Aquatic Mammals 1997, **23.1**, 17–28

Ocular anatomy, retinal ganglion cell distribution, and visual resolution in the gray whale, *Eschrichtius gibbosus*

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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 μm, mostly 20 to 40 μm, mean 31 μm. 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 (under water) this corresponds to 21 and 29 cells/deg^2, which provides retinal resolution of about 13′ in the latero-caudal visual field (nasal retinal area) and 11′ in the rostral visual field (temporal retinal area).

Introduction

Investigation of sensory systems of cetaceans is important to understand mechanisms of their behavior and orientation. To date, studies of cetacean sensory systems are especially important because of 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. 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 plays 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 is 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 & Jansen (1969) and Hosokawa (1951). 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 & 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. 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 last decade resulted in a re-estimation of the role of their vision. Reviewing experimental and behavioral observations, Madsen & 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.

Histological investigations of the mysticete retina are very limited. Mann (1946) was the first to investigate the retina of the fin whale *Balaenoptera physalus*. He described two types of receptors and supposed that the mysticete retina is capable of perceiving visual images. The existence of cones and rods has been reported by Pilleri & Wandeler (1964) in the retina of the fin whale. Apart from the two receptor types, these authors have described ganglion cell characteristics in this species. Some features of the ganglion cells were also described in retinal wholemounts of the minke whale *Balaenoptera acutorostrata* (Murayama *et al*., 1992).

As to the visual acuity of mysticetes, the data were absent until recently because behavioral measurements in large whales are very difficult to obtain. The problem may be solved using a morphological method, i.e., estimation of the visual acuity basing on the ganglion cell density in the retina. Ganglion cell spacing may be used as an indicator of the retinal resolution and thus predicts the visual acuity. Such estimations based on the ganglion cell density have been carried out for some terrestrial mammals (rev. Pettigrew *et al*., 1988) and some cetaceans (odontocetes): *Delphinus delphis* (Dral, 1983), *Phocoena phocoena* (Mass & Supin, 1986), *Inia geoffrensis* (Mass & Supin, 1989), *Tursiops truncatus* (Mass & Supin, 1995), and *Phocoenoides dalli* (Murayama *et al*., 1995).

The purpose of the present study was to investigate the characteristic features and dimensions of the eye of the gray whale, *Eschrichtius gibbosus*; and to assess the ganglion cell distribution in retinal wholemounts to estimate visual acuity; and to study ganglion cell sizes. Preliminary data of this study were published earlier (Mass & Supin, 1990). Apart from that preliminary publication, there was only one study of such type carried out in another mysticete species, *Balaenoptera acutorostrata* (Murayama *et al*., 1992). This paper presents more extensive data obtained from the eyes of the gray whale.

Material and methods

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 wholemounts and one eye was used to measure optic dimensions.

The eyes were fixed in 10% formalin a few hours after death. The wholemounts 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. 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 Pishinger method in 0.06% metilene blue solution under visual control. Shrinkage of large thick wholemounts was avoided by clearing without dehydration in the Apathy's gumsyrup.

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 3×3 samples.

To estimate the retinal resolution, the original wholemount maps were transformed to continuous spherical maps of ganglion cell density in the spheric coordinates. For this purpose, wholemount 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:

$$D = d(\pi R/180^\circ)^2$$

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.

In order to estimate the position of optic points and the posterior nodal distance, 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. Apart from that, external dimensions and eyecup dimensions were measured in the eyes used to prepare wholemounts.

Cell size was obtained by measuring two perpendicular diameters, i.e., the long and short ones, and calculating the mean value.

Results

Eye dimensions

Figure 1 demonstrates a horizontal section of the frozen eye. The eyecup of the gray whale, as well as the eye of other cetaceans, is of hemispheric shape. It is slightly oval: the naso-temporal width (64–66 mm) longer than the dorso-ventral one (60–62 mm). Axial length between the external surfaces of the cornea and sclera was 55–60 mm. Internal naso-temporal eyecup diameter was 46–47 mm and the dorso-ventral 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

