

Auditory sensitivity of a California sea lion to airborne sound

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(Received 1 April 1974; revised 15 July 1974)

Estimates of the California sea lion's (*Zalophus californianus*) sound-detection thresholds in air were determined by the conditioned vocalization technique, covering a frequency range of 4–32 kHz. In air, sensitivity beyond 4 kHz gradually decreased to 24 kHz, with a rapid loss in sensitivity beyond 24 kHz. An average loss of 15 dB in the aerial audiogram of *Zalophus*, compared to its underwater counterpart, indicated that, like the harbor and harp seals' ears, the California sea lion's ear is water adapted. In-air hearing sensitivity of *Zalophus* may be best in the frequency range most characteristic of their vocal signalling during the reproductive season.

Subject Classification: 65.50, 65.22; 80.50.

INTRODUCTION

Although pinnipeds feed in water, their reproductive behavior occurs on land. Thus, their hearing sensitivity should be adapted to airborne and waterborne sounds. Vocalizations by seals (family *Phocidae*) and sea lions and fur seals (family *Otariidae*) occur in air and underwater (Schusterman, Balliet, and St. John, 1970). In particular, tremendous reliance by the California sea lion (*Zalophus californianus*) on acoustical signaling in air (Schusterman and Dawson, 1968; Peterson and Bartholomew, 1969) is circumstantial evidence for relatively fair auditory sensitivity in air by this species.

The ear of terrestrial mammals is adapted for hearing in air, where the specific acoustic resistance is nearly 4000 times less than that of water, while the ear of a totally aquatic marine mammal like the porpoise, *Tursiops truncatus*, is adapted for hearing underwater (Johnson, 1966). Presumably, the porpoise is hard of hearing in air, while terrestrial mammals are relatively insensitive to waterborne sounds. In fact, the only terrestrial mammal (man) ever tested underwater shows a 30-dB loss in this medium relative to its aerial sensitivity (Wainwright, 1958). However, amphibious marine mammals, such as the harbor seal (*Phoca vitulina*) and the harp seal (*Pagophilus groenlandicus*), are as sensitive to waterborne sounds as most terrestrial mammals are to airborne sounds (Møhl, 1968a; Terhune and Ronald, 1972). The question of whether the seal's adjustment for in-air hearing is relatively superior to man's adjustment for underwater hearing has been answered affirmatively by Møhl (1968a). Nevertheless, the conventional upper limit of aerial hearing in the harbor seal is approximately $1\frac{1}{2}$ octaves lower than its conventional upper limit of underwater hearing, and in the range of 1 to 16 kHz, there is about a 15-dB superiority in the harbor seal's underwater sensitivity (Møhl, 1968b).

Recent research indicates that the California sea lion's conventional upper limit of hearing is nearly an octave lower and that its overall sensitivity underwater may be somewhat inferior to that of both the harbor and harp seals (Schusterman, Balliet, and Nixon, 1972). The purpose of the present study was to determine the audibility of the California sea lion in air relative to its underwater audibility and relative to the harbor

and harp seals' audibilities in air.

I. METHOD

A five- to six-year-old male *Zalophus* (Sam) was trained to hold its head underwater in a fixed position and to emit a burst of clicks when it heard a pure tone preceded by a warning light, and to remain silent if it did not hear a tone following the warning light. Conditioned vocalizations proved an extremely reliable technique in enabling investigators to obtain an underwater audiogram from sea lion Sam, covering a frequency range of 250 to 64 000 Hz (Schusterman *et al.*, 1972). Thus, this sea lion was extremely well trained for the present test.

Essentially, the same procedure previously used to determine auditory thresholds underwater in *Zalophus* (Schusterman *et al.*, 1972) was also used to obtain the auditory thresholds of *Zalophus* in air, the principal difference being that the tones were projected in air and the water level of the tank was lowered so that the animal's whole head (including the meatal orifice) remained in air while the neck and rest of its body remained in water. Vocalizations made by sea lions with their mouths closed and out of water may still be projected underwater by the larynx and picked up by a hydrophone (Schusterman and Balliet, 1969).

