# Visual field organization and retinal resolution of the beluga, *Delphinapterus leucas* (Pallas)

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## Abstract

The distribution and size of ganglion cells in the retina of three retinal wholemounts of beluga whales (*Delphinapterus leucas*) were investigated. Cell sizes were from 12 to 48 µm with monomodal size distribution. Ganglion cells concentrated at two spots of high density in the nasal and temporal quadrants, 50 to 60° from the optic disk. Both areas appeared as vertically elongated spots. The mean peak cell density over all wholemounts in the temporal and nasal areas was 400 and 300 cells/mm², respectively. With a posterior nodal distance of 12 m, these cell density corresponded to 17.4 cells/deg² and 12.7 cells/deg², which provided an underwater retinal resolution of 14.4′ (2.2 cycle/deg) and 16.9′ (1.8 cycle/deg) in the temporal and nasal high-density areas, respectively, and aerial resolution of 19.2′ (1.6 cycle/deg) and 22.5′ (1.3 cycle/deg). These data suggest that the beluga whale has slightly poorer visual acuity than other marine odontocetes investigated so far.

Key words: cetaceans, eye morphology, dolphins, vision, retina, wholemount, ganglion cells, cells distribution, cell size, visual acuity.

## Introduction

Traditionally, cetaceans are considered to have excellent hearing and echolocation, but poorly-developed vision which plays a minor role in their life. Recent behavioral investigations of visual discrimination capabilities, visual acuity, and visual system organization of cetaceans proved the visual system of cetaceans to be highly-developed, well-adapted to both aquatic and aerial media, and essential for predator avoidance and successful capture of prey, as well as for social interactions and orientation (Herman *et al*., 1975; Mobley & Helweg, 1990; Herman, 1990; Pack & Herman, 1995; Supin *et al*., 2001).

Studies of visual field organization in marine mammals make it possible to understand specific characteristics of their orientation and behaviour. The organization of visual fields directly relates to the retinal topography and usually is described in terms of the size, shape, and location of areas with the highest resolving power. The location of such areas corresponds to the position of eyes, behavioural traits, and habitat properties (Hughes, 1977; Peichl, 1992; Mass, 1997).

We previously studied some cetaceans and found that they can serve as an unusual example of the visual field organization and of the roles that specific areas of the visual fields play in orientation. Retinal topography mapping showed that, unlike the retina of terrestrial mammals which contains only one area of high ganglion cell density (known as the *fovea*, or *area centralis*), the retina of whales, whether toothed *(odontoceti)* or baleen (*mysticeti*), contains two such areas; one in the temporal part and the other in the nasal part of the retina (Mass, 1997). Presumably, they are differently involved in the aerial and underwater vision (Mass & Supin, 1995; Supin *et al*., 2001). In the underwater vision, both areas are used, whereas the aerial vision relies mostly on one of the two. The use of both areas provides for a wide field of monocular vision under water, which may compensate for the limited range of head movements typical of most dolphins and whales. The ganglion cell counts in the high-density areas make it possible to estimate the retinal resolution. This estimate, in its turn, allows the visual acuity to be calculated. In previous studies, the visual acuity of some cetaceans were estimated (Mass & Supin, 1986, 1989, 1995, 1997, 1999).

The question arises as to whether the presence of two areas of high ganglion cell density in the cetacean retina is a systematic trait or is due to other factors. In this context, an interesting object of study is the beluga whale, *Delphinapterus leucas* (Pallas), that belongs to the family Monodontidae and inhabits Arctic oceans and seas. Compared with dolphins or mysticetes, the beluga whale is less limited in the range of head movements. In addition, this species is characterized by the

lateroventral (rather than ventral, as in other cetaceans) position the eyes (Pilleri, 1982).

Knowledge about visual capabilities of the beluga whale is very limited; however, is crucial for planning strategies for conserving this species. Observations of beluga whales in captivity led to a conclusion that they have rather good visual capabilities (Pilleri, 1982; Marino & Stowe, 1997). However, their retinal resolution was estimated in just one study made on a single retina wholemount (Murayama & Somiya, 1998). Therefore, those data need to be expanded and confirmed.

The goal of this study was to assess the ganglion cell density distribution in beluga whale (*Delphinapterus leucas)* retina and to estimate the visual acuity of this species using retinal wholemounts.

