

## **Bottlenose Dolphin (*Tursiops truncatus*) Double-Slit Pupil Asymmetries Enhance Vision**

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### **Abstract**

Geometries of the iris, retinal cell distributions, and the optical characteristics of the lens and cornea have evolved to optimize the visual adaptations of the bottlenose dolphin (*Tursiops truncatus*) to the oceanic environment. Under high ambient light conditions, the operculum of the iris shields the lens and forms two asymmetrical slit pupils. Under these conditions, light entering the eye is channeled and focused onto the two areas of the retina having a finer retinal mosaic of ganglion cells (typically associated with higher image resolution). The paths of light determined by tracing rays in the reverse direction through these pupils coincide with a dolphin's behaviorally observed preferred viewing directions. These rays aid in determining the interdependence between the graininess of the retinal mosaic and resolution spot sizes in the object space. For oblique forward and downward viewing directions in air, the larger temporal pupil admits light which passes through the weakly refractive margin of a bifocal lens, counterbalancing the optically strong cornea in air. In water, light passing through the optically strong lens core is focused from a wide lateral and downward field-of-vision. Although other explanations for comparable aerial and underwater vision remain plausible, a dolphin eye model incorporating a bifocal lens offers an explanation consistent with ophthalmoscopic refractive state measurements. The model is also consistent with visual acuity study results conducted in air and in water under both high and low ambient light levels. From insight gained after applying a common data analysis technique to visual acuity studies conducted by other researchers and tracing oblique rays through the asymmetric double-slit pupils, a re-examination of explanatory hypotheses for the paradoxical observations of comparable aerial and underwater vision is presented. Based in part on these findings and supportive evidence from dolphin vision researchers, the unique distinguishing characteristics of dolphin vision are summarized.

**Key Words:** vision, bifocal lens, iris asymmetries, bottlenose dolphin, *Tursiops truncatus*, operculum, bioacoustic-imaging

### **Introduction**

Dolphins echolocate under water to locate and identify things of interest in their ecosystem. Vision can be used for similar purposes in both air and water. Bioacoustic-imaging and vision are probably integrated and co-processed in real time as indicated in a study where active echolocation increased when ambient lighting was abruptly decreased (Akamatsu et al., 1992). In another example, it was observed that a dolphin's approach to a maze-obstructed underwater target was much faster and less dependent on active echolocation when not deprived of vision as a sensory input (Azzali, 1992). Captive dolphins familiar with their aquatic environment decrease active echolocation and seem to depend more on sight. This provides excellent opportunities to observe the dolphin's preferred viewing directions both in air and under water. Aerial vision may also take on added importance as enrichment interactions with humans most often take place in air (Pryor, 1975).

Explanations for paradoxical observations of comparable aerial and underwater vision remain a subject of debate. After reexamining the observations and proposed theories from dolphin vision studies, a consolidation of more likely explanations for the capabilities and nature of dolphin vision is presented. Comparisons of similarly structured behavioral acuity studies often require a reanalysis of the data with a common statistical technique and threshold criterion. A classic psychometric function as used in the Madsen (1976) color vision and spectral sensitivity study is described and applied to the behavioral visual acuity studies. The bottlenose dolphin (*Tursiops truncatus*) bifocal lens model (Rivamonte, 1976) is reviewed for light passing obliquely through the double-slit pupil in bright sunlight, and corrected

to illustrate the refraction of light by the front surface of the cornea.

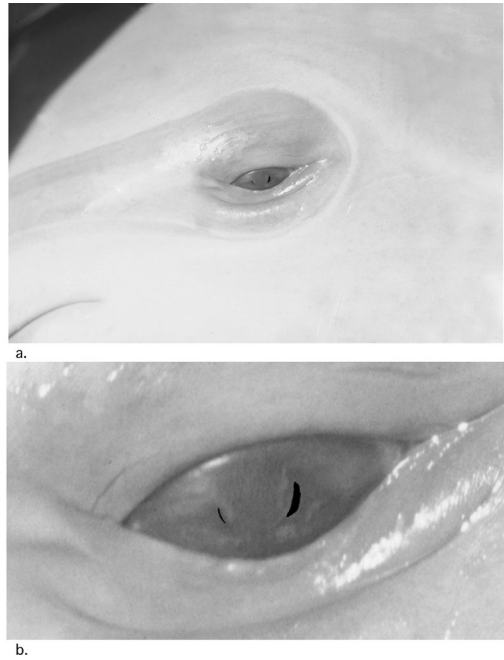
### Materials and Methods

A number of vision studies conducted in Hawaii and cited here involved a dolphin named Puka (Pepper & Simmons, 1973; Peacock et al., 1974; Herman et al., 1975; Madsen, 1976). A photograph (Nikon FTN camera and Nikkor 50-mm F1.4 lens at a 30-mm viewing distance, Kodak Ektachrome film, 50 lp/mm, resolution spot size 0.06 mm, *ca.* 15,000 lux) was taken of Puka's left iris in bright morning sunlight (Figure 1). Even though taken under optimum photographic conditions, this photograph fails to resolve details seen by the unaided human eye. The photograph, however, has sufficient detail to determine the size, shape, and position of the double-slit pupil.

