

BEHAVIORAL CAPABILITIES OF SEALS AND SEA LIONS:
A REVIEW OF THEIR HEARING, VISUAL,
LEARNING AND DIVING SKILLS

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Behavioral capabilities of seals and sea lions (the pinnipeds) are described and summarized in tabular form. Major features of sound detection, pitch perception, sound localization, visual spectral sensitivity, visual acuity, learning potential and constraints on learning and memory, and maximum diving depths are presented for these large-brained amphibious marine mammals. Among those species tested, phocids hear higher frequencies under water than do otariids and the opposite is true for airborne sounds. All pinnipeds are more sensitive to underwater sounds than they are to airborne sounds. There is little evidence to support the notion that most pinnipeds have evolved an echolocation capability. Scotopic sensitivity of several species is correlated with radiant energy in the marine environment. Visual acuity is equally sharp in air and under water, but deteriorates more rapidly in air than in water when the ambient light is decreased. Sea lions generally behave optimally when confronted with ambiguous cues signaling food reward. Although visual form discrimination and generalization is highly developed, thus far abstraction abilities have not been demonstrated easily in pinnipeds. Although many pinnipeds dive to 200-250 m, only the Weddell seal has been observed to dive to 600 m.

Pinnipeds—the seals, sea lions, and walruses—are truly amphibious mammals of the sea. They reproduce (sometimes copulate and always give birth and nurse their young) on land or ice and are third-level consumers in the marine food chain. Until recently, pinnipeds were classified as a separate order (Pinnipedia), but today they are classified within the order Carnivora (Tedford, 1976). This paper concentrates on two of the three taxonomic families of the pinnipeds—the Otariidae or eared seals which include the fur seals and the sea lions, and the Phocidae or earless seals.

During the past 20 years, a large number of laboratory and field observations have been made on the abilities of some pinniped species to obtain, store, integrate, retrieve, and act on information obtained from the environment. The purpose of this paper is to organize this material to obtain a set of profiles on the behavioral capabilities of the best studied of these species. The behaviors most intensively studied are those associated with sensory perception and social communication, learning, and diving.

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Most of the cogent data dealing with these capabilities can be summarized best in table form.

Several caveats must be given before the data are presented. Most observations and experiments in the laboratory have been made on only one or two individuals of a species, and even though these experiments may have been well controlled, generalization to other individuals of the species must be made with caution. In many cases, only one sex was studied and we know large sex differences exist in a number of behavioral, as well as morphological, characteristics among mammals, birds, reptiles, amphibians, and fish. This is particularly true of all of the otariid pinnipeds and several of the phocid pinnipeds who exhibit great sexual dimorphism. In addition to sex differences, there may also be important developmental differences. Several of the studies, for example, on diving capabilities of California sea lions (*Zalophus californianus*) have been done with young individuals (Conboy, 1975). These animals were considerably smaller than adult males of the species. Since diving capabilities are, to some extent, related to body size (Ferren & Elsner, Note 1), figures on maximum diving depths in these and similar experiments may have underestimated the potential capability of larger individuals of the same species.

CHEMORECEPTION

Although little is known about chemoreception in pinnipeds, in some species mothers probably recognize their pups by olfaction (Ono, 1972) and males may determine a female's sexual receptivity by smelling her vulva or her face or both (Miller, 1974). A formal study on taste reception in California sea lions has recently gotten under way (Nachtigall, Note 2).

VISION AND HEARING

The ability to acquire and integrate information at some distance depends to a large extent on an animal's vision and hearing. In pinnipeds, these senses appear to be relatively well adapted for efficient operation in both water and air.

Hearing

Using primarily behavioral preparations, psychophysical data have been obtained on the ability of both otariid species and phocid species to detect underwater sounds of different frequencies, to localize these sounds, and to differentiate sounds of different frequencies. Underwater sound detection thresholds over a wide range of frequencies (audiograms) have been obtained on two otariid species and four phocid species. Critical ratios calculated from masked underwater hearing thresholds were obtained for one phocid and one otariid species. In addition, aerial audiograms have been obtained from four of these six pinniped species.

