discharge to these brief light pulses, respond in a characteristic manner to stimuli balanced for scotopic vision. If the stimuli are above the threshold for the cones, as evidenced both by the presence of color when they are observed by human subjects through the same optical system and by the presence of photopic components in the electroretinogram of the monkey, light of long wavelength is always more effective in stimulating the ganglion cell than the equivalent light of short wavelength (Fig. 1). As the stimuli begin to fall below cone thresholds, as evidenced both by the fading of color in humans and by the presence of scotopic components in the electroretinograms, lights balanced for scotopic vision begin to produce identical effects on the ganglion cell (Fig. 1). The shift from cone to rod action takes place when the retinal stimulus is approximately 106 quanta deg $^{-2}$  pulse $^{-1}$  at 558 nm (nm  $= 10^{-9}$  meter).

The latency of the response is an aspect of ganglion cell function which demonstrates this behavior. Figure 2 shows the latency of a single ganglion cell to monochromatic stimuli, the energies and scotopic effectiveness of which are known. With relatively bright stimuli, the latency is much shorter in response to light of long wavelength than to light of short wavelength, the lights being of equal scotopic strength. At this point the energies required to produce the same response latency at different wavelengths resemble the spectral sensitivity of peripheral cone vision in man (4). As the energies of the stimuli are reduced, the peaks of these curves shift to the light of shorter wavelength and the light of long wavelength progressively ceases to elicit any responses at all. With the dimmest stimuli, latency is determined wholly by the scotopic strength of the light. The pattern illustrates a Purkinje shift of single ganglion cells that occurs without light-adapting the rods; a relatively similar pattern is observed if spike frequency is plotted.

It is interesting that, when a stimulus is suprathreshold for the cones, the action spectrum for eliciting either a constant latency or frequency of firing in a ganglion cell reflects cone function, even though the dark-adapted rod receptors are strongly excited. The large amplitude of the scotopic component of the electroretinogram demonstrates the strong rod activation. Somewhere between the ganglion cell and the electroretinogram, the rod signal is lost when stimuli are relatively bright. The brief burst of ganglion-cell activity, which appears before most of the electroretinograms with such stimuli, suggests that the cell is not only excited but subsequently inhibited rapidly so that only the fastest signal to traverse the retina can produce excitation. After bright stimulation this always reflects cone function. The inhibitory surround of ganglion cells demonstrated in a number of vertebrates (5) and shown to disappear after the rods begin to determine threshold (6) could be responsible.

PETER GOURAS

Ophthalmology Branch, National Institute of Neurological Diseases and Blindness, Bethesda, Maryland 20014

### **References and Notes**

- R. Granit, Acta Physiol. Scand. 7, 216 (1944);
   H. B. Barlow, R. Fitzhugh, S. W. Kuffler, J. Physiol. 137, 327 (1957);
   K. O. Donner and W. A. H. Rushton, *ibid*. 149, 303 (1959);
   R. M. Chapman, J. Opt. Soc. Am. 51, 1102 (1961).
   D. S. Blough and A. M. Schrier, Science 139, 493 (1963).
   P. Gouras, J. Opt. Soc. Am. 55, 86 (1965).

- 493 (1963).
  3. P. Gouras, J. Opt. Soc. Am. 55, 86 (1965).
  4. W. D. Wright, Researches on Normal and Defective Colour Vision (Kimpton, London, 1946); G. Wald, Science 101, 653 (1945).
  5. S. W. Kuffler, J. Neurophysiol. 16, 37 (1953); H. B. Barlow, J. Physiol. 119, 69 (1953); D. H. Hubel and T. N. Wiesel, *ibid.* 154, 572 (1960); H. G. Wagner, E. F. MacNichol, Jr., M. L. Wohlbarsht, J. Opt. Soc. Am. 53, 55 (1963). M. L. (1963).
- 6 H. B. Barlow, R. Fitzhugh, S. W. Kuffler, J. Physiol. 137, 338 (1957).
  7. I thank K. Link and R. D. Gunkel for assist-
- ance.

21 December 1964

# **Underwater Visual Discrimination** by the California Sea Lion

Abstract. Two captive sea lions (Zalophus californianus) presented with a series of size-discrimination tasks showed preferences for the smaller of two targets and gave virtually errorless performances despite changes in the form and relative size of the targets. Further tests revealed that they were capable of discriminating a size-difference ratio as small as 1.06:1.

