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Chapter 13

VISUAL ACUITY IN PINNIPEDS

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I. INTRODUCTION

Until recently, studies of the sensory adaptations of marine mammals have primarily been carried out with the small-toothed whales and have emphasized hearing mechanisms and acoustic orientation almost to the complete exclusion of the visual organ. 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 and is normally considered the most suitable sense organ for environmental orientation. However, previously there was no behavioral evidence of an experimental nature regarding the visual acuity of either the cetaceans or the pinnipeds. Despite experimental evidence suggesting that the behavior of some odontocetes is guided more by sound than by sight (Norris, 1968), Kellogg and Rice (1966) have shown that properly trained dolphins can rapidly solve problems presented to the visual modality, and most recently Spong and White (1969) have done several behavioral experiments concerned with the visual resolving power of the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) and the killer whale (*Orcinus orca*) underwater. Furthermore, although conditions at the water's surface may indicate extreme darkness below, Hobson (1966) reports that considerably more light may be available to the eye located underwater and has described the tendency of sea lions and seals to approach their prey from below, thus silhouetting the prey against the ambient sky light above.

Unlike the cetaceans, which must find food as well as interact socially

in an aquatic medium only, pinnipeds, although feeding exclusively underwater, usually spend a good portion of their time resting and interacting socially in a terrestrial environment. Thus, since they are truly amphibious, pinniped forms such as the California and Steller sea lions and the harbor seal require special sensory adaptations, which are probably quite different from those of the more common toothed whales such as the bottlenosed dolphin and the common porpoise.

Although there is abundant evidence indicating that acoustic signalling and orientation on land by several pinniped forms are critical for the establishment and maintenance of their social organization, the role of visual signalling and orientation on land is less well known (Peterson and Bartholomew, 1967). Naturalistic observations have suggested that the visual acuity of the California sea lion on land is quite poor in daylight and is even worse at night (Peterson and Bartholomew, 1967). On the other hand, the role of acoustic orientation by pinnipeds in finding food at sea is not well understood, and it has been suggested by Hobson (1966) and Schusterman (1967) that some forms probably rely a good deal on visual information for this purpose.

In early experiments dealing with the smallest areas of circles and rectangles that seals and sea lions could consistently detect underwater, it was found that the California sea lion (*Zalophus californianus*), Steller sea lion (*Eumetopias jubatus*), and harbor seal (*Phoca vitulina*) were all capable of detecting area differences as small as 6–9 percent and that *Zalophus* was capable of visually detecting differences of 0.25 cm between bars or rectangles (1.5 cm wide) oriented in the vertical plane (Schusterman, 1968). However, these stimuli may have been either totally or partially irrelevant with regard to measuring visual acuity *per se* since the animals could have been gauging merely the total amount of reflected light from around the area of the stimulus targets, thereby resulting in performance that may have reflected a brightness discrimination. With the use of these stimulus configurations, the animals could, in principle, have discriminated between targets even if their ability to detect fine detail was very poor. Furthermore, in some of the experiments, the animals swam up to the stimulus targets and pushed them; thus there was no way of ascertaining the distance at which the animals made their discriminations. These early efforts at obtaining some information on the underwater visual discrimination capabilities of seals and sea lions were successful in maintaining orienting responses and keeping the sensorimotor requirements relatively constant for different species, in maintaining a clear definition of response, and in keeping the water relatively clear. However, they were largely unsuccessful in keeping the animals at a relatively fixed or minimum distance from the stimuli so that accurate visual angles could be calculated, and in using stimulus configurations in which visual resolving power could be measured uncontaminated by intensity discriminations (Riggs, 1965).

To correct these deficiencies, several changes in methodology were made. In one set of experiments, conditioned vocalizations were used as an objective index of the fact that the animal could discriminate between patterns. In these experiments, the animal was trained to place its head in a head holder so that all responses to the stimuli were made while the head was in a fixed position. In other experiments, the animals were allowed to swim toward and press the stimulus targets; however, a barrier extended out between the stimuli, and the animals were trained to make their decisions at a minimal distance from the acuity targets. In both sets of experiments, the stimulus targets used were a series of grating patterns in which the widths of the lines varied from coarse to fine; the result was that visual acuity, which has been defined as the spatial resolving capacity of the visual system, could be specified in terms of the angular width of the line of the finest grating that could be resolved.

II. UNDERWATER

A. Methodology

In this section I describe a technique used to measure the underwater visual acuity of a 4-year-old male Steller sea lion (Runner) and a 5-year-old male harbor seal (Goldie). Although the general health of both animals was good throughout the training and threshold phases of the study, the corneas of both eyes of the Steller sea lion were slightly "milky," and on a few test sessions during the first threshold phase of the experiments this animal kept its left eye closed while swimming toward the acuity targets. However, binocular and monocular viewing had no effect on the performance of this sea lion. Inspection of the harbor seal's eyes indicated that they were in excellent condition throughout the study. Previously, both animals had received extensive experience with pattern discriminations (the shapes used were painted black on a white background) in which their task was to push one of two targets with the nose in order to receive a fish reward (Schusterman, 1968).

The animals were trained and tested outdoors between the hours of 0800 and 1200 in an oval tank, and were not fed for approximately 20 hr prior to each test session. The tank was constructed of redwood painted white and measuring 4.6 by 9.1 by 1.8 m. Pictures and details of the testing conditions and apparatus have been published (Schusterman, 1967, 1968). The acuity targets were produced from 12.7-cm² photos of Ronchi rulings with the black and white stripes of equal width. The *standard* grating consisted of 300 lines per inch (0.05 mm in width). The lines were invisible to the human eye without the aid of a lens and appeared as a flat gray square. The *variable* gratings consisted of lines varying in width from 25.4 to 0.96 mm. All variable

gratings used during the final acuity threshold tests were compared with the standard by three human observers at a distance that prevented resolution of the lines, and in all cases observers reported that the variable gratings were indistinguishable from the standard grating. Photos of the horizontal striations were centrally fixed and laminated within a 22.8-cm² clear plexiglass, 0.4 cm thick. The area framing the acuity grating was painted flat black. These plexiglass squares could be slipped in and out of an aluminum frame (see Figs. 1 and 2). Thus, the animals saw a 12.7-cm² acuity grating (black and white stripes) surrounded by a large black border.

Two targets were always presented simultaneously so that they projected below the opaque screen, with the center of the target being 30 cm below the water level. At the beginning of a trial, a stimulus panel located behind the opaque screen was lowered to the water level. Attached to the side of the stimulus panel facing the experimenter were two rods holding the targets. Deflection of either rod activated a microswitch that produced an audible click signal. A perpendicular divider of mesh wire projected down to the floor of the tank and 68.6 cm outward from the opaque screen, thus lying between the targets and preventing the animals from swimming laterally from one target to the other. The distance between the centers of any two targets was 67 cm.