It seemed likely that the asymmetries of the double-slit pupil might be helpful in determining the optimal paths of light to the retina. A review of photographs and drawings in the literature support the presence of the *T. truncatus* iris double-slit asymmetry (Rivamonte, 1976; Dawson et al., 1979; Madsen & Herman, 1980; Dral, 1987; Norris et al., 1994). By tracing light through a constricted off-axis pupil, the constrained path of a thin beam of light to an area centralis can be determined. This thin beam of light corresponds to the chief ray used in the characterization optical systems. By definition, a chief ray passes through the center of the entrance pupil and is not blocked by the field stop before reaching the image plane (Jenkins & White, 1957). For the dolphin eye, the field stops and image planes are co-located at the area centralis. Knowing the location of only two points—(1) the center of the area centralis and (2) the pupil—the path of light for best image formation can be determined.

Image formation paths are estimated by tracing light through the double-slit pupils. By tracing rays of light in the reverse direction starting from the area centralis and passing through the constricted pupils, a dolphin's preferred aerial and underwater viewing directions, as observed behaviorally, are correctly predicted. Ray tracing starting from the image or the object space is valid based on the principle of reversibility of light rays. Thus, rather than looking at the size of a blur circle on the retina or the size of an element of the retinal mosaic, a corresponding conjugate resolution spot can be projected onto the object being viewed (Jenkins & White, 1957; Merklinger, 1990). For example, by computing the resolution spot size, an estimate can be made on whether or not a dolphin can resolve a fish held by a trainer in air.

These geometric ray tracings through a lens overcorrected for spherical aberration, either

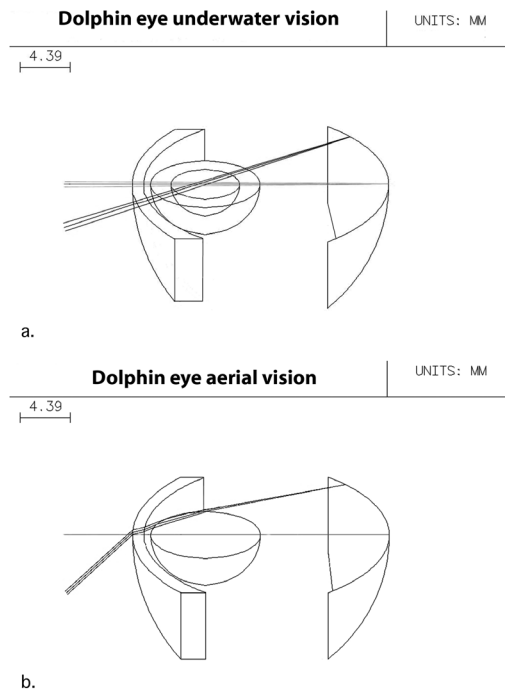


**Figure 1.** Puka's left eye in high ambient light conditions, asymmetric double slit-pupil, retouched to improve contrast: (a) in high ambient light conditions, the rostral stenopaic slit-pupil is functional in air and water for the forward field-of-view and (b) the larger temporal slit-pupil allows light to pass (1) through the lens margin canceling the refractive power of the cornea for the forward and downward field-of-view in air and (2) through the lens core for the rearward field-of-view in water.

through an optically weak lens margin in air or an optically strong spherical lens core in water, support a bifocal lens eye model as an explanation for measured aerial and underwater emmetropia (i.e., in-focus vision). The bifocal lens was initially proposed to explain ophthalmoscopic measurements (Dral, 1972, 1975a) and observed trends in visual acuity data (Peacock et al., 1974; Herman et al., 1975). Emmetropia in air was also observed in the eyes of three other species: (1) the Hawaiian spinner dolphin (*Stenella longirostris longirostris*), (2) rough-toothed dolphin (*Steno bredanensis*), and (3) the beluga (*Delphinapterus leucas*) (Dral, 1975a). Knowing that the dolphin iris admits light through the central region of the cornea of near uniform thickness, the light focusing ability of the odontocete eye can be primarily attributed to the lens core in water, and to both the frontal surface of the cornea and the lens margin in air (Rivamonte, 1976). The initial development of the bifocal eye model incorporated estimates of the cornea's front and rear surface curvatures, thickness, and the index of refraction. The posterior corneal surface

was omitted from the 1976 version of the schematic eye because of its small refractive contribution to the salient characteristics of the model and the tedious nature of the ray tracing calculations. This surface has been reintroduced using optical design software (see Figure 2). Mathematical dolphin eye models, like human eye models, should be predictive of refractive state and behaviorally determined visual acuity measurements.

Custom software was developed to aid in the reanalysis of behavioral acuity data from vision studies conducted by other researchers. Hewlett-Packard *Visual Engineering Environment* (HP VEE) and *MATLAB* programs were used to fit psychometric functions to the data to help determine the best statistical technique. Datasets were analyzed and graphed as linear and log plots using least squares and iterative minimization methods in both the spatial and frequency domains. A comparison of the correlation coefficients of the eight separate plots for each dataset was used to determine the relative goodness of fit and most appropriate statistical technique.



**Figure 2.** Dolphin right eye ray tracing using Oslo optical design software: (a) wide field of view under water for light passing through the lens core and (b) forward and down field-of-view through the lens margin in air; in high ambient light conditions, the rostral stenopaic pupil could also image on the temporal area centralis.