Audiograms. Tables 1 and 2 summarize the key features of the underwater and aerial audiograms. As Terhune and Ronald (1975b) have pointed out, the critical ratio data along with an audiogram allows one to estimate the ability of a species to detect underwater sounds in the presence of either man-made or meteorologically induced ambient noise. In water, four phocid species and two otariid species appear equally sensitive to sounds between 2 kHz and 30 kHz. However, the phocids were generally found to be more sensitive to pure tones that were nearly one-half octave higher than those heard by the otariids. The two otariid species, in contrast, appear to be more sensitive to high frequency airborne sounds than phocids. All pinnipeds that have been subjected thus far to audiometric testing show greater sensitivity to underwater sounds than to airborne sounds (see Table 2).

Frequency discrimination. The frequency discrimination thresholds shown in Table 3 refer to average threshold estimates in the most sensitive range of hearing. These data suggest that two phocids and a California sea lion obtain about the same spectral information from underwater sounds below 30 kHz. However, those phocids tested obtained more spectral information from higher frequencies than did the California sea lion, even when sensation levels were kept relatively constant (Schusterman & Moore, 1978a).

Localization. The resolution of spatial sounds is measured in terms of minimum audible angle (MAA) which is defined as the just noticeable difference between azimuths of two sound sources (Mills, 1958). Table 4 summarizes the data from MAA experiments and suggests that the harbor seal may be better than the California sea lion when tested in water. Aerial MAAs are also available for the harbor seal but not for any other of the pinnipeds. Although the ability of other species of pinnipeds to localize airborne sounds without apparent difficulty seems highly probable, there is no quantitative data currently available on this point.

Behavioral experiments, as well as sound-skull measurements, on a California sea lion by Moore and Au (1975) suggested that sound localization under water depends on intensity cues. Their hypothesis that the California sea lion can discriminate an intensity difference of approximately 3 dB at 16 kHz has been confirmed (Moore & Schusterman, 1976).

Sound production and echolocation. All pinnipeds probably vocalize under water as well as in air. The early evidence for echolocation in California sea lions, Steller sea lions and northern fur seals (Poulter, 1966; Poulter & Del Carlo, 1973; Poulter, 1969) has been criticized (Schusterman, 1968). Several well-controlled studies attempting, in fact, to demonstrate echolocation abilities in California sea lions and gray seals have been unable to support the echolocation hypothesis in these species (Schusterman, 1967b; Scronce & Ridgway, 1980).

Since many species of seals and sea lions become more vocal under water during the breeding season (Watkins & Schevill, 1979; Schusterman & Balliet, 1969), it is likely that much of the underwater sound production of pinnipeds has a reproductive function. However, some phocid species may

TABLE 1
A Summary of Major Features of Underwater Audiograms
(including Critical Ratios) of Pinnipeds

Species	Number of Subjects Tested	Best Range of Sound Detection Thresholds		Approximate High-Frequency Cut-Off	Source
		kHz	dB ^a	kHz	
<u>Otariids</u>					
California sea lion	1	1 to 28	-13 to -24	36 to 40	Schusterman, Balliet, & Nixon, 1972
Northern fur seal	2	2 to 32	-23 to -44	36 to 40	Schusterman & Moore, 1978b
<u>Phocids</u>					
Harbor seal	1	2 to 55	-25 to -37	60	Møhl, 1968
Harp seal	1	1 to 55	-19 to -37	60 to 70	Terhune & Ronald, 1972
Ringed seal	2	1 to 55	-13 to -32	60 to 70	Terhune & Ronald, 1975a
Gray seal ^b	2	2 to 40	-15 to -35	50 to 60	Ridgway, 1973

Critical Ratios (dB)