## Materials and Methods

The material for investigation was collected from four adult belugas (*Delphinapterus leucas*, Pallas) of body length of 225 to 420 cm caught in the Okhotsk Sea. A licence for their capture was provided by the Glavrybvod. Only accidentally dead animals were a source of material.

One eye was used to study its macromorphological features and to determine the main geometric optical parameters, including the posterior nodal distance, which enters the formula for calculating the retinal resolution. The measurements were taken from scanner images of the longitudinal section of the eye fixed in 10% formalin and frozen.

The results reported in this study were obtained by retinal topography method on the wholemounts. This method allows a researcher to determine the ganglion cell distribution over the entire surface of the retina and to assess the cell density in various areas. Retinal wholemounts were prepared by the methods of Mass & Supin (1999).

Ganglion cells were counted and measured with the microscope focused within the ganglion layer. Ganglion cells were counted in small squares (0.15 mm$^2$) regularly spaced 1 mm apart over the entire retina surface. These counts were then transformed into maps of ganglion cell density. Isodensity lines were drawn by interpolation between points of the nearest values of cell density; a custom-made computer program was used for this purpose. The total number of retinal ganglion cells and the total area of the retina were calculated from these counts.

Cell size was obtained by measuring two perpendicular diameters of each cell i.e., the longest and shortest ones, and calculating the mean value. Measurements were made from scanned photographs.

## Results

*Eye morphology and dimensions*

The eye macromorphology of the beluga whale is shown schematically in Figure 1. Many features of the beluga whale eye are common to most of the marine cetacean species studied; however, there are also some distinctions.

The sclera is thick in the beluga whale. The anterior chamber is shallow. The lens is round, with a slight degree of flattening in the anterior-posterior direction. Its transversal and axial diameters are 8 and 7 mm, respectively. The pupil is elongated horizontally and has an operculum. In bright light, the operculum transforms the pupil into two narrow slits in the temporal and nasal part of the iris. In the eyeball measured 32.5 (the horizontal diameter) and 31.0 mm (the vertical diameter), the pupil was 9.0 × 7.5 mm.

Several arteries run through the well-developed iris musculature. The eye fundus is covered almost completely (excluding a small ventral portion) with the tapetum, which is well-developed in the beluga whale eye. These are quite general properties common to most of the cetaceans studied.

The cornea shape deserves special attention. The cornea thickness is nonuniform. Thin (roughly 1 mm) in the central part, the cornea appreciably thickens to the periphery, reaching approximately 3 mm at the boundary with the sclera near the limbus.

The choroid is significantly better developed in beluga whales than in dolphins. The eyeball is much more flattened in the axial direction in beluga whales than in dolphins. As a result, the axial length of the eyecup is significantly smaller than its diameter. In the beluga whale, as in other cetaceans, the eyecup exhibits some degree of dorsoventral flattening: the horizontal diameter is, on average, 2.5 mm larger than the vertical diameter.

Since the refraction index of the cornea is close to that of water, the primary refractive element of the eye under water is the lens. Given this fact, we took the distance from the lens centre to the retina as the posterior nodal distance. This distance was 12 mm in the beluga whale (Fig. 1.).

