

DARK ADAPTATION AND VISUAL SENSITIVITY IN SHALLOW AND DEEP- DIVING PINNIPEDS¹

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ABSTRACT

Pinnipeds forage almost exclusively underwater. Consequently, observing them is difficult and relatively little is known of how they use their senses to locate prey, avoid predators, and navigate while diving. Vision has been presumed to be of primary importance, although previous measurements of visual functioning in pinnipeds have been restricted to just a few shallow-diving species. As diving pinnipeds experience rapid changes in light levels during descent/ascent and low light levels at depth, it has not been clear whether they possess visual capabilities adequate for use while diving, particularly in the case of deep-diving species. To examine this issue, behavioral psychophysics have been used to assess and compare the dark adaptation rates and relative light sensitivities of a deep-diving pinniped (northern elephant seal, *Mirounga angustirostris*), two shallow-diving species (California sea lion, *Zalophus californianus*, and harbor seal, *Phoca vitulina*), and a human subject.

In comparison to the human subject, both the California sea lion and the harbor seal dark-adapted relatively quickly and were more light sensitive. These findings suggest that both of these species are well suited for vision in the moderately dim shallow-water environments in which they dive to forage. In contrast, the elephant seal reached complete dark adaptation in less than half the time taken by the other pinnipeds, and it was significantly more

¹ On a personal level, this paper is related to Ken Norris' thinking about echolocation in marine mammals. He, as well as many others, initially believed that pinnipeds probably used echolocation. He changed his mind in September of 1966 after he heard a presentation by R.J.S. at the Animal Sonar Meetings in Frascati, Italy, about the unlikelihood that California sea lions use echolocation as compared to relying on other sensory modalities, particularly vision, to navigate and forage. As was characteristic of Ken, he saw the humor in all of this and proceeded to draw a fine cartoon (which he showed to R.J.S. later in private). It depicted R.J.S. as Don Quixote and Tom Poulter as himself, fleeing the point of a lance aimed at his rear.

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light sensitive. Unlike the shallower-diving species, the visual abilities of the elephant seal are commensurate with the extreme conditions experienced while deep diving. Thus, we conclude that elephant seals are sufficiently adapted to rely on vision underwater, even while diving to depths in excess of 1000 meters where bioluminescence may be the sole source of ambient light.

Key words: visual sensitivity, dark adaptation, elephant seal, harbor seal, California sea lion.

Pinnipeds (seals and sea lions) forage, travel, and avoid predation under conditions where visibility is greatly reduced. This has led to speculation that when diving nocturnally or to great depths, they must depend on senses other than vision. Unlike echolocating odontocetes (Norris 1969), the hypothesis that the amphibious pinnipeds have also evolved a biosonar system (Poulter 1963, Renouf and Davis 1982) has been largely discounted (Evans and Haugen 1963, Schusterman 1967, Schevill 1968, Wartzok *et al.* 1984). Dehnhardt *et al.* (1998) found that a harbor seal's vibrissae are highly sensitive to water movements and therefore believe that the tactile sense of pinnipeds functionally replaces the visual sense in light-limited environments. However, while taction may be important in benthic foraging (*e.g.*, walrus, bearded seals) and in proximate "sit-and-wait" foraging strategies, particle velocities attenuate rapidly in water and may be difficult to detect above background noise while swimming. Consequently, tactile sensation would likely be of limited use in the location and capture of the free-swimming prey items consumed by many pinniped species (King 1983). Similarly, although the underwater auditory abilities of some pinnipeds are well developed (Kastak and Schusterman 1998), the passive nature of the auditory modality also fails to fulfill the need for an active telereceptive sensory mechanism by which pinnipeds can find prey within the water column.

In contrast to these alternative explanations, there is substantial support for the hypothesis that pinnipeds, like most other carnivores, use vision to orient and locate prey (Walls 1942, Hobson 1966, Schusterman 1967, 1981, Levenson and Schusterman 1997, Davis *et al.* 1999). The cornea and lens of the pinniped eye combine to provide relatively clear vision under water (Piggins 1970, Schusterman and Balliet 1970, 1971, Sivak *et al.* 1989), and the visual pigments of different species provide maximal sensitivity to the wavelengths of light which predominate in their respective foraging environments (Lythgoe and Dartnall 1970, Lavigne and Ronald 1975). However, in addition to the different refractive index and dim conditions found under water, pinnipeds may experience dramatic changes in light levels while diving. Northern elephant seals (*Mirounga angustirostris*), the deepest-diving pinnipeds, regularly dive to 300–700 m and can reach these depths in about six minutes (Le Boeuf and Laws 1994). If elephant seals and other deep-diving pinnipeds are capable of relying on visual cues while diving, they must be not only extraordinarily light sensitive, they must also be capable of dark-adapting faster than the 15–

40-min adaptation times of other mammals, including shallower-diving pinnipeds (Bartlett 1965, LaMotte and Brown 1970, Lavigne *et al.* 1977).