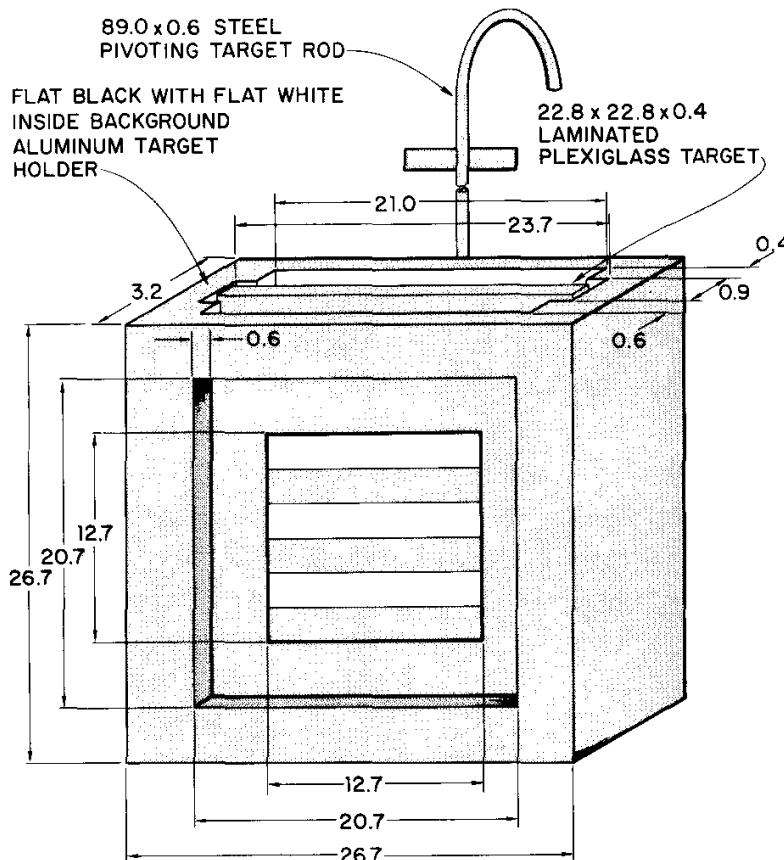


Fig. 1. Schematic diagram of target holder with acuity target in place.

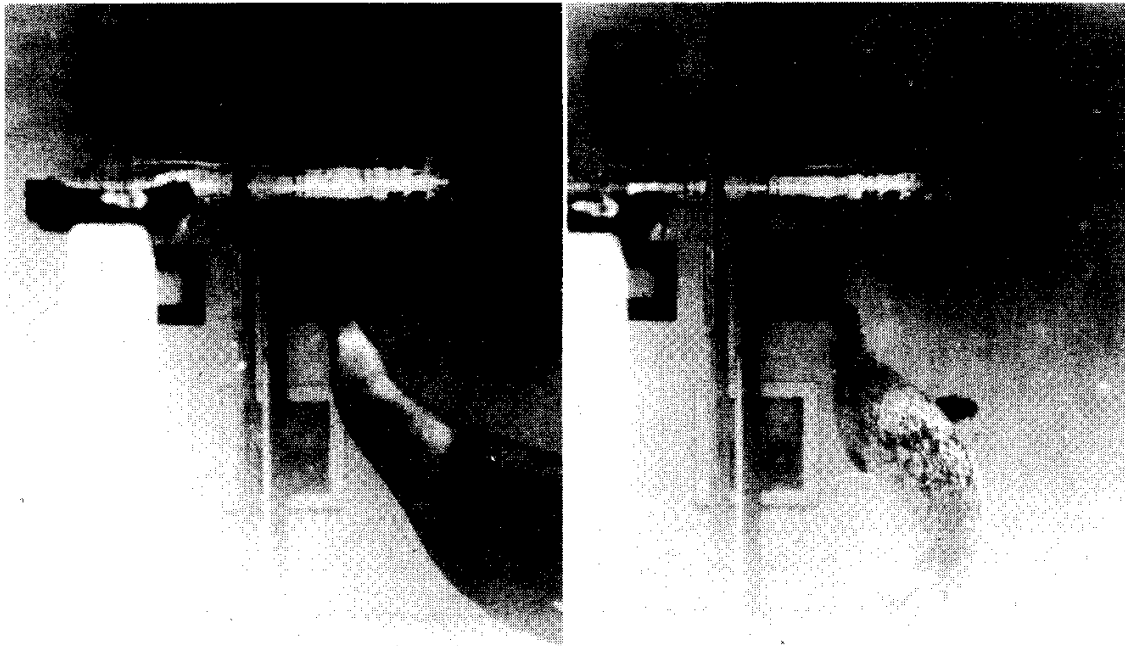


Fig. 2. Underwater photo of harbor seal (left) and Steller sea lion (right) waiting for fish reward after having just pushed acuity target. Note that, at distance photo was taken, gratings cannot be resolved. Head holder with white stand shown in foreground.

The animals had been previously trained to remain at a position about 6 m in front of the stimulus display area until signalled to approach by the sound of the display being lowered into the water. Their task was to push the target with the variable grating (defining a correct response) in order to obtain a fish reward—a 76-g piece of herring (*Clupea pallasii*) for *Eumetopias* and a 16-g piece for *Phoca*. Right and left position of the standard and variable gratings was determined by a Gellerman series, and extreme care was taken to avoid differential auditory, visual, or temporal cues between and during stimulus presentations. Moreover, the variable and standard gratings were changed from one target holder to the other to eliminate any cues associated with the target holders. A trial began when the targets were presented and terminated when they were withdrawn. If the animal, in swimming toward the target, extended its head beyond the outer point of the 68.6-cm-long stimulus divider on the side of the standard grating, then it was forced either to press the target on that side or to swim back to its starting position. If it attempted to switch sides after its head passed the divider, the targets were raised immediately and the response was counted as an “error.” In this manner, animals approaching the targets were trained to make their final decision at a minimal distance from the acuity targets, i.e., at the barrier. Thus the minimum distance between the gratings and the animal was taken

as 68.6 cm (27 inches), and visual angles were calculated for each variable grating on the basis of this distance.

Two observers were always present throughout the entire study. One presented the stimulus display while the other observed the animal from the testing platform, recording correct responses, response latencies (by means of a stop watch), and the presence of orienting responses, which were defined as postural changes of the head or body occurring within 30 cm of the barrier. Previous estimates of reliability in scoring an orienting response by two independent observers yielded agreement of better than 90 percent (Schusterman, 1965*a,b*).

The experiment consisted of three principal phases. During the first phase, the standard and a variable target with striations 25.4 mm wide were presented to the subjects, who were reinforced only for responding to the variable target. The Steller sea lion showed an immediate preference for the reinforced or positive target; he committed only eight scattered errors during the first 67 trials. The harbor seal, on the other hand, showed a slight preference for the standard target, and it took 110 trials and 48 errors before he consistently responded (30 consecutive correct responses) to the variable target. Stimulus control was then gradually shifted to targets having finer striations. Such gradual shifting of stimulus control from relatively easy to more difficult discriminations within a given stimulus dimension has proved to be an extremely efficient technique in training many different animals, including sea lions, for psychophysical experiments in that it tends to decrease or eliminate emotional behavior and may teach the animal to attend to both the location and nature of the critical cue (Blough, 1966; Schusterman, 1968).