Thresholds in air were obtained in the evening in an outdoor 4.6-m × 9.1-m × 1.8-m oval-shaped redwood tank. The loudspeaker used was a JBL tweeter, model 75, with a radiating diameter of 7.9 cm and a power capacity of 20 W above 2500 Hz. The speaker was mounted on the rim of the top of the tank directly facing the headrest position in the tank. The sea lion's head was positioned approximately 1.1 m from the speaker, 2 m from the sides of the tank, and 0.8 m from the top of the tank (see Fig. 1 in Schusterman *et al.*, 1972). Acoustical signals were gated using a Grason-Stadler 829E electronic switch with a rise-decay time of 100 msec. Gate duration was controlled by an Iconix preset counter and logic system. Pure-tone signals were generated by a GR 1312 decade oscillator. Signal level was controlled by two Daven 2-dB step attenuators in series, which lead directly to the loudspeaker. The sound field (at the headrest position) was measured at each test session with a Brüel & Kjaer 2203 sound-level meter containing a type 4131 condenser and type 1613

octave filter. Voltage across the speaker was calibrated before each test session and was continuously monitored using an H-P 132 A dual-beam oscilloscope. Unfortunately, the ambient noise levels at 1 and 2 kHz were considered high enough so that some masking effects at these frequencies were likely. Therefore, valid and reliable auditory thresholds in air were not obtained at frequencies below 4 kHz.

A trial consisted of either the presentation of a light that was turned on for 2.5 sec or the presentation of a light with a tone turned on during the last 0.5 sec of the 2.5-sec light duration. Half the trials were light-only trials. The experimenter began a trial only after the animal's head was in position. A "correct" response was defined as either emitting a burst of clicks within 1.5 sec of tone onset or remaining silent for 3.5 sec after light presentation, and it was reinforced with a small piece of herring.

A modified method of limits similar to the "staircase method" was used to obtain all sound-detection thresholds, defined as the interpolated decibel values at which the sea lion responded correctly 75% of the time at each of the frequencies tested, ranging from 4 to 32 kHz. During each threshold determination, the intensity of the tone was decreased by 4 dB if the sea lion made seven or more correct responses in 10 successive trials. If this criterion was not attained, the intensity of the tone was increased by 12 dB. This latter procedure ensured a stable conditioned vocalization. Thus, the strength of the acoustic signal was changed every 10 trials. Usually, the animal received 75 blank trials and 75 signal trials. Thresholds were obtained this way at least twice for each frequency and the variability between these measurements never exceeded ± 1 dB. The sea lion's performance was extremely stable and there was no reason to believe that the animal's sensitivity would have increased with increased practice.

II. RESULTS AND DISCUSSION

The most important characteristics of the aerial audiogram (Fig. 1) of this sea lion are (a) a 5-dB loss in sensitivity from 4 to 16 kHz, and (b) a steeper rise in

the curve beyond 24 kHz, with a loss in sensitivity of 20 dB/octave, and an even more accentuated threshold rise above 28 kHz, with sensitivity being lost at the rate of 60 dB/octave, leading to a projected effective upper hearing limit of approximately 36 kHz.

While the present study was in progress, an audiogram on two specimens of *Zalophus* was generated by "eyeballing" the oscilloscope image of evoked potentials from the inferior colliculus following pure-tone stimulation in air (Bullock, Ridgway, and Suga, 1971). The results of this electrophysiological study were remarkably similar to the results of the present behavioral study in that *Zalophus* failed to show evoked responses above 35 kHz; best frequency was between 4–6 kHz and thresholds with this method were between 25 and 40 dB SPL. Moreover, these investigators found that, for one of their sea lions, the decrease in sensitivity from 4 to 0.5 kHz was about 5 dB/octave.

