

AERIAL AND UNDERWATER VISUAL ACUITY IN THE
CALIFORNIA SEA LION (*ZALOPHUS CALIFORNIANUS*)
AS A FUNCTION OF LUMINANCE*

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Amphibious Nature of Orientation

Pinnipeds engage in some more or less spectacular activities that presumably depend on a variety of orientation skills. Weddell seals (*Leptonychotes weddellii*) 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.⁷ Northern fur seals (*Callorhinus ursinus*) migrate extensively, sometimes traveling several thousand miles, and adult males show a strong homing tendency, frequently returning and occupying the same territorial location for three successive reproductive seasons.²⁶ Without the aid of special nesting sites, fur seal mothers leave their pups and feed at sea for periods lasting more than two weeks. They then return to specific localities on the rookeries where they meet and feed only their own pups.^{1,16}

These are only a few examples of known orientation and navigation skills performed by some pinniped species. Several other species are known to perform similar feats, albeit on a less spectacular scale. It should be noted that in two of the three examples given, spatial orientation and cue recognition are required both above and below the water surface. Feeding behavior of pinnipeds is, of course, an exclusively aquatic phenomenon, and probably for that reason, is very poorly understood. However, we do know that several species feed either 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, sometimes in relatively clear water and sometimes in relatively opaque water.

On the basis of these brief descriptions of the orientational and navigational abilities of seals and sea lions, 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 would be in contrast to the way we think of the guidance system of predator birds as being visual or the guidance system of some whales and some bats as being acoustical.) Nor would one expect any single sensory system to have become so totally adapted for high resolution in water as to show little or no power of "accommodation" 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 several 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 prevailing at the time the task is being performed.

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One of the initial steps in finding out about the sensory basis of an animal's orientational and navigational skills is to determine its differential and absolute sensitivity by means of experimental procedures making use of a variety of psychophysical techniques. 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. Most of our efforts have been concentrated on one species—the California sea lion (*Zalophus californianus*).

This series of investigations grew out of earlier unsuccessful attempts to demonstrate under controlled laboratory conditions that *Zalophus* was capable of generating a sound under water, listening to the returning echoes, and thereby detecting and discriminating among a variety of objects (echolocation or active sonar).^{17,18} Although *Zalophus* has been shown to be quite vocal, most of its sound production under water may be considered as social communicative signals rather than as echolocation signals.^{18,21} For the present we remain unconvinced that echolocation is relied upon by *Zalophus* to any significant extent for purposes of orientation and navigation.

Visual Orientation

Seals and sea lions have been observed to approach their prey from below, thus silhouetting them against the ambient surface light.⁴ Such observations suggest that at least some pinnipeds depend a good deal on visual orientation when feeding. When the cornea of the vertebrate eye interfaces water rather than air, it loses a great deal of its refractive power because the index of refraction of the cornea is nearly the same as that of water. Pinnipeds have apparently compensated for the loss of the refractive power of the cornea under water by possessing a large spherical lens that apparently provides enough accommodation to focus a reasonably well-defined image on the retina.^{5,12,25} Recent experimental evidence supports the view that several pinniped forms, including the California sea lion (*Zalophus*), Steller sea lion (*Eumetropias jubata*), and the harbor seal (*Phoca vitulina*) have relatively good visual acuity under water in moderate light, up to 85 to 130 ml.^{22,23} All animals observed were capable of consistently resolving gratings subtending visual angles of from 5' to 8' of arc in a variety of behavioral test situations. Moreover, experimental evidence indicates that in moderate light the visual acuity of *Zalophus* in air is essentially the same as it is under water.²³ This finding supports the stenopaeic theory of pinniped aerial visual acuity,^{6,25} which states that in air the effects of the high corneal astigmatism on the retinal image is essentially nullified by the pupil's constricting to a narrow vertical slit. The size and shape of the pupil, as well as the corneal astigmatism, have recently been reconfirmed in refraction experiments on the harp seal (*Pagophilus groenlandicus*).¹²

It is clear then that in terms of resolution of detail in moderate light, the aerial vision of some pinnipeds may be used for the recognition of landmarks for purposes of migration and that their underwater vision is quite well suited for the detection and discrimination of food prey.

Luminance and Visual Acuity

Since *Zalophus*, as well as several other species of pinnipeds, sometimes procures food in relatively dim light⁴ and appears to be quite active at night on land during the breeding season,¹⁰ a question arises regarding the extent to which underwater and aerial visual acuity of this animal 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 acoustical channel for social communication and, therefore, seldom use their aerial vision as compared to land mammals.¹¹ Similarly, under water where several species, including *Zalophus*, are quite vocal,^{3,13,24} 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.¹³

There are various lines of anatomical and behavioral evidence to suggest that under water at least the visual acuity of pinnipeds in extremely low light may be relatively sharp. Walls,²⁵ for example, states the number of layers of cells, as well as the area of the tapetum in seals, is greater than that 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 a nocturnal one 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 on 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 under water. 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 under water. However, if the pupil remains dilated in air as well as under water at very low light levels, then the sea lion should have very poor acuity in air because of the great astigmatism of the cornea.

