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Conditioned Vocalizations as a Technique for Determining Visual Acuity Thresholds in Sea Lions

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*Abstract. Aerial visual acuity and underwater visual acuity were measured in two sea lions (*Zalophus californianus*) by training them to emit click bursts if they saw a striped target or to remain silent if they saw a gray target. The closest grating spacings that could be resolved both in air and under water subtended a visual angle of 5.5 minutes of arc at a distance of 5.5 meters.*

Sea lions (*Zalophus californianus*) are capable of learning to emit underwater click vocalizations in the presence of visual cues (1). Aerial as well as underwater barking by *Zalophus* males can be suppressed, with the degree of suppression dependent upon the social context (2). Thus, exteroceptive cues to the visual or auditory channel can exert strong control over the emission of these sounds by *Zalophus*. How subtle can these cues be and still maintain control over the sound production? Can a wide variety of stimulus configurations be used to acquire control over underwater sound production? Can discriminative con-

trol of vocal behavior be used to determine the absolute or differential sensitivity of *Zalophus* to certain aspects of its environment?

This paper describes several experiments in which a sexually mature male (Sam) and a sexually mature female (Bibi) *Zalophus* were trained to emit a burst of short-duration sound pulses or clicks when viewing targets consisting of black and white stripes, and to remain silent when viewing a target that appeared flat gray. To our knowledge, this is the first report of a threshold determination for a nonhuman animal by means of a conditioned vocalization technique where shock was not

used as an unconditioned stimulus. By training the animal to keep its head in a fixed position while making the discrimination and by varying the width of the stripes, we were able to estimate the finest detail capable of being resolved by the eye of the sea lion which could be communicated to the experimenter by means of a vocal signal. Threshold data were acquired in this manner in air and under water at several distances, thus allowing a direct comparison of visual acuity in the two media. This comparison is particularly important since several observers have suggested that the eye of *Zalophus* is especially adapted for seeing under water and that the visual acuity of this species in air, even in daylight, is of a relatively low order (3).

Although both animals were given similar training, techniques were perfected with Sam. First, underwater clicks were instated by the frustration technique (1), that is, reinforcement was withheld while the animal worked at a target-pressing task—an act that hitherto had yielded a fish reward. This quickly led to the production of click bursts, which were promptly reinforced with a piece of fish. Next, the vocalization was brought under the control of a size cue (1). Vocalizing in the presence of a large target was reinforced, and remaining silent in the presence of a small target was also reinforced. Thus, vocalization or silence in the presence of the appropriate target defined a correct response. In order to ensure adequate visual orientation by the animal and to keep its head in a fixed position while it was responding to the discriminative stimuli, it was next trained to place its head on a headrest while viewing discriminative stimuli. Control of vocalizations was then transferred from size to form (triangle and circle) by a progressive training or fading technique (4). Finally, multiple stimulus control was obtained with the sea lion emitting a signal under water that indicated on each of 72 problems whether it could discriminate between different patterns. One pattern was arbitrarily designated as requiring vocalization and the other as requiring silence for a 5-second period. The first 12 problems consisted of configurations differing only in shape, whereas the next 60 patterns differed in both size and shape. The learning criterion for each problem was 18 consecutive correct responses. The median errors to criterion



Fig. 1. *Zalophus* viewing variable acuity target in air.

of the first 12 problems was 73, on the next ten problems it was 30, and on the final ten problems it was 29.

Before obtaining thresholds on the two sea lions with a series of black and white stripes, we conducted a preliminary experiment in which Sam was trained to emit clicks when it saw a broken rectangle and to remain silent when it saw an unbroken rectangle (10 cm long and 1.5 cm wide). With these test patterns the minimum discriminable visual angles both under water and in air were estimated to be approximately 2 minutes at a distance of 4.5 m. However, in light of our subsequent results, and in accordance with a recent discussion by Riggs (5), it is likely that in using such stimulus configurations, we were not measuring visual acuity uncontaminated by intensity discriminations. During the next series of experiments, stimulus configurations consisted of acuity gratings produced from photos of Ronchi rulings in which the width of the lines varied from coarse to fine. In this way, visual acuity, which has been defined as the spatial resolving capacity of the visual system (6), could be specified in terms of the angular width of the stripes of the finest grating that could be resolved.