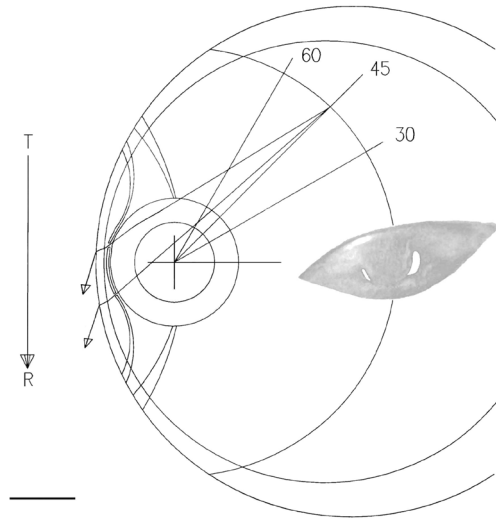
## Results

The study of dolphin vision is complicated by the need to examine several variables at the same time. First, the dolphin uses its visual sense in both air and water. Second, even more than most animals, the dolphin is exposed to a broad range of ambient light conditions, from very bright to very dim. Finally, the dolphin's range of vision is affected in unique ways by its pupil, varying from a large oval to two asymmetric slits—(1) its bifocal lens and (2) its retina—which has two areas of higher resolution.

### *Pupil Shape, Size, and Relative Position*

Aerial and underwater vision of the dolphin is apparently enhanced by the asymmetric constriction of its iris under bright ambient light conditions. The iris changes the shape of the pupil from a large horizontal oval, to a kidney-bean shaped pupil, and then to two near-vertical slits as an operculum extruded by the dorsal iris lowers in front of the lens and the ventral edge rises slightly to meet the operculum until only temporal and rostral slit pupils remain. The two slit pupils are significantly different in size, shape, and orientation. They are displaced slightly forward towards the rostrum with respect to the iris, and presumably the lens. The displacement of the dual pupils towards the rostrum is measured from the left and right horizontal boundaries of the dark (brown) iris and light (white) sclera (Figure 1). The horizontal distance from the center of the rostral pupil to the rostral iris-sclera boundary is shorter than the horizontal distance from the temporal pupil to the temporal iris-sclera boundary. Figure 1 and the iris photographs in Dawson et al. (1997) and Madsen & Herman (1980) illustrate a similar asymmetric lowering of the operculum resulting in the asymmetric pupils. This asymmetry in air results in the rostral pupil becoming more slit shaped, vertically oriented, and thinner. Dral (1975a) observed sideways movement of the operculum, significantly changing the size of either the rostral or temporal pupil. From a geometrical optics standpoint, for example, having a larger rostral pupil in water or a larger temporal pupil in air could improve vision in the forward and downward viewing directions under different ambient light conditions. The asymmetric locations of the slit pupils are illustrated by the passage of the thin beam of light in Figure 3. An unexpected finding is that both the temporal and rostral pupils enable imaging on the temporal area centralis.

The size and shape of the pupils of each eye may differ from each other depending on differences in light levels striking each eye. In general, an eye's sensitivity to light is primarily determined



**Figure 3.** Highly schematic drawing of left eye in air; traces illustrate the passage of light through a low curvature, high index of refraction cornea; high ambient illumination; and dual slit iris. 5-mm scale bar. R = rostral; T = temporal. 30, 45, and 60° off axis lines. Thin beams of light focus on the temporal area centralis.

by retinal processes rather than the amount of light admitted by the pupil. Differences in the state of the left and right irises in the dolphin's eyes may be associated with optimizing the passage of light through different zones of the lens at different light levels (e.g., when herding prey to the surface or shallows, one eye may face downward in water in shade while the other eye targets prey in air at higher light levels). A stopped-down iris in air has a greater impact on improving resolution as the depth-of-field increases and less light is able to pass through the lens core, reducing contrast of the image on the retina. Consequently, as the iris dilates, visual acuity should decrease faster in air than in water because dilation would expose more of the lens core.

#### *Analysis of Visual Acuity Data*

When the acuity data from the behavioral studies are analyzed using the same threshold criteria and regression analysis technique, the final results of similarly conducted studies are in much better agreement, with a higher correlation between the data and the regression lines (Madsen, 1972; Pepper & Simmons, 1973; Peacock et al., 1974; Noordenbos & Boogh, 1974; Herman et al., 1975). The raw data were obtained either from the senior author, read from the published graphs, or found in the report. The loss in accuracy from determining the percent correct from published graphs is counterbalanced by the use of a

common regression analysis with higher correlation (Figure 4). The high contrast grating target data referenced here were analyzed using cumulative log-normal functions having a threshold value corresponding to a variable target correct response level of 50%. This threshold criterion corresponds to a 75% level if both the variable and check targets (gray in appearance; very fine grating widths) are considered. A dolphin's conservative decision strategy during behavioral studies (Schusterman, 1974) supports the use of cumulative log-normal regression analysis.

