Review Article

# Ocular anatomy

S. Bavana Sri[1], R. Sarah Sathiyawathie[1]*, Deepa Gurunathan[2]

ABSTRACT

The eye optics, size, and distribution of ganglion cells in the retina of the gray whale were studied. The hemispheric retina is centered on the quasi-spherical lens which makes it equally possible to create visual images at any part of the retina. Ganglion cell size varied from 14 to 74 m, mostly 20 to 40 m, mean 31 m. Ganglion cells concentrated at two spots of the highest density in the nasal and temporal quadrants, 26–28 mm (65–70) from the optic disk. Mean peak cell densities were 130 and 183 cells/mm$^2$ in the nasal and temporal areas, respectively. With a posterior nodal distance of 23 mm (underwater), this corresponds to 21 and 29 cells/deg$^2$, which provides retinal resolution of about 13 in the laterocaudal visual field (nasal retinal area) and 11 in the rostral visual field (temporal retinal area).

**KEY WORDS:** Anticodons, Nucleotide, RNA polymerase

## INTRODUCTION

Investigation of the sensory systems of cetaceans is important to understand mechanisms of their behavior and orientation. To date, studies of cetacean sensory systems are especially important due to threatened state of this animal group. Apart from that, data on organization of cetacean sensory systems are of interest for comparative anatomy and physiology. However, data on cetacean sensory systems are insufficient. Particularly, data for the mysticete visual system are limited and for many species are completely absent. Some data on whale eye anatomy and optics were collected during the years of whaling.[1] These data resulted in some ideas concerning functional properties of the whale visual system. An opinion was adopted for many years that whales have poor vision and play a minor role in their lives. To date, this opinion does not seem to be true. The idea of immobility of the cetacean's eyeball is an example of a wrong conclusion based on early anatomical findings. Weber (1886) first supposed that the oculomotor functions of cetaceans are reduced. Later Pütter (1903) carried out a comparative investigation of the ocular anatomy of mysticetes and also supposed an immobile ocular bulbus in cetaceans. Walls (1963) supported this idea. He supposed that for whales, the most important gaze direction is downward, and the eyeball is canted ventrally or nasoventrally, which helps out in tilting the visual axis. However, the idea of eyeball immobility in cetaceans was not confirmed by numerous later investigations of Jansen and Jansen (1969) and Hosokawa (1951).[2] It was shown that whales have a whole set of completely developed oculomotor muscles and nerves. These muscles provide the mobility of the cetacean eyeball comparable to that in other mammals. Apart from that, direct behavioral observations indicated clearly that eyes of dolphins and killer whales are mobile (Slijper, 1962; Madsen and Herman, 1980; Dawson, 1980). Some other early conclusions concerning the visual abilities of mysticetes were not confirmed either. Walls (1963) hypothesized regression of the visual function in mysticetes due to their "trawling" method of feeding. However, morphological and optical adaptations of the cetacean visual system to the underwater environment were found, indicating the importance of the visual system for these animals. Mysticetes have the quasi-spherical lens with a high refractive index.[3] The hemispheric eyecup, wide pupil, and well-developed tapetum were interpreted as adaptations to conditions of low illumination under water (Waller 1980; 1984). Contrary to early hypotheses, experimental studies and field observations of cetaceans during the past decade

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[1]Department of Research, Saveetha Dental College and Hospital, Saveetha Institute of Medical and Technical Sciences, Chennai, Tamil Nadu, India, [2]Department of Pedodontics, Saveetha Dental College and Hospital, Saveetha Institute of Medical and Technical Sciences, Chennai, Tamil Nadu, India

***Corresponding author:** Dr. R. Sarah Sathiyawathie, Department of Research, Saveetha Dental College and Hospital, Saveetha Institute of Medical and Technical Sciences, 162 Poonamallee High Road, Chennai – 600 077, Tamil Nadu, India. Tel.: +91-9884156513. E-mail: dr.sarahrobin@gmail.com

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resulted in a reestimation of the role of their vision. Reviewing experimental and behavioral observations, Madsen and Herman (1980) summarized that cetaceans use their vision for orientation and navigation, coordination of group movements, identification of conspecifics and individuals, communication, etc. These observations concern both odontocetes and mysticetes.[4]