In the second phase, a modified method of limits was used to obtain a range of acuity targets necessary for estimating thresholds (defined as the interpolated values at which the animals responded correctly 75 percent of the time) during the third and final phase of the study. There were a total of 62 sessions for the Steller sea lion and 50 sessions for the harbor seal. Both animals showed significant improvement from the early sessions to the later sessions, with performances stabilizing during the last ten to 20 sessions. At each session a series of acuity gratings was presented, starting with stripes 3.2 mm in width. The stripes were made finer or broader, depending on whether the animal succeeded in making eight or more correct responses in ten successive trials. A session was terminated only after an animal had succeeded at a given acuity grating. The minimum number of trials at a session was 60, and on a few occasions an animal was given as many as 90 trials. By this means, threshold estimates for the two animals were bracketed at between 5.5' and 8.5' of visual angle.

During the final phase, an underwater visual acuity threshold for each animal was obtained by the psychophysical method of constant stimuli.

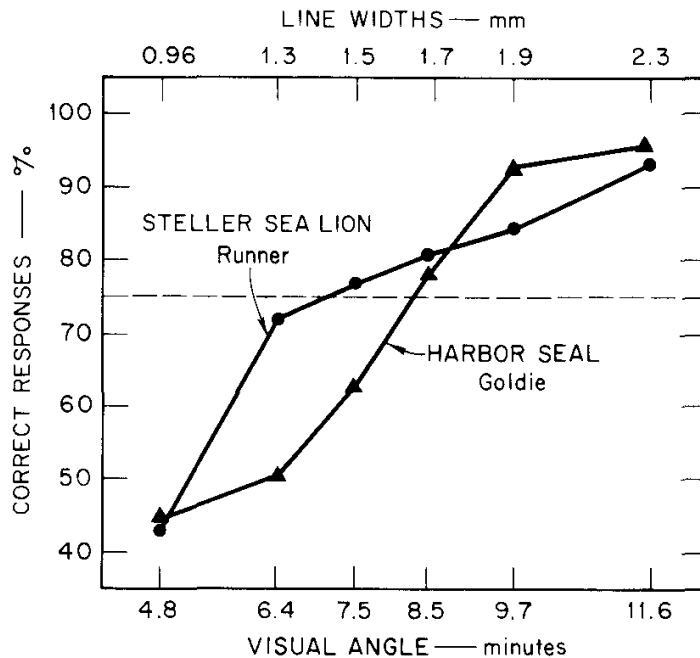


Fig. 3. Correct responses as a function of visual angle calculated at a distance of 68.6 cm.

Following a ten-trial warm-up period with a suprathreshold target, each of six variable gratings with line widths as listed on the top abscissa of Fig. 3 was paired randomly from session to session with the standard for ten consecutive trials, for a total of 70 trials per session. A total of 15 sessions was run for each animal.

Ambient light measurements were taken with an SEI photometer during and immediately after the final threshold phase was completed. Although most of the tank was in sunlight, even on clear days acuity targets were always presented in the shade of the testing platform. Ambient light measurements around the stimulus display area were taken from behind the back window of the tank when it was filled with water, and yielded readings of 130 m μ L on clear days and 85 m μ L on overcast days.

B. Results

The underwater visual acuity threshold curves obtained by the method of constant stimuli for one *Eumetopias* and one *Phoca* are shown in Fig. 3. Several comparisons may be made from these curves: (1) *Eumetopias*, despite its slightly "milky" eyes, performed significantly better than chance ($P < 0.01$) with line widths that subtended a visual angle of 6.4' of arc, but *Phoca* did not achieve performance significantly better than chance until tested with broader stripes subtending a visual angle of 7.5'; (2) whereas the acuity curve for *Phoca* showed the typical ogive function resulting from a psychophysical experiment, the curve obtained for *Eumetopias* was negatively accelerated;

(3) both animals were capable of resolving stripes that subtended a visual angle of 8.5' of arc with relatively good accuracy; (4) threshold estimates measured in minutes of visual angle over the 15 test sessions were 7.1 for *Eumetopias* and 8.3 for *Phoca*.

Threshold values during the first eight and the last seven test days were 7.5' and 6.5' for *Eumetopias* and 8.6' and 8.1' for *Phoca*. Although there is some evidence of improvement, especially in the case of *Eumetopias*, the differences revealed in these comparisons were not significant and indicate relatively stable acuity performance by both animals during the final threshold phase. This resulted presumably from the rather long and intense training and early threshold phases.

Pinnipeds, while swimming underwater, frequently acquire orienting and fixating responses of the head and eyes in order to discriminate effectively (Schusterman, 1955a,b, 1966). Conflict and discrimination difficulty are critical factors in the production and maintenance of orienting responses (Tolman, 1948). On this basis, one would predict that orienting responses by the seal and sea lion during the present experiment would be maintained at a relatively high level when they were attempting to detect acuity targets below or just above threshold as compared to suprathreshold targets. The results, plotting orienting responses as a function of visual angle, are shown in Fig. 4 and bear out this hypothesis. Significantly more orienting responses were made on the most difficult discrimination than on each of the two easiest discriminations ($P < 0.05$, sign test). Predictably, their response latencies were also increased as the stripes of the acuity targets became finer (see Table I), with latencies for both animals being significantly longer on the most difficult discriminations as compared to the easiest discrimination ($P < 0.05$,

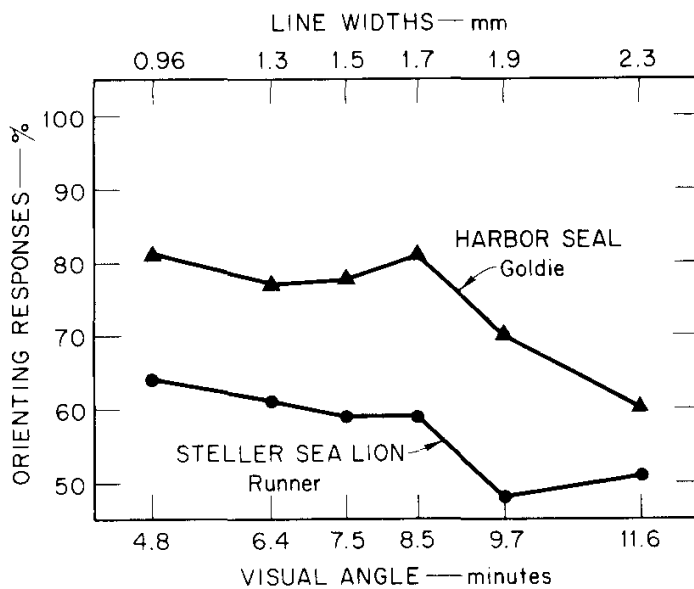


Fig. 4. Orienting responses as a function of visual angle.

