The Visual System of Dolphins

A Review by James T. Fulton

J.1 Introduction

The visual system of the dolphin, particularly the bottle-nosed dolphin, *Tursiops truncatus*, has been observed extensively in the field from a behavioral aspect. However, from a physiological perspective, Pryor quoted one researcher as follows: “Compared to our knowledge of vision in terrestrial animals, our fundamental knowledge of the cetacean’s highly evolved and very different eye is ‘pathetic.’” This situation appears to be largely unchanged in 2009. There are many unresolved questions that prevent a detailed description of the performance of the dolphin visual system. As a result, the literature of dolphin vision should be considered largely exploratory rather than descriptive.

Three major compilations have appeared relating to the sensory abilities of marine mammals; Thomas & Kastelein in 1990, Thomas, Kastelein & Supin in 1992 and Supin, Popov & Mass in 2001. As noted by a long time participant in the field, the investigators “are biologists and tank cleaners.” They may be described a bit more precisely as behavioral anthropologists with undergraduate backgrounds in biology—and tank cleaners. Very few specialists in histology, neurology or physiology have made a career in this field.

Due to this situation, concepts have crept into the literature that are perplexing. The dolphin eye when fully light adapted has been described as analogous to a pin hole camera. However, a pin hole camera does not have a lens behind the pin hole, it is defined as a camera that is refraction free (although it is limited by diffraction)—all optical rays pass straight through the aperture of a pin hole camera. The resulting image covers a very wide field of view that is not limited to the area around a chief ray. The dolphin eye when fully light adapted is a conventional eye with a fully developed lens system and a very effective aperture stop. It is not a pin hole camera by definition. It can be described in optical science as a conventional camera with a pin hole aperture in front of the lens. A pin hole aperture mask is frequently used in optometry where it is called a Hartmann mask. It may consist of one pin hole or an array of pin holes. If each pin hole in the array is turned into an interferometer, the resultant instrument becomes a Shack-Hartmann interferometer. This instrument is very useful for measuring the properties of the lens system of a camera. A simpler variant of a Hartmann mask based instrument is described below by Cronin, Fasic & Howland.

The dolphin eye has been described repeatedly as exhibiting two fovea based on a novel criteria, that the concentration of large ganglion neurons at two locations on the neural portion of the retina define two fovea. Rivamonte described this dual fovea configuration along with the unusual operculum as constituting a bifocal visual system. The dolphin retina, like all mammalian retinas is reversed (Section 1.7). All of the neural tissue of the retina is in the optical path leading to the photoreceptors. The hallmark of a fovea is that there are NO neural cells in the optical path leading to that fovea, ganglion or otherwise. In fact, the fovea is characterized by an absence of vascularization, as well as neurons, in this “area centralis.” The photoreceptors are supported by diffusion of blood plasma through the non-neural tissue and even more importantly from the retinal pigment epithelium layers on the...
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scleral side of the retina. Surveys of the cetacean retina by conventional retinoscopic imaging have not reported any fovea in Cetacea.

The spectral performance of the dolphin visual system has been investigated primarily from the behavioral and coarse psychophysical perspectives (Madsen, 1976). The Madsen (1976) color vision study boiled down to a visibility spectrum study when, after more than 15,000 trials under several different behavioral protocols, the single subject continued to respond to perceived target brightness and failed to take advantage of spectral color cues presented. It exhibited a visual luminosity function similar to other mammals. In field studies, “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)” were observed. Needless to say, the response of dolphin eyes is photon-based and should be expressed in quantum-based and not energy-based units.

Thomas, Kastelein & Supin have provided a phylogenetic tree of the cetacean families. Supin, Popov & Mass give a brief but informative textual discussion of the major families of cetacea (pg 3). Leatherwood & Reeves provide a more extensive phylogenetic discussion of cetacea.

Cetacea have greatly evolved from their presumed ungulate ancestor to match the requirements of their new ecological niche. Both the performance and physiology of their visual and auditory capabilities have changed remarkably and their olfactory capability is believed to be vestigial at best.

The eyes of dolphins have evolved from those of the typical ungulate to share many of the features of more predatory families and species. The eyes share a set of six muscles with other mammals but their tasks appear to have been modified. Dolphin eyes are not known to exhibit torsional motion (rotation around the optical axis). Additional adaptations may have occurred to satisfy ecological needs. The sclera is particularly thick and the intraocular pressure (relative to the environment) is known to be very high compared to terrestrial mammals (Dawson et al., 1992). The non spherical shape of their sclera limits eye rotation up and down and left and right about the center of the sclera or choroid.