## METHODOLOGY HISTORY

The material, four eyes, was collected in 1989 from two adult gray whales that died near the Lorino settlement in Chukotka, Russia. Three eyes were used to prepare retinal whole mounts and one eye was used to measure optic dimensions. The eyes were fixed in 10% formalin a few hours after death. The whole mounts were prepared by method of Stone (1965) with our modification (Mass, 1992). Before the retina was excised, its orientation was noted. Then, the cornea, iris, lens, and vitreous body of the eye were removed and the retina was excised from the eyecup.[5] The retina was flattened on a slide, with the ganglion cell layer upward, covered with filter paper, and kept under a weight for several hours in 10% formalin solution. Radial cuts allowed flattening the retina on the slide. After that, the retina was dried and stained by the Pischinger method in 0.06% methylene blue solution under visual control. Shrinkage of large thick whole mounts was avoided by clearing without dehydration in the Apathy's gum syrup. The ganglion cells were counted in 0.15 mm$^2$ square samples on a 1 mm step grid over the whole retina. The results of counting were converted into number of cells per mm$^2$. These data were used for mapping the distribution of ganglion cell density in the retina as well as for calculating the total number of ganglion cells in the retina. Smoothing of the maps was carried out by averaging the number of cells in blocks of three samples.[6] To estimate the retinal resolution, the original whole mount maps were transformed to continuous spherical maps of ganglion cell density in the spherical coordinates. For this purpose, whole mount maps were transformed by a computer program in such a way as to remove radial cuts and restore a hemisphere approximating the entire retina. In these spherical maps, the cell density was specified in cells/deg$^2$: $D = d (R/180)^2$ where: D is the density in cells/deg$^2$, d is the density in cells/mm$^2$, and R is the retinal radius in mm. To estimate the position of optic points and the posterior nodal distance (PND), one eye was frozen and sectioned horizontally. Then, half of the eye had been removed, photographs were taken, and measurements were made from these photographs.[7] Apart from that, external dimensions and eyecup dimensions were measured in the eyes used to prepare whole mounts. Cell size was obtained by measuring two perpendicular diameters, i.e., the long and short ones, and calculating the mean value.

## RESULTS

### Eye Dimensions

A horizontal section of the frozen eye was made. The eyecup of the gray whale, as well as the eye of other cetaceans, is of hemispheric shape. It is slightly oval: The nasotemporal width (64–66 mm) longer than the dorsoventral one (60–62 mm). Axial length between the external surfaces of the cornea and sclera was 55–60 mm. Internal nasotemporal eyecup diameter was 46–47 mm and the dorsoventral one was 44–45 mm. The lens was very convex but not truly spherical. Its transverse diameter was about 13 mm and axial diameter about 10 mm. The distance from the center of the lens to the retina was estimated as 23 mm. The cornea was elongated in the nasotemporal direction. Its nasotemporal diameter was 28–30 mm and the dorsoventral one was 20–21 mm. The peripheral rim of the cornea was much thicker (2–2.5 mm) than the central part (around 1 mm).[8,9] The pupil was horizontally elongated and had the operculum. The shape of the retina was complex. Its major part, except the far periphery, had a shape of an incomplete hemisphere, about 150 across. A peripheral rim of the retina was bent inward. The radius of the retinal hemisphere was assessed to be 23 mm. The tapetum was blue-gray and well developed. It covered a major part of the eyecup except the ventral region and the region adjacent to the optic disk. Similarly, to other cetaceans, the retina of the gray whale contained mostly large neurons. The most typical were cells 20–40 m in size, although cells up to 74 m were found as well. The cells were of various shapes. Most of them were polygonal in shape with clearly visible sites of originating of 3–6 dendrites. Oval cells were rare, and even more rare were round cells. The cells were characterized by a broad rim of cytoplasm with well-stained Nissl granules. Clearly visible light nucleus with dark nucleolus could be disposed both in the soma center and eccentrically.