A normal distribution is completely described by only two parameters: (1) its mean and (2) its SD. The mean is associated with a location on the number line and the SD with shape (e.g., narrow or wide). Each of these two parameters can be independently changed recursively (i.e., by trial and error) when the trial fits the data. Use of logarithmic probability graph paper, algebraic approximations (Zelen & Severo, 1970), and the simplex algorithm (Caceci & Cacheris, 1984) facilitated a least squares fit of the untransformed visual acuity data (Figure 4). Although the least squares method (LSM) and the simplex algorithm minimize the sum of the squared differences between the regression line and the measured data, the LSM requires the transformation of the cumulative log-normal function into a linear function. This linear transform plots as a straight line on logarithmic probability graph paper facilitating graphical analysis. Transforming a cumulative log-normal function into a straight line disproportionately weights measurements in the tails of the distribution (i.e., behaviorally determined measurements approaching zero or 100% correct). At these two extremes, differences between measurements and the corresponding value of the transformed log-normal function become disproportionately large. By implementing the simplex algorithm or using converging estimates of the mean and SD to minimize the sum of squared difference between measurements and the untransformed log-normal function, better agreement was realized between similarly conducted visual acuity studies. For example, the reported visual acuity angle of 18 min by Pepper & Simmons (1973) becomes 12.4 min. This value is similar to the Peacock et al. (1974) and Herman et al. (1975) values of between 12.2 and 12.7 min measured at a somewhat shorter viewing distance under similar high ambient light conditions with the same dolphin. It was interesting to note that in the frequency domain (line pairs per degree), the easier to implement LSM produced similar results to the iterative technique with only slightly lower correlation.

The trend in the SD for the different measured acuities with respect to viewing distance

(Rivamonte, 1983) could be interpreted as the result of retinal image processing, a function of differences in receptor field sizes and resolution of image detail. Increased image processing at the retinal level is suggested by the types and range of ganglion cell sizes (Dral, 1977). When inverse Fourier transforms of the resultant regression lines in the frequency domain are performed, estimates of retinal blur circles are determined. These can be used in the convolution (a two-dimensional analytical blurring) of the grating targets or for that matter any digitally captured scene. Though possibly an artifact of the mathematical modeling, the overall three-dimensional profile of the blur circles indicates lateral inhibition of the ganglion cell receptor fields.

Several unexpected trends were noted after analyzing the visual acuity data. First, contrary to what might be expected, SD dramatically increase as visual acuity improves (Figure 4). Why there is more variability as imaging becomes sharper seems paradoxical. As a consequence, there are more misses on the easier to resolve targets for higher acuity datasets than lower acuity datasets. Second, why is the correlation better when the LSM is applied in the frequency domain?

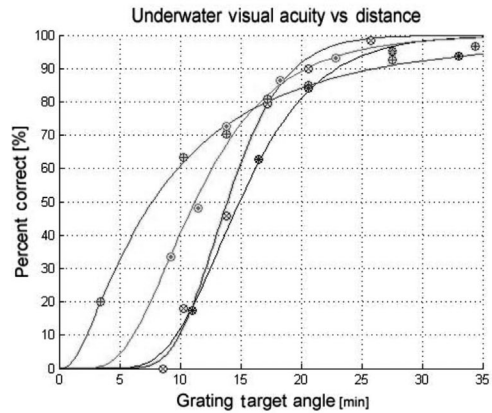
### Discussion

An explanation for the proposed equal aerial and underwater image sizes is followed by a case-by-case description of the fields-of-view. Finally, a listing of the distinguishing characteristics of dolphin vision is preceded by a comparison between human and dolphin vision.

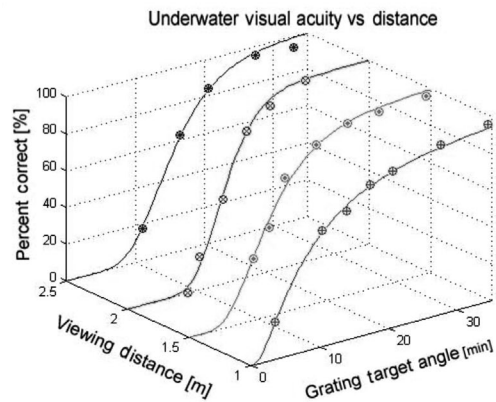
#### *Aerial and Underwater Image Sizes*

For undersea human divers, the air space of the facemask preserves the corneal refractive power of the eye when the diver is under water. Distances from the planar glass faceplate of the facemask to underwater objects appear foreshortened in proportion to the ratio between the refractive index of water and that of air. Objects appear approximately one third closer and, because of this, one third larger under water (Jenkins & White, 1957).

For a dolphin, the front surface refractive power of the cornea is significantly altered during sea surface transitions from approximately 17.5 diopters in air to essentially zero diopters in water. Although uncertainties in curvature and refractive index values limit detailed modeling of the dolphin eye for the very oblique rays discussed here, results from behavioral studies indicate comparable best aerial and underwater acuities (Herman et al., 1990). Basically, the principal planes and nodal points of the dolphin eye are pulled towards the stronger optical power of the cornea in air,



a.



b.

**Figure 4.** Cumulative log-normal regression lines (Peacock et al., 1975; Herman et al., 1976) in water visual acuity data; *MATLAB* orthographic and isometric plots of simplex fit. Two data points were dropped being greater than 5 SD from their respective regression lines.

resulting in images roughly the same size for the dolphin eye in both air and water.