Table I. Response Latencies (in sec) as a Function of Pattern Discriminability

Line width (mm)	Visual angle (°)	Harbor seal "Goldie"		Steller sea lion "Runner"	
		Mean	SD	Mean	SD
0.96	4.8	8.1	1.4	6.4	1.9
1.3	6.4	7.7	2.1	6.1	1.5
1.5	7.5	7.8	2.0	5.9	1.0
1.7	8.5	8.1	1.8	5.9	1.6
1.9	9.7	7.0	1.8	4.7	1.5
2.3	11.6	6.0	1.8	5.1	1.1

sign test). The extremely high level of orienting responses as well as the relatively longer latencies on the most difficult discriminations reflect an attempt by both animals to swim as close as possible to the stimulus display area in order to resolve the finer gratings prior to making a decision at the edge of the barrier. Occasionally, in the case of *Eumetopias*, if the animal swam past the edge of the barrier on the side of the standard target, it would swim to within about 50 cm of the target and then turn away from the target and swim back to the start position.

III. AERIAL VS. UNDERWATER

A. Methodology

This section describes several experiments in which a sexually mature male (Sam) and female (Bibi) *Zalophus* were trained to emit a burst of short-duration sound pulses or clicks (see Schusterman, 1968, for a review of training procedures) when viewing targets consisting of black and white stripes and to remain silent when viewing a target that appeared flat gray. By training the animal to keep its head in a fixed position while making the discrimination and by varying the width of the stripes, an estimate was obtained of the finest detail that could be resolved by the sea lion eye. Threshold data were acquired in this manner, both in air and underwater at several different distances, thus allowing for direct comparison of visual acuity in the two media (see Fig. 5).

Testing was outdoors between 0800 and 1200 hr in the oval redwood tank described previously. Animals were not fed for 20 hr before a test. Acuity targets were the same as those used for testing underwater visual acuity in the Steller sea lion and harbor seal.

A "correct" response was defined as either emitting a burst of clicks



Fig. 5. California sea lion viewing variable acuity target in air.

to the variable stimulus or remaining silent in the presence of the standard stimulus. Sam was required to remain silent for a 5-sec period. Bibi was required to remain silent for only a 3-sec period. The change in response for Bibi was necessary because when she remained silent she jerked her head back and forth and moved forward toward the target; these movements only occurred while she was silent. If an animal produced a burst of clicks, it would usually do so within less than 0.5 sec following stimulus presentation, which was always by the successive method (i.e., one at a time). Two experimenters worked from behind an opaque screen, presenting stimuli, recording responses, observing the animal, and reinforcing all correct responses. Sound production was continuously monitored by means of a hydrophone. The same procedure for testing visual acuity was used underwater and in air, the only difference being that in air the water level of the tank was lowered so that the targets were in air and the animal's eyes remained in air while the neck and the rest of its body remained in water. Despite the fact that in the aerial testing the animal's mouth was out of water, its neck was in water, and it is known that vocalizations made by sea lions with their mouths closed and out of water may still be projected under water by the larynx and thereby be picked up by a hydrophone (Schusterman and Balliet, 1969; Schusterman *et al.*, 1970).

Like the previously described study of underwater visual acuity, this experiment consisted of three phases. First, the standard and a variable

target with striations 25.4 mm wide were presented, and the sea lions were reinforced for vocalizing and remaining silent in response to the appropriate target. Once stimulus control of vocalization was obtained with this variable target, it was gradually shifted to targets having finer striations.

In the next phase, a modified method of limits was used to obtain a range of acuity targets necessary for estimating thresholds during the final phase of the study. Threshold bracketing by this method was primarily accomplished with the sea lion's head being maintained at a fixed distance of 4.5 m from the targets. However, distances of 1.9 and 5.5 m were also used. It is important to note that both animals showed a significant practice effect *only* during aerial testing. At the beginning of a test session, it was found that performance in air was generally more erratic than it was underwater. Therefore, a worm-up period was used in air, with both animals being required to perform at an 80 percent level of accuracy before proceeding to the more difficult discriminations during a given test session. These early results suggest that *Zalophus* learns to orient to visual patterns slower in air than it does underwater (possibly to adjust or compensate for astigmatic blurring); this may be the reason that naturalists have suggested that the aerial vision of these animals is very poor in daylight (Peterson and Bartholomew, 1967; Hamilton, 1934). When performances stabilized, threshold estimates were bracketed between 5' and 8' of visual angle, with little difference between aerial and underwater performance.

During the final phase, acuity thresholds were obtained by the psychophysical method of constant stimuli. Following a ten-trial warm-up period with a suprathreshold target, each of four variable gratings with line widths as listed on the top of Fig. 6 was paired randomly from session to session with the standard for ten consecutive trials and then repeated within each session, for a total of 90 trials per test session. A total of 20 sessions were run, with testing in air and water alternated daily. Thresholds were obtained at three different distances in the following sequence—3.1, 5.5, 1.9, and 5.5 m. Thus two separate thresholds were computed at the distance of 5.5 m.

B. Results

Visual acuity threshold curves are shown in Fig. 6. In general, there appears to be relatively little difference between underwater and aerial acuity at the closest and farthest distances measured. However, at the middle distance, 3.1 m, performance is significantly superior for both animals underwater than in air. The poorer aerial acuity at 3.1 m may be accounted for by the fact that the animals were tested by the method of constant stimuli for the first time at that distance. Performances were best at 5.5 m (see Table II).

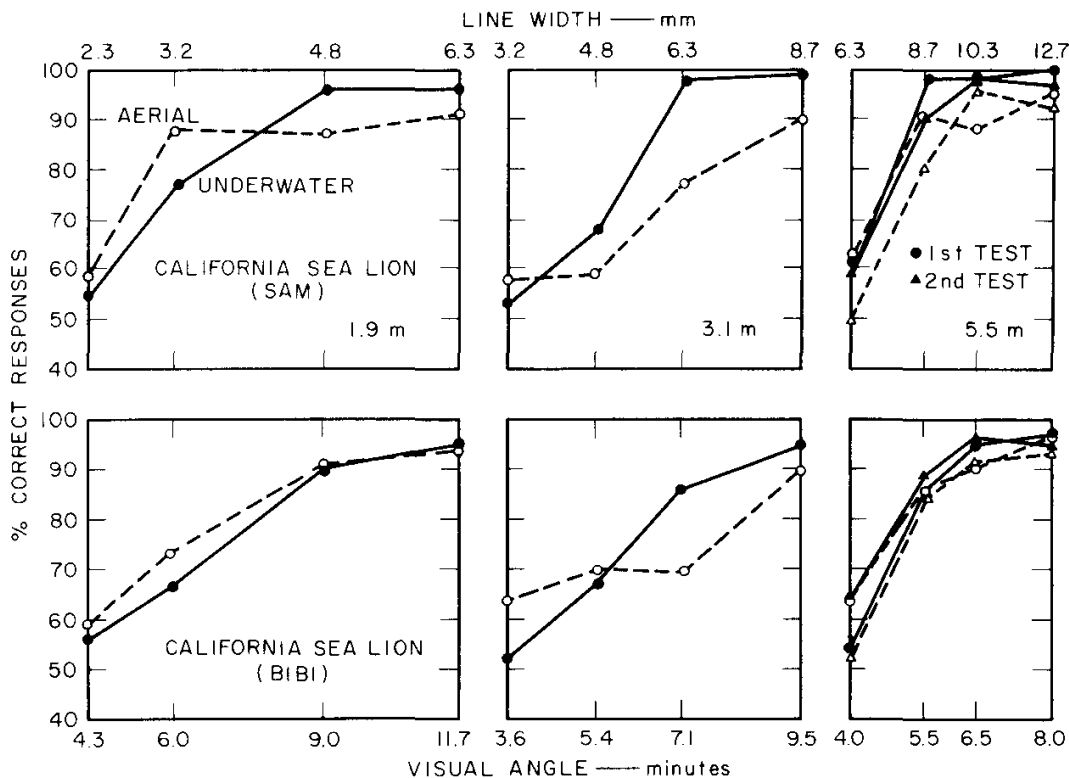


Fig. 6. Comparison of aerial and underwater visual acuity threshold curves at three different distances.