### Distribution of Ganglion Cells

The mean total area of the three investigated retinal whole mounts was found to be 2520 mm$^2$. Ganglion cell totals in the three whole mounts varied from 165,000 to 184,000 with a mean of 174,000. The mean ganglion cell density averaged over the whole area of the retina and among three whole mounts were 70 cells/mm$^2$. Counting ganglion cells throughout the retina at 1 mm steps revealed that cell distribution varied in different parts of the retina. A representative pattern of ganglion cell distribution is shown by a whole mount map. A characteristic feature of the map is the presence of two areas of cell concentration: One area was located in the nasal part of the retina and another one in the temporal part. Both areas of cell concentration were located near the equator of the retina.[10]

# DISCUSSION

## Eye Optics

The optic structure of the eye of the gray whale is similar in general to that described in other cetaceans, both odontocetes and mysticetes (Mayer, 1852; Pütter, 1903; Rochon-Duvigneaud, 1939, 1943; Pilleri and Wandeler, 1964; Waller, 1980; Dawson *et al*., 1972; Vasilyevskaya, 1988; Mass and Supin, 1995). A distinctive feature of the eye of the gray whale and other large mysticetes is very thick sclera. This feature, however, does not influence directly the eye optics. A common feature of the eye optics of both odontocetes and mysticetes is a hemispheric retina centered on the quasi-spherical lens. The cornea apparently plays a minor role under water due to small difference of its inner and outer curvatures and small difference of refractive indices of the media in front of and behind the cornea. Although refraction at the cornea cannot be neglected completely in cetaceans (Kröger and Kirschfeld, 1994), the thick lens is obviously the main refractive structure of the cetacean eye. In these conditions, the nodal point of the eye coincides with the center of the lens. Since the hemispheric retina is centered on the same point, the overall optic structure of the eye is symmetric relative to the lens center, and light rays of any direction can be equally focused at corresponding parts of the retina. It is noteworthy, however, that the cornea of the gray whale is much thicker at its periphery than at the center, thus functioning as a weak dissipating refractive structure. According to Kröger and Kirschfeld (1994), this function of the cornea is important for refraction correction.

## Ganglion Cell Size

A characteristic feature of the retina of the gray whale is the very large size of ganglion cells. In the present study, we found ganglion cells as large as 14–74 m (means 30.9 m). Large (mean 42.9 m) and giant (up to 80 m) ganglion cells were also observed in the retina of the minke whale *Balaenoptera acutorostrata* (Murayama *et al*., 1992). Very large (50–80 m) and giant (up to 160 m) cells were observed in the retina of the fin whale *Balaenoptera physalus* (Pilleri and Wandeler, 1964). The large size of ganglion cells is a common feature of many cetacean species. Ganglion cells up to 60–75 m were described in the retina of the common dolphin *Delphinus delphis* (Dral, 1983).[11]