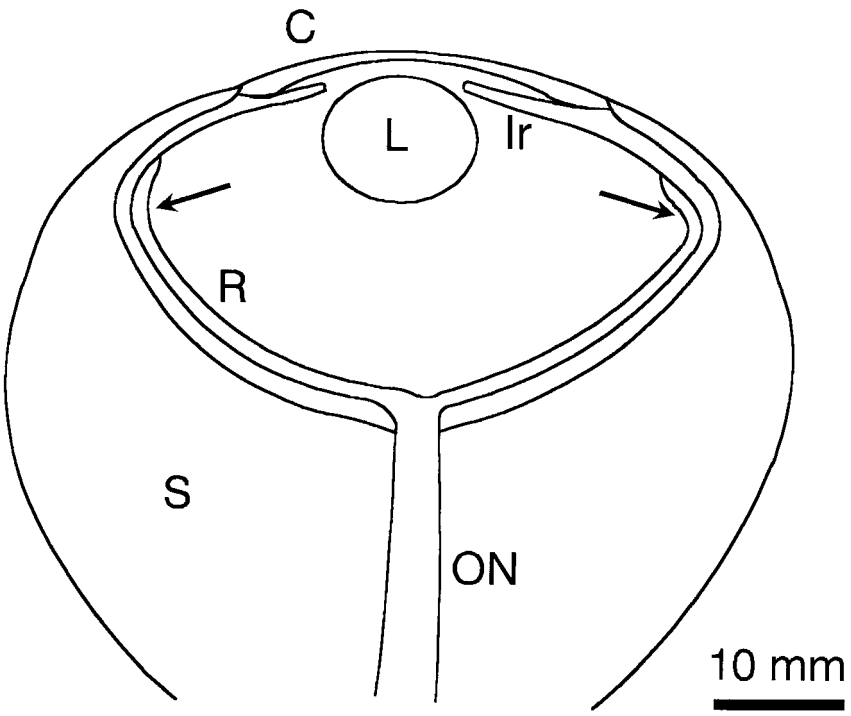

Figure 1. Horizontal section of a whale's eye (redrawn from a photograph). Right eye, the nasal pole leftward. C–cornea, Ir–iris, L–lens, R–retina, ON–optic nerve, S–sclera. Arrows delimit a part of the retina that can be approximated by an incomplete hemisphere (approx. 150° relative to the lens center).

center of the lens to the retina was estimated as 23 mm.

The cornea was elongated in the naso-temporal direction. Its naso-temporal diameter was 28–30 mm and the dorso-ventral 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). 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.

Ganglion cell characteristics

Similarly to other cetaceans, the retina of the gray whale contained mostly large neurons. The most typical were cells 20 to 40 μm in size, although cells up to 74 μm 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 to 6 dendrites (Fig. 2). 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 wholemounts was found to be 2520 mm^2. Ganglion cell totals in the three wholemounts 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 wholemounts was 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 wholemount map in Fig. 3. 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