This may be related to latency of vocalization. Although no measurements were made, our general impression was that the animal vocalized more rapidly following stimulus presentations at 1.9 and 3.1 m than at 5.5 m.

Whether or not variable targets were easily distinguished from the standard had little effect on the rate of false alarms (vocal responses to the standard target) by both sea lions. Thus Fig. 7 shows that even though the probability of vocalizing to a variable target (a hit) decreased directly as a function of decreasing visual angles, the probability of making a false alarm remained relatively constant. This means that during difficult discriminations the sea lions did not respond randomly, as one might expect, or persist

Table II. Aerial and Underwater Visual Acuity Thresholds in Minutes of Visual Angle

Distance (m)	Sea lion Sam		Sea lion Bibi	
	Air	water	Air	Water
1.9	5.2	5.8	6.1	7.0
3.1	7.0	5.8	7.8	6.1
5.5 (test 1)	4.8	4.6	4.8	5.0
5.5 (test 2)	5.3	4.8	5.0	4.7
Median	5.25	5.30	5.55	5.55

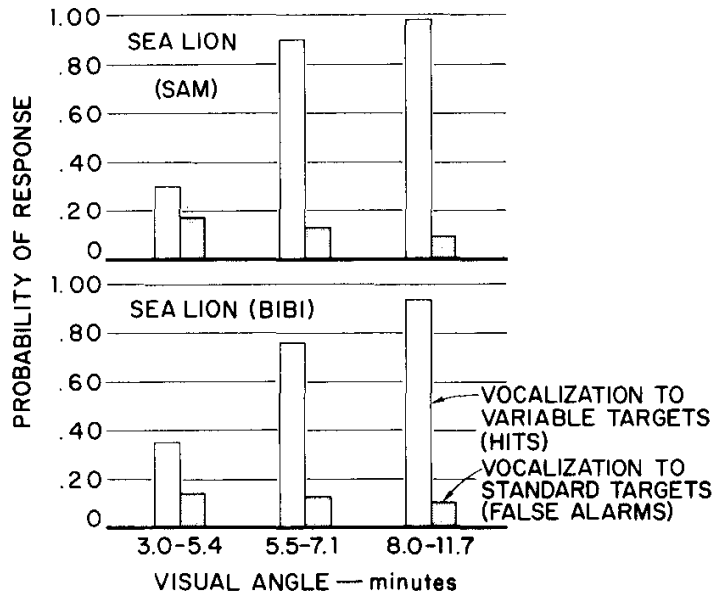


Fig. 7. Relationship between hits and false alarms as a function of visual angle.

in a vocal response. Rather, they did what they were trained to do; i.e., they generally remained silent when viewing a gray patch.

It is well known that without goggles human visual acuity is enormously impaired under water. A preliminary test was made with one human subject, using the same acuity targets previously presented to the sea lions. At a distance of 0.7 m, the subject could quite accurately differentiate the standard target when line widths subtended a visual angle of 7.5' but could not make such a discrimination when each line subtended a visual angle of 6.2'. At distances of 4.5 and 5.5 m, the subject reported that he could not even see the outline of the targets.

IV. LUMINANCE

A. Introduction

All of the previously described studies on visual acuity have been conducted at relatively high levels of luminance. Since *Zalophus*, as well as several other species of pinnipeds, sometimes procures food in relatively dim light (Hobson, 1966) and appears to be quite active at night on land during the breeding season (Peterson and Bartholomew, 1967), the question arises as to the extent to which underwater and aerial visual acuity of these animals is limited by luminance. This question is of particular importance since it has been suggested that when on land many forms of pinnipeds have become especially dependent upon the acoustic channel for social communication and therefore use their aerial vision very little compared to land mammals

(Peterson and Bartholomew, 1969). Similarly, underwater, where several species including *Zalophus* are quite vocal (Evans, 1967; Poulter, 1968; Schusterman *et al.*, 1970), it has been suggested that when illumination is poor or *almost* nonexistent, these animals, like the odontocete whales, orient to food sources by means of an active sonar system; i.e., they use their own reflected sounds to locate the prey (Poulter, 1966).

There is anatomical and behavioral evidence to suggest that the visual acuity of pinnipeds in extremely low light may be relatively sharp, at least underwater. Walls (1963), for example, states that the number of layers of cells, as well as the area of the tapetum, is greater in seals than in some land mammals having a nocturnally adapted eye. Walls goes on to say that the adaptations of the pinniped eye that make it appear to be nocturnal compensate for the reduced intensity produced by the narrow pupil in air as well as that produced by the reduction of light when the animal dives to relatively great depths. Walls does not comment about how well pinnipeds may be able to see under low levels of luminance except to indicate that with these nocturnal adaptations the animal should have relatively good visual acuity under low levels of luminance while underwater. On the other hand, if the pupil remains constricted in air under low levels of light, then it would be expected that the reduced amount of light should result in poorer visual acuity in air than underwater. However, if the pupil remains dilated in air as well as underwater at very low light levels, then the sea lion should have very poor acuity in air because of the great astigmatism of the cornea (Johnson, 1901; Walls, 1963).

In previous experiments dealing with the effects of luminance on visual acuity, the stimulus configurations used were not appropriate to the visual acuity task *per se*; therefore, it is not surprising that the differences found between the visual acuity of *Zalophus* in air and underwater were not significant, even at levels of luminance down to approximately 10^{-6} mL (Schusterman, 1968, 1969). However, in the present study, which sought to determine aerial and underwater visual acuity thresholds of *Zalophus* under a wide range of luminance, the stimulus configurations used consisted of gratings—the same targets that were used in the previously described experiments.