The animals were not fed for 20 hours before a test. Testing was conducted outdoors between 8 a.m. and 12 noon, in an oval tank, 4.6 by 9.1 by 1.8 m deep, constructed of redwood

and painted white. 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 (118 lines per centimeter) (0.05 mm in width). The lines were invisible to the human eye without the aid of a lens and the grating appeared as a flat gray. Variable gratings consisted of lines varying in width from 25.4 mm to 2.3 mm. When compared with the standard at distances at which the lines could not be resolved, three human observers reported that the variable gratings were indistinguishable from the standard grating.

The horizontal gratings were laminated within sheets of 22.8-cm² clear plexiglass with a black frame surrounding the acuity grating. These plexiglass squares could be slipped into a 26.7-cm² black aluminum frame. When the stimulus was presented the animal saw a 12.7-cm² acuity grating with a large black border surrounding it (see Fig. 1). Ambient light around the stimulus display area was measured with a photometer (Scientific Enterprises, Inc.) from behind the back window of the tank. Acuity targets were always presented in the shade of the testing platform. When the tank was filled with water, the readings were 130 mlam on clear days and 85 mlam on overcast days; when it was not filled with water, the readings were 200 mlam on clear days and 150 mlam on overcast days.

A "correct" response was defined as either emitting a burst of clicks in the presence of the variable stimulus, or remaining silent in the presence of the standard stimulus. Sam was required to remain silent for 5 seconds. Bibi was required to remain silent for only 3 seconds. The change in response for Bibi was necessitated by the fact that 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 second after stimulus presentation, which was always by the successive method. 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 under water 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. Although the animal's mouth was out of water in the aerial testing, its neck was in water and click vocalizations made by sea lions with their mouths closed and out of water may still be projected under water by the larynx and be picked up by a hydrophone.

The visual acuity studies consisted of three phases. First, the standard target and a variable target with striations 25.4 cm wide were presented and the sea lions were reinforced for vocalizing and remaining silent to the appropriate targets. Once stimulus control of vocalization was obtained with this target, it was 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 valuable technique in the training of many different animals, including sea lions, in psychophysical experiments involving traditional motor responses (such as pushing a target manipulandum) in that it tends to decrease or eliminate emotional behavior and may teach the animal to attend to both the location and the nature of the critical cue (7).

Table 1. 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

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. At the beginning of a test session, performance in air was generally more erratic than it was under water and both animals showed a significant practice effect only during aerial testing. Therefore, a warming-up period was used in tests 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 at a slower rate in air than it does under water, which may be the reason why naturalists have suggested that the aerial vision of this species in daylight is very poor (3). When performances stabilized, threshold estimates were bracketed between 5 and 8

minutes 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. After a ten-trial warming-up period, with a suprathreshold target, each of four variable gratings with line widths as listed on the top of Fig. 2 was paired randomly with the standard for ten consecutive trials. The pairings were repeated within each session for a total of 90 trials per test session. A total of 20 sessions were held with testing in air and water alternated daily. Thresholds were obtained at three distances in the following sequence: 3.1, 5.5, 1.9, and 5.5 m. Thus, two separate thresholds were obtained at 5.5 m.

Visual acuity threshold curves are shown in Fig. 2. In general, there appears to be little difference between underwater and aerial acuity at the closest and farthest distances measured. However, at the middle distance, 3.1 m, performances were significantly better under water 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 1) and may have been related to latency of vocalization. Although we made no measurements of the speed of vocalization, our general impression was that the animal vocalized more rapidly after stimulus presentations at 1.9 and 3.1 m as compared to 5.5 m.

Even though the probability of vocalizing to a variable target (hit) varied directly as a function of visual angle, the probability of vocalizing to the standard target (false alarm) remained relatively constant. If we disregard air-water and distance factors, at visual angles of 8.0 to 11.7 minutes, the hit and false alarm probabilities were 0.93 and 0.10, respectively, for Bibi and 0.98 and 0.09 for Sam, whereas at visual angles of 3.6 to 5.4 minutes hit and false alarm probabilities were 0.35 and 0.14 for Bibi and 0.30 and 0.17 for Sam. Thus, when the sea lions had difficulty resolving grid lines, they reported this by generally remaining silent rather than by responding randomly or persisting in a vocal response.