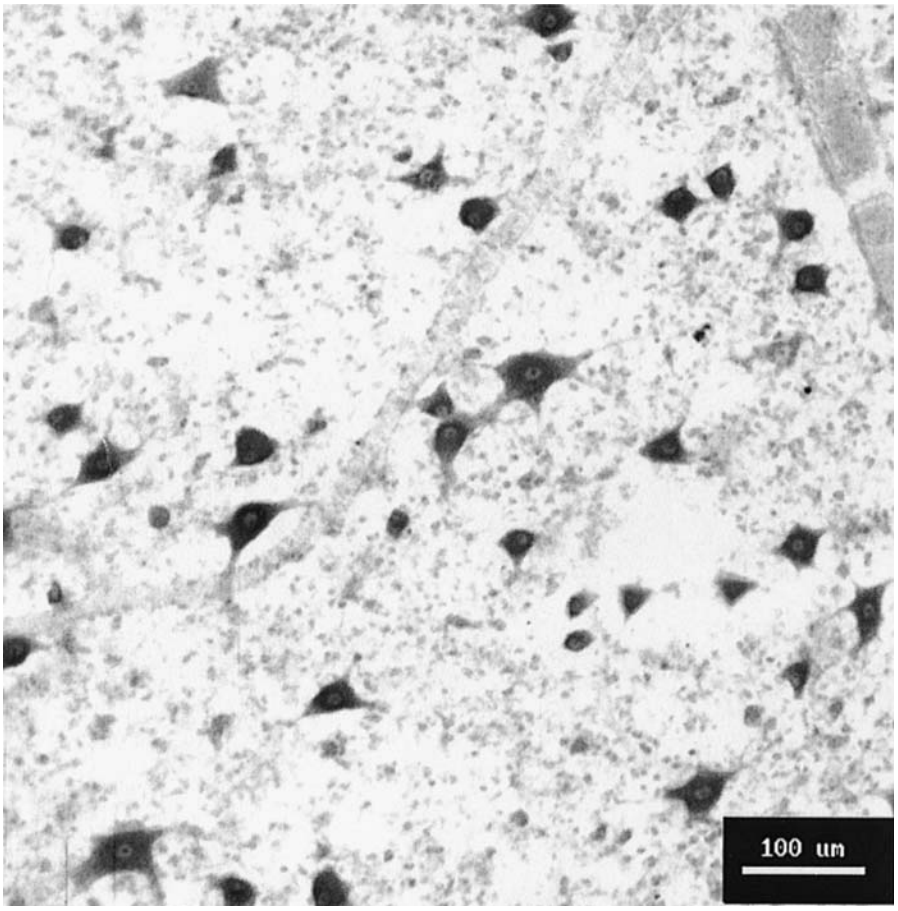

Figure 2. Light micrograph from the ganglion cell layer of a Nissl-stained retinal wholemount of a gray whale. Cell density about 70 cells/mm^2.

part. Both areas of cell concentration were located near the equator of the retina.

The peak cell densities in the wholemount of Fig. 3 were 142 and 200 cells/mm^2 in the nasal and temporal areas respectively. In all wholemounts, peak cell density in the nasal area was lower than in the temporal one. The averaged peak cell densities for the three wholemounts were 130 and 183 cells/mm^2 in the nasal and temporal areas respectively.

The high density areas were distinguished clearly against the background. Outside these areas, cell density declined markedly. In both central and peripheral parts of the retina, cell density was less than 50 cells/mm^2.

Distribution of cell density with two areas of cell concentration can be illustrated by profiles of cell density across the naso-temporal equator (Fig. 4). This figure combines data obtained in all wholemounts. The plots show two distinct peaks of cell density in the nasal and temporal areas, steep decrease of cell density towards the retinal periphery and very low density in the central part adjacent to the optic disk.

Figure 5 shows a spherical map of ganglion cell density obtained by transformation of the wholemount map shown in Fig. 3. Upon constructing continuous spherical maps of the retina, it was supposed that the mean radius of the retinal hemisphere was 23 mm. At this radius, the arch of 1° corresponds to the distance of 0.4 mm along the retinal surface, and 1 deg^2 corresponds to 0.16 mm^2. Note that according to Fig. 1, only the part of the retina within the circle of 75° represents the incomplete hemisphere; the periphery outside this circle corresponds to the retinal rim bent inward.

The map shows that the areas of high cell density are situated in the nasal and temporal parts of the retina, near its naso-temporal equator. The cell density peaks were 65 to 70° from the geometric