*Ganglion cell characteristics*

A distinctive property of the beluga whale retina was the large size of ganglion cells (Fig. 2). In the wholemounts studied, the ganglion cell size ranged from 12 to 48 μm. Large cells contained abundant cytoplasm, in which intensely stained Nissl bodies were clearly discernible. The pale nucleus with a prominent nucleolus stood out against a darker cytoplasm background. As a rule, three to five processes emanated from large neurons. Undoubtedly, these large neurons were ganglion cells. No
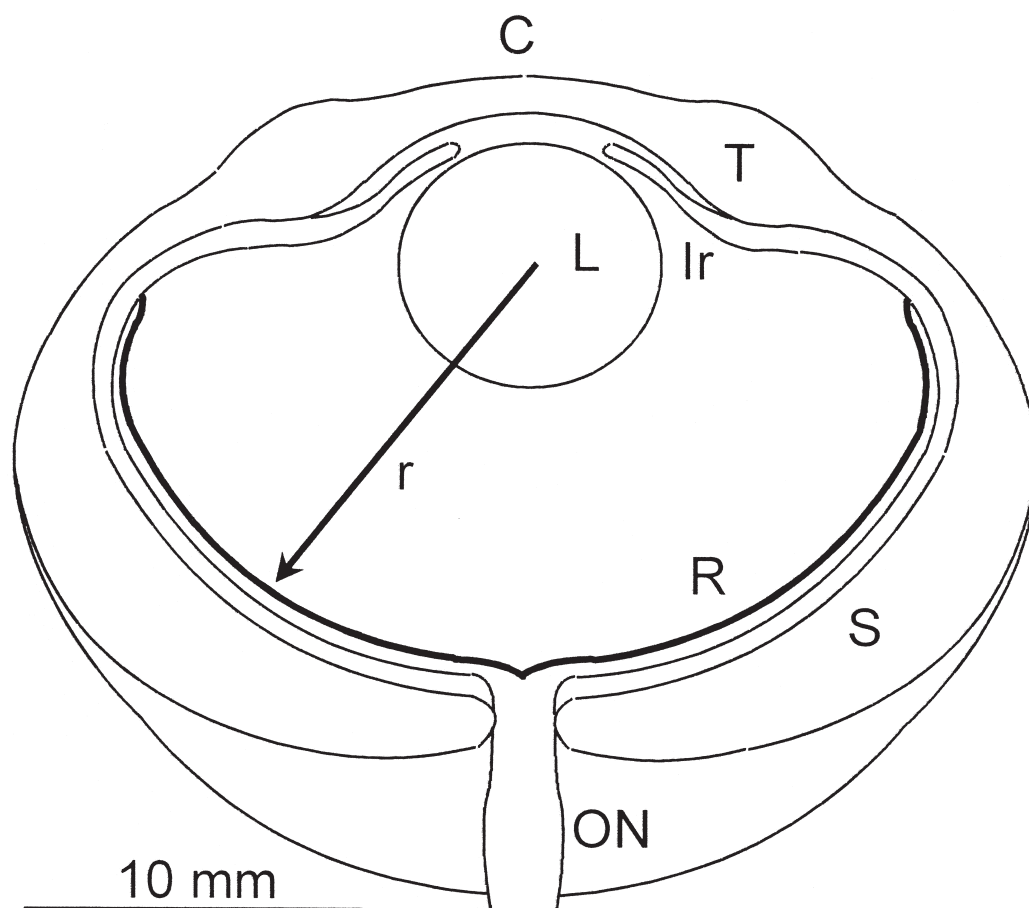
**Figure 1.** Sagittal section of the beluga eye (redrawn from scanner images). C=cornea, Ir=iris, L=lens, ON=optic nerve, S=sclera, R=retina, T=peripheral thickening of the cornea, *r*=the hemisphere radius.

small round dark cells resembling glial or amacrine cells were detected.

*Ganglion cells distribution*
The ganglion cell number in three investigated wholemounts was found to be from 103 700 to 124 640, with a mean of 122 360 cells (Table 1). The mean total retinal area was 916 mm$^2$.

A typical cell density map constructed using the results of ganglion cell counting is shown in Figure 3. The cell concentrations are depicted by isodensity lines and by hatching of different densities. The cell density in the ganglion cell layer was relatively low in the beluga whale; notwithstanding, sparse and dense areas could be distinguished, among which two high-density areas were the most prominent. One of them was in the temporal segment of the retina, close to its horizontal diameter;

and the other one in the nasal segment. Both areas appeared as vertically elongated spots. In the retinal wholemount shown, the peak cell densities observed in the temporal and nasal areas were 479 and 352 cells/mm$^2$, respectively. As can be seen in Table 1, the cell density averaged over all wholemounts studied was higher in the temporal segment than in the nasal one (about 400 and 300 cells/mm$^2$, respectively). Being the highest at the centre of each spot, the cell density rapidly declined to its periphery and remained low throughout the rest of the retina. The ventral segment of the retina was especially sparse.