B. Methodology

The animal tested was a 4-year-old male *Zalophus* (Spike) that had been previously trained and tested on size and line-length discrimination tasks both underwater and in air (Schusterman, 1968). The experiments were conducted in a light-tight tank, which was periodically inspected and corrected for light leaks. Figures 8 and 9 show the principal features of the apparatus, including the target presentation board. At the beginning of each trial, the board

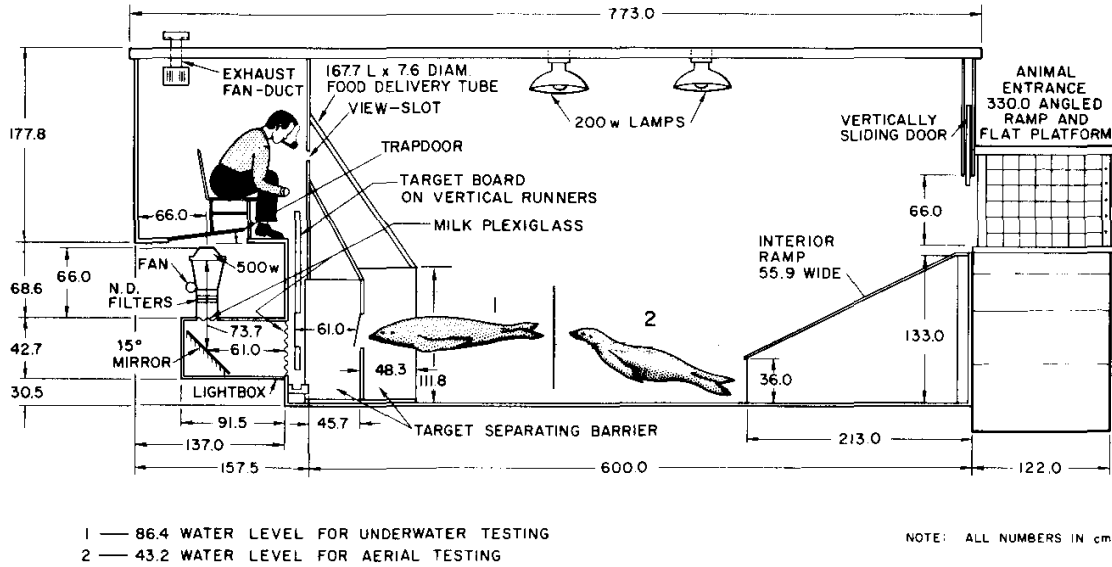


Fig. 8. Schematic diagram of dark tank and apparatus to test sea lion visual acuity under different levels of background luminance. Side view.

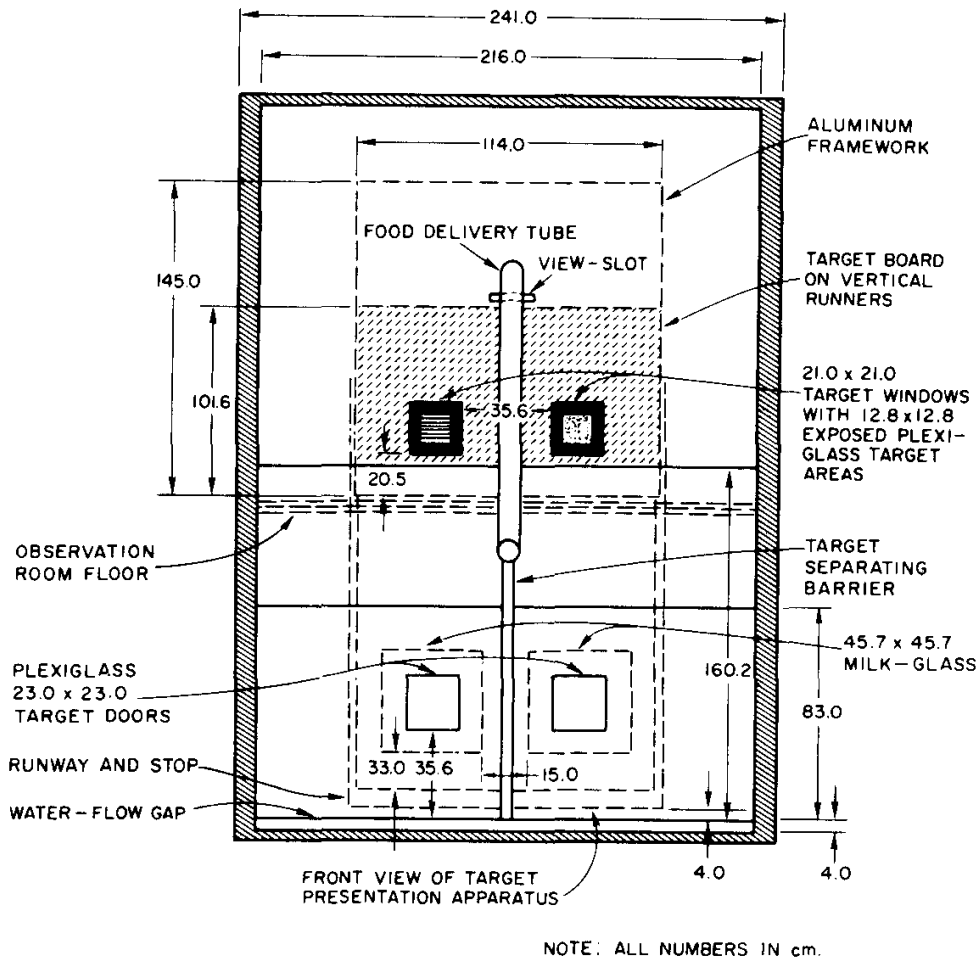


Fig. 9. Schematic diagram of apparatus to test sea lion visual acuity under different levels of background luminance. Front view.

holding the target was lowered from behind an opaque screen. Once the targets were in place, the animal indicated its choice by pressing one of two clear plexiglass windows situated 61 cm in front of the target array. Thus the minimum distance between the acuity gratings and the animal at a constant distance of 61 cm. The response windows were hinged at the top and wired so that a 5-cm displacement activated a microswitch and lit a red 12-W light in the experimenter's compartment. Activation of the microswitch defined the indicator response by the sea lion. An opaque barrier extended out 48.3 cm between the hinged windows and was effective in preventing the sea lion from responding to both windows in rapid succession.

The acuity targets were illuminated from behind by a 500-W General Electric iodine cycle floodlight which was kept at a constant line voltage of 110 and which shone down through a funnel arrangement to a light box. The light was then reflected by a mirror onto two milk plexiglass plates. The intensity of the light falling on the milk plexiglass plates behind the acuity targets was varied with neutral density filters, which were inserted into the funnel arrangement, thus intercepting the light rays before they reached the reflecting surface.

Luminance was calibrated periodically, using either an SEI light meter or a Minolta spot meter. Initially, aerial and underwater measures were taken through a periscope. At the highest intensity used in the experiment, the aerial reading was 0.4 mL higher than the underwater reading.

The animal had been trained to hold at a starting position approximately 4 m in front of the target presentation apparatus. This starting position was near the front of the interior ramp (see Fig. 8). To begin a trial, the experimenter lowered the target board, which released a normally closed microswitch, thus turning on the 500-W lamp. This event signalled the animal to swim forward, either with his head underwater or in air, depending upon the test condition. The animal's task was to strike the window directly in front of the variable target in order to obtain a piece of herring. The experimenter immediately reinforced this response by dropping a piece of herring through the food delivery tube. A response to the standard target was counted as an error and was not reinforced. At the conclusion of the trial, regardless of whether the response was correct or incorrect, the display board was raised. This automatically turned off the 500-W lamp and turned on a 25-W red bulb in the experimenter's compartment, enabling him to record the response and change the position of the target. Position of the targets was randomly determined.