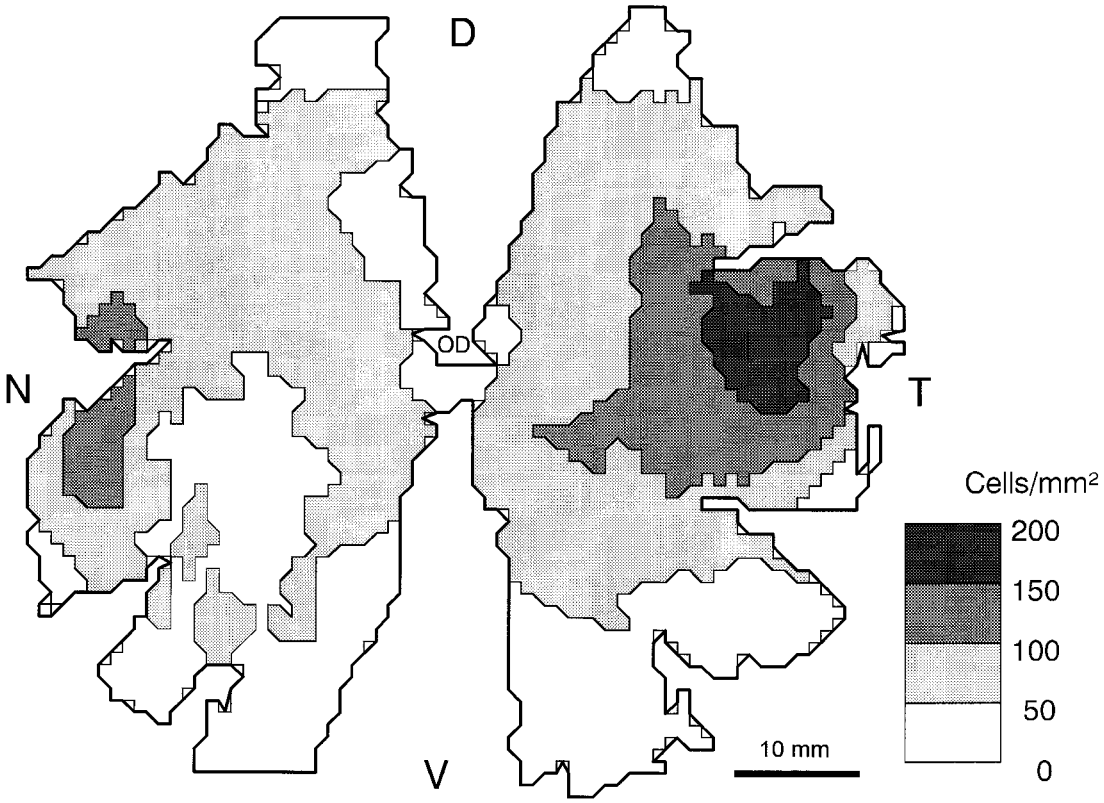

Figure 3. Map of ganglion cell density in a retinal wholemount. Cell density is designated according to the scale on the right. N, T, D, V–nasal, temporal, dorsal and ventral poles of the retina; OD–optic disk.

center. The peak cell densities were 23 cells/deg^2 in the nasal area and 32 cells/deg^2 in the temporal area.

Such maps were construction for all three wholemounts. The averaged peak cell density among the three wholemounts were 21 and 29 cells/mm^2 in the nasal and temporal areas respectively. Location of the high density areas was similar in all the wholemounts. Therefore it was possible to average the data among all the wholemounts. Figure 6 presents the averaged continuous spherical map. Similarly to the map of an individual wholemount (Fig. 5), the areas of high cell density were situated near the naso-temporal equator, with cell density peaks located 65 to 70° from the center of the retina. The maximum cell density in the averaged map was 20 cells/deg^2 in the nasal area and 28 cells/deg^2 in the temporal one. This is somewhat less than the means of peak values indicated above (21 and 29 cells/deg^2). The difference arose since spatial positions of the density peaks did not coincide precisely in different wholemounts. In the retinal periphery and near the optic disc, the cell density was 6 to 10 cells/deg^2.

