The possible therapeutic action of GH on the first filial generation of previously undernourished rats may explain, in part, the findings of an earlier study from the same laboratory in which differences in the adult behavior of GH offspring were observed (*3*), but would not account for the apparent improvements in adult behavior found in other studies in which there were no adverse nutritional circumstances (*4, 5*). However, it has been demonstrated that the maternal behavior of GH mothers differs from that of control mothers throughout the first 2 weeks postpartum (*13*); and, given the importance of early experience in the determination of adult behavior, these different patterns of maternal behavior may account for the permanent changes that have been observed in the offspring born to and reared by GH mothers.

The administration of GH, then, produces at least two definite effects in the rat: (i) prolonged gestation leading to postmaturity of the offspring and (ii) alterations in the maternal behavior of the GH mother. It is possible that prenatal treatment with GH may produce other changes in the adequately nourished rat which have not been detected this far. Also, GH preparations derived from different sources or species may exert differing qualitative and quantitative (*19*) influences possibly because of contamination by other pituitary hormones. However, in view of our failure to demonstrate any obvious influence of GH on prenatal development of body or brain (*6*), and the data reported here (*6*), it is doubtful that structural or functional differences in the offspring of normally nourished rats can be ascribed to changes produced prenatally by GH.

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Bottlenosed Dolphin: Double-Slit Pupil Yields Equivalent Aerial and Underwater Diurnal Acuity

Abstract. *In bright daylight, and at best viewing distances, the bottlenosed dolphin resolves visual gratings approximately equally well in air and in water. Aerial resolution improves with increased viewing distance, while underwater resolution improves with decreased viewing distance. The double-slit pupil overcomes the gross myopia in air measured by ophthalmoscope and produces the indicated effects of viewing distance.*

We present here the first behavioral evidence that daylight visual resolution acuity of the bottlenosed dolphin, *Tursiops truncatus*, is approximately equally good in air and water. Although informal observations of captive bottlenosed dolphins suggest good aerial acuity, measurements of the eye by ophthalmoscope reveal a gross aerial myopia of 16 to 20 diopters (*1, 2*). This large refractive error in air derives from the considerable power of the cornea added to that of the large, spherical lens. In water, where the cornea is ineffective as an optical device (its refractive index is approximately that of water), measurements by ophthalmoscope indicate emmetropia (*1*) to moderate hypermetropia (*2*). Functionally, these measurements predict con-