While pupillometric evidence supports these predictions (Levenson and Schusterman 1997), explicit comparisons of the visual sensitivities of deep and shallow-diving pinnipeds have not previously been performed. Hypothetically, even the deepest-diving pinnipeds possess visual abilities sufficient for use while diving. To test this hypothesis conclusively, we have used behavioral techniques to measure and compare the light sensitivities and dark-adapting abilities of some shallow and deep-diving pinnipeds. A harbor seal (*Phoca vitulina*) and a California sea lion (*Zalophus californianus*), both shallow divers (Feldkamp *et al.* 1989, Boness *et al.* 1994), as well as a deep-diving northern elephant seal and a human subject were examined.

METHODS

Subjects

The subjects for this experiment were a four-year-old female northern elephant seal (Burnyce), an eight-year-old male harbor seal (Sprouts), a 10 yr-old female California sea lion (Rio), and a 22-yr-old female human subject. The pinnipeds were held in two large seawater pools at Long Marine Laboratory, Santa Cruz, Ca. They were maintained on a vitamin-supplemented daily diet of 2–5 kg of frozen fish. The animals were trained using food reinforcement to perform all experimental behaviors. The human subject was given verbal instructions.

Materials

Experiments were conducted inside a 1.5-m deep, light-sealed tank partially filled with seawater.³ One end of the tank's light-proof cover was hinged so that it could be raised to allow subjects to enter/exit the tank. When the lid was closed and sealed, dark-adapted human observers reported little or no ambient light visible within the enclosure. All sensitivity measurements were made in air. However, as the light sensing responses of pinnipeds appear to be similar in air and under water (Lavigne and Ronald 1972), the sensitivity measurements obtained here should apply to vision in either medium. As shown in Figure 1, a PVC chin rest was used to position the subjects approximately 25 cm from where the visual stimuli were projected. The response ball (see *Procedure*) was located 10 cm to the right of the stimulus projector. In the darkness during experiments, the subjects were observed on a closed-circuit television system with an infrared (IR) sensitive video camera and IR illumination from a 100 W IR-only spotlight (Fig. 1). Fish rewards for correct behaviors were delivered through a light-tight fish feeding apparatus.

The visual stimuli used for testing were created with a 20 W tungsten-halogen lamp and were directed towards the subject through a light-guiding

³ The tank contained no water while the human subject was tested.