Both wholemount maps (Fig. 3) and spherical maps (Figs 5, 6) show that we did not find a streak connecting the two high density areas, clearly visible in dolphins and described in the minke whale by Murayama *et al.* (1992).

Ganglion cell size

A total of 1200 cells were measured in three retinal areas with different cell densities (400 cells in each sample). Most of the cells were of large size. Although maximal cell size observed in the wholemounts was 74 μm, in the selected samples, cell size varied only from 14 to 56 μm since cells larger than 50 μm were very rare. Cells smaller than 14 μm were not found. The majority of cells were within the range of 20 to 40 μm.

Figure 7 presents frequency vs cell size histograms for ganglion cells in three areas (A–C). The cell size distributions were monomodal in all samples, however, there was a slight tendency of separation of large cells (larger than 40 μm) in to a distinct group.

There was little difference between cell size distributions and mean sizes in areas of high and low cell

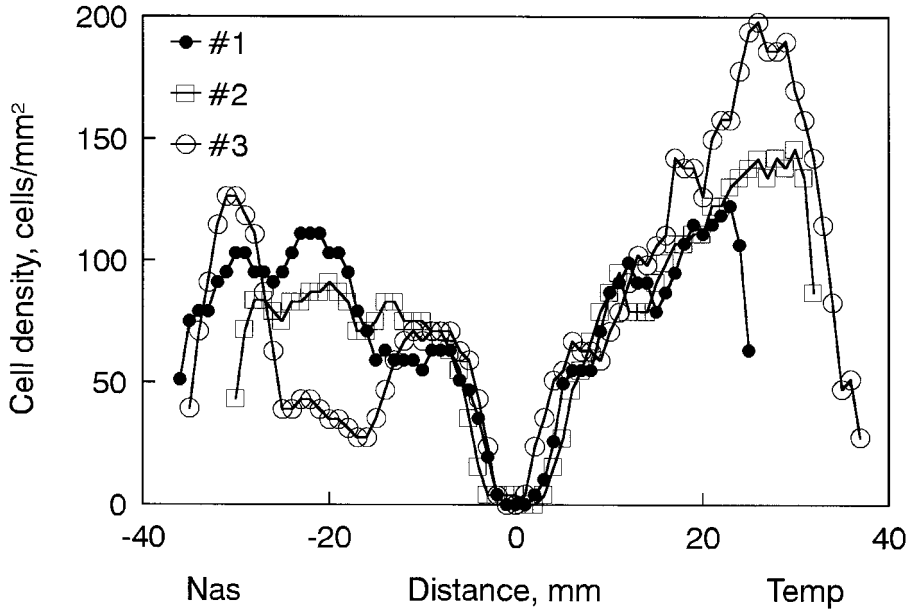

Figure 4. Ganglion cell density distribution along the horizontal equator in the whale's retina. *Nas*–nasal, *Temp*–temporal direction. Plots obtained from three wholemounts are designated by different symbols.