Another hypothesis suggests that one of the best visual areas provides satisfactory visual acuity in air. It was shown that dolphins have good vision in air (Herman *et al*., 1975). It had to be explained how the eye optics of dolphins prevents aerial myopia which derives from the refractive power of the cornea surface in air added to that of the lens. Some of the hypotheses were discussed earlier (Mass and Supin, 1995); among them, the following are noteworthy: (1) Closer position of the temporal fundus to the lens (Waller, 1980); (2) less refractive power of the cornea surface in its frontal part (Dawson, 1987); (3) strong pupillary construction in air results in double-slit shape of the pupil rendering light to pass through the margin of the lens, which is optically weaker than its central core (Rivamonte, 1976); and (4) the pinhole apertures of the constricted pupil improve visual acuity. All the suggested mechanisms work for oblique rays passing through the nasal part of the pupil to the temporal best vision area of the retina. Thus, the specific position of the best vision areas in the dolphin retina may be connected with their combined underwater and aerial vision. However, it remains unclear whether mysticetes have satisfactory aerial vision. Matthiessen (1893) investigated in detail the mysticete eye optics in *B. physalus* and showed that the mysticete eye is emmetropic in water and very myopic in air. He concluded that whales are unable to see clearly objects in air and can only see some movements and the horizon line. Rochon-Duvigneaud (1939; 1943) also suggested that cetaceans had no capacity for aerial vision and that a clear retinal image could not be formed. Experimental investigations of mysticete visual behavior are absent since these animals have never been kept in captivity for investigations. However, there were some observations made from ships that mysticete whales may “spy-hop” by raising the head vertically out of the water (rev. Madsen and Herman, 1980). It suggests that mysticetes may use their vision in air. It is unknown yet whether mysticetes have eye optics which makes it possible to prevent aerial myopia. However, based on the similarity of the mysticete eye optics with that of dolphins, it is reasonable to suppose that mysticetes have mechanisms of preventing aerial myopia similar to those hypothesized for dolphins. Direct investigations are necessary to decide whether these hypotheses can be applied to mysticetes. Data on ganglion cell density in the best vision areas and other parts of the retina make it possible to calculate the retinal resolution of the gray whale. The retinal resolution can be estimated as mean angular spacing of ganglion cells, i.e., s = 1/DY; where, s is angular spacing and D is cell density per $deg^2$ of visual angle. The latter depends on cell density and PND. As shown above, the cetacean eye optics makes it possible to adopt PND equal to the radius of the retinal hemisphere. In this case, cell density in degrees of the visual field is the same as in terms of the retinal hemisphere, i.e., in the nasal retinal area, peak cell density is 21 cells/$deg^2$, and in the temporal area, it is 29 cells/$deg^2$. These values correspond to retinal resolution of 0.22 = 13 in the nasal area and 0.19 = 11 in the temporal one. At the retinal periphery and around the optic disk, retinal resolution is worse: Cell density of about 10 cells/$deg^2$ corresponds to the resolution of 0.32 = 19. The optical system of the eye and retinal resolution is two main factors determining visual acuity. Supposing that these two factors are in correspondence, the values of retinal resolution mentioned above can be adopted as a first approximation of visual acuity of the gray whale. Thus, the best visual acuity of the gray whale can be estimated as about 11 in the frontal part of the visual field (corresponding to the temporal best vision area of the retina) and about 13 in the laterocaudal part of the visual field (corresponding to the nasal retinal area). These estimations indicate that the visual acuity of the gray whale is a little worse than, but comparable to, that in some other cetaceans, for example, about 7 in *B. acutorostrata* (Murayama *et al*., 1992), 8–12 in *Tursiops truncatus* (Herman *et al*., 1975; Mass and Supin, 1995), and close to that 11–14 in *Phocoena phocoena* (Mass and Supin, 1986). It suggests that visual abilities of the gray whale (perhaps, of other mysticetes as well) are comparable with those of dolphins which actively use their vision and demonstrate fine image recognition. The estimations presented above concern visual acuity of mysticetes in water since their eye optics is obviously adapted to the underwater vision. We refrain from discussion of visual acuity of mysticetes in air since very little is known of their aerial refraction.

## REFERENCES

1. Dawson WW, Brindorf LA, Perez JM. Gross anatomy and optics of the dolphin eye (*Tursiops truncatus*). Cetology 1972;10:2-12.
2. Jamieson GS, Fisher HD. The retina of the harbor seal *Phoca vitulina*. Can J Zool 1971;49:19-23.
3. Madsen CJ, Herman LM. Social and ecological correlates of cetacean vision and visual appearance. In: Herman LM, editor. Cetacean Behavior: Mechanisms and Function. New York: Wiley Interscience; 1980. p. 101-47.
4. Thomas JA, Kastelein RA, Supin AY. Marine Mammal Sensory Systems. New York: Plenum; 1992. p. 119-35.
5. Mass AM, Supin AY. Topographic distribution of size and density of ganglion cells in the retina of a porpoise, *Phocoena phocoena*. Aquat Mammals 1986;12:95-102.
6. Chapeville F, Lipmann F, Von Ehrenstein G, Weisblum B, Ray WJ Jr., Benzer S, *et al*. On the role of soluble ribonucleic acid in coding for amino acids. Proc Natl Acad Sci U S A 1962;48:1086-92.
7. Flinta C, Persson B, Jörnvall H, von Heijne G. Sequence determinants of cytosolic N-terminal protein processing. Eur J Biochem 1986;154:193-6.
8. Grunberger D, Weinstein IB, Jacobson KB. Codon recognition by enzymatically mischarged valine transfer ribonucleic acid. Science 1969;166:1635-7.
9. Kozak M. Point mutations close to the AUG initiator codon affect the efficiency of translation of rat preproinsulin *in vivo*. Nature 1984;308:241-6.
10. Kozak M. Point mutations define a sequence flanking the AUG initiator codon that modulates translation by eukaryotic ribosomes. Cell 1986;44:283-92.
11. Kozak M. An analysis of 5'-noncoding sequences from 699 vertebrate messenger RNAs. Nucleic Acids Res 1987;15:8125-48.

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