The location of the high-density areas draws particular attention. They were far (12 to 15 mm) apart from the centre of the retina and relatively close to its periphery. In all the mounts studied, the high-density areas were similar in size, shape, and location.
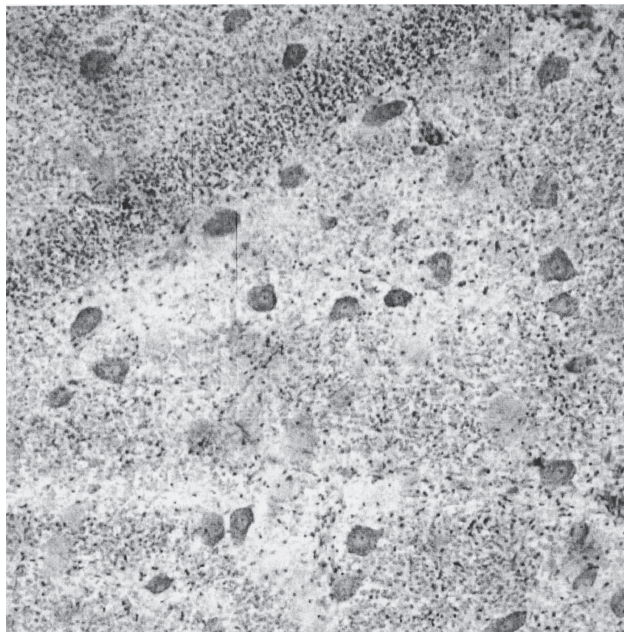
A



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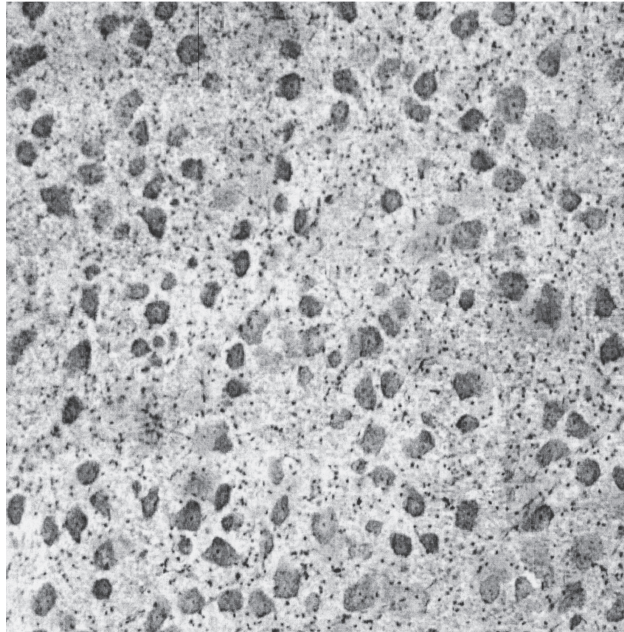


100 µm

**Figure 2.** Light micrograph from the ganglion cell layer of a Nissl-stained retinal wholemount of a beluga whale. A—in a temporal high-density zone; B—in a peripheral low-density zone.

**Table 1.** Counting data of three retinal wholemounts of beluga whales.

| | Temporal zone | | | | Nasal zone | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Number | Cells/ mm$^2$ | Cells/ deg$^2$ | Resolution arc min | Resolution cycle/deg | Cells/ mm$^2$ | Cells/ deg$^2$ | Resolution arc min | Resolution cycle/deg | Area mm$^2$ | Radius mm | Number of cells |
| 1 | 315 | 15.4 | 15.2 | 2.1 | 225 | 11.0 | 18.0 | 1.7 | 1181 | 12.7 | 124 640 |
| 2 | 479 | 21.6 | 12.6 | 2.4 | 352 | 15.5 | 15.3 | 2.0 | 800 | 12.2 | 138 750 |
| 3 | 414 | 15.2 | 15.4 | 2.0 | 320 | 11.7 | 17.4 | 1.6 | 768 | 11.0 | 103 700 |
| Mean | 403 | 17.4 | 14.4 | 2.2 | 299 | 12.7 | 16.9 | 1.8 | 916 | 12.0 | 122 360 |

*Retinal resolution*

To estimate retinal resolution, the maps of retinal wholemounts were transformed to continuous spherical maps of ganglion cell density in the spherical coordinate domain. Wholemount maps were transformed by a computer program to remove radial cuts and restore a hemisphere approximating the entire retina. Upon constructing continuous spherical maps of the retina, it was supposed that the mean radius of the retinal hemisphere was 12 mm.