densities. In all the investigated samples, mean cell size was within a range of 30 to 31.6 μm (i.e., differed within 5.3%) with a standard deviation of distributions of 5.3 to 6.4 μm. Similar cell size in all the samples makes it reasonable to average all the data. It results in the distribution with the mean of 30.9 μm with SD of 5.8 μm.

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 & Wandeler, 1964; Waller, 1980; Dawson *et al*., 1972; Vasilyevskaya, 1988; Mass & 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-spheric lens. The cornea apparently plays a minor role under water because of 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 & 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 & 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 to 74 μm (means 30.9 μm). Large (mean 42.9 μm) and giant (up to 80 μm) ganglion cells were also observed in the retina of the minke whale *Balaenoptera acutorostrata* (Murayama *et al*., 1992). Very large (50–80 μm) and giant (up to 160 μm) cells were observed in the retina of the fin whale *Balaenoptera physalus* (Pilleri & Wandeler, 1964). The large size of ganglion cells is a common feature of many cetacean species. Ganglion cells up to 60–75 μm were described in the retina of the common dolphin *Delphinus delphis* (Dral, 1983),

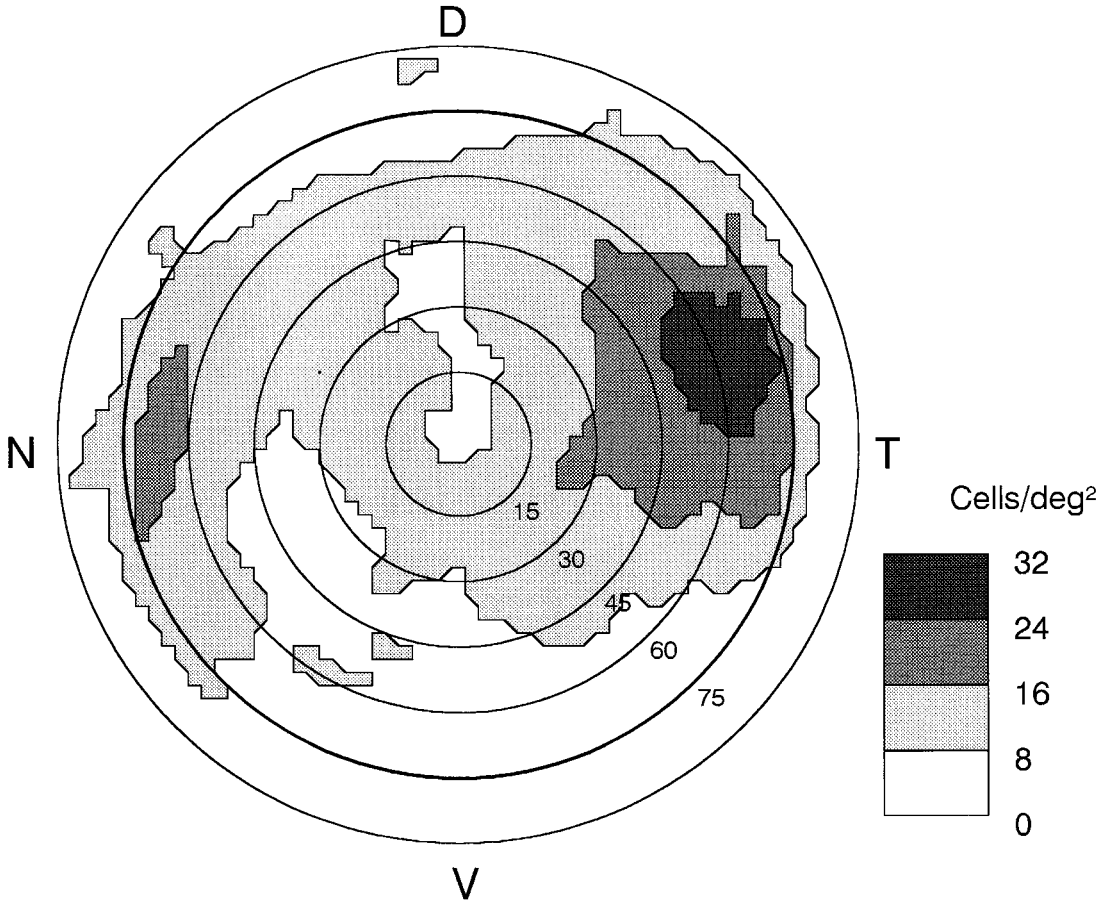

Figure 5. Continuous spherical map of ganglion cell density. The wholemount shown in Fig. 3 was used for transformation. The spheric coordinates are shown in the map, the coordinate center corresponds to the optic disc. N, T, D, V–nasal, temporal, dorsal and ventral poles of the retina. Note that only the part within the circle of 75° (i.e., 150° across) corresponds to the part of the retina that can be approximated by an incomplete hemisphere, this circle is shown by a thick line.

bottlenosed dolphin *Tursiops truncatus* (Dawson *et al.*, 1982; Mass & Supin, 1995), Baiji dolphin *Lipotes vexillifer* and finless dolphin *Neophocaena phocaenoides* (Gao & Zhou, 1987). The retina of other cetacean species has rather large ganglion cells as well (Waller, 1982; Mass & Supin, 1986, 1989).

It is noteworthy that representatives of another group of aquatic mammals, the pinnipeds, have also large retinal ganglion cells, up to 45–50 μm (Nagy & Ronald, 1970; Jamieson & Fisher, 1971; Mass, 1992; Mass & Supin, 1992). Probably the large size of ganglion cells is a common feature of aquatic mammals.

It seems unlikely that large size of ganglion cells in aquatic mammals relates to the body and eye size. In the retina of large terrestrial mammals, e.g. bovines (Hebel & Hollander, 1979) and the elephant (Stone & Halasz, 1989) ganglion cells do not exceed 25 to 30 μm.

It should be noticed that cell size distribution in the gray whale shows a tendency to separation of a small group of large (more than 40 μm) cells. A similar tendency was observed in other aquatic mammals: the northern fur seal *Callorhinus ursinus* (Mass & Supin, 1992) and bottlenose dolphin *Tursiops truncatus* (Mass & Supin, 1995).

The functional significance of large ganglion cells in aquatic mammals remains to be investigated. We can suppose, however, that for animals with large body size, such as mysticetes, rapid transmission of nerve pulses through thick axons of large ganglion cells is of importance. Dawson *et al.* (1982) suggested that the giant cell-axon systems of the