Species	Number of Subjects Tested	Center Frequencies Tested				Source
		4 kHz	8 kHz	16 kHz	32 kHz	
<u>Otariids</u>						
Northern fur seal	2	20	20	25	27	Moore & Schusterman, 1978
<u>Phocids</u>						
Ringed seal	2	30	32	34	35	Terhune & Ronald, 1975b

^a db re 1 μ Bar

^b Evoked potential audiogram

be echolocators. For example, since Weddell seals are not only the deepest divers of the pinnipeds, but also have a rich underwater vocal repertoire (Thomas, Note 3), Weddell seals may have some sort of echolocating ability. Moreover, some populations of harbor seals (*Phoca vitulina richardi*) feed on fish and are capable of navigating in very murky waters (Fancher, Note 4). Although studies on their underwater vocalizations suggest only limited sound production (Schusterman, Balliet, & St. John, 1970), these animals may also warrant further investigation regarding their potential echolocation capability. However, pinnipeds have neither evolved

TABLE 2
A Summary of Major Features of Aerial Audiograms of Pinnipeds

Species	Number of Subjects Tested	Best Range of Sound Detection Thresholds		Approximate High-Frequency Cut-Off	Average Hearing Loss in Air ^a	Source
		kHz	dB ^b	kHz	dB	
<u>Otariids</u>						
California sea lion	1	4 ^c to 16	30 to 35	32 to 36	19	Schusterman, 1974
California sea lion	1	2 to 16	16 to 19	32	--	Schusterman & Moore, 1980
Northern fur seal	2	2 to 20	6 to 13	36	10	Schusterman & Moore, 1980
<u>Phocids</u>						
Harbor seal	1	2 to 16	16 to 26	20	15	Møhl, 1968
Harp seal	1	1 to ?	29 to 42	?	> 30	Terhune & Ronald, 1971

^a These threshold losses in air relative to under water are based on the best range of hearing in air.

^b dB re .0002 dynes/cm²

^c Lowest frequency tested

TABLE 3
Frequency Discrimination in Pinnipeds

Species	Frequencies Tested Within Best Frequency Range kHz	Threshold ($\Delta F / F$) $\times 10^3$	Source
<u>Otariids</u>			
California sea lion	16 to 28	20	Schusterman & Moore, 1978a
<u>Phocids</u>			
Harbor seal	1 to 57	13	Møhl, 1967
Harp seal ^a	8 to 55	39	Terhune & Ronald, 1976

^a Two individuals were tested.

the kind of sound emissions nor the underwater hearing capability that would give them the type of "sophisticated" sonar ability that has been displayed by some species of toothed whales (Moore, 1980; Murchison, 1980; Nachtigall, 1980; Schusterman, 1980).

Despite these findings, the notion that "most pinnipeds have developed a sophisticated echolocation ability" is still prevalent (e.g., see Repenning, 1980). However, a few instances of blind individual seals and sea lions not suffering from lack of food should *not* be interpreted as evidence for an evolved echolocation system by means of natural selection, but rather as an ontogenetic modification in which the individual comes to learn to rely on sound localization as well as other nonvisual cues to find food. This point of view is consistent with the finding that blind persons are generally superior to normally sighted individuals in their ability to localize sound and that persons blind at birth acquire echolocative skills which are superior to persons who become blind later in their ontogenetic development (Rice, 1969).

TABLE 4
A Summary of Underwater and Aerial Localization Data for Pinnipeds

Species	Frequency kHz	MAA Thresholds (in Degrees)		Source
		Underwater	In Air	
California sea lion	0.5	12		Moore & Au, 1975
	1.0	4		"
	2.0	>45		"
	3.5	26 ^a		Gentry, 1967
	4.0	42		Moore & Au, 1975
	6.0	12 ^a		Gentry, 1967
	8.0	14		Moore & Au, 1975
	16.0	18		"
	Clicks	9		Moore, 1975
Harbor seal	2.0	3 ^a		Møhl, 1964
	Clicks	9		Terhune, 1974
	0.5		5 ^a	Møhl, 1964
	Clicks		3	Terhune, 1974

^a Threshold estimates calculated by the author using average z scores (Woodworth & Schlosberg, 1954)

Vision

Two major functions of the eye which have been studied in a few species of pinnipeds are those dealing with spectral sensitivity and spatial or visual acuity. The studies have used a variety of measurement techniques, including psychophysical, pupilometric, histological, and biochemical.