Figure 4 shows a spherical map of ganglion cell density obtained by transformation of the wholemount map shown in Figure 3. In this spherical map, the cell density was specified in cell/deg$^2$ and is shown by hatching according to the scale at the bottom. Distance from the centre of the retina is shown in spherical coordinate (degrees). Its appears that the zones of the highest cell density were situated in the temporal and nasal quadrants of the retina, near its horizontal equator, and 50° to 60° away from the geometric centre. The peak cell densities were 21.6 cell/deg$^2$ in the temporal area and 15.5 cell/deg$^2$ in nasal one.

Knowing the ganglion cell density in the high-density areas, we assessed the angular distance between ganglion cells using a relationship:

$$\alpha = 180°/\pi r \sqrt{d},$$

where, $\alpha$ is the angular distance, $d$ is the cell density (cells/mm$^2$) and $r$ is the posterior nodal distance (mm). For mean peak cell density $d=400$ cells/mm$^2$ in the temporal high-density area, $d=300$ cells/ mm$^2$ in the nasal area, and $r=12$ m, we obtained $\alpha_t=14.4'$ and $\alpha_n=16.9'$ for the temporal and nasal high-density areas, respectively.

Another commonly used estimate of the retinal resolution is the resolvable spatial frequency (in cycles per degree):

$$f = 1/2\alpha$$

(the factor of 2 appears since at least two points are necessary to encode one cycle of spatial frequency).

The visual acuity $\alpha_t=14.4'$ corresponds to a spatial-frequency resolution $f_t=2.2$ cycle/deg and the acuity $\alpha_n=16.9'$ corresponds to $f_n=1.8$ cycle/degree (for the temporal and nasal high-density areas, respectively). These estimates of the retinal resolution of the beluga whale eye are valid for underwater vision, when the main refractive structure of the eye is its lens and, hence, the nodal point is the lens centre.

In air, refraction at the cornea surface shifts the nodal point. Its position cannot be determined without knowing the corneal curvature, which has not been measured accurately. However, given the water to air refraction index ratio of 1.33, we can assume as a first approximation that the retinal image size under water is 1.33 times that in air. If so, we have in air $\alpha_t=19.2'$ ($f_t=1.6$ cycle/degree) for the temporal high-density area and $\alpha_n=22.5'$ ($f_n=1.3$ cycle/ degree) for the nasal high-density area.

*Ganglion cell size*

Cell sizes were measured in two retinal wholemounts (number 1 and number 3, according to Table 1) obtained from two different animals. A total of 2400 cells were measured in six areas with different cell densities (400 cells in one sample). Figure 5 presents frequency-vs-size histograms for ganglion cells in various part of the retina, with high and low concentration: (A) in the temporal high cell-density region where the cell density was 455 cells/ m$^2$; (B) in the nasal high cell-density region where the cell density was 330 cells/mm$^2$; and (C) in a peripheral (nasal) part of the retina where the cell density was about 90 cells/mm$^2$. In all samples, the cell size ranged from 12 to 48 μm. Cells larger than 40 μm were very rare. Cells smaller than 12 μm were not found. Figure 5 shows that the cell size distributions were monomodal in all samples.