Seals and sea lions emit series of short pulses while apparently searching for underwater objects-usually food (1). These pulses appear to be similar in many ways to the sonar clicks of the porpoise as described by Kellogg (2) and are considered by Poulter (3)to be ideally suited for the echo detection of objects under water. If seals and sea lions do have a superior sonar system, then a question arises as to the role that underwater vision plays in the abilities of these animals to navigate and find food. Although anatomical and physiological evidence suggests that most pinnipeds have good underwater vision (4), there have been no previous experiments dealing with the sea lion's visually guided behavior in an underwater environment. We have, therefore, studied the ability of sea lions to differentiate among targets of various sizes while monitoring their underwater sounds.

All testing was conducted in an oval tank constructed of redwood and measuring 4.57 m by 9.14 m and 1.83 m deep (Fig. 1). The interior of the tank was painted white; during testing it was filled with 81.8 kiloliters of fresh water, and animals could be observed and photographed by means of six windows spaced around the perimeter of the tank. A hydrophone (5) was usually available for recording and monitoring underwater sound signals.

We used two female California sea lions (Zalophus californianus), which, at the time of their arrival at our laboratory (26 February 1964) had been in captivity for approximately 3 weeks; each weighed 25 kg. They were approximately 17 to 20 months old when training was initiated. The sea lions were usually deprived of food for 22 hours before a test session.

The experimenter worked from behind an opaque screen which was set out 15.2 cm from the dock area and extended down to the water line (see Fig. 1). Targets were presented simultaneously so that they projected below the opaque screen and were at least 38 cm below 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, 114 cm in length and 0.64 cm in diameter. The targets were cut from 20-gauge sheet metal and were attached to the lower portion of each rod by means of set screws. Deflection of either rod activated a microswitch and produced a light signal behind the stimulus panel. A perpendicular divider of 3.8-cm pine projected 45 cm downward from the water level and 45.7 cm outward from the opaque screen, thus lying between the targets and preventing the animals from moving laterally from one target to the other. The distance between the centers of any two targets was 57.2 cm (Fig. 2).

Prior to formal testing both animals were trained to push with their noses

against a single square-shaped target (42.8 cm<sup>2</sup> in area). The position of the target was randomly determined within blocks of ten trials. Preliminary training was discontinued when subjects immediately began approaching the submerged stimulus display from a starting position 5 to 6 m in front of the testing platform or dock. Between trials the subjects remained near the starting position until they were signaled to approach by the sound of the stimulus display being lowered into the water. During formal testing the sea lion's task was to push one of two targets (differing in size) in order to obtain a small piece of herring (Clupea pallasi) weighing approximately 5 g. The stimulus display was immediately withdrawn following either a correct or an incorrect response. The position of the target was an irrelevant cue throughout all phases of this investigation.

After preliminary training on a single target, subjects were tested with two pairs of black circular targets and two pairs of black triangular targets. A test session consisted of 50 trials and learning criterion was designated as 90 percent correct responses at a given test session. The sequence of testing, target magnitudes, and results are shown in Table 1.

Although we originally planned to train sea lion B to respond to the large target and sea lion C to the small target, on the initial discrimination task both animals showed a strong preference for the small target. This preference resulted in virtually errorless performance by sea lion C and persistent incorrect responding and subsequent non-test-oriented or emotional behavior by sea lion B. For this reason, after the first 20 trials, sea lion B also received fish rewards for responding to the smaller target of each pair. As Table 1 shows, on the basis of this size preference, the performance of both animals was virtually errorless despite changes in the relative size and form of the targets. In general, the preference for a very small target as compared to a very large target is consistent with the notion that, in novel situations, increasing excitation or large amounts of stimulation lead to avoidance behavior, and low or decreasing degrees of excitation will elicit approach responses (6).