Spectral sensitivity. Until recently, pinnipeds were considered to have pure rod-dominated visual functioning. Recent histological studies, however, have shown both rod- and cone-like receptors in the eyes of two

phocids—the harbor seal (Jamieson & Fisher, 1971) and the harp seal (Nagy & Ronald, 1975). Psychophysical data on the relative sensitivity of the harp seal to various wavelengths under scotopic (dim light) and photopic (bright light) conditions has shown a Purkinje shift or change in maximum sensitivity from 525 to 550 nm between scotopic and photopic conditions indicating the existence of at least two types of photopigments (Lavigne & Ronald, 1972). In addition, psychophysical data on critical flicker frequency on another harp seal indicated two photoreceptors (Bernholz & Matthews, 1975). Further support for dual photoreceptors comes from a “break” in the dark adaptation curve for the harp seal (Lavigne & Ronald, 1972) in which maximum sensitivity was not attained until the seal had been in darkness for 30 to 40 min, and from the effects of wavelengths between 425 and 650 nm on pupillomotor responses from three phocids—two harp seals, two harbor seals, and two ringed seals (Lavigne, 1973). In this experiment, maximum sensitivity in all three phocid species occurred in the region of 500 to 525 nm (the blue-green part of the spectrum). The seals were less sensitive to the red end of the spectrum (650 nm) than to the blue (450 nm).

Spectral sensitivity may also be determined in terms of the wavelength of the light which is maximally absorbed. For example, in many fish maximum scotopic sensitivity correlates well with the spectral distribution of radiant energy in the environment. Deep sea fish thus tend to have blue-sensitive pigments while marine fish living in surface waters and bogs have greener pigments, and the maximum absorption of visual pigments of freshwater fish are shifted toward still longer wavelengths. These observations have resulted in the so-called “sensitivity hypothesis” (Lythgoe, 1972) and McFarland (1971) suggests the hypothesis holds for cetaceans. Consideration of pinniped feeding and migratory habits suggests that the sensitivity hypothesis may also be applied to them. Table 5 gives the maximal light absorption by visual pigment in five phocids and two otariids. As the table shows, all the coastal-dwelling species and the shallow to medium divers (for food) have rod visual pigments with maximum absorption between 496 and 501. The two otariid species are green-shifted with respect to the phocid pigments. The only “deep sea” rhodopsin was found in the elephant seal and this may be an adaptation to its pelagic and deep diving habits. Surprisingly, the deep diving Weddell seal showed an absence of “deep-sea” visual pigment. However, as Clarke (1970) has noted, polar waters are more green than the blue of tropical oceans.

Recently, rod-dominated spectral sensitivity curves were psychophysically determined in dim and bright light for two species of phocid—the spotted seal (*Phoca largha*) and the harbor seal (*P. vitulina concolor*). Peak sensitivity centered at 530 nm with no Purkinje shift (Wartzok, Note 5). The stimulus presented was either moving or stationary and the investigator suggests that these results mean that fully dark-adapted seals would be capable of visually detecting a moving object on a moonlit night at depths of 360 m in clear oceanic waters and 80 m in clear coastal waters.