A major void in the current literature is a definitive discussion of the location of the eyes of Tursiops truncatus relative to the skull and the outer conformation of the animal. There is reasonably broad agreement in the literature that the eyes move in ways other than simple rotation of the globe within a fixed spherical eye socket. It is likely this motion is coordinated with the skin conformation to provide optimum conditions for alternately high speed swimming and analytical examination of rostral targets at minimal speed swimming. While the eye is not spherical and able to rotate in a spherical socket like a human eye, the socket itself may be under muscular control (in conjunction with the contour of the skin. Cranford et al. have been active in computer aided tomography of the dolphins head, but with most attention focused on its acoustic properties. They have defined a set of horizontal, vertical and transverse planes and illustrated their coordinates with a transverse plane passing through the eyes of the dolphin. Their dorsal schematic in figure 3 suggests the optical axis of the eye of Delphinus delphis is 75 degrees from the long axis of the body but a higher precision measurement is required under a variety of in-vivo conditions.

As a phylogenetic family, the dolphins do not depend on vision as their primary sensory facility. Their acoustic sensing is far more important in their ecological niche. This fact is demonstrated by the so-called river dolphins who have evolved to the point they are functionally blind, although they have lived with this characteristic for millennia.

Rivamonte reviewed much of the work in the field in 2009, and focused on one of the outstanding dichotomies. How does the dolphin see clearly in both air and water when "the dolphin eye has no obvious means to compensate for the large difference in refractive power of the cornea between air and water?" This question will be examined below.

Kroger & Kirschfeld (1993) provided a schematic of the eyes of Phocoena phocoena relative to the long axis of the body. They show the optical axis of the eyes at equal angles of less than 45 degrees from the body axis (compare to 75 degrees in Cranford). No angular dimensions are provided and no stereo vision is suggested. However, stereoptic vision could be obtained in the real system for optical axes less than 30 degrees from the body axis. As seen in Figure J.1.1-1, the dolphin may exhibit better stereoptic vision in air than in water because of the change in index of refraction of the medium. Kastelein et al. noted this possibility in 1990 (page 477). The performance of the cetacean eyes are significantly degraded at an angle of 60° from the optical axis; the angle of maximum resolving

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power proposed by some investigators.

Except for the motions of the eyes, the dolphin visual system appears to be typically mammalian except for one peculiar adaptation believed to be shared with octopus and possibly other shallow water marine species. It exhibits an operculum that is much more effective than the typical circular or oval mammalian iris. Whereas the human iris operates over a range from 8 to 2 mm in diameter giving a brightness control at the retina on the order of 16:1, the dolphin iris/operculum is able to achieve a brightness control range exceeding 100:1. Dawson et al. have provided data suggesting the time constants of the iris/operculum are similar to those of human and operate at similar light levels.

The dolphins literal habitat involves a very large illumination range, from the depths of the ocean (down to several hundred feet) to bright direct sunlight during periods of breathing and even intermittent aerial flight. The iris/operculum appears to be maximally closed at light levels on the order of 15,000 lux (15,000 lumens/m² or 1400 foot-candles).

While the literature tends to negate the importance of the cornea under water, Litwiler & Cronin take a different and possibly more informed view. They summarized current knowledge in this area. “The cornea, however, may also contribute to image formation even underwater. Unlike the terrestrial cornea, which is relatively thin throughout, the dolphin cornea is thicker at the periphery than at the center, being more strongly curved on the posterior surface than the anterior surface (Kroger and Kirschfeld 1994). In addition, the periphery of the cornea has a higher refractive index than the center (Kroger and Kirschfeld 1992). Together, these result in an unusual optical system in which the cornea acts as a diverging lens and contributes negative refractive power to the overall optics of the eye. The negative power of the cornea may compensate for the excessive refractive power of the lens, and correct the optics of the eye to near emmetropia in water. Several hypotheses have been suggested to account for this aerial acuity, including a constricted pupil (Herman et al. 1975, Rivamonte 1976, Dawson et al. 1987, Kroger and Kirschfeld 1993), localized flattening of the cornea (Dawson et al. 1987, Kroger 1989), variation in focal position with direction of view (Dral 1972, Pack and Herman 1995), and a fine, continuous accommodative mechanism, such as movement of the lens within the eye (Dral 1972, Mass 1997). While some of these hypotheses are supported by experimental results (e.g., corneal flattening, Kroger 1989; variation with direction of view, Dral 1972), researchers have questioned the validity of others (e.g., lenticular accommodation, Dawson 1980; constricted pupil, Murphy and Howland 1991; Rivamonte 1976),” Litwiler & Cronin go on, “In general, there is a lack of observations and data on the accommodative capacity of the dolphin visual system. “Our results are inadequate to demonstrate whether or not dolphins accommodate in air, but they strongly suggest that these animals lack the ability to adjust the focus of the eye underwater.”