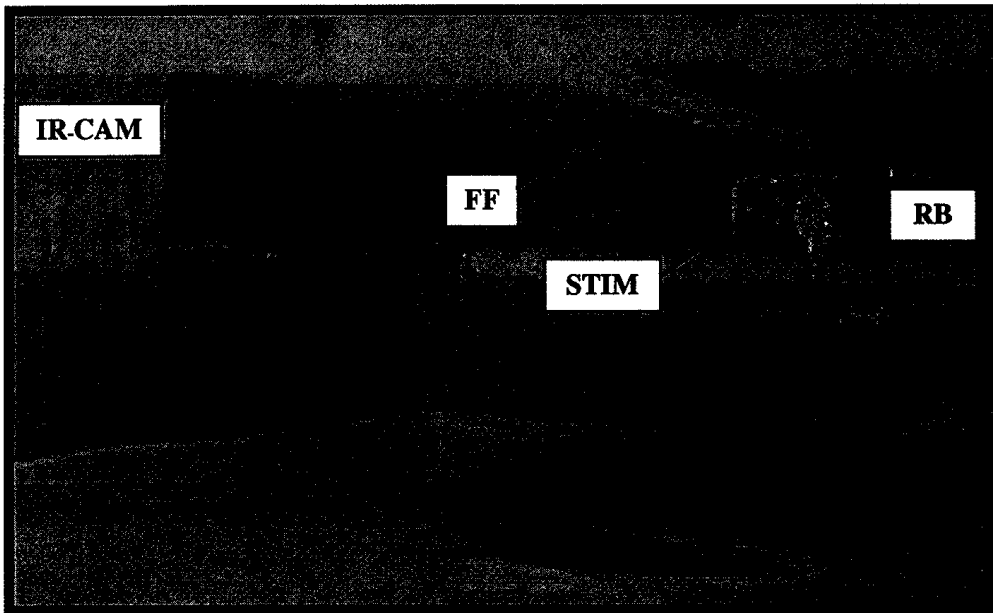


Figure 1. Video image (taken in normal daylight) of a harbor seal inside the test enclosure waiting for a visual stimulus (STIM). A chin rest located directly below the response ball (RB) was used to maintain a consistent position for each subject's head during trials. A waterproof wooden box with one glass side contained the infra-red sensitive camera and infra-red-only light source (IR-CAM) that were used to monitor the subjects in darkness. Above and to the left of the subject is the barrel of the light-tight fish feeding apparatus (FF).

cable with a 1.2-cm diameter collimating lens on the distal end. Stimulus-intensity levels were manipulated in ~ 0.25 log unit increments by placing neutral-density filters between the light source and the entrance to the light guiding cable. Actual stimulus intensities ($\text{W}/\text{m}^2\cdot\text{sr}$) were determined between sessions with a United Detector Technologies radiometer. Stimulus duration was regulated at the entrance of the light-guiding cable with a 35-mm camera shutter. For non-stimulus trials, the shutter was still triggered but an opaque filter was used to prevent light transmission into the light-guiding cable.

Procedure

For threshold testing, the animal subjects were trained using operant conditioning techniques in a go/no-go paradigm. The "no" response was controlled by the absence of a light stimulus. The "yes" response (touching the response ball) was controlled by the onset of the visual stimulus: a 250-msec flash of white light that subtended 1.5° of visual angle in the subject's visual field. Individual trials lasted 4–8 sec. Subjects were reinforced equally for correct responses at the end of both stimulus and non-stimulus trials. The human subject was given verbal instructions to perform a similar task.

Subjects were light-adapted in ambient daylight ($50\text{--}300 \text{ W}/\text{m}^2$) for at least one hour before each experimental session. The pupils of pinnipeds are capable

of substantial constriction to regulate retinal illumination (Lavigne and Ronald 1972), and this capacity varies considerably among species (Levenson and Schusterman 1997). Consequently, we were skeptical of our ability to achieve equivalent levels of light adaptation between experiments and between species with the use of controlled lighting. Mydriatics could not be used to artificially dilate the pupils, as we were interested in observing the animals' natural dark-adapting processes. Therefore, we opted to use daylight which, although variable, would roughly approximate the maximal light-adapting conditions these animals might experience in the wild.

Once inside the light-sealed enclosure, white-light thresholds were obtained using a modified method-of-constants procedure (Stebbens 1970). A series of five light levels centered about an estimated threshold value was pre-selected for each subject for each interval to be tested. For the seals and the sea lion, the light levels selected for each interval were presented in random sequence over successive experiments until each had been shown a minimum of eight times (*i.e.*, at least 40 signal trials per threshold estimate). For the human subject, light levels were similarly determined and each was presented at least four times (20 signal trials per threshold estimate). Final threshold estimates (50% correct detection levels) with standard deviations were obtained using the probit analysis and bootstrapping procedures of Foster and Bischof (1991). Estimates were obtained for each subject after one and two minutes in darkness and at successive two-minute intervals thereafter until sensitivity ceased to change ± 0.1 log units for at least 8 min. Dark-adapted sensitivity was calculated for each subject as the mean sensitivity observed over the final 8 min of testing. As multiple experimental sessions were required, the initial 3:1 ratio of go to no-go trials was manipulated for each animal to maintain false alarm rates of approximately 10%–20% in an attempt to minimize inter-session changes in response criteria (Schusterman 1974).

RESULTS

Figure 2 shows the threshold estimates (± 1 S.D.) obtained for each subject throughout the dark-adaptation process. The elephant seal reached maximum sensitivity within just 6 min. The California sea lion, harbor seal, and human subject took 16 min, 18 min, and 22 min, respectively, to fully dark-adapt. Threshold estimates for the harbor seal at 22 min and for the human subject at 24 and 26 min are missing due to insufficient sampling during these intervals. Bi-phasic second-order polynomial regressions were performed to create the dark-adaptation curves for the human subject ($r^2 = 0.97$), harbor seal ($r^2 = 0.94$), and California sea lion ($r^2 = 0.96$) shown in Figure 2. The first apparent sensitivity plateaus in the dark-adaptation curves of the harbor seal and sea lion were selected as their respective cone/rod transition points under the assumption that their stenopaic pupils would substantially limit the time necessary for complete cone adaptation to occur (Hecht *et al.* 1937, LaMotte and Brown 1970). A monotonic regression was performed for the elephant