One of the reasons for conducting the present experiment was to compare the aerial audiogram of the California sea lion with its underwater counterpart (Schusterman *et al.*, 1972) in order to determine whether its hearing sensitivity is principally water adapted, as previously suggested. Taking into account differences in intensity units based upon the different acoustic impedances of water and air, Table I clearly shows that an otariid pinniped, like *Zalophus*, manifests a substantial hearing loss in air, similar to that shown by phocid pinnipeds, and like the phocid ear, the otariid ear must be adapted for hearing underwater and is perhaps susceptible to some measure of acoustical-impedance mismatch in air. Moreover, in contrast to many terrestrial mammals, pinnipeds, having a long narrow auditory meatus and either totally lacking or having a considerably reduced pinna, are likely to have a reduced sensitivity to airborne sounds in a relatively free-field situation (Repenning, 1972).

Although methodological differences and small samples make it unsafe to draw any definite conclusions about the absolute sound-detection thresholds in air for different pinniped species, inspection of Fig. 1 and Table I reveals several interesting comparative aspects

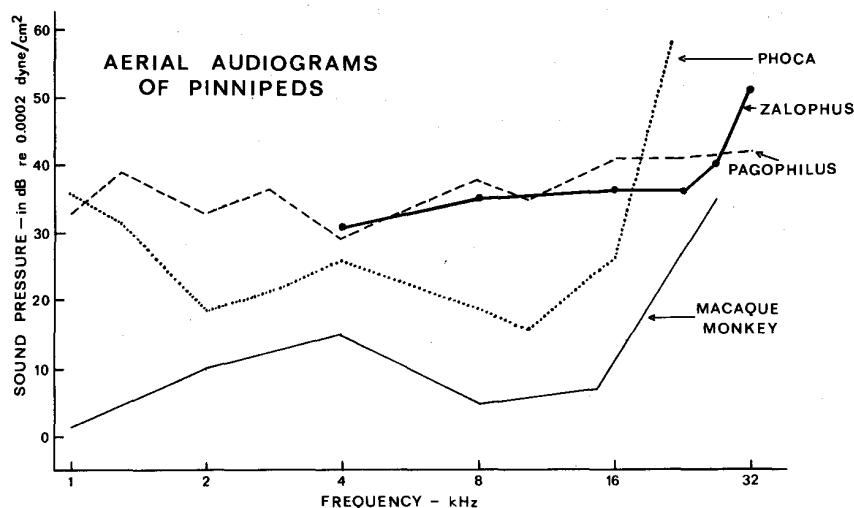


FIG. 1. Comparison of aerial audiograms of three species of pinnipeds, including *Zalophus* (this study), *Phoca* (Møhl, 1968a), and *Pagophilus* (Terhune and Ronald, 1971). Audiogram of macaque monkey (Stebbins, Green, and Miller, 1966) shown for reference to hearing in old-world primates.

TABLE I. Comparison of hearing losses in air relative to underwater auditory thresholds in *Zalophus* (Schusterman *et al.*, 1972), *Pagophilus* (Terhune and Ronald, 1972) and *Phoca v.* (Møhl, 1968).

Frequency (kHz)	Hearing loss (in dB)		
	<i>Zalophus</i>	<i>Pagophilus</i>	<i>Phoca v.</i>
1	...	19	16
2	...	29	8
4	9	18	17
8	18	33	16
11	...	30	...
16	22	34	26
23	...	39	...
24	15
28	18
32	14	32	...

in terms of the shapes of the audibility functions of seals and sea lions. It appears that both *Zalophus* and *Pagophilus* are somewhat sensitive to sounds in the frequency range of approximately 20–30 kHz, whereas *Phoca v.* is relatively insensitive to frequencies above 20 kHz. However, in the middle range of hearing (1–8 kHz), *Zalophus*, like *Phoca v.* and *Pagophilus*, shows poorer hearing to airborne sound than to waterborne sound (15–25 dB). Between 2 and 16 kHz, all three pinniped species show aerial sound-detection thresholds to be 10–30 dB higher than macaque monkeys (Stebbins, Green, and Miller, 1966).