While the literature leans to no method of accommodation in the bottlenose dolphin eye, this is short-sighted. Living biological systems require largely automatic methods of optimization, the eyes cannot be pre-aligned and pre-focused at the factory like a man-made camera. Effective imaging requires the optical image be brought to focus within 15–25 microns (0.015–0.025 millimeters) of the entrance aperture of the photoreceptors for an F/3 optical system. This quality of adjustment must be maintained throughout the life of the animal (including periods of growth) and over the entire retina operating at optimal resolution. A mechanism or protocol is required to achieve this goal in any mammal. Dral, a histologist with a veterinary bent, described the fields of view of the bottle nose dolphin under a variety of light conditions in 1975. As noted by Dral, “a mechanism for accommodation, which is lacking in the ciliary body, might be present in the iridal musculature.” These combined tissues are sometimes labeled the trabecular matrix. West et al. have explored the relevant tissue recently.

Maintaining focus may be a demanding requirement in the bottlenose and other animals attempting to maintain high

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acuity over a wide field of view. Humans are only required to maintain optimum focus over the central 1.2 degree diameter of the fovea.

Very little is known about the structure of the retina except it has the same layered structure as other terrestrial mammals. It does exhibit an effective tapetum lucidum to enhance its low light level performance. The topography of the neural portion of the retina is unusual in that it contains very large ganglion neurons grouped into two areas of the retina. The location and area of the blind spot has not been precisely identified. It is nominally dorsal along the sagittal plane of the eye. No area of minimal vascularization of the neural retina (suggestive of a fovea) have been identified to date.

J.2 The general form of the Cetacean eye

The axial dimensions of the dolphin eye are remarkably similar to the human eye. The minimum focal distance for dolphin is on the order of one meter in water and probably greater than two meters in air. Rivamonte’s 1976 working model assumes the lens is spherical and consists of two concentric volumes, an inner core of ~3.0 mm radius and an outer core of ~4.8 mm radius. He gives the outer radius of the cornea as 19.2 mm. He gives the overall refractive power as 83.4 in water and 93.9 in air. Rivamonte (1976) gives the focal length of the eye as 22.42 mm in water and 18.48 mm in air (although these values are subject to refinement and interpretation). Rivamonte notes the focal length in air, using only the outer core of the lens, is 22.48 mm. This is a reasonable condition at high light level based on the presence of an operculum rather than a simple iris.

Figure J.2.1-1 provides a multi-panel schematic that can be compared to a similar Figure 2.4.1-4 for the human eye in Chapter 2 of Processes in Biological Vision. The figure is adapted from Rivamonte, 1976. Note: the values for the cardinal points, principle points and nodal points only apply to the paraxial condition (within about one degree of the optical axis). These values do not apply to the off-axis condition except in the case of a perfectly spherical lens in a uniform medium.

It is important to differentiate between the term spherical lens, referring to a ball-shaped lens, and a spherical lens, referring to a lens with at least one spherical shaped surface (and not an asphere). This overlap in terminology is unfortunate.

The cornea of the dolphin appears to exhibit an unusually large radius of curvature and the lens is much more spherical than a typical terrestrial mammal, more similar to that of many fish. The currently documented optical characteristics of the cornea and lens are not adequate to define the performance of the dolphin eye in detail. As a result, the best interpretation of the visual system is a parametric model rather than a precise optical prescription.

The literature includes many observations from anatomists describing the first order shape of the lenses of marine mammal eyes as “spherical.” More careful observations by optical engineering aware investigators give a second order description of these lenses as ellipsoidal. The most recent third order descriptions show the anterior and posterior surfaces of these lenses have different radii, indicating more complex forms than a simple ellipsoid. These third order descriptions are more compatible with the complex non-spherical retinal cups measured in many cetaceans.

The uppermost frame shows the eye in water where the cornea has been eliminated as it is assumed to have the same index of refraction as the external water and the internal anterior humor. The lens is treated as spherical and consisting of an inner spherical core with a radius of ~3.0 mm and an outer margin with an outer radius of ~4.8 mm. The principle points and nodal points of such a system are at the center of the lens. Rivamonte gives the radius of the retina as 16.1 mm centered on the center of the lens.

The F/# of an optical system, the ratio of the focal length to the maximum aperture, indicates the light gathering power of the system. For the system in water, the F/# = 3.0. This value is not significantly faster than that of the human eye in air. Thus, the dolphin eye is not optimized specifically for operating in low light environments typical of the deep sea. The dolphins are shallow water inhabitants, making only occasional deep dives (frequently with human encouragement). Their dominant sensory modality in deep water is their echolocation capability.

The F/# of 3 is only achieved along the optical axis of the system. For large field angles, the aperture is greatly reduced and vignetted (partially blocked) due to the location of the bulk of the lens so far behind the iris.

There is considerable comment in the literature concerning the field of view of the dolphin eye both in water and in air. Comparisons of the field of view of cetacean and human eyes are awkward. The eyes are optimized for entirely different ecologies. The cetacean eye attempts to maintain a relatively high resolution over a very wide field of view on the order of 100 degrees. The human eye seeks a very high resolution only over a small region associated with
the fovea (nominally 1.2 degrees in diameter) and a much lower resolution over a wide field of view on the order of 110 degrees.