TABLE 5
Wavelength of Maximal Light Absorption by Visual Pigment in Pinnipeds

Species	Maximum Absorption (nm)	Habits	Source
<u>Otariids</u>			
California sea lion	497, 501	Coastal waters, shallow dives	Crescitelli, 1958
Northern fur seal	499.9	Coastal waters, shallow to medium dives	Lavigne & Ronald, 1975
<u>Phocids</u>			
Harp seal	496.6	Polar and coastal waters, medium dives	Lavigne & Ronald, 1975
Harbor seal	495.7	Coastal waters, bays, rivers, fresh water, shallow to medium dives	Lavigne & Ronald, 1975
Grey seal	496.8	Coastal waters, medium dives	Lavigne & Ronald, 1975
Weddell seal	495-496	Polar waters, deep dives	Lythgoe & Dartnell, 1970
Southern elephant seal	485-486	Open ocean and coastal waters, deep dives	Lythgoe & Dartnell, 1970

The only evidence for color discrimination by a marine mammal was a psychophysical demonstration of a blue-orange differentiation by a female spotted seal (Wartzok & McCormick, 1978). An attempt to obtain color discrimination from another spotted seal (a male) failed. Color discrimination ability of seals is apparently similar to that of cats in that the seals tend to respond to brightness cues rather than hue.

Visual acuity. The spatial resolving power of the eye or how well detail can be seen has been measured properly, i.e., by spatial gratings or similar stimulus configurations (see Riggs, 1965) in only one phocid and two otariids. The threshold estimates obtained in these psychophysical experiments are shown in Table 6 and include underwater and aerial comparisons for the California sea lion. Acuity was measured in minutes of visual angle so that the smaller the angle the better the resolving power of the eye.

There is some indication that as the viewing distance was increased, acuity improved, and for one California sea lion, although acuity decreased both under water and in air as illumination decreased, the effect was much more precipitous in air than in water. These results demonstrate that underwater visual resolution in all three species is similar to that of some visually active carnivores on land, such as the domestic cat (Schusterman,

1972). The aerial vision was also found to be quite sharp under moderate illumination but quite poor under low illumination (Schusterman & Balliet, 1971).

TABLE 6
Visual Acuity in Pinnipeds

Species	Number of Subjects Tested	Visual Angle in Minutes of Arc		Viewing Distance (m)	Ambient Light (ml)	Source
		Underwater	In Air			
<u>Otariids</u>						
California sea lion	2	6.4	5.7	1.9	85-130	Schusterman & Balliet, 1970a
		5.9	7.4	3.1		
		4.8	5.0	5.5		
California sea lion	1	9.0	11.0	0.61	3	Schusterman & Balliet, 1971
		10.9	17.8		3×10^{-2}	
		11.7	24.5		3×10^{-3}	
		13.0	31.2		3×10^{-4}	
		18.5	47.8		3×10^{-5}	
		31.5	75.0		3×10^{-6}	
Steller sea lion	1	7.1		0.61	85-130	Schusterman & Balliet, 1970b
<u>Phocids</u>						
Harbor seal	1	8.3		0.61	85-130	Schusterman & Balliet, 1970b

CONDITIONING AND LEARNING

Behavioral reflexes are elicited and are usually defined as a temporal correlation of stimulus and response (S-R) such that a reliable response will immediately follow a specific stimulus event. A startle reflex or startle response is a sudden move or jump to a normally frightening or surprising stimulus like an intense or strange sound or sight. Behavioral reflexes may become conditioned by means of Pavlovian "procedures." Operant responses are emitted and frequently depend on discriminative stimuli to set the occasion for their reinforcement and subsequent conditioning. The distinction between operant and Pavlovian conditioning is blurred and frequently difficult to maintain either in the laboratory or in terms of naturalistic observations. Furthermore, as one observes animals in the laboratory or in the field, some learned behaviors necessitate the use of terms such as memory, attention, abstraction, and cognition, suggesting that S-R principles of conditioning and learning may need revision or expansion to include these conceptualizations.

Habituation and adaptation. These terms mean getting used to something. Individuals of some pinniped populations or species may habituate to loud or novel sounds or the approach of humans at a faster rate than other populations or species. Thus, upon repeated exposures to the stimulus, a fright response decreases. Some species may adapt to a captive environment more readily than others, and the use of the term adaptation in this context reflects a whole host of complex behavioral and physiological

responses that are the phenotypical expression of both endogenous and exogenous influences.