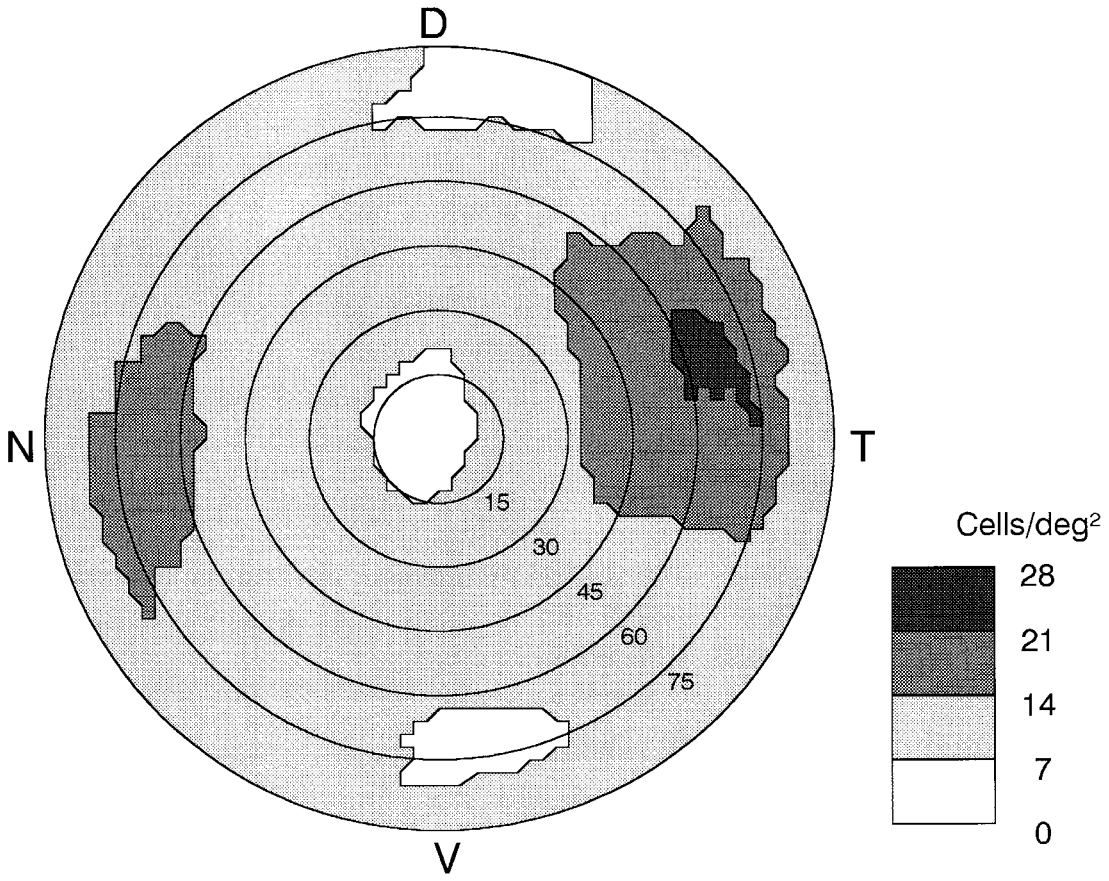

Figure 6. Continuous spherical map obtained by averaging the data from three wholemounts. Designation as in Fig. 5.

whale retina may be similar to the 'Y' cell-axon system in terrestrial mammals.

Number of ganglion cells

The present study gives estimation of a total number of ganglion cells in the retina of the gray whale. To date such data were absent for mysticetes, although the number of fibers in the optic nerve was estimated for some mysticete species. According to these data, the total number of optic fibers is 420 000 in *Balaenoptera borealis* (Morgane & Jacobs, 1972), 326 000 in *Balaenoptera acutorostrata* (Jansen & Jansen, 1969), and from 157 000 (Pütter, 1903) to 252 000 (Jacobs & Jensen, 1964) in *Balaenoptera physalis*. Most of these values exceed the number of 174 000 ganglion cells found in the gray whale. The number of optic nerve fibers may not coincide precisely with that of ganglion cells because of possible presence of centrifugal fibers; however, in other cetaceans rather good agreement was found between the number of ganglion cells (Mass & Supin, 1995) and the number of optic nerve fibers (Dawson, 1980; Dawson *et al*., 1982; Gao & Zhou, 1991). Thus, the number of ganglion cells in the gray whale may be really less than in some other mysticetes.

Functional significance of the two areas of ganglion cell concentration

The data presented herein reveal two areas of high ganglion cell density in the gray whale retina. These areas are located in the nasal and temporal quadrants of the retina. A similar pattern was found by the same method in another mysticete species, the minke whale *Balaenoptera acutorostrata* (Murayama *et al*., 1992).

This pattern is similar to that found in many dolphins: the common dolphin *Delphinus delphis* (Dral, 1983), bottlenose dolphin *Tursiops truncatus* (Dral, 1977; Mass & Supin, 1995), harbor porpoise *Phocoena phocoena* (Mass & Supin, 1986); and the Dall's porpoise *Phocoenoides dalli* (Murayama *et al*., 1995). All these odontocetes have two spots of high cell density in the retina, one in the nasal

