

Rapp. P.-v. Réun. Cons. int. Explor. Mer, 169: 165-168. 1975.

PINNIPED SENSORY PERCEPTION

R. J. SCHUSTERMAN

Departments of Biology and Psychology, California State University at Hayward, Hayward, California 94542, U.S.A.

INTRODUCTION

In a very real sense, an animal's environment is defined and ultimately limited by the properties of its sensory systems. An animal cannot orient toward sounds it cannot hear or configurations it cannot see, nor can it react differentially to sound-pressure waves or light quanta which are perceived to be the same. In mammals, the capacity to obtain and integrate environmental information at some distance and to behave effectively on the basis of such information increase the likelihood of species survival and reproduction.

Light and sound propagation in the atmosphere and in the hydrosphere differ to such extent that special mammalian sensory adaptations are necessary for efficient operation in both media. Contemporary pinniped species combine two characteristics which occur together in no other mammals. They reproduce on land or pack ice, and they are third-level consumers in the marine food chain. Thus, the visual and auditory sensory systems of some pinniped forms must be adapted to both a marine and a terrestrial environment. Each pinniped species has evolved in a particular ecological niche, within which it feeds, reproduces and avoids its enemies. The degree to which the interaction of several sensory systems of high acuity are available to members of a species greatly influences all of these activities. Furthermore, in terms of size and complexity of neural elements, it is likely that in pinnipeds sensory exploration can interact with past experience to open up new possibilities to an individual, such as eating a new type of food, abandoning an old rookery, or colonizing a new beach.

In order to acquire a more complete biological understanding of the environmental features affecting the migration, feeding and reproduction of pinnipeds, one must carefully determine and, whenever possible, quantify the relationship between those features of the marine environment either social or nonsocial, which serve as cues for pinniped navigation and orientation and those which do not. Detection, localization and recognition of landmarks, obstacles, the ocean bottom,

predators, prey and conspecifics are of critical importance for the continuing survival of all modern pinniped species.

There are several descriptions of social and non-social orientation-skills and navigation-skills performed by pinniped species representing the subfamilies Otariinae, Arctocephalinae, Phocinae and Monachinae. Male *Zalophus* migrate from as far north as British Columbia to breed on the southern California Channel Islands where they depend on vocal and postural displays for acquiring and maintaining territories necessary for reproductive success (Bartholomew, 1967). *Callorhinus* migrate several thousand miles, with adult males occupying the same territorial location for at least three successive reproductive seasons (Peterson, 1968). Fur seal mothers leave their pups to feed at sea for two weeks or longer, eventually returning to specific localities on the rookeries where they meet and feed only their own pups (Bartholomew, 1959; Rand, 1967). *Halichoerus* establish rookeries on rocky coasts and sandy coves, sometimes moving rather extensively inland at night, with bulls using natural markings in the terrain as territorial boundary demarcations (Cameron, 1967). Perhaps the most spectacular orientation-skills are manifested by Weddell seals, which explore, feed, socialize and generally find their way around under the Antarctic ice, diving to depths as great as 600 m for as long as one hour (Kooyman, 1966; Ray, 1966). In these examples of spatial orientation-skills (be they navigational or socially communicative) detection, localization and recognition of cues are required both above and below the water surface.

Feeding behavior of pinnipeds is an exclusively aquatic phenomenon and probably for that reason is very poorly understood. However, we do know that several species feed in large groups or singly, depending on the availability of prey, and that feeding may be a nocturnal or diurnal activity. In general, pinnipeds take shallow-water, coastal food organisms.

On the basis of these brief descriptions of the orientational and navigational abilities of pinnipeds,

one might expect that no single set of internal or external receptor mechanisms would be relied upon as the exclusive or even as the primary basis of pinniped sensory orientation. This is in contrast to the way we think of dogs tracking on the basis of olfactory cues, or the guidance system of predator birds as being visual, or the guidance system of some whales and some bats as being acoustical. Nor might one expect any single sensory system to have become so totally adapted for high resolution in water as to show little or no resolving power in air. Rather, the three principal distance receptors—visual, auditory, and olfactory—would each be expected to play important roles both in air and under water. Hearing may possibly play the most important role, since sound is the most efficient form of energy for long-range orientation. On the other hand, the eye, by nature of its large, spatially ordered, point-to-point representation of the environment, often yields instantaneous and panoramic information at considerable distances. Thus, it is likely that pinniped forms utilize a variety of exteroceptive, proprioceptive and interoceptive cues in a rather complex fashion, depending upon the particular orientation task and the “noise” levels which prevail at the time the task is being performed.