Although most species and populations of pinnipeds are easily startled or frightened into the sea by loud or novel sounds or the appearance of humans, a few groups are not. For example, humans may approach adult and subadult male northern elephant seals within 2-4 m without much response (the males either remain with their eyes closed, become alert and orient to the stimulus or show a mild threat vocalization consisting of a snorting sound while remaining in a prone position). Australian sea lions (*Neophoca*) at Seal Bay on Kangaroo Island, off South Australia are nonresponsive to humans approaching within 1-2 m. However, only 80 km away on the same island sea lions flee into the water immediately following the sight of a human (Stirling, 1972). The California sea lions on San Nicolas Island (the outermost of the California Channel Islands) are also afraid of man, but a different population of California sea lions in the Galapagos is not (Peterson & Bartholomew, 1967). The harbor seal is probably one of the most alert species of pinniped on land, periodically interrupting its rest or sleep to raise its head and scan the horizon even in captivity (Schusterman, 1968). The amount of vigilance behavior in harbor seals has been attributed to seasonal changes, age, maternal care, and frequency of human-related disturbances (Fancher, Note 4). To some extent, these factors also appeared to play a role in the flight reaction of California sea lions on the Channel Islands (Peterson & Bartholomew, 1967). All of these observations suggest that to some extent startle or flight reactions habituate at different rates in different species and in different populations as a function of age, sex, season, and time of day.

Habituation of the startle and/or flight response in the field is likely to be somewhat predictive of an individual's general tameness in captivity, as well as its trainability. However, there are so many variables affecting such behaviors in the field that our *current* knowledge of this kind of learning may not be too helpful in predicting how responsive individuals of a given species are to human "handling" in the acquisition of relatively complex tasks while they are in captivity.

The data in Table 7 summarizes the author's impressions on the potential tameness and trainability in captivity of several species of pinniped in which there are abundant individuals. Perhaps the most important special considerations for nearly all those species listed are related to age, sex, and reproductive season. A captive colony of male California sea lions, for example, showed seasonal fattening and aggressive displays starting at 5 years of age (Schusterman & Gentry, 1971). Surely, some of the problems associated with tameness and trainability can be overcome with skill and patience on the part of the trainer (Allen, 1977). However, the ranking in Table 7 is an attempt to generalize over individuals, sex, age, and populations within a given species. Another important special consideration is likely to be whether the individual, regardless of species, has been reared by humans soon after birth. In this regard, it is important to note that, in general, otariid pups have a much longer suckling period than phocid pups and thus may be more amenable to the effects of early human socialization.

At any rate, such factors as the duration of mother-pup bonding and the emergence of early sex differences in play patterns of pinnipeds (Gentry, 1974; Reiter, Stinson, & LeBoeuf, 1978; Schusterman, 1968; Wilson, 1974) are likely to play constraining or facilitating roles in the training of captive seals and sea lions.

TABLE 7
Degree of Potential and/or Actual Tameness and Trainability of Selected
Species of Pinnipeds when in Captivity

Species	Tameness ^a	Trainability ^b	Source
<u>Otariids</u>			
California sea lion	Excellent	Excellent	Schusterman, 1968
Steller sea lion	Poor	Good	Schusterman, 1968; Allen, 1977
South American sea lion (<i>Otaria f.</i>)	Poor	Good	Vaz-Ferreira, 1975; Johann, 1979
Northern fur seal	Fair	Good	Schusterman & Moore, 1978b; Cover, 1977; Bailey & Peiterson, 1977
Cape fur seal (<i>Arctocephalus pusillus</i>)	Excellent	Excellent	Ian Stirling, Gerry Kooyman, Ted Miller ^c
Kerguelen fur seal (<i>Arctocephalus gazella</i>)	Excellent	?	Gerry Kooyman ^c
Harbor seal	Excellent	Excellent	Schusterman, 1968; Betty Constantine ^c
Spotted seal (<i>Phoca largha</i>)	Excellent	Excellent	Wartzok & McCormick, 1978
Ringed seal (<i>P. hispida</i>)	Excellent	Excellent	Terhune & Ronald, 1975a
Harp seal (<i>P. groenlandica</i>)	Excellent	Excellent	Lavigne, 1973
Gray seal	Good	Excellent	Ridgway ^c ; Shusterman et al, 1970
Leopard seal	Poor	Good	Gaskin, 1972; Gerry Kooyman, Bill Evans ^c
Weddell seal	Excellent	?	Kooyman, 1968