#### *Fields-of-View*

*Bright Sunlight Bifocal Oblique Frontal Vision in Air*—Under high ambient light conditions in air, the constricted iris allows light to travel through the larger temporal pupil and the weakly refractive lens margin. The passage of light through the temporal pupil and lens margin before focusing on the temporal area centralis is an optically corrected alternative to the more direct path through the stenopaeic rostral pupil and lens core in air (Figure 3). Compensation for corneal refraction in air by an overcorrected lens margin is supported by ophthalmoscopic measurements of emmetropia in air under reduced lighting for corresponding oblique forward and downward viewing directions (Dral,

1972, 1975a, 1975b, 1977). These emmetropic forward and downward viewing directions in air and water are also predicted by a schematic eye model whose lens margin can focus on the retina in air, while an optical path through the lens core focuses on the retina in water (Rivamonte, 1976; Dral, 1987). This model allows agreement with behaviorally measured aerial visual acuities, even though the dolphin eye does not have an active mechanism which can change the position or shape of its rigid lens to accommodate for viewing distance (Dral, 1987; Cronin & Fasick, 1998; Litwiler & Cronin, 2001) or to compensate for the difference in refractive power of the cornea in air and water.

*Dim Light Bifocal Oblique Frontal Vision in Air*—Under low ambient light conditions in air, for very oblique forward and downward viewing directions, the geometry of the large symmetrically oval pupil admits light that passes primarily through the optically weak lens margin. The anterior position of the lens places it in close proximity to the cornea and iris, which in conjunction with oblique viewing direction, blocks light that would otherwise pass through the lens core. This geometry effectively limits the passage of light refracted by the cornea to the optically weak lens margin, canceling the otherwise high aerial refractive power of the cornea. The strongest evidence of this emmetropic viewing mechanism in air was obtained during ophthalmoscopic examinations (Dral, 1972, 1975a, 1975b). In air, emmetropia has only been measured in directions corresponding to forward and downward viewing directions. These results are also behaviorally supported by the dolphin's directional viewing preferences and its ability to perform tasks requiring good vision under low-light conditions (Dawson, 1979). By personal observation, Puka had no trouble responding to subtle hand signals which were shaded from artificial lights on a dark night.

*Bright Sunlight Stenopaic Frontal Vision in Air*—A second functional optical path in air at high illumination is also possible. The highly stopped-down rostral slit acts as a stenopaic pupil and allows light a direct path through the central core of the lens with reduced degradation of the image. However, the rostral slit pupil cannot constrict sufficiently to produce the blur circles predicted by the retinal mosaic or by behavioral acuity studies as the eye would theoretically become diffraction-limited. This second path might be better suited for underwater vision, where the eye would simply be a stopped-down, fixed focus optical system.

The rostral stenopaic pupil could function in air in bright sun to widen the field-of-vision because a pinhole type aperture has no preferred optical axes and is less dependent on the eye's refractive

elements. As previously noted, a dolphin's best optically corrected vision in air involves the passage of light striking different regions of the cornea, but passing through the optically weak lens margin covering a forward and downward visual field under both high and low ambient light conditions. Interestingly, for frontal vision, the best optical image formation in air in bright sunlight is through the temporal pupil and not the stenopaic rostral pupil as might be expected.

One of the more elaborate stenopaic mechanisms advanced was the double-slit pupil explanation for the variation in acuity with viewing distance by means of overlapping retinal images (Herman et al., 1975). This as well as other explanations remain under consideration (Dawson, 1980). Early theories proposing that a stenopaic mechanism could compensate for the additional refractive power of the cornea in air should probably not be abandoned out of hand for another explanation such as "light passing through different portions or layers of the lens" (Herman, 2000) without good reason to drop a previously held plausible explanation. Another possible stenopaic explanation for good aerial vision yet to be explored is the effective reduction in pupil cross-sectional size for very oblique forward or downward viewing directions in dim light when the iris is dilated.

*Frontal and Lateral Vision in Water*—The frontal and lateral field-of-vision is mapped onto the high-resolution temporal and low-resolution central retina for both high and low ambient light conditions in water. The frontal field-of-vision extends downward as illustrated by Dral (1975a). The forward image space is also cross-modally monitored by active echolocation (Azzali, 1992; Harley et al., 1996; Pack et al., 2002). The general nature of frontal and lateral underwater vision can be bracketed at the extremes of ambient illumination:

- Under low ambient light conditions in water, the dilated iris allows light to pass through the highly refractive lens core onto most of the retina, covering a wide frontal and lateral field-of-vision. As optically modeled and refractively measured, the lens core is sufficiently strong on axis to compensate for the overcorrected margin and the negative refraction of the posterior surface of the cornea in water.
- Under high ambient lighting conditions in water, light entering through the narrow rostral slit pupil passes through the highly refractive lens core onto the temporal retina, and less onto the central regions of the retina than when the iris is fully dilated. If a dolphin rapidly goes from bright light conditions

at the surface to a dim condition underwater, the iris may not have sufficient time to dilate, and a stenopaic pupil would not allow an optimum level of light to reach the retina. For every light and image contrast level, the retina has an optimally sized ganglion summation region and sensitivity. Under low ambient light conditions, the perception of a blurred but brighter retinal image can be better than a sharper but dimmer image. It seems that almost every adaptive feature of an eye for bright light conditions has a detrimental consequence under low-light conditions. The relatively slow dolphin iris reflex could be an adaptation for frequent returns to brighter surface conditions for respiration rather than merely a result of the thinness and minimal musculature of the iris.