In obtaining the size threshold, we took advantage of this preference, which, as far as our experimental treatment was concerned, may be consid-



Fig. 1. A sea lion in the experimental tank waiting for a trial to begin. The experimenter is in the process of changing targets.

ered an "untrained" discrimination and therefore was probably influenced by fewer irrelevant variables than are most trained discriminations. We sustained the indicator response (pushing the target) by reinforcement procedures throughout testing. Differential size-thresholds were obtained by the psychophysical method of constant stimuli. The animals were always required to respond in accordance with their previous training. Each variable stimulus was paired with the standard stimulus for ten consecu-

## Table 1. Description of training.

Trai	ining stimuli		Sea lion B		Sea lion C	
Problem sequence	Areas of paired targets (cm <sup>2</sup> )	No. of trials	No. of correct responses	р	No. of correct responses	р
Circles	289.8* and 6.35	20	4	<.05		
Circles	289.8 and 6.35*	50	45	<.01	47	<.01
Triangles	289.8 and 6.35*	50	48	<.01	50	<.01
Triangles	179.8 and 10.20*	50	49	<.01	47	<.01
Circles	179.8 and 10.20*	50	50	<.01	50	<.01

\* Responses to these stimuli were reinforced.

Table 2. Values of standard and variable stimuli and percentage of responses to smaller stimulus (circles).

Stimulus characteristics			Sea lion B			Sea lion C		
Stimuli	Area (cm²)	Ratio of variable to standard	No. of trials	Responses to smaller stimuli (%)	р	No. of trials	Responses to smaller stimuli (%)	р
-6	16.5	1:2.59	100	99	<.01	100	100	<.01
-5	26.6	1:1.61	120	98.3	<.01	200	91.5	<.01
-4	34.1	1:1.26	100	95	<.01	200	89	<.01
-3	38.0	1:1.13	200	82	<.01	200	83	<.01
-2	40.3	1:1.06	120	70.8	<.01	100	62	<.05
-1	41.7	1:1.03	20	50	>.05			
Standard	42.8	1:1						
1	43.9	1.03:1	20	60	>.05			
2	45.4	1.06:1	120	71.7	<.01	100	58	>.05
3	48.4	1.13:1	200	77.5	<.01	200	77	<.01
4	54.3	1.27:1	100	94	<.01	200	92	<.01
5	69.1	1.61:1	120	93.3	<.01	200	93.5	<.01
6	111.5	2.60:1	100	99	<.01	100	99	<.01



Fig. 2. A sea lion approaching the smaller of two targets. The size ratio of the larger to smaller target is 1.13:1.00.

tive trials and, generally, four pairs were presented at each test session for a total of 40 trials per session. Random sequences of paired presentations were given from session to session.

In the first experiment dealing with size threshold, black circular disks were used as the stimuli. The results of this experiment are presented in Table 2, which shows that, as the magnitude of the size-difference ratios decreases, there is a corresponding decrease in correct responses. The table also reveals that both animals were capable of discriminating a size-difference ratio as small as 1.06:1.

To appreciate the fineness of this discrimination, we compared our results with sea lions underwater to those results obtained by Klüver (7) with two Java monkeys. The monkeys were given a great number of size discrimination problems with two rectangles. On one problem, with one of the smallest difference ratios-on the order of 1.06:1---one animal got 70 percent correct in 420 trials and the other got 61 percent correct in 365 trials. Surprisingly, the scores were almost identical to the two sea lions at the same difference ratio. It should be noted that Klüver's monkeys were generally at a fixed distance of approximately 1.23 m from the stimuli, whereas the sea lions started their approach at approximately 5 to 6 m away and rarely got closer than 1 m before making a choice.

A second experiment dealing with size threshold was conducted with black triangular targets. In this experiment we forced the animal to make a decision at least 1.23 m prior to its giving the indicator response. This was accomplished by replacing the previously used perpendicular divider with one which projected 1.23 m outward from between the stimulus targets and all the

Our results suggest that under natural illumination (sunlight) the ability of the California sea lion to discriminate objects underwater on the basis of size may be as good as the ability of some monkeys to discriminate objects in air on the basis of size. Indeed, these behavioral data confirm the anatomical evidence (4) suggesting that pinnipeds have compensated for the loss of the refractive power of the cornea underwater by having a large spherical lens which produces enough accommodation to form a reasonably well-defined image on the retina.

Throughout these experiments (8) underwater monitoring revealed no sounds suggestive of pulses or clicks used for the purpose of echo-location. On infrequent occasions, we did obtain bubble sounds and underwater barks.