A modified method of limits was used to obtain visual acuity thresholds (defined as the interpolated values at which the animal responded correctly 75 percent of the time) for each of six different luminance levels, ranging from 3 mL to 3×10^{-6} mL. Prior to the start of all test sessions in which limu-

nance was either 3×10^{-2} mL or less, the animal was dark-adapted for 30 min. Dark adaptation was carried out for only 10 min when luminance was at 3 mL. At each test session, the luminance remained constant, and stripes were made finer if the animal succeeded in making eight or more correct responses in ten successive trials, and made broader if the animal committed three or more errors in ten successive trials. Thus, acuity gratings were changed every ten trials. A session was terminated only after the animal had succeeded at a given acuity grating. The minimum number of trials at a given test session was 60, and on a few occasions the animal was given as many as 120 trials. The same neutral density filter was used on two successive test sessions, first in air and then for testing underwater. After obtaining a threshold at a given luminance level, it was decreased by either 1 or 2 log units. Following the first determination of the luminance function, a complete replication was obtained.

C. Results

The main results of this experiment are shown in Table III and Fig. 10. Table III contains the total number of trials and the percentage of correct responses for all visual angles tested under each of the six levels of background lighting. Figure 10 plots aerial and underwater visual acuity thresholds in terms of visual angle as a function of the six levels of background luminance. Both aerial and underwater visual acuity decreased (i.e., targets subtending small visual angles became increasingly difficult to resolve) with decreasing background luminance. However, these luminance functions for visual acuity were dramatically affected by whether the sea lion was viewing the targets underwater or in air. Underwater, visual acuity dropped quite slowly between 3 and 3×10^{-4} mL, and even under the very dim conditions

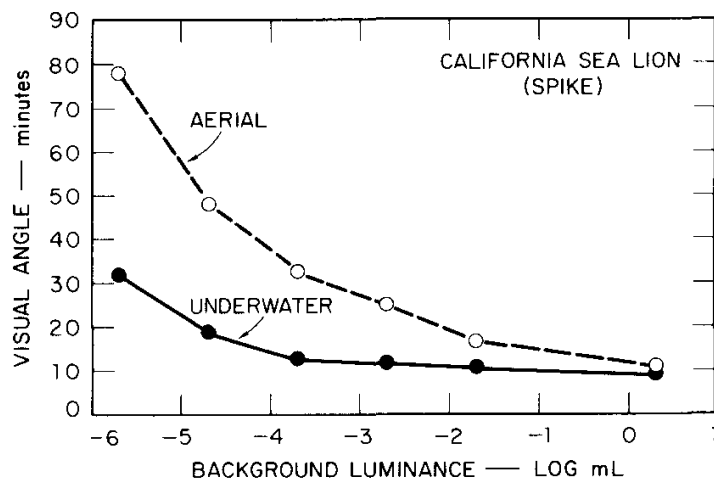


Fig. 10. Aerial and underwater visual acuity thresholds as a function of background luminance.

Table III. Correct Responses of California Sea Lion Spike as a Function of Visual Angle and Luminance^a

Line width (mm)	Visual angle at 61 cm	Luminance (mL)											
		3		3×10^{-2}		3×10^{-3}		3×10^{-4}		3×10^{-5}		3×10^{-6}	
		No. trials	Percent correct	No. trials	Percent correct	No. trials	Percent correct	No. trials	Percent correct	No. trials	Percent correct	No. trials	Percent correct
Underwater													
10.3	58.2'											10	100
8.7	47.8'											60	90
6.3	36.3'											120	83
4.8	26.5'											70	92
3.2	18.0'			40	98	20	100	20	100	60	97	150	92
2.3	13.0'			80	93	50	96	100	95	150	73	150	66
1.9	11.0'	20	100	90	77	80	58	40	58	50	50	20	45
1.7	9.6'	100	93	50	66	30	67						
1.5	8.6'	90	60	10	50	10	50						
1.3	7.2'	30	53										
0.96	6.7'	10	50										
In air													
25.4	2°23.0'											60	97
19.1	1°47.5'											110	89
12.7	1°11.5'											100	72
10.3	58.2'											60	67
8.7	47.8'											20	50
6.3	36.3'			20	100	10	100	50	94	110	75		
4.8	26.5'			80	88	90	94	140	84	40	60		
3.2	18.0'	70	97	110	80	60	55	10	50				
2.3	13.0'	90	83	60	45								
1.9	11.0'	100	77										
1.7	9.6'	50	60										
1.5	8.6'	10	40										

^a All visual angles were calculated at a distance of 61 cm.

a target subtending a visual angle of 13' could still be resolved by the sea lion in luminance as low as 3×10^{-4} mL. In contrast, the aerial visual acuity of the sea lion, although nearly the same as that underwater at the highest luminance tested (3 mL), dropped precipitously between 3×10^{-3} and 3×10^{-6} mL. Thus, even targets subtending as wide a visual angle as 18' to 27' could not be resolved by the sea lion in air in the dim light of 3×10^{-4} mL.

V. SUMMARY AND DISCUSSION

A series of behavioral experiments was conducted using three California sea lions, one Steller sea lion, and one harbor seal to determine the extent to which these pinniped forms can visually resolve fine detail under a variety of conditions. The task for each of the animals was to give a differential response to a striped or a gray target of equal brightness. All targets consisted of lines or grating patterns in which the widths of the black and white lines were equal, regardless of the number of lines. The task of resolving such gratings is generally recognized as one of the most critical aspects of visual acuity, and is less subject to errors involving intensity discriminations than most other types of tasks used to measure visual acuity (Riggs, 1965). In all the experiments conducted, visual angles were readily computed since the animals were always kept at a given or known distance from the acuity targets prior to making a differential response.

The effects of several variables on pinniped visual acuity were studied, both singly and in combination; these included aerial vs. underwater viewing, distance from target, and background luminance. The effects of these variables proved relatively minimal with the exception that luminance had a profound differential effect on aerial and underwater visual acuity in the California sea lion.

In the luminance range of approximately 3–130 mL, all members of the three species studied were capable of consistently resolving gratings subtending visual angles of from 5' to 9' of arc underwater in a variety of testing situations. Although these visual acuity thresholds in terms of visual angle are considerably inferior to many of the primates (man, 26''; chimpanzee, 28''; rhesus monkey, 34''), in terms of the currently available comparative data on visual acuity functions, these pinnipeds compare quite favorably with the several species of land mammals reputed to have rather sharp aerial vision, such as the elephant (10'), antelope (11'), red deer (9.5'), and the domestic cat (5.5') (see Rahmann, 1967, for a review of the literature on comparative visual acuity).

The finding that all three sea lions could resolve lines subtending visual angles of less than 7', whereas *Phoca* could not, suggests that possibly

the visual capability of pinnipeds underwater may differ significantly at the family level and may be related to different feeding or social behavior patterns. However, further study on several additional species with a larger number of subjects is necessary before any such generalizations can be made.