One of the initial steps in finding out about the sensory basis of an animal's orientation-skills, either feeding or social, and navigation-skills is to determine the differential and absolute sensitivity of an animal by means of experimental procedures using a variety of psychophysical methods. We have recently embarked on such a research program in an attempt to assess the visual and auditory acuity of pinnipeds both in air and under water.

RESULTS AND DISCUSSION

Vision

Although we still know very little about the migratory, feeding, and reproductive habits of cetaceans, it is clear that feeding and social orientation as well as the navigational skills of some odontocete whales depend, to a large degree, on acoustical information (Norris, 1969). On the other hand, several pinnipeds are thought to rely on acoustical cues for social orientation on land and visual cues for feeding orientation at sea.

Some pinnipeds are nocturnal and opportunistic feeders and have been known to approach their prey from below, thus silhouetting them against the ambient surface light above (Hobson, 1966). Our recent experimental results on two otariids (*Zalophus californianus* and *Eumetopius jubatus*) and one phocid (*Phoca vitulina*) indicate the potential significance, as

well as the limitations, of the visual channel in these pinnipeds for feeding and social orientation and migration (Schusterman and Balliet, 1970a, 1970b).

In previous experiments, we have shown that when the ambient light was approximately 10^2 mL, the visual angles at behavioral thresholds under water for *Zalophus*, *Eumetopius* and *Phoca* were between 5 and 8 min of arc. At approximately the same level of ambient light, the visual acuity of *Zalophus* was the same in air as it was under water. These results tended to support the notion that in the relatively bright light of 10^2 mL, the closing down of the pupil to a very narrow vertical slit eliminated the natural astigmatism of the sea lion's eye. As a result, the level of aerial visual acuity under clear daylight conditions is quite sufficient for resolving gross shore features at distances of up to 32 km, and the level of underwater visual acuity under clear water conditions is quite suitable for detecting and differentiating between a variety of food prey at some distance. However, as previously mentioned, several species are nocturnal feeders and the question of their visual orientation at night is critical. Furthermore, it seemed likely that if light intensity was decreased, the pupil should widen, resulting in poorer visual acuity in air than under water owing to corneal astigmatism of the sea lion eye. Experimental results with *Zalophus* showed that decreasing luminance down to 10^{-4} mL had little effect on underwater visual acuity while having a most profound deleterious consequence on aerial visual acuity (Schusterman and Balliet, 1971; Schusterman, 1972). For example, at this luminance *Zalophus* was capable of resolving target-gratings subtending a visual angle of 13 min of arc under water compared to a figure of 36 min of arc in air. Thus, *Zalophus* has a remarkable visual capability for resolving detail under water in extremely darkened conditions. On the other hand, *Zalophus* aerial vision at night seems quite unsuitable for resolving even gross shoreline features at extremely close distances. Even when luminance was at 3 mL, the highest light intensity used in the experiment, the underwater visual acuity was significantly superior to the aerial acuity. When only a small quantity of light is available, one would predict from these results that: a) *Zalophus* will visually orient to food sources; b) *Zalophus* either will not show migratory movements or else will not depend upon shore features for navigational cues; c) *Zalophus* will depend more upon vocal, olfactory and tactual signalling rather than visual signalling in reproductive behaviour [the latter has been observed in the field (Peterson and Bartholomew, 1969)].

Combining our present knowledge of pinniped vision under water with a recent review by Clark (1970) on measurements of the intensity and spectral