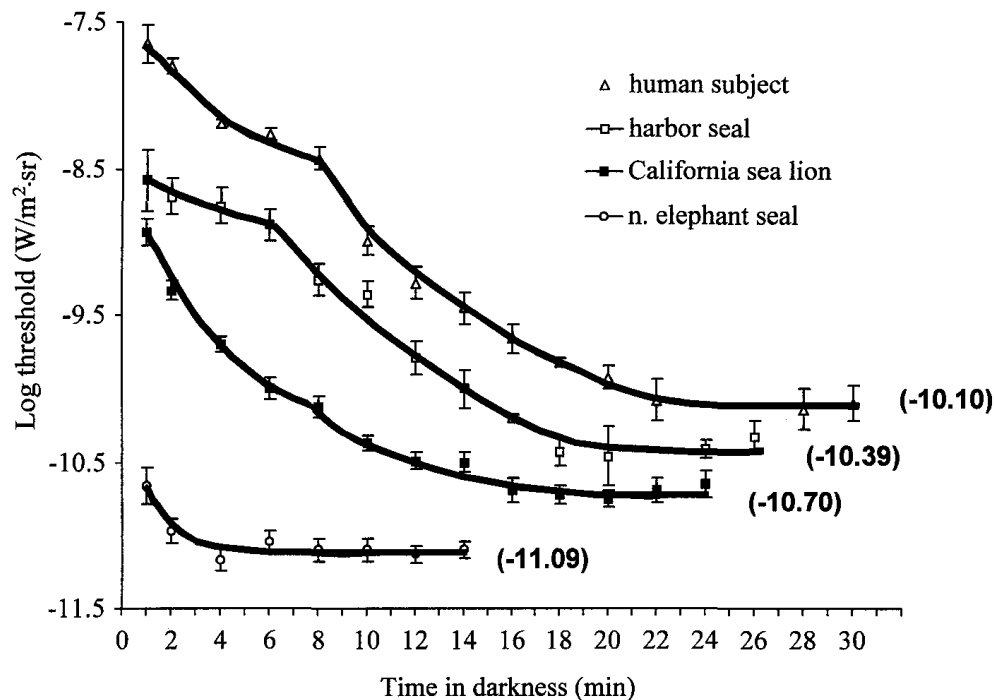


Figure 2. Threshold estimates (± 1 S.D.) and corresponding dark adaptation curves for the northern elephant seal, harbor seal, California sea lion, and human subject. Mean dark-adapted thresholds are shown in parentheses for each subject at the end of its respective dark adaptation curve.

seal data ($r^2 = 0.81$), as the truncated nature of this seal's adaptation prohibited a bi-phasic analysis.

Mean dark-adapted thresholds are indicated in Figure 2 for each subject. Using one-way ANOVA and then Tukey multiple comparison tests (Zar 1996), the dark-adapted thresholds of the four subjects were found to be significantly different from each other (all P values < 0.001).⁴ False alarm rates for the elephant seal, harbor seal, and California sea lion were 20%, 10%, and 9%, respectively.

DISCUSSION

The dark adaptation curves of the human subject, harbor seal, and California sea lion in Figure 2 are similar to those obtained for humans and pinnipeds in other investigations (Bartlett 1965, Lavigne *et al.* 1977). The rapid sensitivity increases that occur during the first minutes of adaptation are most likely the result of the subjects' respective pupillomotor responses. Day to day differences in pre-testing conditions may also have contributed to the vari-

⁴ Note that the high levels of significance between these means were, to some degree, the result of low within-subject variability created by the original criterion by which these data were chosen.

ability of threshold estimates observed during this time. With the exception of these initial points, however, the adaptation curves of the human subject, harbor seal, and California sea lion appear quite similar and suggest that the biochemical mechanisms which dark adapt their photoreceptors are probably similar. The heightened light sensitivity of the pinnipeds may be attributed to their large pupils, well-developed choroidal tapeta, and highly rod-dominated retinas (Walls 1942). Interspecies differences in these characters may also account for the differences observed among pinnipeds.