*Rearward Vision in Water*—The dolphin pupil has a slight overall rostral displacement relative to the lens which tends to favor the rearward underwater viewing direction at the expense of a better geometry for aerial vision in this quadrant. At all levels of ambient lighting, rearward vision makes use of the rostral area centralis:

- Under low ambient light conditions in water, a wide rearward emmetropic field-of-vision has been measured for the dolphin eye through a dilated pupil (Dral, 1975a). The optical path is through the temporal region of the dilated pupil and lens core with image formation on the rostral area centralis.
- Under high ambient light conditions, the temporal pupil also enables rearward viewing underwater. This optical path is through the larger temporal pupil and lens core, with image formation on the rostral area centralis. The larger temporal pupil, even in bright light, acts more like a stopped-down aperture than a pinhole pupil.

Forward and rearward vision play a key role in a dolphin's near and far perception of its environment, but vision must play an even greater role in the routine activities of a deaf dolphin. A deaf bottlenose dolphin captured in the wild with others appeared to be normal in size, weight, and behavior (Ridgway & Carder, 1997), but it was only later determined that this dolphin did not make any of the typical whistle, chirp, and click sounds of its conspecifics. This dolphin would only respond to trained auditory cues when able to see the other dolphins performing the behavior. When it rested with the other dolphins, it would assume a vertical orientation, perpendicular to the water's surface, assuming a "spar buoy" posture. For a dolphin having no passive echolocation faculty, this atypical resting position could be in response to a need to visually detect threats

from below. The dolphin's sense of sight is functional at birth, but echolocation is acquired over its development. This may be explained in part because biosonar requires both a modulated signal source and a sensor, whereas vision only requires a sensor. Especially in clear, familiar aquatic environments, vision is most likely equal in functional importance to biosonar and requires less energy expenditure than active echolocation. As more deaf dolphins are being found in nature, the idea that a deaf dolphin is a dead dolphin is not necessarily true. As a blind dolphin is yet to be reported, a blind dolphin may lack a sensory input vital for survival.

*Theories Advanced to Explain Dolphin Vision*—The eye of the bottlenose dolphin has some interesting asymmetric anatomical features. First, the dolphin has two irregular retinal regions that have finer mosaics of ganglion cells (indicating areas of enhanced image resolution), a temporal area centralis, and a rostral area centralis (Dral, 1977; Mass & Supin, 1990, 1995; Supin et al., 2001). These would correspond functionally to the centrally located area centralis in the human eye. More striking is the double-slit pupil formed by an operculum of the iris shielding the central core of the lens under high ambient light conditions. The size and location of the double-slit pupil and the placement of the two areae centrali contribute to a bifocal optical model that can explain the equally good aerial and underwater vision of the dolphin.

Kroger & Kirschfeld (1992, 1993, 1994) measured a high index of refraction and posterior curvature for the cornea of the harbor porpoise (*Phocoena phocoena*), which make the cornea a very negative optical element in water. Emmetropia in water was established by measurements indicating a correspondingly stronger positive lens. A similar counterbalancing of refractive indexes between the lens core and cornea of the dolphin bifocal lens model would not adversely affect its bifocal functionality. A possible benefit of a highly refractive, low-curvature cornea would be in the oblique fields of view in air. Very oblique rays that would otherwise be deflected too steeply to pass through the lens margin exit the cornea at a shallower angle with respect to the lens margin (Figure 3). A greater acceptance angle for very oblique rays may also be an eye trait in other species having a high index of refraction with a low-curvature front optical surface (Sivak, 1976). With this in mind, a review of the dolphin bifocal eye model article (Rivamonte, 1976) reveals errors in a drawing that illustrates thin beams of light passing through the lens margin. Although the schematic eye model computations in this paper are correct, the schematic illustration of rays passing through the lens margin in air does not show them

being strongly refracted by the cornea. In addition, one of these rays is curiously focused on a very low-resolution region of the retina. There are other hypotheses explaining the paradoxical observation of comparable aerial and underwater dolphin visual acuity of approximately 8 min of arc (Herman, 1990). The paradox is that the dolphin eye has no obvious mechanism to compensate for the large difference in refractive power of the cornea between air and water. Based on measurements and modeling of the *P. phocoena* eye (Kroger & Kirschfeld, 1992, 1993, 1994; Wartzok & Ketten, 1999), van de Pol et al. (1995) developed an eye model to explain comparable aerial and underwater visual acuities. Relying on a negatively refractive divergent cornea, rather than being very nearsighted in air and in focus in water, this dolphin eye model is in focus in air and very farsighted in water. Other explanations involve one or both stenopaic (i.e., pinhole) pupils (Dawson et al., 1972; Herman et al., 1975). One of the possible pathways investigated here also supports a stenopaic pupil explanation for emmetropic aerial vision at high ambient light levels. Stopping-down of the dolphin iris increases the depth-of-field and reduces aberrations. Common to both theories are the dolphin's behaviorally observed and optically modeled preferred viewing directions (Dral, 1977; Dawson, 1980; Pryor, 1990). A key distinction between the bifocal lens and stenopaic pupil theories is that the bifocal lens is capable of explaining observed visually guided behaviors in air under low ambient light conditions when the pupil is expanded (Dawson, 1979). Though other mechanisms may be involved, the computed blur circle diameters corresponding to the behaviorally measured acuities are much smaller than would be predicted by the minimum dimension of the stenopaic rostral pupil (Rivamonte, 1976). As the rostral pupil is a near vertical slit, the series of blur circles making up the shadow of this slit on the retina will favor vertical features in the object space (e.g., vertical gratings). The role of a constricted pupil in reducing aberrations and increasing the depth-of-field remains an important element in marine mammal vision (Gislen & Gislen, 2004). With a single fixed focal distance in air and another in water, a dolphin's extent of good vision is significantly improved by a stopped-down iris. A stopped-down iris can also constrain the passage of light to specific layers (e.g., the lens margin) of the bifocal lens for best resolution.