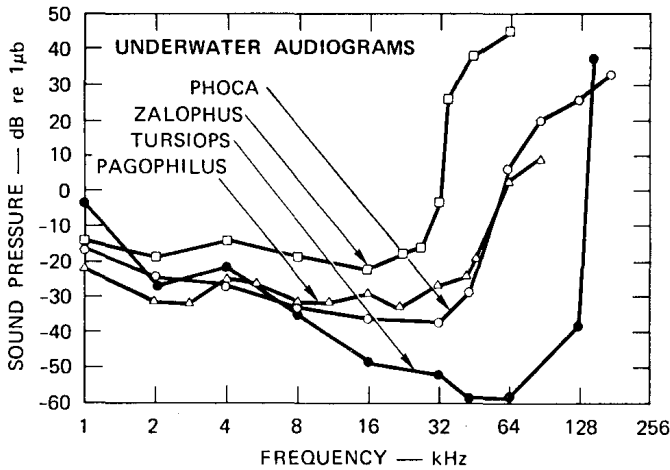


Figure 131. Comparison of underwater audiograms of *Zalophus* (Schusterman et al. 1972), *Phoca v.* (Møhl, 1968), *Pagophilus* (Terhune and Ronald, 1972) and *Tursiops truncatus* (Johnson, 1966).

distribution of natural light as it enters the sea, penetrates to various depths and is back-scattered upward, it must be concluded that, at least under relatively clear coastal-water conditions, some pinnipeds can recognize small surface nekton, such as herring, sardines and squid even on cloudy nights at depths of about 200 m, if they are effectively silhouetted. Under ideal conditions in the open ocean, small objects which were effectively silhouetted could be readily detected by pinnipeds at depths slightly greater than 1000 m. Furthermore, although little is known about the spectral sensitivity of seals (Lavigne and Ronald, this volume), it should be noted that in the temperate and polar seas and in coastal waters where pinnipeds are most likely to be found, the spectral region of greatest intensity moves toward the longer wavelengths, ordinarily lying between 500 and 560 nm (Clarke, 1970).

Hearing

Two phocids, *Phoca* and *Pagophilus* (Møhl, 1968; Terhune and Ronald, 1972) and one otariid, *Zalophus* (Schusterman et al., 1972), have been studied in enough detail to know their sound detection thresholds over a wide range of relatively pure-tone frequencies. Comparison of the auditory perception of these three pinnipeds with a delphinid, *Tursiops truncatus* (Johnson, 1966) reveals that the former are more sensitive to low-frequency sounds below 4 kHz while the latter is absolutely more sensitive to a wider frequency range, especially above 32 kHz (see Fig. 131). The overall significance of these results in terms of the feeding orientation of some pinnipeds and delphinids is clear. Since high-frequency sounds allow for greater resolution from a reflected echo, and since both *Tursiops* and *Zalophus* frequently prey on marine animals of

the same size, *Tursiops* is much more likely to depend upon an active biological sonar system during feeding orientation than is *Zalophus* (see Schusterman et al., 1972 for further details). However, when the turbidity of the water is great, *Zalophus* may orient to the low-frequency sounds emitted by many shallow-water vertebrates and invertebrates, or not eat at all. Thus, information about the sensory perception of marine mammals, when combined with information about marine environmental conditions, may allow one to predict what kind of food sources they are likely to exploit. Such predictions may be confirmed or negated by field observations, including stomach-content analysis and fecal analysis.

Physiological evidence that does not support the echolocation hypothesis in *Zalophus* and perhaps *Phoca* comes from recent work by Bullock, Ridgway and Suga (unpublished 1971) in which they obtained acoustically evoked potentials in the inferior colliculus and the lateral lemniscus from these two pinnipeds. Briefly, they found that, although the midbrain centers gave good evoked potentials to sounds which were slow rising, of long duration and low frequency (4–6 kHz), the auditory midbrain system of these pinnipeds, as compared to the porpoise, was not as sensitive to steepness of rise of a sound, or to frequencies above 30 kHz or to frequency modulation. Nor was the evoked response of pinnipeds specialized for extremely brief sounds and rapid recovery as it is in the porpoise.

There are now published in-air audiograms for both *Phoca* (Møhl, 1968) and *Pagophilus* (Terhune and Ronald, 1971). Table 16 compares the aerial data of of these two phocids with some unpublished data of mine on aerial hearing of *Zalophus*. The best sensitiv-

Table 16. Comparison of aerial audiograms and hearing losses relative to underwater audiograms of *Zalophus* (Schusterman, unpublished data), *Pagophilus* (Terhune and Ronald, 1971) and *Phoca* (Møhl, 1968). Thresholds and hearing losses are expressed in dB re 0.0002 dynes/cm²