In previous experiments dealing with the effects of luminance on visual acuity, stimulus configurations were used that were not appropriate to the visual acuity task per se; therefore, it is not surprising that only insignificant differences were obtained between the visual acuity of *Zalophus* in air and that under water even at levels of luminance down to approximately 10⁻⁶ ml.^{19,20} However, in the present experiment, which sought to determine aerial and underwater visual acuity of *Zalophus* under a wide range of luminance, stimulus configurations consisting of grid lines were used and visual acuity could be specified in terms of the angular width of the line of the finest grating that could be resolved.

Methodology

The animal tested was a four-year-old male *Zalophus* that had been previously trained and tested on size and line-length discrimination tasks both under water and in air.¹⁹ The experiments were conducted in a light-tight tank that was periodically inspected and corrected for light leaks. Figures 1 and 2 show the principal features of the apparatus, including the target presentation board. Acuity targets were produced from 12.7 cm² photos of Ronchi rulings, with 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 grey. Variable gratings consisted of lines varying in width from 25.4 mm to 0.96 mm. When compared with the standard at distances preventing resolution of the lines, three 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. A black frame surrounded the acuity grating. At the beginning of each trial, the board holding the targets 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,

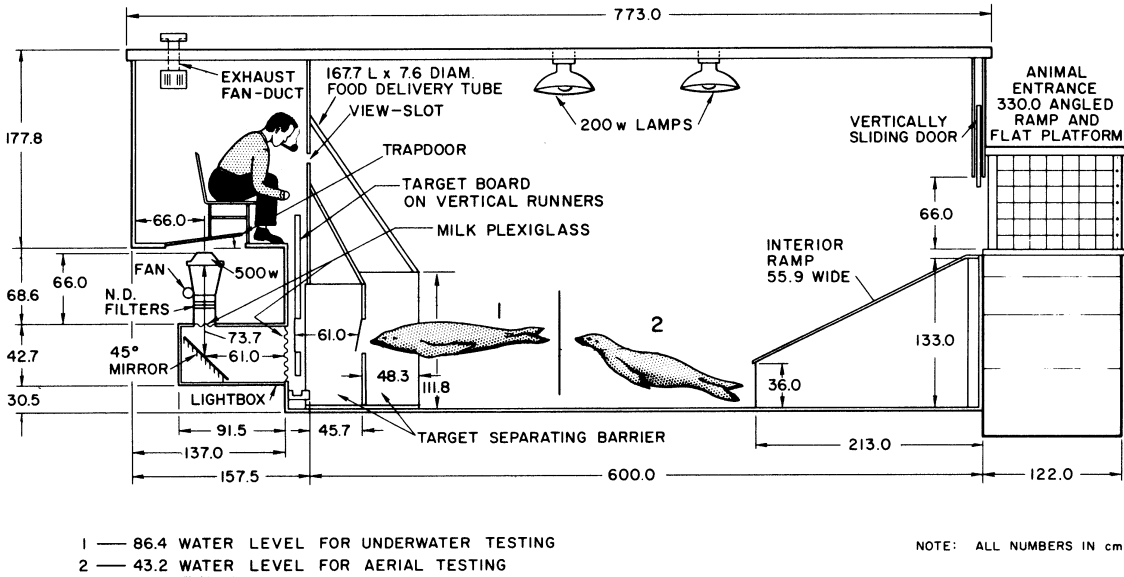


FIGURE 1. Schematic diagram of dark tank and apparatus to test sea lion visual acuity under different levels of background luminance. Side view.