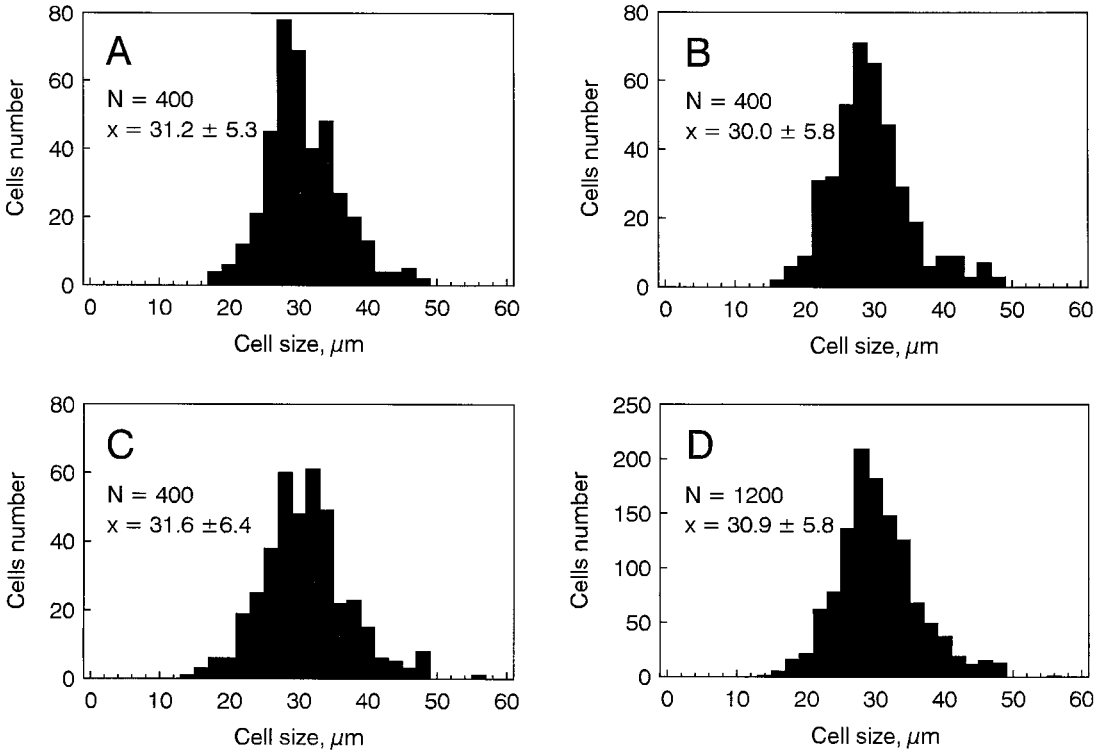

Figure 7. Histograms of ganglion cell size distribution in a few areas of the whale's retina. A–in the temporal high density area; B–in the nasal high density area; C–in a nasal low density area; D–averaging of the histograms A–C.

andthe other in the temporal quadrant with a streak connecting these two areas and passing below the optic disk.

There are, however, some differences in the retinal organization of odontocetes and mysticetes. Peak cell density in the gray whale (below 200 cells/mm^2) is markedly lower than in investigated odontocetes (700–800 cells/mm^2). Nevertheless, these areas of cell concentration are well defined in the gray whale. Apparently the lower cell density in the gray whale as compared to small cetaceans relates to the larger eye size in the whale. Being presented in the angular measure as cells/deg^2, the peak cell density in the gray whale (21 and 29 cells/deg^2 in the nasal and temporal areas respectively) is very close to that in the harbor porpoise (Mass & Supin, 1986, 1990). However, even presented in the angular measure, the peak cell density in the gray whale is less than in the bottlenose dolphin (43 cells/deg^2, Mass & Supin, 1995) indicating lower retinal resolution.

It is important that the centrally symmetric optics of the whale's eye are appropriate to create focused images at any part of the retina, including the areas of cell concentration which are disposed far from the retinal center. Apparently, these areas provide higher visual resolution than other retinal regions and may be considered as the best vision areas.

The position of the best vision area correlates with the shape of the pupil of the gray whale. The dilated pupil of the gray whale takes the shape of a horizontally oriented slit thus providing satisfactory illumination of equatorially located best vision areas. It was shown in dolphins (Dawson *et al.*, 1979) and the sperm whale (Rochon-Duvigneaud, 1939) that at higher light intensity, the centrally located operculum constricts the aperture in such a way that it takes a shape of two small slits at the temporal and nasal extremes of the pupil. These two slits are located just opposite the two best vision areas of the retina thus providing the illumination of these areas.

As to reasons why cetaceans have two best vision areas, there were several hypotheses proposed for dolphins which have similar retinal organization. In particular, it may be that the presence of the two best vision areas compensates the restricted mobility of the head of cetaceans (Mass & Supin, 1995). Together with eye movements, these two areas can provide acute vision in various parts of the visual field.

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 & 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 pin-hole 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 *Balaenoptera 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 & Herman, 1980). It suggests that mysticetes may use their vision in air.

It is unknown yet whether mysticetes have eye optics which make 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.

Retinal resolution and visual acuity estimation in the gray whale

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.:

$$s = 1/D^{\frac{1}{2}},$$

where s is angular spacing and D is cell density per deg^2 of visual angle. The latter depends on cell density and posterior nodal distance (PND). As shown above, the cetacean eye optics make 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 are 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 latero-caudal 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; e.g. about 7′ in *Balaenoptera acutorostrata* (Murayama *et al*., 1992), 8–12′ in *Tursiops truncatus* (Herman *et al*., 1975; Mass & Supin, 1995); and close to that (11–14′) in *Phocoena phocoena* (Mass & 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 are 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.

Acknowledgement

This study was supported by the Russian Foundation for Basic Research, Grant #95-04-11127.

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