The upper frame also shows the horizontal view of the dolphin eye in air according to Rivamonte. The presentation shows the lens as consisting of two spherical zones and the cornea as a meniscus lens. The inner zone has an index of 1.524, the outer zone an index of 1.451, and the cornea has an index of 1.336. Using his values and a lens program originally on an HP-65 hand calculator, he calculates the location of the focal plane as $F'$, nominally thee millimeters short of the focal plane. This distance is so large, the animal would be functionally blind (no detail in the perceived image, a uniformly illuminated plane) rather than myopic.

In a note, Rivamonte says a ray parallel to the optical axis and passing through the lens 3.9 mm from its center (essentially avoiding the core) focuses at the retina. This would suggest, the operculum could be used as an aperture stop that blocks all paraxial light from passing through the core of the lens. The resulting paraxial scene would be in focus. However, off-axis light would not focus at the retina, and specifically would not focus at the two proposed fovea. These situations are illustrated in the lower half of the figure.

The lower half of the figure shows a matrix of four conditions. In water, the cornea is assumed to be ineffective. The lens is the only optical element. Its geometric symmetry causes any chief ray of an optical bundle (passing through the center of the lens) to mimic a paraxial ray. It passes straight through the lens. All of the rays come to focus the same distance from the center of the lens. Therefore, the retina must be perfectly spherical to perceive the image properly if the lens is spherical. The artwork suggests the non-vignetted field of view of the dolphin eye in water is on the order of ±30 from the axis.

At low light level, the dolphin eye in air operates similarly except for the optical power of the cornea. The cornea changes the focal length of the system and also changes the perceived external field angle for a given location on the retina. This change in field angle would be zero on axis but would cause the foveas to image different field positions than when viewing in water. As is noted at lower right, the operculum has the potential to block the paraxial and some parallel rays from reaching the retina. This provides an effective sun shield for the retina near the axis but may not protect the two proposed fovea.

**J.2.1 The version range of the cetacean eye**

The literature describes considerable flexibility of the eyes within the skull and outer contour of the dolphin. Dawson et al., 1972; and Dawson, 1980, reported the eyes were capable of bulging. Dawson (1980) also noted what he called the heavily developed external musculature of the eye of *Tursiops*. However, there is opposing literature suggesting the eyes of *Tursiops* are nominally fixed in pointing. Note carefully that while the retina of *Tursiops* is not spherical the outer surface of the eye is. The degree of roundness is shared with few other animals and is similar to that of the human. This roundness suggests considerable rotary range for its eye within a fixed socket.

While the eyes are supported by three sets of muscles, as in all mammals, the set used for torsion (rotation about the optical axis) has apparently been converted to other uses. There are indications that rather than significant rotation of the optical axis up and down and left and right about their centroids, the position of the eyes and the outer skin
contour can rotate into a more forward looking direction in order to aid stereoscopic vision. Yablokov et al. ascribed a protraction-retraction function to these muscles, based on observations that the eyes protrude substantially when viewing forward\textsuperscript{14}. They suggested the overlap in the visual field might be as high as 20-30 degrees in this situation. The above assertions are in Mass & Supin (1990, page 524). Supin, Popov & Mass (page 235) suggest each eye of *Trusiops truncatus* can be displaced up to 15 mm under muscle control. They did not define the axes they were discussing. Figure J.2.1-2 shows the eyes in the proposed forward position. This figure also illustrates the outer ears of the dolphin (binaural acoustic receivers) as refractive lenses in accordance with the texts, “Hearing: A 21\textsuperscript{st} Century Paradigm” and “Processes in Biological Hearing” by this author. The figure shows the hydrodynamic profile of *Tursiops truncatus* is changed dramatically when moving at low speed and interrogating objects ahead of it, compared to its profile when swimming at high speed.

interesting view is the artistic rendition of *Tursiops truncatus* swimming toward the artist by Reynolds et al\textsuperscript{15}. Their figure 11 shows a dolphin with an asymmetric external head. The one eye is oriented much more toward the direction of travel than the other and the outer skin reflects this difference in conformation.

**Figure J.2.1-3** provided by Jack Kassewitz of the The Speak Dolphin Project is even more defining. The dolphin is obviously looking at the volleyball above the horizontal plane of the animal’s head at zero range employing a sight line along the crease in the external contour of its head. Note the white of the dolphins eye indicating the degree of rotation of the eye toward the rostral direction.

![Figure J.2.1-3](image)

The reflection directly above the animal’s eye may suggest some change in the external contour of the eye socket as well in this dolphin configuration but this is unclear from the photograph alone. The question of an asymmetrical head can not be addressed from this picture alone.