The results, indicating that the visual acuity of the California sea lion in daylight is similar underwater and in air and that aerial acuity is not deleteriously affected at a distance of 5.5 m, *do not support* the view that the eye of pinnipeds is especially adapted for seeing underwater only and that in air the vision of these amphibious marine mammals is subject to gross dioptric errors, including myopia and astigmatism. It is true, however, that all *Zalophus* subjects initially had difficulty resolving grid lines in air and that special "warm-up" sessions had to be instituted before their aerial acuity matched their underwater acuity. This suggests that, in air, pinnipeds make special postural and visual accommodative adjustments in order to fix a relatively clear image on the retina. Aerial and underwater comparisons of the visual acuity in *Zalophus* under good or moderate lighting conditions are supportive of the stenopaic theory of pinniped aerial visual acuity (Walls, 1963; Johnson, 1901). According to this theory, underwater—where the cornea plays no role in focusing an image on the retina—the relationship between the position of the retina and the refractive strength of the lens is such that the animal will have a sharp retinal image. On the other hand, in air—where the cornea makes the eye strongly myopic and astigmatic—the pupil closes down to a narrow vertical slit (stenopaic vision). Therefore, the refractive power of the cornea in the short axis of the slit is irrelevant since the narrow width acts as a pinhole, thus providing the eye with a huge depth of focus in that meridian. Although the optics of the cornea does play a role in the axis parallel to the length of the slit, the astigmatism in that axis combined with the spherical power of the cornea makes the eye approximately emmetropic in that meridian.

Behavioral evidence from one California sea lion on the ability of pinnipeds to resolve detail under low levels of background luminance in air and underwater strongly suggests that decreasing luminance down to 10^{-4} mL has only a slight effect on underwater visual acuity but has a most profound, deleterious effect on aerial visual acuity. At this light level, the aerial vision of *Zalophus* is somewhat poorer than that of the rat under moderate luminance (20–36'—see Rahmann, 1967). but their underwater vision is nearly as good as that of the rhesus monkey and baboon in air (8–13') at 10^{-4} to 10^{-5} mL (Behar, 1968). With decreasing background luminance, the relative rate of decline in the underwater visual acuity of the sea lion is considerably less than that of humans and several nonhuman primate forms (Behar, 1968). These findings on the sea lion are consistent with anatomical evidence suggesting that the highly 'specialized "pinniped eye" is structurally

adapted for efficient functioning in dim light. However, this is true only with regard to their underwater vision. Their dioptric and accommodative mechanisms appear to be such that although they are adaptive for seeing in air under moderate levels of luminance, they are not adaptive for seeing detail under low levels of luminance, either because the pupil remains constricted in air under low levels of light, thus reducing the amount of light entering the eye, or because the pupil becomes fully dilated in dim light in air, resulting in a significant corneal astigmatism.

It is particularly significant to note that the present behavioral results are consistent with the present knowledge about the retinal structure and organization of some pinniped eyes. A recent histological analysis (Landau and Dawson, 1970) of retinas from the California sea lion, the northern fur seal, and the harbor seal revealed no area centralis in any of these pinniped forms, with only rod-shaped receptors being observed. They determined that the ratio of these receptors to ganglion cells was approximately 100:1, a figure similar to estimates of human parafoveal receptor-to-ganglion cell ratios. Landau and Dawson note that visual acuity in rod monochromat humans is similar to the visual acuity of the cat and several pinniped forms, all of which have quite similar receptor-to-ganglion cell ratios.

Because there is not enough information available about the marine ecology of *Zalophus*, *Eumetopias*, and *Phoca*, it is difficult at this time to draw any definite conclusions regarding the ways in which these three pinniped forms use their vision underwater for general orientation, feeding, and social communication. All three species emit vocal signals underwater as well as in air (Schusterman and Balliet, 1969; Schusterman *et al.*, 1970), and there is strong experimental evidence that underwater acoustic signalling plays a role in the social behavior of *Zalophus*. Furthermore, depending on the temporal and geographic factors, the degree of water turbidity may place severe limitations on the visually guided feeding behavior of these animals. This would be especially true of *Phoca*, which sometimes lives in rather muddy bays and estuaries (Scheffer, 1958). Whether *Phoca*, when searching for prey under such conditions, relies on its passive hearing abilities, which have been experimentally shown to be more than reasonably adequate for detecting and localizing sounds underwater (Møhl, 1968), or on echolocation or some other sensory system is still problematic (Poulter, 1968; Schevill *et al.*, 1963). Our results, however, demonstrate that underwater visual resolution in all three species is similar to that of some visually active carnivores on land, such as the cat, and is quite suitable for detecting even relatively small food prey at some distance. The aerial vision of these amphibious mammals also appears well suited for the detection of predators, such as man, as well as for recognizing conspecific individuals or classes of individuals and for recognizing landmarks for purposes of migration. It is likely that many

species of sea lions as well as some seals appear to have poor visual acuity in air under daylight conditions, especially with regard to their reactions to human observers, not because their visual acuity capacity is poorly developed for seeing in air in terms of dioptric and accommodative mechanisms and retinal anatomy and organization, but because of selective attention factors. I have suggested elsewhere (Schusterman, 1968) that the reason the aerial visual discrimination of sea lions in daylight appears to be inferior to that of harbor seals is because of the great amount of vigilance behavior shown by harbor seals in the wild and in captivity. The harbor seal, in contrast to sea lions and some other seals, is constantly searching its environment by means of vision and audition, and is therefore much more likely to detect subtle environmental changes.

The present results indicate the potential significance of the visual channel in pinnipeds for such behavioral functions as feeding, predator detection, social communication, and navigation. As has been pointed out elsewhere, each sensory modality has its own special advantages and disadvantages (Marler and Hamilton, 1966). It is likely that pinnipeds as well as other marine mammals use the acoustic or visual channel as receptors, depending upon the situation, or use both channels by combining them in a complementary fashion.

To my knowledge, these are the first visual acuity threshold estimates obtained on any marine mammals using acuity gratings. In earlier experiments, I used a minimum separable discrimination, with patterns consisting of broken and solid black rectangles, 1.5 cm wide and 10 cm long, on a white background. With these test patterns, the minimum discriminable visual angles were estimated to be slightly less than 2' for both *Phoca* and *Zalophus*. Moreover, there was virtually no difference between the aerial and underwater visual acuity of *Zalophus*, even with background luminance as low as 10^{-6} mL. Using a series of discriminations consisting of two such rectangles versus one, with the space between the two rectangles being progressively reduced, Spong and White (1969) found a minimum discriminable visual angle of approximately 6' at a distance of 46 cm in two cetaceans, the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) and the killer whale (*Orcinus orca*). Width and height dimensions of the rectangles used during the final threshold phases of the experiments were 1.3 cm for each of the two rectangles and 2.5 cm for the one rectangle, with the height of the rectangles remaining at 31 cm. In a recent discussion of the types of test patterns and tasks used for measuring visual acuity, Riggs (1965) points out that the resolution of only two fine lines depends on the dimensions of the lines, among other things. Broadening of the lines would tend to lower the minimum discriminable threshold, and visual acuity measured in this way probably involves a brightness or intensity discrimination. In view of these considera-

tions and in light of the present results, it seems quite likely that with the types of test patterns used in our earlier attempts to obtain underwater visual acuity thresholds in pinnipeds, the obtained threshold values considerably overestimated their visual resolving power. Perhaps a similar criticism may be leveled at the only experiments thus far reported on the visual acuity of cetaceans (Spong and White, 1969).

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