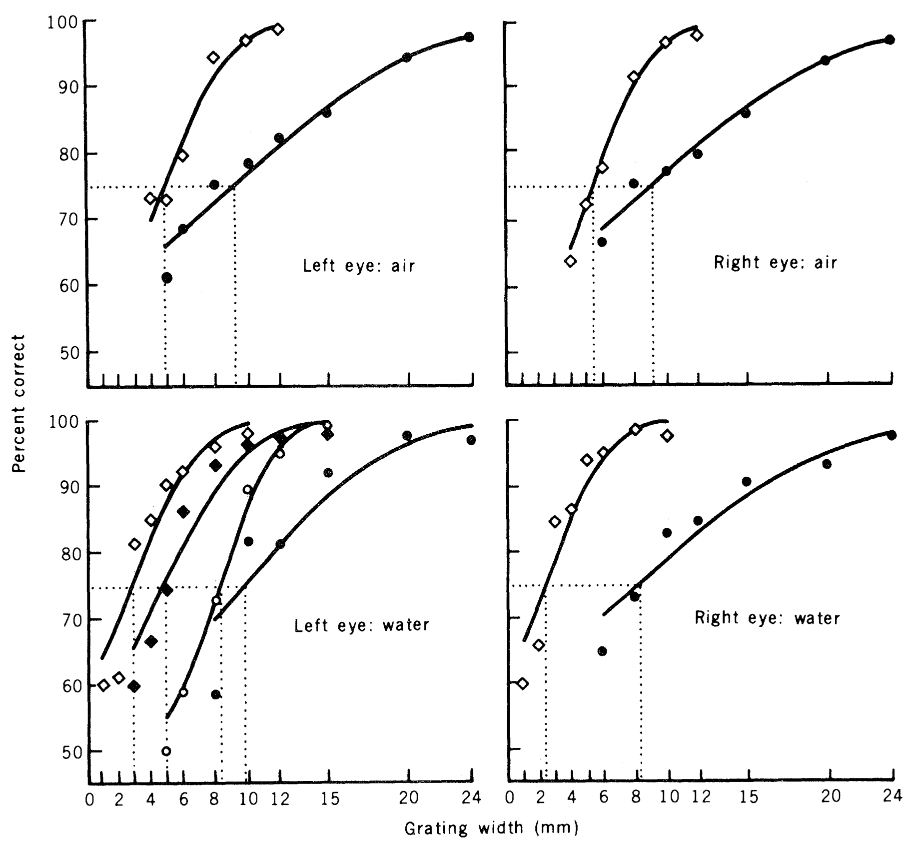

Fig. 1. Percentage of correct responses with each comparison target as a function of left or right monocular viewing, air or water medium, and viewing distance (◇ = 1 m; ◆ = 1.5 m; ○ = 2 m; ● = 2.5 m). Resolution thresholds for the criterion 75 percent correct are shown.

siderably poorer resolution capabilities in air than in water. Also, aerial resolution capability should decrease with increased viewing distances, while underwater resolution should either be invariant or improve with distance.

Our behavioral tests measured aerial and underwater daylight resolution capabilities at viewing distances of 1 to 2.5 m from grating targets. Acuity ranged from 12′ to 19′ in air, and from 8′ to 14′ in water, depending on viewing distance (*3*), but the effects of viewing distance in each medium were opposite to those expected. Corrections for the increased apparent size of the targets in water yielded nearly equivalent best-resolution capabilities in the two media. The surprisingly good aerial resolution and the paradoxical effects of viewing distance within media were interpreted as optical effects of the double-slit pupil, observed in bright illumination.

The bottlenosed dolphin tested was an adult female of 12 to 14 years, named Puka, previously tested in a preliminary study of aerial acuity (*4*). Ophthalmoscopic examination revealed no visual anomaly. We tested the animal outdoors, between 1000 and 1500 hours, in a large seawater tank at the University of Hawaii (*5*). Median incident light measurements in the partially shaded testing area were 1750 lux in air and 1500 lux in water (*6*).

The 24-cm square viewing targets were high-contrast black-and-white gratings milled from phenolic (*7*). Two targets with grating widths of 0.5 mm and 1 mm, respectively, were used as standards. These corresponded to visual angles ranging from 0.7′ to 3.4′, for viewing distances between 1 and 2.5 m, well below the expected resolution capabilities of the animal, and presumably were seen as homogeneous gray surfaces. Comparison targets had grating widths of 2, 3, 4, 5, 6, 8, 10, 12, 15, 20, and 24 mm. The 1-mm standard was considered a comparison target when the 0.5-mm standard was used.

A single grating target, with bars vertically oriented, was mounted on a track and lowered from behind an opaque screen into the testing area for 6 seconds. The target was 10 cm above the water surface for viewing in air and 50 cm below it for viewing in water. Following exposure of a standard target, a press on a paddle to the left of the target was correct, while exposure of a comparison target required a press on a paddle to the right. Correct responses produced a fish reward, while errors yielded a 30-second time-out before the next trial.

Resolution capability was determined by progressively decreasing the width of the comparison target grating over blocks of ten trials while maintaining a constant standard, until performance during a block fell to 70 percent correct or less. The standard and the comparison target were always presented in a quasi-random, balanced sequence within each block. For each unique condition tested, resolution was measured by this procedure a minimum of 32 times, but generally considerably more, and the pooled data used to estimate thresholds. The conditions tested, in order, were left eye in water at viewing distances of 2, 2.5, 1.5, and 1 m; right eye in water at 2.5 and 1 m; right eye in air at 1 and 2.5 m; and left eye in air at 2.5 and 1 m.

We obtained monocular viewing by requiring the animal to bite a rigidly fixed dental-type plate. The grating target was then exposed. The plate maintained either the left or right eye at the desired viewing distance from the target, and at a viewing angle of approximately 75°. The elevation of the bite plate determined whether the eye was in air or in water.

Figure 1 shows the percentage of correct responses as a function of the width of the comparison target gratings, for all conditions tested. Percentages were based on the combined correct responses to standard and comparison targets within a block. Ogives (cumulative normal distribution functions) were fitted to the data by a minimization technique (*8*), and thresholds were defined as the value of the function (in grating width) at the 75 percent correct response level.