**J.2.2 Computed prescriptions for the cetacean eye**

Several prescriptions of the optics of dolphins have appeared in the literature. As in the human eye, all of the prescriptions found applied to the paraxial performance of the eye (chief rays within one degree of the optical axis). This is virtually the trivial case in the wide visual angle eye of the dolphin. The numbers used by the different investigators are primitive from the perspective of an optical designer, seldom exceeding three decimal place accuracy for the index and two decimal places for radii and positions in millimeters.

Rivamonte provided a prescription for the eye in 1976 that has been recently repeated in a 2009 paper\textsuperscript{16}. The model was not sufficiently precise and treated the cornea as entirely transparent with an index of refraction the same as the


\textsuperscript{16}Rivamonte, L. (2009) Bottlenose dolphin (*Tursiops truncatus*) double-slit pupil asymmetries enhance vision Aquatic Mammals vol 35(2), pp 269-280
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sea and the anterior humor. He noted, the dolphin lens tends to be ovoid in shape with its long axis orthogonal to the long axis of the ovoid cornea. However, he modeled the lens as a perfect sphere.

Rivamonte (1976) and Kroger & Kirschfeld (1990’s) both performed ray trace analyses of cetacean eyes as part of their doctoral degree apprenticeships. In both cases they developed their own ray trace programs rather than use more sophisticated industrial ray tracing programs. Rivamonte employed a programmable hand held calculator (HP-65) and Kroger & Kirschfeld used their own program and a desktop computer. Both groups indicated insufficient computer power for thorough analyses. These programs did not provide the optimization routines or sophisticated output graphics associated with the industrial programs of the respective time periods. Neither program processed skew optical rays.

Rivamonte’s analyses was developed on the assumption that the cornea was ineffective under water and the lens was spherical in shape. Kroger & Kirschfeld moved forward by describing a more realistic cornea and an ellipsoidal lens, which they soon replaced with a generally ellipsoidal form that recognized the axial and naso-temporal radii that were different for the anterior and posterior portions of the lens. None of these analyses provided optical prescriptions with a Petzval surface (surface of best optical focus for the lens system) that overlaid the focal plane of the retina within tolerable values (with errors less than the depth of focus of the optical system). Lacking convergence between the Petzval and focal surfaces, the results of these exploratory analyses can only be used as first order estimates of the actual optical systems of cetaceans. Their prescriptions will not be tabulated here.

Kroger & Kirschfeld (1992) reviewed the work of several investigators and have provided prescriptions for the cetacean eye that were evolving rapidly. Their review did not address the model of Rivamonte. They used an index for the cornea of 1.3800 in 1989 (part of a thesis submission) and 1.5300 in 1992. They also show the cornea as a negative lens with an aspheric inner surface and suggest it has little effect on the overall performance of the eye. They admit their description of the inner cornea surface is only a rough estimate. They specified the wavelength used in their ray tracing as 480 nm.

Both of the above groups relied upon ray tracing programs they generated themselves. This seems remarkable when excellent commercial ray trace programs were readily available. Kroger & Kirschfeld even note the limitations of their program, it could not handle skew rays and gave no information about image quality across the field of view. This is in considerable contrast to the data expected from commercial programs.

Kroger & Kirschfeld conclude, “it seems to be a reasonable proposition that a cornea of considerable, negative refractive power is a common feature of most, if not all modern cetacean species. Aspherical surfaces, gradient index optics, oblique axes of highest resolution, and the combination of a diverging lens (cornea) with the converging crystalline lens all make the cetacean eye an interesting, but complicated subject to study.”

Kroger & Kirschfeld (1993) provided a more refined prescription for the cetacean eye. It lead directly to their even more refined prescription and schematic of the eye of *Phocoena phocoena* of 1994. The 1994 paper only addresses the eye in water but it resolves several important issues, although it still uses less than adequate dimensional precision. It also collected data on the eyes when internally pressurized to the previous *in-vivo* state. Unfortunately, they did not form a plastic cast of the vitreous chamber under pressure and then take dimensions from the cast with a coordinate measuring machine. They carried the relevant indexes to four decimal accuracy and many millimeter dimensions to two decimal accuracy, but some of the critical radii are only given to one decimal accuracy. The prominent improvements are the recognition that the lens is not spherical in shape but is ellipsoidal, the retina is not symmetrical but is also ellipsoidal, and the use of an Abbe refractometer does not offer adequate precision for optical applications. The retina is treated as made up of two independent halves of different radii in the horizontal plane (leading to a less than precise description of the retinal focal surface). Although not stressed in the text, the optical system is shown graphically to be highly vignetted in the retinal areas some have proposed to be regions of maximum visual acuity (~±50° in the horizontal plane). Their interferometric technique for determining the index of refraction of small local areas is in accordance with best optical design practice.