^a Tameness refers to an animal reliably accepting approach by strangers and handling by familiar trainers.

^b Trainability refers to the ease with which an animal can be brought under stimulus control by operant and Pavlovian conditioning procedures.

^c These sources are personal communication.

Discrimination and detection experiments. A large number of behavioral experiments have been conducted with pinnipeds that are referred to in the section on vision and hearing. These experiments have demonstrated that the following species (see Table 7) can be conditioned to respond differentially to rather specific stimulus events in either the auditory or the visual modality: California sea lion, Steller sea lion, northern fur seal, harbor seal, spotted seal, ringed seal, harp seal, and gray seal. In most of these experiments, the conditioned responses consisted of

some sort of paddle push with the chin or nose. In some experiments with California sea lions, food reinforcement was used to rapidly condition vocalizations consisting of underwater and aerial clicks and barks (Schusterman, 1978).

Attention. Data have been obtained with two California sea lions during which a series of "probe" trials were inserted at several points in a fading program that was used to effect nine errorless reversals of a form discrimination (Schusterman, 1967a). The data suggested that the sea lions differed in the point at which they shifted attention from a size cue to the reversed forms and that the sea lions shifted their attention gradually from size to form over the course of fading. Most recently, in experiments on qualitative versus directional cues (Dobrzecka, Szwejkowska, & Konorski, 1966), California sea lions and northern fur seals paid no attention at all to the quality of sounds (pulsed versus continuous tones) coming from different locations if the animals had been trained to respond spatially and the response manipulanda were located adjacent to or in the vicinity of the sound source (Schusterman, Note 6).

Memory. Instead of presenting a pair of stimulus shapes for a given number of trials, one can present each pair of stimuli for just a single trial. Thus, the first pair is presented, followed by the second pair, and then a third, and so forth, through a given "list" of discriminations. Once a list has been run through, it can be repeated for a second run, then a third run, and so forth. This technique is similar to the serial learning of paired associates frequently used to study memory with human subjects. In an experiment with one California sea lion, one harbor seal, and one Steller sea lion, problems involved either 5, 10, or 20 stimulus pairs. As expected, the longer the list the more difficult it was to learn and remember. All three animals, however, were capable of remembering a list of 20 stimulus pairs without a single error (Schusterman, Note 7).

Decision making. In a series of studies, Schusterman and his colleagues showed that a California sea lion uses a maximum-likelihood decision rule during classifications of ambiguous acoustic signals. In laboratory experiments, in which the payoff matrix was varied either by varying the amount of reinforcement (Schusterman, Barrett, & Moore, 1975) or by varying the probability of reinforcement (Schusterman, 1976), the sea lion changed its decision rule quite rapidly (within a single test session consisting of 120 trials) in order to optimize its total payoff or food intake. Sensitivity to acoustic signals was relatively unaffected by these rapid shifts in decision rules. Variation in signal probability also resulted in changes of decision rules, but at a rate which was considerably slower than when the payoff matrix was modified (Schusterman & Johnson, 1975). In a recent experiment on decision-making under conditions of uncertainty, it was demonstrated that a California sea lion was relatively indifferent as to whether it received large amounts of food infrequently or small amounts frequently (Schusterman & Moore, Note 8). These results are consistent with the ecological principle of optimization (see, for example, the book by Krebs & Davies, 1978) and the psychological principle known as the "matching law" (Herrnstein, 1970).