Another explanation for the paradox involves the displacement of the rigid lens by the operculum (Dral, 1972). This explanation was prompted by the observation of small transient changes in the refractive state of the eye during ophthalmoscopic measurements. These measurements could not be

easily explained because of the anatomical observation of the complete lack of ciliary musculature usually associated with lens deformation or displacement (Dral, 1972; Kastelein et al., 1990). These transient changes may have been artifacts of the measurement process which in part relies on the accommodative state of the observer's eye.

Not only does the dolphin lack any obvious mechanism to compensate for air-water transitions, but it also lacks a means for the much smaller focal changes it required to accommodate for differences in viewing distances. Photorefractive measurements (Cronin & Fasick, 1998; Litwiler & Cronin, 2001), refractive state determinations (Dawson, 1972), and behavioral visual acuity data trends indicate that the dolphin eye does not actively accommodate for changes in viewing distance. For underwater visual acuity determinations (e.g., every 0.5 m from 1.0 to 2.5 m), the trend in measured values follows a curve similar to an optical system focused at just under a meter (Peacock et al., 1974; Herman et al., 1975).

A large foreshortening of the distance between the lens and retina by means of the eye's strong extra ocular muscles is also unlikely. This mechanism would require a large off-axis deformation of an incompressible eye, an eye strengthened by an atypically thick sclera. The thick sclera rounds and reinforces the attachment of strong extra ocular muscles to an otherwise ellipsoidal shaped eye. The combination of high intraocular pressure (Dawson et al., 1992) and a sclera thickened to form a more spherically shaped eye (Dawson et al., 1972; Dral, 1975a, 1987) may have evolved in response to factors like hydrodynamic stresses, the benefits of lateral eye bulging, and better eye mobility afforded by a ball and socket configuration.

*Comparison of Dolphin Vision to Human Vision*—Differences between dolphin vision and human vision include varying degrees of coordinated eye movements, partial independence of left and right iris responses to ambient light levels, very high intraocular pressure (Dawson et al., 1992), and reduced or absent color vision (Madsen, 1976; Simons, 1977; Fasick et al., 1998; Griebel, 2002; Griebel & Schmid, 2002). The Madsen (1976) color vision study boiled down to a spectral sensitivity study when, after more than 15,000 trials under several different behavioral protocols, Puka continued to respond to perceived target brightness and failed to take advantage of spectral color cues presented. Griebel & Schmid (2002) have since demonstrated that *T. truncatus* are able to distinguish between spectral blue and near ultraviolet stimuli of equal brightness. Spectral and light level sensitivity differences between dolphins and humans were dramatically



evident during a spectral sensitivity study when a dolphin reliably intensity-matched a very bright red stimulus, which illuminated the water in the tank, to a very dim blue stimulus that the researchers had to look directly into the projection apparatus to observe (Madsen, 1976).

The human fovea is associated with stereoscopic vision and binocular depth perception. Both of these functions are associated with precise, coordinated alignment of both eyes, and eyes having a high-resolution, narrow field-of-vision. The lack of a fovea within the temporal area centralis may explain in part why the dolphin has reduced eye mobility and low binocular eye coordination (Dawson et al., 1981). Dolphins probably lack true stereoscopic vision where objects appear to float in three dimensions (Supin et al., 2001; Sacks, 2006).

Other differences include a teardrop or spoon-bottom-like shaped cornea, oily viscous protective tears, behaviorally measured astigmatism in water but not in air, and an eye capable of bulging. The dolphin lens tends to be ovoid in shape with its long axis orthogonal to the long axis of the ovoid cornea. This orientation of the lens and cornea could explain the behavioral and ophthalmoscopic indications of no apparent aerial astigmatism (Dral & Dudok van Heel, 1974; Rivamonte, 1983).

In a sense, a dolphin's vision can be compared to that of a human wearing blue filtered GEN II night vision goggles, being fixed focus, very blue light sensitive, lower in resolution, and monochromatic (Rivamonte, 1993). Dolphin vision can also be compared to human vision in old age when the human lens becomes rigid and unable to refocus for different viewing distances (Dawson, 1980). A dolphin's underwater fixed focus is estimated to be  $< 1$  m in water, and  $> 2.5$  m in air (Peacock et al., 1974; Herman et al., 1975).

The iris of the killer whale (*Orcinus orca*) is similar in appearance to that of the bottlenose dolphin in high illumination. Unlike the bottlenose dolphin, however, the killer whale lacks the upper body flexibility to rotate its head downward with respect to the long axis of its body to redirect its gaze. With a significant portion of its body above the sea surface in a near vertical orientation during a spy hop, the killer whale is required to look downward (ventrally) to observe prey on ice floes. The killer whale should have similar but higher visual acuity than the bottlenose dolphin because of its longer focal length eye. Like the bottlenose dolphin, its temporal pupil offers the best geometry for aerial vision.