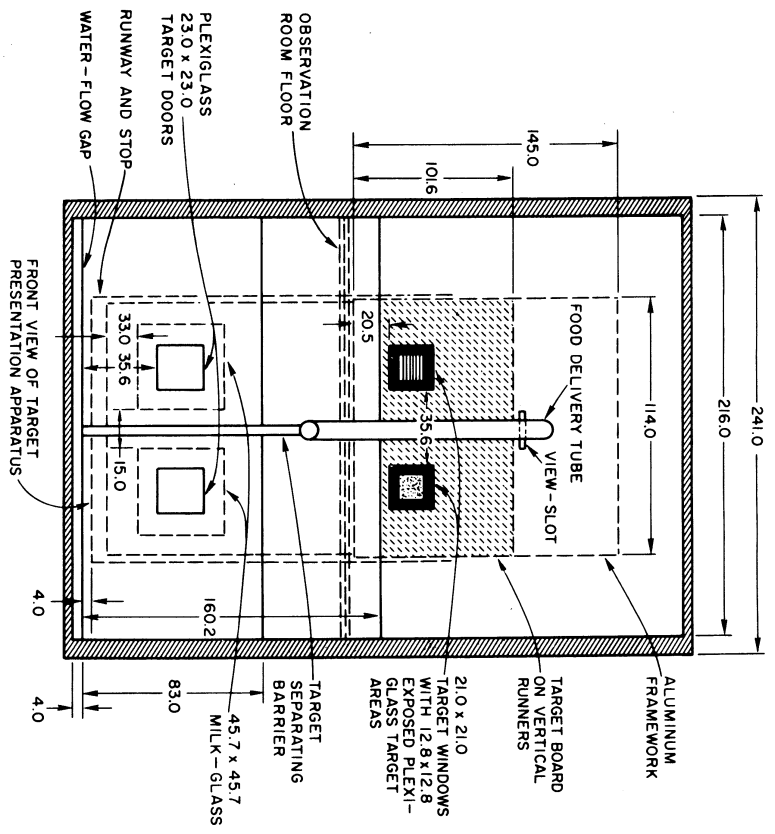


Figure 2. Schematic diagram of apparatus to test sea lion visual acuity. Front view.

the minimum distance between the acuity gratings and the animal was maintained 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-volt 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 light source for background lighting was a 500-watt General Electric iodine cycle floodlight kept at a constant line voltage of 110 that shone down through a funnel arrangement to a light box. The intensity of the light falling on the milk plexiglass plates behind the acuity targets was varied with neutral density filters that 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 more 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 (FIGURE 1). A trial began by lowering the target board, which released a normally closed microswitch thus turning on the 500-watt lamp. This event signaled the animal to swim forward, with his head either under water 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-watt lamp and turned on a 25-watt 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% 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 background luminance was either 3×10^{-2} or less, the animal was dark-adapted for 30 minutes. Dark adaptation was carried out for only ten minutes when background luminance was at 3 ml. At each test session, background 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 under water. After obtaining a threshold at a given luminance level, it was decreased by either one or two log units. Following the first determination of the luminance function, a complete replication was obtained.

Results

The main results of this experiment are shown in FIGURES 3 and 4. FIGURE 3 shows the percentage of correct responses for most of the visual angles tested under each of the six levels of background lighting. FIGURE 4 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 or not the sea lion was viewing the targets under water or in air. Under water, visual acuity dropped quite slowly between 3 and 3×10^{-4} ml. 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 under water 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.

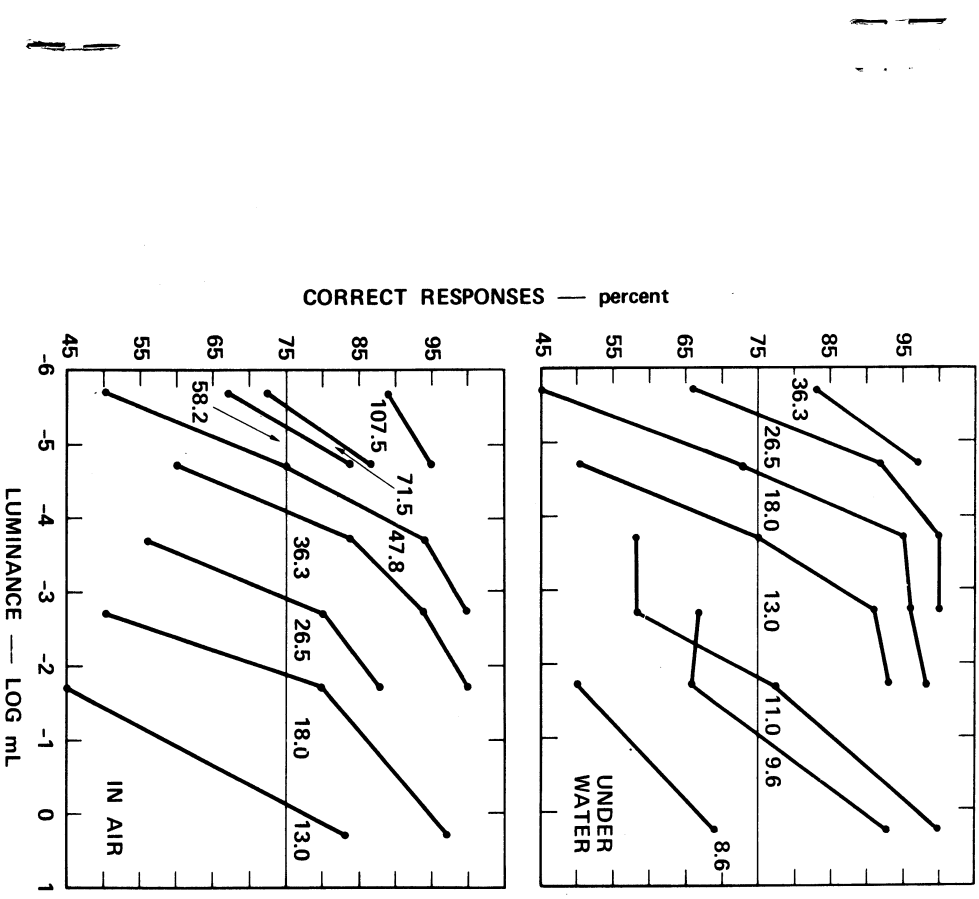


FIGURE 3. Luminance functions of sea lion for acuity targets subtending visual angles indicated.