The results with *Zalophus* reported here are in support of the stenopaic theory of pinniped aerial visual acuity (8). According to this theory, under

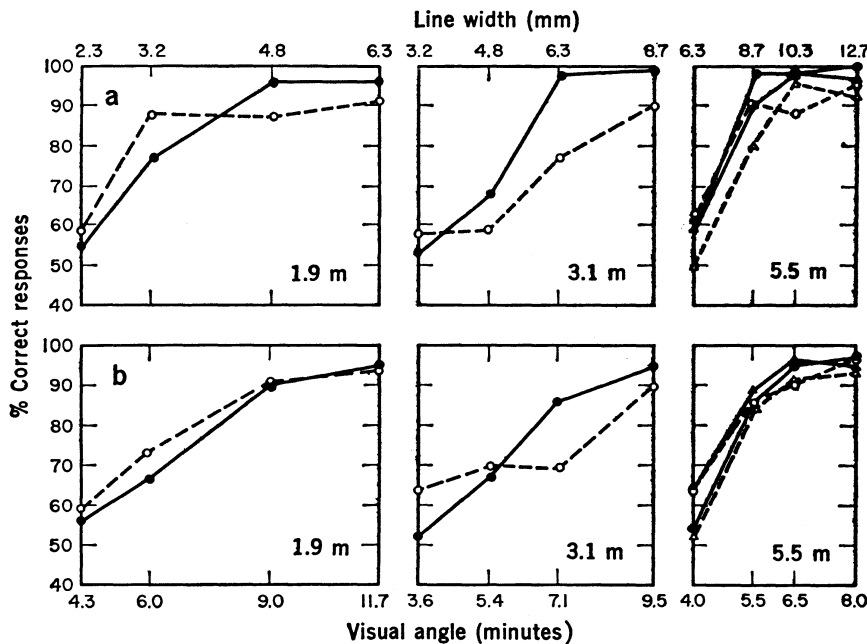


Fig. 2. Comparison of aerial and underwater visual acuity threshold curves for (a) California sea lion Sam and (b) California sea lion Bibi at three different distances. (Solid circles) Underwater tests at 1.9 and 3.1 m and first underwater test at 5.5 m; (open circles) aerial tests at 1.9 and 3.1 m and first aerial test at 5.5 m; (solid triangles) second underwater test at 5.5 m; (open triangles) second aerial test at 5.5 m.

water where the cornea plays no role in focusing an image on the retina (9), 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 very narrow slit (stenopaic vision). Therefore, the refractive power of the cornea in the direction of 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 do 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.

In terms of resolution of detail in moderate or good light, the underwater vision of *Zalophus* is similar to the aerial vision of the cat (10) and appears quite well suited for the detection and discrimination of food prey and predators as well as for the recognition of conspecific individuals or classes of individuals. The aerial vision of this species may also be used for these tasks, as well as for the recognition of landmarks for purposes of migration. These statements are intended only to upgrade the relative importance of the visual channel of these behavioral functions, and not to downgrade the acoustic channel. Each sensory modality has its own special advantages and disadvantages (11), and, depending upon the situation, it is likely that pinnipeds as well as other marine mammals use either the acoustic or the visual channel as a distance receptor, or use both channels by combining them in a complementary fashion.

The experiments reported here clearly show that a very vocal pinniped such as *Zalophus* has a high degree of control over its sound-production mechanism, and that its vocal behavior is susceptible to rather subtle variations in stimulus control. It appears likely that the sound emissions of some other pinnipeds as well as the odontocete whales may also be subjected to a fine degree of stimulus control, and thus may be used to determine their abso-

lute or differential sensitivity to certain selected aspects of their environment. Therefore, psychophysical experiments may be conducted in air or under water without the use of cumbersome manipulanda normally associated with the measurement of discriminative behavior in these animals. When desired, a marine mammal may be trained to remain in a relatively fixed position for long periods of time without swimming to the manipulandum, or, on the other hand, well-placed hydrophones can pick up the controlled sound emissions of a free-swimming animal despite the relatively great distances that separate the animal and the source of the controlling stimuli.

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9. It is well known that if one does not use goggles human visual acuity suffers enormously under water. We made a preliminary test 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 from stripes subtending a visual angle of 7.5 minutes but could not make such a discrimination when the stripes subtended a visual angle of 6.2 minutes. At distances of 4.5 and 5.5 m the subject reported that he could not even see the outline of the targets.
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