencies in the seal than in boneconduction stimulated humans.

Hearing by bone conduction in submerged subjects is known to be a very real possibility from a great many experimental results with humans (Deatherage et al. 1951; Hamilton, 1957; Reysenbach de Haan, 1957; Wainwright, 1958; Montague and Strickland, 1961; Møhl, 1964; Feinstein, 1966). The well developed directional hearing in the seal (Møhl, 1964) and its high auditory sensitivity in water compared to the absent or rudimentary directional hearing and low auditory sensitivity in submerged humans lead to the conclusion that if bone conduction plays a part in underwater hearing in seals as well as in terrestrial mammals (exemplified by humans) this principle seems to be differently applied in the two cases.

## SUMMARY

The audibility function of a Common Seal has been obtained in air from 1 to 22.5 kc/s and in water from 1 to 180 kc/s, using an operant conditioning technique. Best sensitivity in air is at about 12 kc/s (threshold: 11 db SPL); best sensitivity in water is at 32 kc/s (threshold: -37 db re 1 $\mu$Bar), suggesting a water-adapted ear with some accomodation power for hearing in air. The rise in threshold above best frequency in water is 60 db/octave up to 64 kc/s, but only 12 db/octave between 90 and 180 kc/s, the limit of the instruments used. The results are discussed in relation to human auditory thresholds in air and in water, and for bone conduction.

## ACKNOWLEDGMENTS

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# STRIDULATION AND HEARING IN THE TENREC,

## *Hemicentetes semispinosus*[*]

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The streaked tenrec, *Hemicentetes semispinosus,* is a small insectivore found on the island of Madagascar, and has the peculiar ability to produce sounds by stridulation (Gould and Eisenberg, 1966).

The common name is derived from the markings on the back, which consist of seven bands running from front to rear and alternating black and light yellow. The head and back are well protected with sharp spines distributed among the hairs, and of about the same length, 10 to 12 mm, except those forming a ruff over neck and shoulders, which are two or three times as long. When the animal is disturbed the spines are erected, especially those of the ruff, and at the same time the fore part of the body is thrust upward repeatedly in a quick jerky fashion. This "humping" has the effect of thrusting the spines of the ruff into the skin of an enemy that approaches from above. A heavy leather glove is essential to catching and handling the creature, and even with this protection a person often finds himself impaled by a spine or two that has worked itself through the leather.

The stridulating organ consists of a group of about 14 spines that form three rows in the middle of the back toward the rear. These spines are heavier than the others, measuring about 0.3 mm in diameter at their thickest region as compared with 0.1 mm for the other spines. They are moved vigorously by underlying muscles so that their tips rub together, producing high-frequency sounds. The stridulation was readily elicited by any sort of sudden or disturbing stimulus such as a quick movement near

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