Discussion and Conclusions

Behavioral evidence from one California sea lion on the critical question regarding the ability of pinnipeds to resolve detail under low levels of background luminance in air and under water strongly suggests that decreasing luminance down to 10^{-4} ml has only a slight effect on underwater visual acuity, whereas it 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 mod-

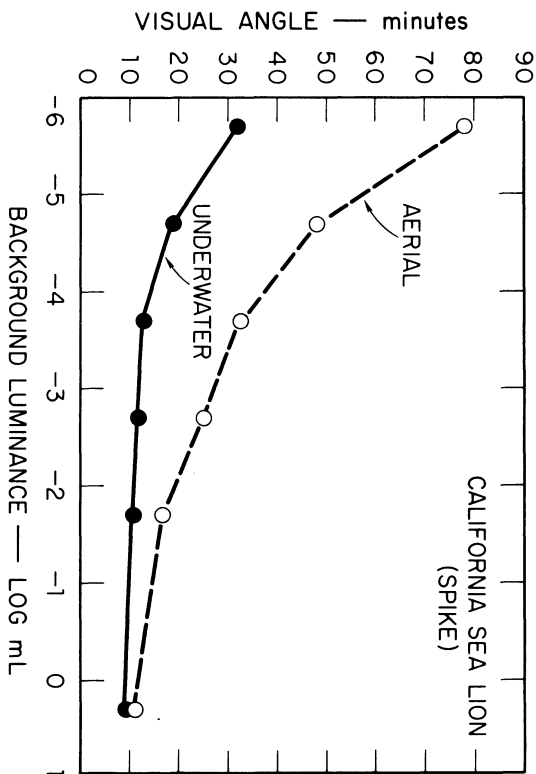


Figure 4. Aerial and underwater visual acuity thresholds as a function of luminance.

erate luminance ($20'$ to $36'$),¹⁵ while its underwater vision is nearly as good as those of the rhesus monkey and baboon in air ($8'$ to $13'$) at the same level of luminance.² 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 other primates.² 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 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 what is presently known about the retinal structure and organization of some pinniped eyes. A recent histological analysis by Landau and Dawson⁸ 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 Dawson⁸ also note that visual acuity in rod monochromat humans, as determined by Hecht in 1948 and presented by Pirenne,²⁷ is similar to the visual acuity of the cat and several pinniped forms, all of which have quite similar receptor-to-ganglion-cell ratios.

The present results indicate the potential significance, as well as the limitations, of the visual channel in pinnipeds for feeding orientation, social orientation, navigation, and migration. As has been pointed out elsewhere, each sensory modality

has its own special advantages and disadvantages.⁹ It is likely that pinnipeds and other marine mammals use the acoustic or visual channel as a primary distance receptor, depending upon the situation, or use both channels by combining them in a complementary fashion.

Summary

Visual acuity thresholds in *Zalophus* were obtained for luminance levels ranging from 3 ml to $3 \times 10^{-6} \text{ ml}$. Decreasing luminance down to 10^{-4} ml has only a slight effect on underwater visual acuity, whereas it has a most profound deleterious effect on aerial visual acuity. These findings 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 the animals' underwater vision.

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Discussion

DR. HOWLAND: I didn't understand about the astigmatism of this eye and thus I'd like to know just how much power the corneal-air interface has in terms of total dioptric power of the eye? Is it a round cornea as in humans?

DR. SCHUSTERMAN: No, it is not a round cornea. It has a very flat portion that gives rise to the astigmatism and that is essentially a vertical, flattened portion that runs congruent with the slit vertical pupil.

DR. HOWLAND: In your targets you had a raster of lines, and I think in the pictures we saw they were horizontal. Does it make a difference if, as you say, the eye is astigmatic whether the lines are horizontal or vertical?

DR. SCHUSTERMAN: It's the horizontal lines that should give rise to a blurring effect; vertical lines should not. We started out with vertical lines and then we were going to switch back and forth. We got locked onto horizontal lines and finished the study before I remembered to go back to vertical lines. I don't think it makes much difference, as we knew that the theory told us that it would only be horizontal lines.