Figure J.2.1-4 modifies their figure 5 to highlight certain additional features. Neither the lens or the nominal retina are spherical in this horizontal plane view. The lens is ellipsoidal as suggested by the dotted portion of a circle shown to the left. Kroger & Kirschfeld assume the lens is circular in the plane transverse to the optical axis with a radius of 4.51 mm. In the sagittal plane, they describe the anterior axial radius as 3.92 mm and the posterior axial radius as -4.26 mm (using ray trace notation). The lens is supported by two ligaments. Immediately above the ligaments and in contact with the anterior surface of the lens is the fully dilated iris (I). The radius of the fully dilated iris is given as 3.95 mm. The space between the lens and the inner surface of the cornea is minimal, only leaving space for the sphincter muscle tissue of the iris. The cornea is shown by its anterior surface (Ca) and posterior surface (Cp).

The cornea is also described as ellipsoidal with an...

Figure J.2.1-4 Horizontal plane ray tracing for Phocoena phocoena showing vignetting at ±50°. See text. Modified from Kroger & Kirschfeld, 1994.
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The retina is given less precisely as having an axial radius of -11.2 mm, a nasal radius of 12.5 mm and a temporal radius of 13.6 mm. It is shown in the figure as the solid line labeled R. The dashed line labeled R’ is a mirror image of R drawn to highlight the fact the retina is not circular in this plane.

The full axial ray bundle illustrates how the incoming rays are bent slightly away from the axis due to the negative power of the cornea, limited in diameter by the iris, converged by the lens, and arrive at the retina as a nominally F/3 cone. The partial ray bundles are drawn for two situations, on the left for an average cornea index of refraction of 1.53 and on the right for a corneal index of 1.50. The results shown indicate the ray bundles generally achieve best focus (Minimum diameter ray bundle) at a Petzval surface that follows the retina labeled R on the right and R’ on the left. The optics as modeled is forming a nominally circular Petzval surface in the horizontal plane even though the focal surface of the retina is described as circular in this plane.

As modeled by Kroger & Kirschfeld, the eye of *Phoconea phoconea* is badly out of focus at the two extremes of its field of view. Further analysis will be required to determine how this eye achieves its well recognized performance in behavioral tests. Kroger & Kirschfeld noted their model “serves as only a rough approximation of the harbor porpoise eye.”

J.2.3 Measured optical properties of the eye

The predicted optical properties of the dolphin eye to date suggest poorer optical performance than observed in the real world, particularly the ability of the dolphin to strike with precision at small targets in air as much as 20 feet above the surface of an evaluation pool.

The angular resolution of the dolphin eye has been described very briefly by many (generally without any description of the field angle at which the estimate applies). In the absence of a fovea, the limiting resolution of the eye is nearly constant over a wide field angle (subject to vignetting and focus errors). In 2001, Supin, Popov & Mass gave the resolution as 8.2 min of arc in water and 12.5 min of arc in air (page 283). Rivamonte (1976) gives a Table attributed to Peacock, Yunker, Madsen & Herman showing statistically determined resolutions for each eye of one dolphin at several distances20. They used a 24 cm square target of high contrast consisting of milled bars with widths in the 2 to 24 mm range. Thus the targets consisted of as few as ten and as many as 100 repeating bar patterns with bar lengths of 10 to 100 times the bar spacing. The targets were presented to the dolphin at an angle of 75 degrees from rostral, either 10 cm above or 50 cm below the water surface. The best values were in the 8 min of arc and 12 min of arc areas as above.

These values compare with a value of 3.125 min of arc for the on-axis human eye performing at 20/20 (6/6 in metrics) using a standard Snellen eye chart in air and low photopic illumination. The Snellen eye chart describes the outside dimension of a square containing three bars and two spaces, a more demanding test than the two bars and a space employed in the animal tests. Studies have been made on the comparison between Snellen eye chart and long repeating bar patterns for use in aerial reconnaissance. They suggest the resolution of the dolphin eye at 75 degrees from rostral is about ten to twenty times poorer than the human eye at the center of the fovea. This would be reasonable for an animal without a fovea. A similar resolution is found at 18-30 degrees eccentricity from the center of the fovea in humans21.

Crude efforts to compute the resolution of the bottlenose dolphin eye based on ganglion cell density have routinely given values about two to three times lower than the resolution measured in the field22.

Cronin, Fasic & Howland have developed a very practical method of determining the optical power of the aquatic

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eye without touching or constraining the animal. The technique showed clearly that these small dolphins were emmetropic in water (typically within one or two diopters hyperopic) and significantly myopic in air. Both Cronin et al. and Litwiler & Cronin used the same form of multi-LED retinoscopy without any precise control of the field angle of the eye they were exploring.