Upon completion of the experiments, sea lion B was presented with a sizediscrimination task on moonless nights and did emit trains of pulses while swimming toward the targets. One tentative hypothesis concerning the click emission of sea lions seems to emerge from these investigations. Namely, that sea lions emit clicks primarily when visual cues are scarce or unavailable, but depend principally upon their visual sense for purposes of detecting and discriminating underwater objects.

RONALD J. SCHUSTERMAN WINTHROP N. KELLOGG

CHARLES E. RICE

Stanford Research Institute Menlo Park, California 94025

#### **References and Notes**

- W. E. Evans and R. Haugen, Bull. S. Calif. Acad. Sci. 62, 165 (1963); T. C. Poulter, Science 139, 753 (1963); W. E. Schevill, W. A. Watkins, C. Ray, ibid. 141, 50 (1963).
   W. N. Kellogg, Porpoises and Sonar (Univ. of Chicago Press, Chicago, 1961).
   T. C. Poulter, Inst. Elec. Electron. Eng. Trans. 10, 109 (1963).
   G. Walls, The Vertebrate Eye (Cranbrook Inst. Science, Bloomfield Hills, Mich., 1942).

- Science, Bloomfield Hills, Mich., 1942), Inst. 446.
- 5. The following equipment was used for moni-The following equipment was used for moni-toring and recording underwater sounds. Hy-drophones: (i) Channel Industries 275 (20 cy/sec to 150 kc); (ii) Fishphone (750 cy/sec to 6.5 kc). Recorders: (i) Vega at 60 inches per second (1.5 m/sec) (150 cy/sec to 150 kc); (ii) Ampex 601 at 7.5 inches per second (20 cm/sec) (30 cy/sec to 18 kc). Pream-(20 cm/sec) (30 cy/sec to 18 kc) plifier: Burr-Brown Model 100. Amp Pream-Amplifier and
- binder: Burr-Brown Model 100. Amplifer and speaker: Webster-Chicago 66-1A.
  b. Bindra, Motivation: A Systematic Reinter-pretation (Ronald, New York, 1959); E. W. Menzel, J. Comp. Physiol. Psychol. 55, 1044 (1962)
- (1962).
  H. Klüver, Behavior Mechanisms in Monkeys (Univ. of Chicago Press, Chicago, 1933).
  Supported by NSF grant GB-1437. We grate-fully acknowledge the assistance of Garth Rader who helped in testing the animals.
- 7 December 1964

## **Prenatal Auditory Sensitivity** in Chickens and Ducks

Abstract. Recordings from chick and duck fetuses inside the egg revealed an increase in the rate of bill-clapping and vocalization when the fetuses were aurally stimulated by the maternal call of their species on the day before hatching.

Several days before hatching, the head of the fetal chick and of the fetal duck moves into the air space at the large end of the egg. At this time fetuses of both species begin uttering low-intensity peeps or cheeps (1). In at least one species of duck the incubating parent begins uttering a lowintensity call coincident with the pipping of her eggs, that is, before her young have hatched (2). In line with these findings and to expand our knowledge of prenatal sensory function, it seemed worthwhile to determine whether chicks and ducklings are capable of hearing prior to hatching. Workers in neurophysiology investigating the visual modality have demonstrated electrical changes of the eve and optic lobe of highly developed chick (3) and duck (4) fetuses upon stimulation by relatively intense flashes of white light from a source located several inches from the exposed heads of the fetuses. It is possible that the auditory system of the avian fetus develops at least as fast as (if not faster than) its visual system, partly because the fetus can stimulate itself aurally but is not normally subject to patterned visual stimulation until after hatching.

Though the present study is not parametric in any sense, the positive results concerning the presence of auditory sensitivity in highly developed chick and duck fetuses seem sufficiently clearcut to warrant report now, pending completion of a more extensive examination of the various stimulative and developmental parameters which are involved.

Fifteen White Rock chicken eggs and 15 Peking duck eggs, which had been subjected to a preincubation chilling procedure to increase precision in aging (5), were candled on the day before hatching to determine the position of the fetuses in the air space (6). A small opening was made in the shell in the proximity of the bill or beak and then a sufficient amount of shell and inner membrane was removed to insert the needle electrodes, as shown in Fig. 1.