There was some difference between cell size distributions and mean sizes in areas of high and low cell densities. The cells were, on average, somewhat smaller in the high-density areas (25.0 μm) than in the peripheral low-density areas (29.6 μm).
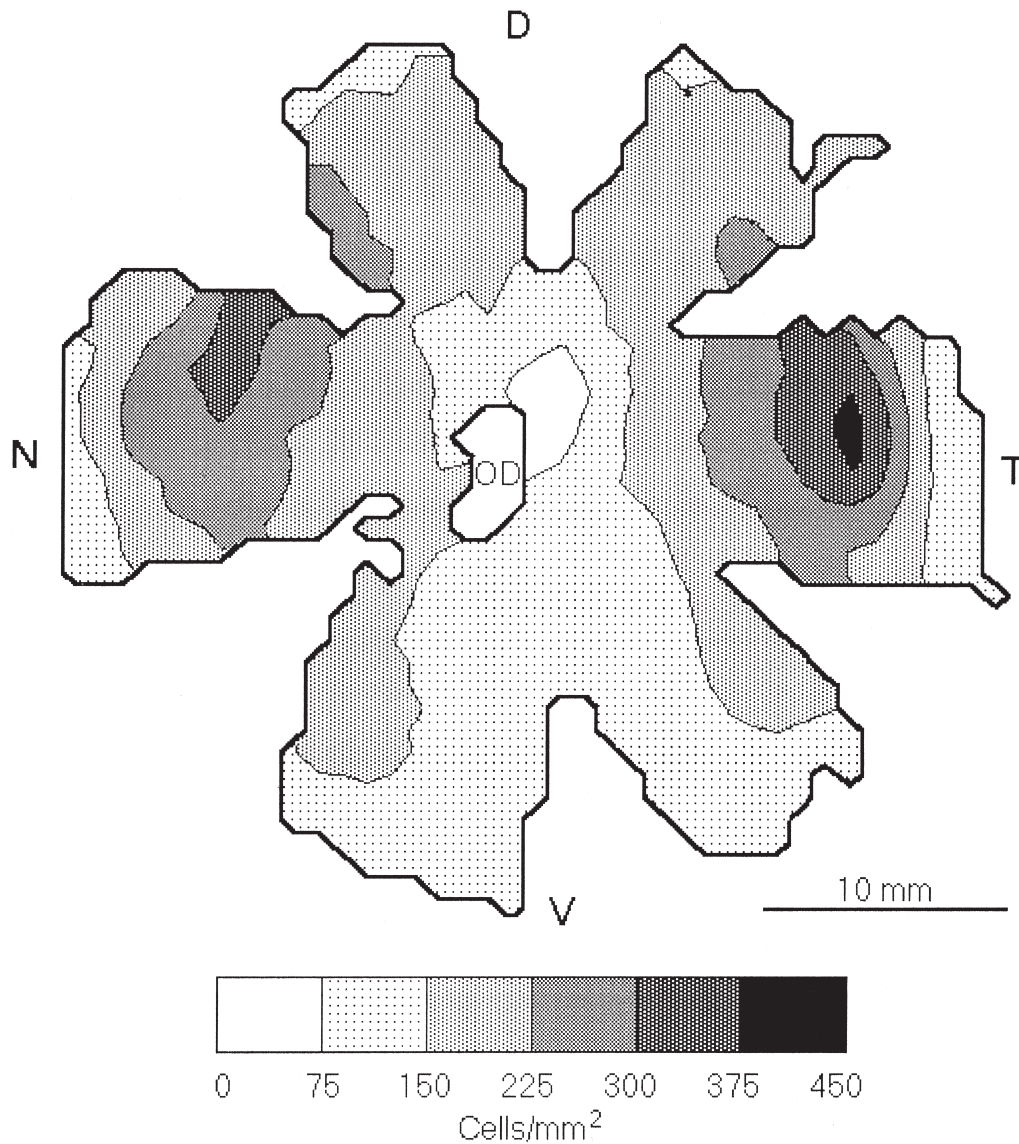
**Figure 3.** Map of ganglion cell density in a retinal wholemount. Cell density is designated according to the scale below. N, T, D, V=nasal, temporal, dorsal and ventral poles of the retina; OD=optic disk.

### Discussion

There are just a few studies of the layered structure of the beluga whale retina (Pütter, 1903; Pilleri, 1964). Its morphological and functional integrity was proved in those studies by demonstrating the presence of all the known retinal layers, each of which is well-developed in this species. Rod and cone photoreceptors also were detected in the beluga whale retina. However, retinal whole mounts have not heretofore been described for the beluga whale.