An agreed description of the cornea of the cetaceans is difficult to produce. The cornea varies from a thin meniscus only a few cells thick with the same index of refraction as sea water (taken as 1.336 by Rivamonte) to a negative lens with a minimum thickness on axis of 0.35 mm reaching 1.2 mm thick at the chamber angle and an index of 1.530 (Kroger & Kirschfeld), to various positive and even zero power lenses (Supin, Popov & Mass, pg 283) over at least a portion of its surface area. The 1987 paper of Dawson et al. is particularly useful in understanding the ability of the dolphin to see rostrally in water and air. They examined several members of *Tursiops* and *Zalophus* (sea lion). “All *Zalophus* corneas showed no reliable regular astigmatism (overall mean power is 21.7 D, SD = 4.4, N = 53) but exhibited a flat, circular region about 6.5 mm in diameter along the nasal aspect of the horizontal meridian. Refraction through this corneal region showed aerial emmetropia, which accounts for equivalent marine and aerial visual resolution in this species.” They noted considerable damage to the corneas in mature cetaceans due to abrasion.

Kastelein et al. assert, “the lens of the harbor porpoise is typically ellipsoid with major dimensions of 7.5 by 7.0 mm in the adult.”

Dawson (1988) described the intracocular pressure of *Tursiops truncatus* as at least 50 mm Hg higher than in humans. Kastelein et al. (1990, pg 475) have noted the high internal pressure within the dolphin eye may be to cope with the high hydrodynamic pressure exerted on the eye during swimming rather than to cope with the high hydrostatic pressure encountered in diving to depth in water.

**J.3 Characteristics of the retina in dolphin**

Amazingly little histological investigation of the retina has been reported in the literature. Mass & Supin described the situation in 1990. “Cetacean retinæ have no avascularized areas in high cell density sites (Dawson, 1987). High cell density zones were unknown until recently. Attempts to localize these zones in marine mammals by studying cross-retinal cuts yielded no results (Landau & Dawson, 1970). This gave rise to the hypothesis that the retina of marine mammals has no area centralis.” This is correct. However, Mass & Supin went on. “However, Peers (1971) observed some irregularity of ganglion cell distribution in the retina of *Tursiops truncatus*. Only studies on the topography of ganglion cells in total retinal preparations made it possible to discover zones of high ganglion cell density in marine mammals.” Their paragraph was carefully worded. However, there is no correlation between ganglion cells and the fovea. In fact, an area of dense ganglion cells is the antithesis of an area centralis or fovea in mammals. The only rational conclusion based on the literature is there are no fovea in the cetacean eyes studied to date (2009). The literature has not yet reported the precise location of the “blind spot” in the dolphin eye, the location of the origin of the optic nerve on the surface of the retina. Based on the imagery of Kastelein et al., the optic nerve exits near the center of the optic cup in at least one plane of the eye of *Phocoena phocoena*. This condition may create a blind spot along the optical axis of the eye. Kastelein et al. stress the absence of any area centralis (fovea) in the eye of this related species.

This work does not support the assertion by Mass & Supin that areas of high ganglion cell density are known in terrestrial mammals as the area centralis or the visual streak. The area centralis and visual streaks are characterized by no neural cells in the neural overlay and little vascularization.

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Mobley & Helweg have drawn a similar conclusion concerning any area centralis or fovea. “Observations of the ocular fundus of some cetacean species have failed to reveal clear evidence of an area centralis- - the retinal area found in many terrestrial mammals that appears to be specialized for high resolution of detail.” The first clause is definitive. There is no question that the area centralis in mammalian eyes is the area specialized for high resolution of detail. They noted the density of large ganglion cells on the retina of dolphins is actually quite low (by an order of magnitude) compared to the density of similar ganglion cells (except possibly for size) in cats\textsuperscript{27}. They went on. Additionally, recent examinations of the ocular fundus of Tursiops truncatus and Grampus griseus failed to show the reduced vascularization in these areas normally characteristic of an area centralis, thus suggesting that the areas proposed by Dral and Mass et al. may not function as areas of high resolution.”

Figure J.2.1-5 reproduces a cross section of the retina of Phocoena phocoena from Kastelein et al. that is highly disturbed at the focal plane formed by the photoreceptors. (typically colocated with the Outer Limiting Membrane at this scale). It shows a conventional mammalian retina except for the larger number of photoreceptor soma in the layer marked ONL and a lower number of cells in the layers marked INL and GL. The number of cell layers in the ONL of humans is typically three instead of the 12 noted by Kastelein et al. A nominally perfect F/3 optical cone has been added with the cone intersection at the OLM. “Best focus” for this lens would extend about 15-30 microns above and below the intersection. It appears the image was selected to accentuate the one large ganglion cell.