Abstraction. Visual form discrimination and generalization are well developed in California sea lions (Schusterman, 1968). The closest demonstration to abstraction in pinnipeds, however, has come from the research of Betsy Constantine at Northeastern University and the New England Aquarium. Briefly, she has been able to train five harbor seals and one gray seal to match-to-sample using black and white squares as visual stimuli. However, when vertical and horizontal stripes were used as stimuli, i.e., when the seals were confronted with new configurations, their performance deteriorated suggesting that they may lack the abstraction abilities readily demonstrated in humans, chimpanzees, and dolphins (see Herman, 1980; and also see Kellogg & Rice, 1963).

DIVING

The last reviews concerned with maximum diving depths of pinnipeds were done by Harrison and Kooyman (1968) and Kooyman and Anderson (1969). Although there are a great many physiological and behavioral ecology variables which influence the maximum diving depths reported, the methods used and the age and sex of the animals are perhaps the most important when considering generalizations regarding maximum diving depth capabilities for a given species. For example, diving characteristics of three species of fur seals were recently studied, but the object of the study was to determine female diving patterns and not the diving characteristics in adult males (Kooyman & Gentry, Note 9). Many of the maximum diving depths had been observed indirectly either by animals being hooked on a line by fishermen or inferred from feeding habits or from experimentally simulating the dive. These methods of observation are obviously suspect. However, new techniques have been developed in which either a depth recorder is attached to the free swimming animal (Kooyman, 1968) or the animal is trained by operant conditioning techniques to dive in the open ocean in the presence of an acoustical signal (Ridgway, 1972).

Table 8 is fashioned after Kooyman and Anderson's Table III (1969) and gives the maximum diving depths reported for the pinnipeds. On the basis of an individual's size and the method of observation, the values shown in Table 8 are in several instances likely to be underestimates of maximum diving depth capabilities. However, the figure given by Kooyman for the Weddell seal is probably a maximum figure since it is based on a free-diving older male.

SUMMARY

Although the behavioral capabilities of many species of pinniped have not been studied and of those that have been studied the sample size has been very small, there are still enough data available to make some preliminary statements about the sensory, learning, and diving capabilities of pinnipeds. This report summarizes, primarily in tabular form, what is currently known about these performance capacities. Specifically, major

TABLE 8
Maximum Diving Depths Reported for Pinnipeds and Method of Observation

Species	Depth (in meters)	Method of Observation	Source
<u>Otariids</u>			
California sea lion	250	Trained	Ridgway, 1972
Steller sea lion	183	Hooked on line	Kenyon, 1952
Northern fur seal	190	Attached depth recorder	Kooyman, Gentry, & Urquhart, 1976
Cape fur seal	204	Attached depth recorder	Kooyman, Gentry, Note 9
Kerguelen fur seal	68	Attached depth recorder	Kooyman, Gentry, Note 9
<u>Phocids</u>			
Harbor seal	206	Experimentally simulated	Kooyman, Schroeder, Denison, Hammond, Wright, & Bergman, 1972
Ringed seal	90	Inferred from food habits	McLaren, 1958
Harp seal	150 & 275	Inferred from food habits, hooked on line	Sergent, 1973; Nansen, 1925
Bearded seal	100-200	Inferred from food habits	Kosygin, 1971
Hooded seal	75	6-month pup with attached depth manometer	Scholander, 1940
Gray seal	213	Trained	Ridgway, Note 10
Northern elephant seal	183	Hooked on line	Scheffer, 1964
Weddell seal	600	Attached depth recorder	Kooyman, 1968

features of sound detection, pitch perception, sound localization, visual spectral sensitivity, visual acuity, learning potential and constraints on learning and memory, and maximum diving depths are presented in eight tables. New studies, in the areas of learning potential, methodological and biological constraints on learning and memory (particularly on the effects of early experience), diving capabilities in adult or large males, and audiometry (both passive and active, i.e., echolocation) on additional pinniped species are sorely needed if we are to have a more complete picture of pinniped behavioral capabilities.

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