Fre- quency kHz	<i>Zalophus</i>		<i>Pagophilus</i>		<i>Phoca</i>	
	Thres- hold	Hearing loss	Thres- hold	Hearing loss	Thres- hold	Hearing loss
1.....	-	-	33	19	36	16
2.....	-	-	33	29	19	8
4.....	31	9	29	18	26	17
8.....	35	18	38	33	19	16
11.....	-	-	35	30	16	-
16.....	36	22	41	34	26	26
23.....	-	-	41	39	58	-
24.....	36	15	-	-	-	-
28.....	40	18	-	-	-	-
32.....	51	14	42	32	-	-

ity for *Phoca* is at 11 kHz and for *Pagophilus* and *Zalophus* the best sensitivity is at 4 kHz. Several other interesting comparisons emerge concerning the hearing of seals and sea lions in air. First, both *Pagophilus* and *Zalophus* are fairly sensitive to sounds above 20 kHz, whereas *Phoca* is relatively insensitive to such high-frequency tones. Second, *Pagophilus* shows an average loss of 30 dB in its aerial hearing, whereas both *Zalophus* and *Phoca* show an average loss of 14–15 dB in their aerial hearing.

Terhune and Ronald (1971) claim that *Pagophilus* mothers can detect their pups' cries, and since the bleating of *Phoca* pups has been reported by Bishop (1967) to be audible to the human ear up to a distance of 2 miles, it is very likely that their mothers can hear them at some considerable distance. The pup cries of *Zalophus* have a good deal of sound energy between 1 and 4 kHz, the latter being perhaps the frequency of best sensitivity in adult *Zalophus*. However, if there is a consistent 15–30 dB loss in the aerial hearing of pinnipeds then, considering ocean and wind noise, the notion that the loud, repetitive "honking" threats of *Mirounga angustirostris* bulls may also function to attract breeding females several miles at sea (LeBoeuf, 1971) seems somewhat tenuous.

Finally, a comment about aerial hearing and male barking in several species of sea lions and fur seals (see Schusterman and Dawson, 1968; Schusterman and Balliet, 1969; Peterson and Bartholomew, 1969; Stirling and Warneke, 1971). These vocal territorial displays have a rapid onset, are highly repetitive, and often have a frequency range greater than 4 kHz. A series of barks can be readily localized in space by binaural detection of differences of intensity, phase and time of arrival, and may contain information related to individual recognition. Male *Zalophus* barks are extremely loud and directional. *Zalophus* barks not only to generally advertise itself, but the barks are frequently directed at individual animals. Using a Bruel and Kjaer sound level meter with different filters, we measured barking intensity at a distance of approximately 2 m. At this distance, our largest bull, Growler (about 8 years old), barked consistently with intensities averaging 103 dB re 0.0002 dynes/cm² at 1 kHz and 89 dB at 4 kHz when the meter was placed directly in front of the animal's head. When the meter was placed at a 90° angle to the sea lion's head, there was a 7 dB fall off at 1 kHz and a 9 dB fall off at 4 kHz. These figures may be compared to measurements made on an adult male dog (Norwegian elkhound). The barking intensity of the dog was 94 dB at 1 kHz and 74 dB at 4 kHz when the sound level meter was placed in front of its head. When the meter was placed at a 90° angle to the dog's head there was a 1 dB fall off at 1 kHz and 5 dB fall off the 4 kHz.

ACKNOWLEDGEMENTS

This research was supported by a U.S. Office of Naval Research Contract N00014-72-C-0186.