**J.4 Characteristics of the optic nerve**

Kastelein et al. (1990, pg 466) describe the optic nerve of the harbor porpoise as consisting of 136,000 axons surrounded by a dense intertwining of bloodvessels. This compares to the nominal one million axons in the human optical nerve. Guofu & Kaiya have provided a comprehensive study of the optic nerve\textsuperscript{28}. They indicate no particular dominance by large fibers in the optical nerve of the cetaceans. They show typical log-normal diameter distributions with peaks near 1-3 microns. No obvious sign of a bimodal distribution is found.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{retina.png}
\caption{Retina of Phocoena phocoena. OLM; outer limiting membrane. ONL; outer neural layer. OPL; outer plexiform layer. INL; inner nuclear layer. IPL; inner plexiform layer. GL; ganglion layer. Scale; 100 microns. From Kastelein et al., 1990.}
\end{figure}


J.5 The role of the large ganglion cells in the retinas of Cetacea

A group of large ganglion cells appear in the ganglion layer of many cetacean eyes. The group has a bimodal distribution roughly parallel to but displaced from the horizontal plane of the eye. The purpose of this presumed family of ganglion cells serving a common purpose is unknown. Supin, Popov & Mass have recently reviewed the distribution of these neurons\(^{29}\).

While the diameter of the soma of a ganglion neuron catches the attention of an investigator, it is the diameter of the axon that is characteristic of the performance of the neuron. The diameter is highly correlated with the velocity of propagation of these stage 3 projection neurons. See Sections 9.3 & 14.5 in “Processes in Biological Vision.”

Ganglion neurons are not normally associated with light sensitivity in retinas. They are associated with the collection of signals from various distributions of photoreceptor axons (proceeding from the inner segments of the photoreceptors of the outer nuclear layer to the synapses of the outer plexiform layer) following stage 2 signal processing by bipolar and amacrine neurons (located in the inner nuclear layer).

Supin, Popov & Mass assert that the signal capture area of the ganglion neurons is indicative of the resolution of the cetacean eye. They then discuss the receptive field of the dendritic arborization of the neuron based on a variety of generalities. This is a very unusual proposal that has appeared occasionally in the literature since it originated in the 1960′s. The concept has been pursued primarily by Mass & Supin. As they note in 1995, “This feature has not been described in other mammals.” And, “The functional significance of large ganglion cells in aquatic mammals remains obscure.” In 2003\(^{30}\), Mass & Supin noted the population of large ganglion neurons in the retina of the harp seal was quite small, “(on the order of a few percent).” Most ganglion cells have a capture area on the order of 100 to 1000 times the soma diameter. On the other hand, in ganglia supporting the photoreceptors in the human fovea, a single ganglion neuron supports a single photoreceptor of known diameter, typically 2 microns. More evidence is called for before associating the diameter of a ganglion neuron soma with the best resolution of a cetacean eye.

An alternate purpose for the large ganglion cells of the cetacean eye may be collecting signals that relate to the mechanism used to align and to focus the cetacean eye under a wide range of circumstances. Typically, the signals are collected in the mammalian retina for processing by the accommodation subsystem used to drive the accommodation muscles located near the trabecular matrix of the eye (Section 7.4.9 of “Processes in Biological Vision”). The result is an active closed loop servomechanism used throughout the life of the animal. While the means of accommodation within the cetacean eye during growth as well as normal daily activities is unknown, the necessity of maintaining the conjunction of the Petzval surface of the optical system and the focal surface of the retina congruent within the acceptable depth of focus error of the optics suggests a sophisticated accommodation subsystem is required to optimize this non-spherical retina.

J.6 The CNS of the dolphin

Morgane, Jacobs & Galaburda have provided a graphic description of the dorsal brain of *Tursiops truncatus*\(^{31}\). It is significantly less convoluted than the human brain. Leatherwood & Reeves have provided an equivalent ventral view.

As might be expected, the cerebral cortex of *Tursiops truncatus* assigns a smaller area to the visual modality and a larger area to the auditory modality than found in humans. Glezer et al. have provided an annotated image of the cerebral cortex from the rear\(^{32}\). Figure J.2.1-6 provides an annotated schematic of its brain modified from Supin,


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Popov & Mass\textsuperscript{33}.

Morgane & Glezer provide a marginally different description of the same brain\textsuperscript{34}. Some variants show the visual area stopping at the sulcus endolateralis (SEL) while others show it extending to the sulcus lateralis (SL).

Supin, Popov & Mass have also indicated one somatosensory region of the brain of *Tursiops truncatus* (page 286). It is the region shown at the top just beyond region 1 in this figure.

Morgane, Glezer & Jacobs have provided a major study of the anatomy of the visual cortex of the bottlenose dolphin brain\textsuperscript{35}.

J.3 Signal Levels and Polarities

![Figure J.2.1-6](image) Localization of the auditory and visual projections on the cerebral cortex of *Tursiops truncatus*. Dorsal view. Right half; mapping of sulci and gyri. Left half; mapping of sensory modality inputs and major sulci for reference. 1; area of short-latency hearing. 2; area of long-latency hearing. Uniform shaded area; area of visual cortex. Modified from Supin et al., 2001.

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