Møhl (1968b) and others have noted that, due to the acoustic-impedance mismatch, the sensitivity of a water-adapted ear (e.g., seals and sea lions) to airborne sounds, or the sensitivity of an air-adapted ear (e.g., monkeys, apes, and men) to waterborne sounds, should produce an expected transmission loss of 30 dB. Indeed, at 2 kHz, Wainwright (1958) found about a 37-dB hearing loss when humans were tested in water. At 4 kHz, the harbor seal, harp seal, and the California sea lion are considerably more sensitive to airborne sounds than are humans to waterborne sounds. This has led Møhl (1968b) to suggest that, unlike strictly terrestrial mammals (e.g., man) or strictly aquatic mammals (e.g., porpoises), the amphibious pinnipeds may have separate inputs for hearing underwater and in air. Support for this model has come from Møhl and Ronald (1972). They blocked various sound-transmission routes both in air and underwater, and by recording cochlear microphonic potentials in harp seals, they found that, whereas the meatal orifice played a significant role for aerial hearing, reception of waterborne sounds was best by the skin area just below the meatal orifice and running adjacent to the ascending part of the meatal tube. From the standpoint that underwater the external auditory meatus plays a limited role, if any, in the process of sound conduction in the ears of seals, the results of Møhl and Ronald (1972) are similar to recent results showing that sound reception in the submerged porpoise is initiated in tissue in the region of the head (McCormick, Wever, Palin, and Ridgway, 1970).

An important aspect of the present results is related

to vocal signaling in the otariid pinnipeds. Repetitive barks of *Zalophus* bulls emitted in air are similar to those emitted underwater, and the interindividual variation in both media suggests recognition of territorial neighbors (Schusterman and Balliet, 1969). At a distance of approximately 2 m, the SPL of an adult male California sea lion bark at 1 kHz is 103 dB *re* 0.0002/cm² and 90 dB at 0.5 and 2 kHz (Schusterman, in press). There are similarities in structure between the barks of *Zalophus* (Peterson and Bartholomew, 1969), the Australian sea lion, *Neophoca cinera* (Stirling, 1972), and those of several southern fur seals (*Arctocephalus gazella*, *A. pusillus doriferus*, and *A. forsteri*), as reported by Stirling and Warneke (1971). For all species, the spectral characteristics of the barks range from approximately 200 Hz to 8 kHz.

In *Zalophus*, the female's pup-attraction call has its greatest energy components between 500 Hz and 4 kHz. The mother-response call by the pup has an acoustic structure very much like that of the pup-attraction call (Peterson and Bartholomew, 1969). Mother-response calls and pup-attraction calls of *Neophoca cinera*, *A. p. doriferus*, *A. forsteri*, and *A. gazella* also have their greatest energy components between 500 Hz and 4–8 kHz, depending on the species (Stirling, 1972; Stirling and Warneke, 1971). The female calls, in particular, have generally been described by all field investigators as loud and intensive with a good deal of interindividual variation.

Spacing among breeding males and pup viability strongly depend on the vocal-auditory communication channel, which is extremely noisy due to wind, surf, and population density. Therefore, it is not surprising to find that not only are the airborne vocalizations of *Zalophus* (and probably other otariids as well) loud and repetitive during the reproductive season, but that a good portion of their vocal spectral energy (especially the harmonics) lies in the range of their best aerial hearing.

ACKNOWLEDGMENTS

This research was supported by ONR contract NO0014-72-C-0186. The author thanks R. F. Balliet and B. Johnson for their help in conducting the experiment and Dr. Earl Shubert for his advice and for the loan of some equipment.