Figure 2 shows the visual angles for the threshold gratings. For both eyes, underwater acuity decreased 3′ to 4′ from 1 m to 2.5 m, while acuity in air improved by 4′ to 6′ over the same distances. The best resolution capability in water was 8.2′ (at 1 m) and that in air was 12.5′ (at 2.5 m).

The best underwater capability approaches the maximum acuity of 6′ predicted from receptor-to-ganglion cell ratios of approximately 100/1 in the ret-

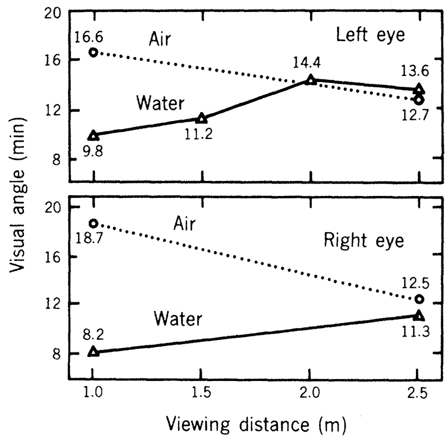

Fig. 2. Resolution thresholds, in visual angle, for each condition tested.

ina of *Tursiops* (*9*). Other odontocete (toothed) cetaceans tested for underwater daylight acuity, the white-sided dolphin (*Lagenorhynchus obliquidens*) and the killer whale (*Orcinus orca*), have yielded thresholds of 5′ to 6′ (*10*). If these values are increased by 3′ to 4′ to correct for the use of viewing targets having confounding brightness cues (*11*), the underwater resolution capabilities of these two odontocete species would agree well with our results for the bottlenosed dolphin. All odontocete cetaceans tested so far fall within the 5′ to 9′ range of underwater daylight acuity reported for various pinniped species (*11*).

Our results showed the best resolution capability of the bottlenosed dolphin in air to be somewhat inferior to the best capability in water. However, the interaction of the optical properties of air, water, and the eye (*2*) dictates that, at a given viewing distance, the image in water will be approximately 1.33 times larger than the image in air (*12*). Correcting for these different image sizes, by multiplying thresholds in water by 1.33, or else multiplying aerial thresholds by 0.75, yields nearly equivalent best-resolution capabilities in the two media.

The finding that viewing distance affects acuity in both media indicates that no fine, continuous accommodation mechanism is available. Fine accommodation has not been observed during ophthalmoscopic examination (*2*), and mechanisms for fine lens deformation or displacement seem to be lacking (*1*). However, the good aerial acuities reported here require some gross, discrete accommodation method for overcoming the great power of the cornea-lens combination in air. The pupil can serve this function. When dilated, the pupil is a horizontally oriented crescent (*13*), but under bright illumination it closes completely in its central portion leaving a small, irregularly shaped aperture at its nasal and at its temporal extreme (*1*). Measurements of these two pupillary apertures, obtained from daylight photographs of the eye in air, revealed a maximum dimension in the horizontal plane of approximately 0.5 mm, and in the vertical plane of approximately 1.4 mm. The two apertures were separated horizontally by approximately 5.3 mm. The "pinhole" size of these apertures yields a large depth of field, and their displacement suggests that they may be treated as double slits, the optics of which are well known (*14*).

The application of the double-slit model to the dolphin eye can be outlined as follows. With a cornea-to-retina distance of approximately 22 mm (*2*), the refractive error in air results in the image plane lying approximately 5.2 mm in front of the retina, for an object at infinity. In this plane, focused images from each pupillary slit are superimposed, but then diverge as they continue past the image plane to the retinal plane, forming two retinal images. At a viewing distance of 1 m, the two retinal images of our 24-cm square targets will overlap by approximately 71 percent, producing blur over the major portion of the combined image. The overlap decreases to approximately 25 percent at 2.5 m, confining the blur to a small, central portion of the combined image and allowing greater opportunity for resolution of individual bars of the grating targets. Completely separated images will occur at a viewing distance of approximately 3.3 m, suggesting that daylight aerial resolution might be further improved at this increased viewing distance.