REFERENCES

- Bartholomew, G. A. 1959. Mother-young relations and the maturation of pup behavior in the Alaska fur seal. *Anim. Behav.*, 7:163–171.
- Bartholomew, G. A. 1967. Seal and sea lion populations of the California Islands. pp. 229–244. *In* Symposium: Biology of the California islands. Proc. Symp. Biol. Calif. Isl. held at the Santa Barbara Botanic Garden, 1965. Santa Barbara Garden, Santa Barbara.
- Bishop, R. H. 1967. Reproduction, age determination, and behavior of the harbor seal, *Phoca vitulina*, in the Gulf of Alaska. Univ. Alaska, M.Sc. Thesis.
- Cameron, A. W. 1967. Breeding behavior in a colony of Western Atlantic grey seals. *Can. J. Zool.*, 45:161–73.
- Clarke, G. L. 1970. Light conditions in the sea in relation to the diurnal vertical migrations of animals. pp. 41–50. *In* Symposium: Biology of sound scattering in the ocean. Proc. Int. Symp. Biol. Sound Scattering in Ocean. Ed. by G. B. Farquhar. U.S. Navy, Washington, D.C.
- Hobson, E. S. 1966. Visual orientation and feeding in seals and sea lions. *Nature*, (London), 210: 326–27.
- Johnson, C. S. 1966. Auditory thresholds of the bottlenosed porpoise (*Tursiops truncatus*). U.S. Nav. Ord. Test. Stn., Tech. Publ., 4178:1–28.
- Kooyman, G. L. 1966. Maximum diving capacities of the Weddell seal, *Leptonychotes weddelli*. *Science*, (New York), 151: 1553–54.
- Lavigne, D. M. & Ronald, K. 1975. Visual sensitivity in the harp seal *Pagophilus groenlandicus*. This volume, pp. 254–56.
- Le Boeuf, B. J. 1971. The aggression of the breeding bulls. *Nat. Hist.*, 80:83–94.
- Möhl, B. 1968. Hearing in seals. pp. 172–95. *In* The Behavior and Physiology of Pinnipeds. Ed. by R. J. Harrison, R. C. Hubbard, R. S. Peterson, C. E. Rice and R. J. Schusterman. Appleton-Century-Crofts, New York.
- Norris, K. 1969. The echolocation of marine mammals. pp. 391–423. *In* The Biology of Marine Mammals. Ed. by H. T. Anderson, Academic Press, New York.
- Peterson, R. S. 1968. Social behavior in pinnipeds with particular reference to the northern fur seal. pp. 3–53. *In* The Behavior and Physiology of Pinnipeds. Ed. by R. J. Harrison, R. C. Hubbard, R. S. Peterson, C. E. Rice and R. J. Schusterman. Appleton-Century-Crofts, New York.
- Peterson, R. S. and Bartholomew, C. A. 1969. Airborne vocal communication in the California sea lion, *Zalophus californianus*. *Anim. Behav.*, 17:17–24.
- Rand, R. W. 1967. The cape fur seal, *Arctocephalus pusillus*. *Investl Rep. Div. Sea Fish. Afr.*, 60:1–39.
- Ray, C. 1966. Stalking seal under Antarctic ice. *Nat'l Geogr.*, 129:54–65.
- Schusterman, R. J. 1972. Visual acuity in pinnipeds. pp. 469–92. *In* Behavior of Marine Animals. Vol. 2. Ed. by H. E. Winn and B. L. Olla. Plenum Press, New York.
- Schusterman, R. J. and Dawson, R. G. 1968. Barking, dominance, and territoriality in male sea lions. *Science*, (New York), 160:434–36.
- Schusterman, R. J. and Balliet, R. F. 1969. Underwater barking by male sea lions (*Zalophus californianus*). *Nature*, (London), 222:1179–81.

- Schusterman, R. J. and Balliet, R. F. 1970a. Visual acuity of the harbor seal and the Steller sea lion under water. *Nature*, (London), 226:563-64.
- Schusterman, R. J. and Balliet, R. F. 1970b. Conditioned vocalizations as a technique for determining visual acuity thresholds in the sea lion. *Science*, (New York), 169:498-501.
- Schusterman, R. J. and Balliet, R. F. 1971. Aerial and underwater visual acuity in the California sea lion (*Zalophus californianus*) as a function of luminance. pp. 37-46. *In* Orientation: sensory basis. Ed. by H. E. Adler. N.Y. Acad. Sci., Ann., 188.
- 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.*, 17:339-50.
- Stirling, I. and Warneke, R. M. 1970. Implications of a comparison of the airborne vocalizations and some aspects of the behavior of the two Australian fur seal species (*Arctocephalus* sp.) on the evolution and present taxonomy of the genus. *Aust. J. Zool.*, 19:227-41.
- Terhune, J. M. and Ronald, K. 1971. The harp seal, *Pagophilus groenlandicus* (Erleben, 1777). X. The air audiogram. *Can. J. Zool.*, 49:385-90.
- Terhune, J. M. and Ronald, K. 1972. The harp seal, *Pagophilus groenlandicus* (Erleben, 1777). III. The underwater audiogram. *Can. J. Zool.*, 50: 565-69.