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AMPHIBIOUS NATURE OF VISUAL ACUITY IN THE ASIAN "CLAWLESS" OTTER

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Amphibious Nature of Visual Acuity in the Asian "Clawless" Otter

THE ability to acquire information at some distance and to behave accordingly increases the probability of species survival and reproduction. The propagation of light and sound differs to such a great extent in air as compared with underwater that special sensory adaptations are necessary for an animal to operate effectively in both media.

Recently there has been great interest in the amphibious nature of visual and auditory acuity in a variety of aquatic animals, including turtles[1], river otters[2], sea otters[3], mink[4], porpoises[5], pinnipeds[6] and man[7,8]. The latter, for example, shows an expected 30 dB hearing loss under water[7]; also when not wearing goggles the loss of refractive power of the cornea under water[9] cannot be sufficiently compensated by the accommodative power of the lens so that, at a distance of 0.7 m, human visual acuity in water suffers an eight-fold decrease compared with that in air, and at a distance of 5 m humans are virtually unable to resolve sufficient detail to differentiate form from background[8]. Thus man, like other terrestrial mammals that have not developed special adaptations for seeing under water, is hypermetropic in water while being emmetropic in air. On the other hand, truly amphibious mammals like the pinnipeds, which feed exclusively under water and carry out many reproductive functions on land, have essentially an emmetropic eye under water while possessing special dioptric mechanisms for seeing detail in air.

Pinnipeds have developed a permanently changed curvature of the lens for seeing under water. On the other hand, otters are thought to have a similar device to turtles, in having well developed ciliary and sphincter muscles which squeeze the anterior part of the air adapted lens, giving it a focal length similar to that of a spherical lens[5].

The visual acuity of the Asian "clawless" otter has been measured both in air and under water under a light intensity level of 100–200 mL (ref. 2), and it was found that the closest grating spacings that could be resolved in both media subtended visual angles ranging from 14–16 arc min. As this special adaptation of otter underwater vision is thought to be achieved primarily by the action of the powerful iris sphincter closing down on and distorting the lens, a question arises as to the effects of ambient light on the iris sphincter. If the pupil fully dilates under low light levels, then the lens would not become sufficiently spherical, thus resulting in the otter's eye becoming hypermetropic in water. This would in turn lead to the hypothesis that as luminance decreased under water, visual acuity in otters would deteriorate at a more rapid rate under water than it would in air. To test this, we measured the aerial and underwater visual acuity of two mature male Asian "clawless" otters (*Amblonyx cineria cineria*) in three ambient light conditions.

The testing tank apparatus, general testing procedures and acuity targets were the same as those used previously[2]. Acuity targets were produced from 12.7^2 cm photos of Ronchi rulings with black and white stripes of equal width. The standard grating consisted of 300 lines per inch, the variable gratings of lines varying in width from 12.7 mm to 4.8 mm. Targets were presented simultaneously by lowering a target board from behind an opaque screen. The only modifications were to control ambient light intensities, simply by covering the top of the apparatus with a double layer of 8 mill black vinyl sheeting. The amount of light entering the tank and reflected from the targets was controlled by opening the top cover a given amount. At the start of each test session the experimenter dark adapted and an assistant would then slide back the black vinyl cover until the desired light level was obtained. The light intensities were 0.3, 0.03 and 0.009 mL. Daily light readings were taken with an SEI meter which was checked against a Macbeth illuminometer.

The otters were maintained at fixed distances of 1.7 m and 1.3 m at the highest light level, 1.3 m at the next highest light level and at 0.76 m at the lowest light intensity. A modified psychophysical method of limits was used to obtain visual acuity thresholds.

In most conditions each animal's threshold was defined as the interpolated values at which the animal responded correctly 75% of the time. If an otter never achieved a value of 75% correct responses or better, however, then the threshold was defined in terms of visual acuity targets resulting in discrimination performance which was significantly better than chance ($P<0.01$).

At each test session ambient light levels remained relatively constant, and stripes were made finer if the animal succeeded in making seven or more correct responses in ten successive trials. The otters were dark adapted 30 min before each test session.

The main results of the experiment (Table 1) clearly support the idea that visual acuity in otters, although showing an air-water equivalence in relatively bright light,

Table 1 Aerial and Underwater Visual Acuity Thresholds* as a Function of Ambient Light Levels

Luminance (mL)	River otter, Tom Air	River otter, Tom Water	River otter, Jerry Air	River otter, Jerry Water
100–200†	14	15	15	16
0.3	18	18	17	17
0.03	23	33	23	33
0.009	39	57	38	58

* In minutes of visual angle.
† Data from Balliet and Schusterman[2].

degrades at a considerably more rapid rate in water than in air. The lack of visual accommodation in otters under water in the dark may be due to pupillary dilation resulting in insufficient squeezing of the anterior portion of the lens by the iris sphincter muscles. On the other hand, one might argue that the present findings are not due to the lack of lens accommodation, but result from insufficient pupillary dilation in the dark, thus reducing the amount of light entering the submerged eye. This explanation assumes that squeezing of the lens by the pupil aperture occurs either voluntarily or is triggered reflexively soon after the otter goes under water.

It is interesting to compare the present experiments with otters whose eye is emmetropic in air with special adaptation for seeing under water, with similar experiments using seals and sea lions whose eyes are emmetropic under water with special adaptations for seeing in air.

In the California sea lion (*Zalophus californianus*) aerial acuity deteriorated at a much more rapid rate than underwater acuity in the luminance range of 3 to 0.000003 mL (ref. 6). These results are consistent with the idea that as pupil size in seals and sea lions varies with ambient light intensity regardless of whether the eye is submerged[10], the narrow vertical slit pupil in air provides good visual acuity in relatively brighter light, but in dim light the pupil is dilated and aerial visual acuity is reduced by the astigmatism of the cornea. Although the pupil is dilated under water, the corneal astigmatism of sea lions plays virtually no role because of the similar refractive indices of the cornea and water.

Thus a comparison of the effectiveness of the visual systems of modern aquatic mammals suggests that only when tested under a wide range of lighting conditions is there a correlation between the degree of adaptedness of different amphibious species to aquatic and terrestrial habitats.

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