In water, refractive error is absent or nearly absent (*1*, *2*). However, since fine accommodation is lacking, the image will lie on the retina at only one viewing distance. Assuming from our results that this distance is 1 m, although it could be less, then at greater viewing distances the image plane will move progressively forward of the retina. Our calculations indicate that at infinity the image plane lies approximately 1 mm in front of the retina, so that, in contrast to the aerial situation, at viewing distances beyond 1 m there is little room for divergence of the images from each slit before they strike the retina. Nevertheless, slightly increased displacements of the images on the retina will occur with increased viewing distances beyond 1 m, yielding increasing blur of the image. The double-slit model thus accounts for the observed poorer resolution with increased viewing distance in water and also for the improved resolution with increased viewing distance in air.

The double-slit pupil of the dolphin sacrifices the constant acuity over distance obtainable with a single, centrally located pupillary slit, like that observed in pinniped species (*11*). However, the double slit yields a considerably brighter image (in the image plane) than does the single slit, and also yields a wider field of view (*13*). This seems a favorable compromise adaptation for the bottlenosed dolphin, which can rely on echolocation in water to detect distant objects, and which encounters relatively few nearby objects of interest in air in the open aquatic environment.

Since the double-slit effect disappears as the pupil dilates, aerial acuity should decrease rapidly with lowered levels of illumination, because of the increased optical role of the cornea. In water, the eye is emmetropic at favorable viewing distances, even with the pupil dilated (*1*). Resolution losses with decreasing illumination should therefore occur much less rapidly in water than in air, as with pinnipeds (*11*). Considerably reduced underwater resolution in very dim illumination has been found for *Tursiops* (*15*), but systematic comparisons of aerial and underwater acuity under various levels of illumination are not available.

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5. Transmissibility of the naturally filtered seawater, measured daily with a Hydro Products 612S transmissometer having a tube with a 1-m pathlength, ranged from 49 to 80 percent (mean, 65 percent), depending on the algal growth between weekly tank cleanings. The lower value yields an underwater visibility range for humans of roughly 5 m, and the upper limit roughly 8.5 m. Underwater performance of the animal was not significantly correlated with the different transmissibility values.
6. Incident light measurements in air and water were made daily using a Clairex 705L photocell with translucent diffuser, located at the position of an exposed grating target. Current readings from the photocell were calibrated in daylight with a United Detector Technology-40A optometer.
7. Michelson contrast, the preferred measure for grating targets, was 0.33. It was measured as $(L_{\max} - L_{\min})/(L_{\max} + L_{\min})$, where $L_{\max}$ was the luminance of a white bar and $L_{\min}$ the luminance of a dark bar of a grating target.
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Purposive Behavior as a Basis for Objective Communication Between Chimpanzees

Abstract. *The rate at which a chimpanzee approaches a hidden, distant goal varies according to social conditions and according to whether the goal is a novel object or food. This behavior furnishes a social group with sufficient information for simultaneous and successive discriminations between leaders and between goals.*

It is often assumed that without a symbolic code of vocalizations, manual gestures, or other displays which "stand for" particular objects and relations, primates are incapable of communicating about things that are not present to the senses (*1*). Consider, however, any molar behavior, for example, locomotion (*2–5*). To most human observers, walking seems purposive, that is, it appears to have some external referent. Walking is syntactic, or possesses global organization. It is informative; for example, its velocity and acceleration suggest to us how interested an animal is in his goal, and consistency of direction suggests to us where the goal might be located. There can also be considerable displacement between this "signal" and its "referent"; the signaler's behavior can be highly devious and subject to learning, hence arbitrary and noniconic; and finer details of the animal's behavior can supplement or qualify the information available from locomotion and reduce our uncertainty about the environment still further. In short, locomotion can, if one so chooses, be said to possess most if not all of the major logical "design features" by which Hockett and Altmann (*6*) have tried to characterize language; and the ability of nonverbal animals to "tell" each other the precise nature and location of their goals is limited only by the richness of the signaler's purposive movements and the receiver's knowledge of the signaler and the environment in which he is operating.

In this report we extend our previous studies of inter-chimpanzee communication (*3–5*) and show that: (i) A chimpanzee leader's rate of locomotion provides the rest of his group with a sufficient basis for simultaneous and successive discriminations between novel toys and food, which are both highly preferred classes of objects. (ii) This result cannot be fully predicted