- Bullock, T. H., Ridgway, S. H., and Suga, N. (1971). "Acoustically evoked potentials in midbrain structures in sea lions. (*Pinnipedia*)," *Z. Verh. Physiol.* 74, 372–387.
- Johnson, C. S. (1966). "Auditory thresholds of the bottlenosed porpoise (*Tursiops truncatus*)," U. S. Naval Ord. Test Station Tech. Pub. 4178, 1–28.
- McCormick, J. G., Wever, E. G., and Ridgway, S. H. (1970). "Sound conduction in the dolphin ear," *J. Acoust. Soc. Am.* 48, 1418–1428.
- Møhl, B. (1968a). "Auditory sensitivity of the common seal in air and water," *J. Aud. Res.* 8, 27–30.
- Møhl, B. (1968b). "Hearing in seals," in *The Behavior and Physiology of Pinnipeds*, R. J. Harrison, R. C. Hubbard, R. S. Peterson, C. E. Rice, and R. J. Schusterman, Eds. (Appleton-Century-Crofts, New York), pp. 172–195.

- Møhl, B., and Ronald, K. (in press). "The harp seal, *Pagophilus groenlandicus* (Erxleben, 1777). XVII. Peripheral auditory system," in *The Biology of the Seal*, K. Ronald and A. Mansfield, Eds. (ICES, Copenhagen).
- Peterson, R. S., and Bartholomew, G. A. (1969). "Airborne vocal communication in the California sea lion, *Zalophus californianus*," *Animal Behav.* **17**, 17-24.
- Repenning, C. A. (1972). "Underwater hearing in seals: functional morphology," in *Functional Anatomy of Marine Mammals*, R. J. Harrison, Ed. (Academic, London), Vol. 1, pp. 307-331.
- Schusterman, R. J. (in press). "Pinniped sensory perception," in *The Biology of the Seal*, K. Ronald and A. Mansfield, Eds. (ICES, Copenhagen).
- Schusterman R. J., and Balliet, R. F. (1969). "Underwater barking by male sea lions (*Zalophus californianus*)," *Nature* **222**, 1179-1181.
- Schusterman, R. J., and Dawson, R. G. (1968). "Barking, dominance and territoriality in male sea lions," *Science* **160**, 434-436.
- Schusterman, R. J., Balliet, R. F., and St. John, S. (1970). "Vocal displays under water by the gray seal, harbor seal and Steller sea lion," *Psychonomic Sci.* **18**, 303-305.
- Schusterman, R. J., Balliet, R. F., and Nixon, J. (1972). "Underwater audiogram of the California sea lion by the conditioned vocalization technique," *J. Exp. Anal. Behav.* **17**, 339-350.
- Stebbins, W. C., Green, S., and Miller, F. L. (1966). "Auditory sensitivity of the monkey," *Science* **153**, 1646-1647.
- Stirling, I. (1971). "Studies on the behavior of the South Australian fur seal, *Arctocephalus forsteri* (Lesson) I. Annual cycle, postures and calls, and adult males during the breeding season," *Aust. J. Zool.* **19**, 243-266.
- Stirling, I., and Warneke, R. M. (1971). "Implications of a comparison of the airborne vocalizations and some aspects of the behavior of the two Australian fur seals, *Arctocephalus SPP.*, on the evolution and present taxonomy of the genus," *Aust. J. Zool.* **19**, 227-241.
- Terhune, J. M., and Ronald, K. (1971). "The harp seal, *Pagophilus groenlandicus* (Erxleben, 1777). X. The air audiogram," *Can. J. Zool.* **49**, 385-390.
- Terhune, J. M., and Ronald, K. (1972). "The harp seal, *Pagophilus groenlandicus* (Erxleben, 1777). III. The underwater audiogram," *Can. J. Zool.* **50**, 565-569.
- Wainwright, W. N. (1958). "Comparison of hearing thresholds in air and water," *J. Acoust. Soc. Am.* **30**, 1025-1029.