*Characteristics of Dolphin Vision*—In summary, knowledge gained primarily during behavioral acuity and spectral sensitivity studies (Madsen, 1972, 1976; Pepper & Simmons, 1973; Peacock

et al., 1974; Noordenbos & Boogh, 1974; Herman et al., 1975; Griebel & Schmid, 2002) indicate a visual sense with (1) comparable aerial and underwater acuities; (2) a wide field-of-vision with a best resolution of approximately 8 min of arc in both air and water in the forward and downward direction (Herman et al., 1990); (3) two areae centrali and a bifocal lens; (4) preferred viewing directions that allow light to pass through the lens margin in air and lens core in water; (5) an inability to actively accommodate for different viewing distances (Cronin & Fasick, 1998; Litwiler & Cronin, 2001); (6) a fixed focus of approximately  $< 1$  m in water and  $> 2$  m in air; (7) preferred viewing directions corresponding to areas on the retina capable of better resolution; (8) voluntary head and body positioning for optimal vision; (9) the ability to eye bulge to improve viewing geometries (Dawson et al., 1972; Dawson, 1980); (10) best aerial vision in the forward and downward viewing direction; (11) no astigmatism in air; (12) a peak quantum corrected dim light sensitivity at 487.4 nm (495 nm energy-based) and a peak bright light sensitivity at 493.4 nm (500 nm energy-based); (13) a spectral sensitivity that follows a rod Dartnall function for wavelengths longer than spectral blue; (14) a small Purkinje shift for wavelengths greater than blue-green, indicating no or minimal color vision; (15) an inability to distinguish between color hues for wave lengths longer than spectral blue; (16) an ability to distinguish between blue and ultraviolet stimuli at the same brightness (Griebel & Schmid, 2002); (17) relatively small differences in spectral sensitivities in the region of the broad violet-blue-green sensitivity peak; (18) very high violet-blue-green light sensitivity and very low orange-red light sensitivity; (19) a high sensitivity to brightness differences; (20) insensitivity to light from red light emitting diodes (Cronin & Fasick, 1998); (21) rapid loss of visual resolution, but improved sensitivity, with decreasing light levels; (22) the capability to visually recognize subtle hand signals in air on a dark night as well as in bright sun light; (23) lateral inhibition of the ganglion receptor fields; (24) comparable aerial and underwater image magnifications; (25) conservative, low false alarm rate response bias (Schusterman, 1974); and (26) acuity and spectral sensitivity data having high correlation with cumulative log-normal distribution functions. A more interdisciplinary coverage is presented by Supin et al. (2001).

## Conclusions

By tracing rays in a reverse direction from the temporal area centralis of the retina through the wide temporal and stenopaic rostral pupils of the iris at high light levels, a dolphin's forward aerial

and underwater optimum viewing directions and object space resolution can be predicted. These same oblique paths and corresponding viewing directions could also be used under low ambient light conditions through a dilated iris. As the iris dilates, visual acuity drops off sharply, especially in air. This drop off in acuity with light level can be attributed to optical adaptations of an eye evolved to function at extremes of ambient illumination in both air and water. The rostral area centralis is positioned to best provide underwater viewing in the rearward direction, providing additional sensory input from a sector not covered by a dolphin's use of active echolocation. In the most ecologically relevant forward and downward viewing directions, best aerial and underwater visual acuities of approximately 8 min are achieved under high ambient light conditions by means of a double-slit pupil and a bifocal lens. For this forward sensory field, there is evidence that underwater vision and bioacoustic-imaging are integrated in real time. An iterative least squares statistical analysis of the raw data plotted on cumulative log-normal graph paper was applied to the behavioral acuity data from similarly conducted studies. These behavioral studies were conducted at different grating target distances and ambient light levels. The studies help determine dolphin eye performance characteristics which cannot be inferred with any certainty from *post-mortem* material. Ophthalmoscopic, keratometric, and photorefractive measurements provided *in vivo* estimates of geometric optical parameters. When taken together, the geometric dolphin eye model and the behavioral acuity data indicate that aerial and underwater images are probably comparable in size and detail for this dual fixed focus optical system. This image space information enables estimates of resolution spot sizes in the object space. The proposed comparable image sizes, whether the eye is in air or water, would contribute to a stable visual environment where the visual field remains steady and independent of eye, head, or body movements. From a geometrical optics standpoint, the dolphin eye will remain a subject of active research and debate because of the present limited knowledge of the gradient indices of its optical elements and the role of the operculum.

#### Acknowledgments

I thank those whose work in the early 1970s sparked my interest in attempting to understand how a dolphin named Puka viewed her world: first and foremost A. D. G. Dral, Netherlands Institute for Sea Research, The Netherlands; W. H. Dudok van Heel, Dolfinarium at Harderwijk, The Netherlands; L. H. Herman and other researchers at the Kewalo Basin Marine Mammal Laboratory

in Honolulu, including C. J. Madsen, M. F. Peacock, M. P. Yunker, and R. K. R. Thompson; W. W. Dawson, University of Florida, Gainesville; J. G. Sivak, University of Waterloo, Canada; and K. Pryor, Sea Life Park and Oceanic Institute, Hawaii. Dr. Carolyn Madsen's comments and assistance in writing this article are greatly appreciated.

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