Presuming the processes which dark-adapt the photoreceptors of pinnipeds are similar to those of other mammals, the rapid dark adaptation of the pinnipeds must be related to their large ranges of pupillary dilation (Levenson and Schusterman 1997). Large pupillary ranges are known to increase dark adaptation rates in other mammals (LaMotte and Brown 1970), although none has been found to exhibit adaptation as rapid as that observed here for the elephant seal. The dark adaptation of this seal appears more similar to that observed for human subjects light-adapted in dim conditions than for subjects adapted in full daylight (Bartlett 1965). One possible explanation for this observation is that the highly contractile pupils of elephant seals may limit retinal illumination to such an extent that even in daylight their rod photoreceptors are not completely saturated and their vision is partially rod-based. The limited bleaching of the rods would explain how these seals are capable of reaching maximum visual sensitivity so quickly after prolonged exposure to bright light. Recent studies indicating that harbor seals possess only a single cone photoreceptor type (Crognale *et al.* 1988, Peichl and Moutairou 1998) support this conclusion: If harbor seals possess only a single cone type, the reported ability of these seals to make color discriminations in bright light (Wartzok and McCormick 1978) must be a product of their ability to simultaneously perceive both cone and rod neuronal signals under these conditions (Crognale *et al.* 1998). Alternatively, there may be biochemical or neurological differences in the visual systems of elephant seals which facilitate their rapid dark adaptation.

While further research is necessary to understand the photoreceptive mechanisms of pinniped vision, the ecological implications of their visual abilities are clear. The enhanced light sensitivities and rapid dark-adapting abilities of the pinnipeds examined here support the conclusion that their visual systems are well suited for use in the conditions experienced while diving. The shallow-diving harbor seal and California sea lion, while less light sensitive and slower to dark-adapt than the elephant seal, still possess sufficient visual abilities for use in the moderately light-limited environments in which they dive to forage. The elephant seal possesses keen light sensitivity for vision at depths where little or no ambient sunlight may be available. Moreover, the elephant seal is capable of adapting from daylight conditions to maximum sensitivity in only six minutes, roughly the same time it takes these seals to dive from the surface to foraging depth (LeBouef and Laws 1994). Although sample size was limited, the contrasting abilities of the shallow and deep-diving species confirm pupillometric findings that the visual capabilities of these pinnipeds are di-

rectly related to the needs incurred by their respective diving behaviors (Levenson and Schusterman 1997).

In addition to acute light sensitivity and rapid dark adaptation, elephant seals possess highly blue-shifted visual pigments like those of deep-sea fish to facilitate vision in the dimly illuminated mid-water regions (Lythgoe and Dartnall 1970). Until only recently, the meso/bathypelagic depths (200–1,000 m) where elephant seals and other deep-diving mammals forage have often been considered to be devoid of adequate sunlight for vision (*e.g.*, Denton 1990). However, with increasing exploration of these areas, it is no longer uncommon to find animals adapted for vision at these depths (Bowmaker 1995). Even in conditions where downwelling solar radiation is limited or absent, light produced by bioluminescent organisms can provide substantial background illumination for vision (Widder *et al.* 1989, 1992). Not surprisingly, many of the prey items consumed by elephant seals are bioluminescent or associate with the highly bioluminescent deep-scattering layer (Rodhouse *et al.* 1992, Le Boeuf and Laws 1994).

Whether ambient light is solar or biological in origin, the conclusion that elephant seals are foraging visually at great depths raises the possibility that other deep-diving marine mammals may have also adapted their visual systems for seeing at these depths. Underwater video recordings of Weddell seals (*Leptonychotes weddellii*) indicate that these deep-diving seals also use vision to find prey (Davis *et al.* 1999) and there is anecdotal evidence of California sea lions performing visually-oriented tasks at depths of more than 300 m (Hugueley *et al.* 1997). With respect to cetaceans, Norris and Møhl (1983) have suggested that the biosonar systems of some deep-diving whale species (*e.g.*, sperm whales, beaked whales) may be designed for prey debilitation rather than detection, thus implying that other sensory modalities such as vision must be used to locate prey. Although relatively little is known of the visual abilities of these whales, at least one species, a Baird's beaked whale (*Berardius bairdi*), has been found to possess highly blue-shifted visual pigments (McFarland 1971).

Of course, while visual cues may be of primary significance during foraging and traveling, we do not propose that pinnipeds or any other marine mammals rely solely on their visual sense while under water. As pointed out by Dehnhardt *et al.* (1998), tactile sensation may be of considerable proximal importance to pinnipeds, and auditory cues are known to play a significant role in foraging, traveling, predator avoidance, and communication (Schusterman 1981). However, while many aspects of the visual capabilities of pinnipeds remain to be examined, we do conclude from our findings here that even the deepest-diving pinnipeds are adequately adapted for visual functioning at depth, and thus that there is no need for compensatory non-visual explanations of their underwater sensory orientation.

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