The total number of ganglion cells in the beluga whale retina averaged about 122 000, which is close to the total number of the optic nerve fibers in this species (137 000) reported by Pütter (1903). This coincidence supports our identification of large neurons as ganglion cells.
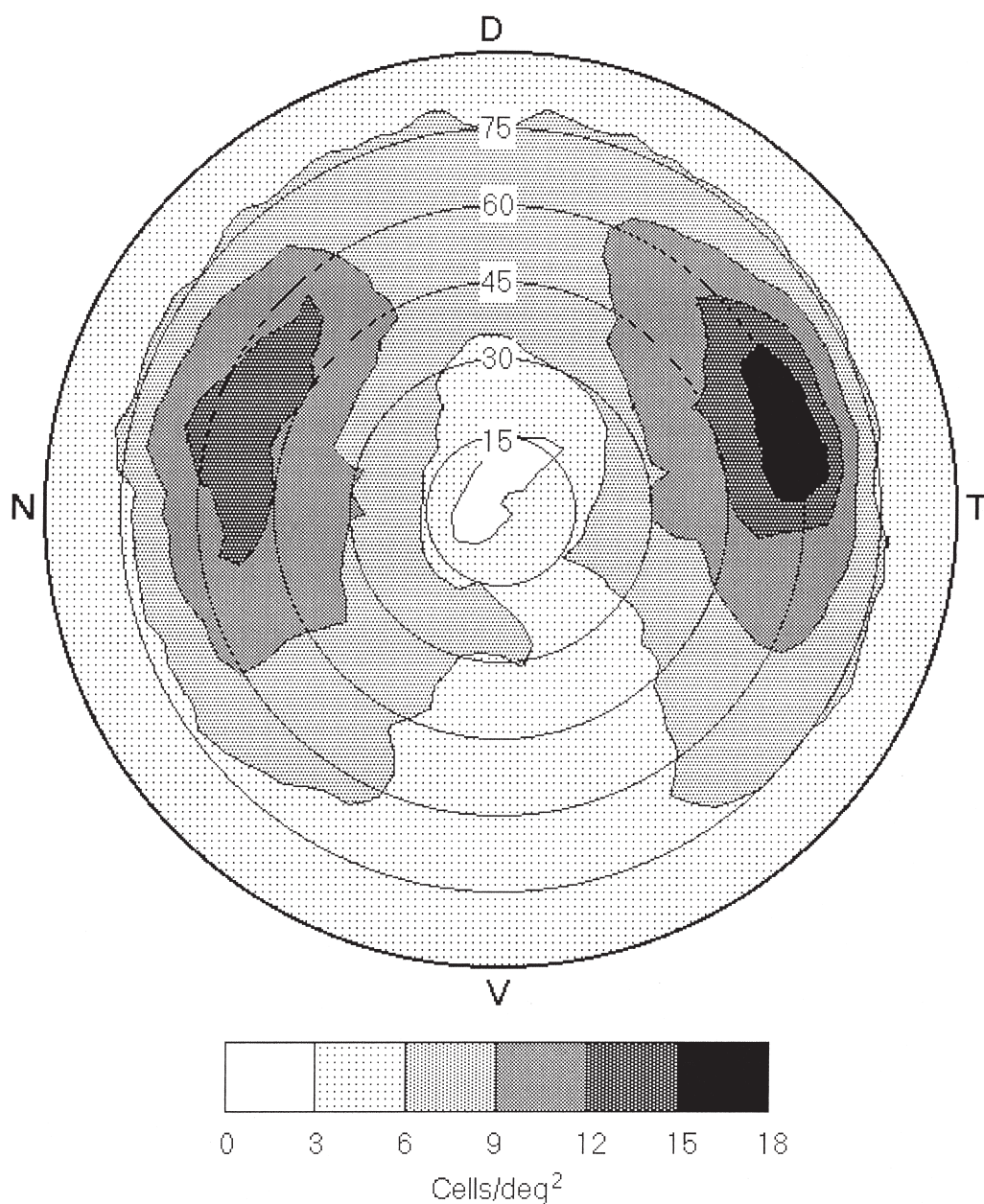
**Figure 4.** Ganglion-cell density distribution as projected onto the visual field in a beluga whale. Cell density (cells/deg$^2$) is designated according to the scale below. Distances from the centre of the retina are shown in spherical coordinates (degrees). D, V, N, and T=dorsal, ventral, nasal, and temporal poles of the retina, respectively.

According to the data presented herein, the beluga, that belongs to the family Monodontidae, has two areas of high ganglion cell density in its retina. That is, the retinal topography in general is the same as in a number of other odontocete families, such as Delphinidae (*Tursiops truncatus,*

*Delphinus delphis, Lagenorhynchus obliquidens, Pseudorca crassidens, Sotalia fluviatilis*), Phocoenidae (*Phocoena phocoena, Phocoenoides dalli*), (Dral, 1977, 1983; Mass & Supin, 1986, 1995; 1999; Murayama *et al.*, 1995; Murayama & Somiya, 1998), as well as in a few mysticete species,
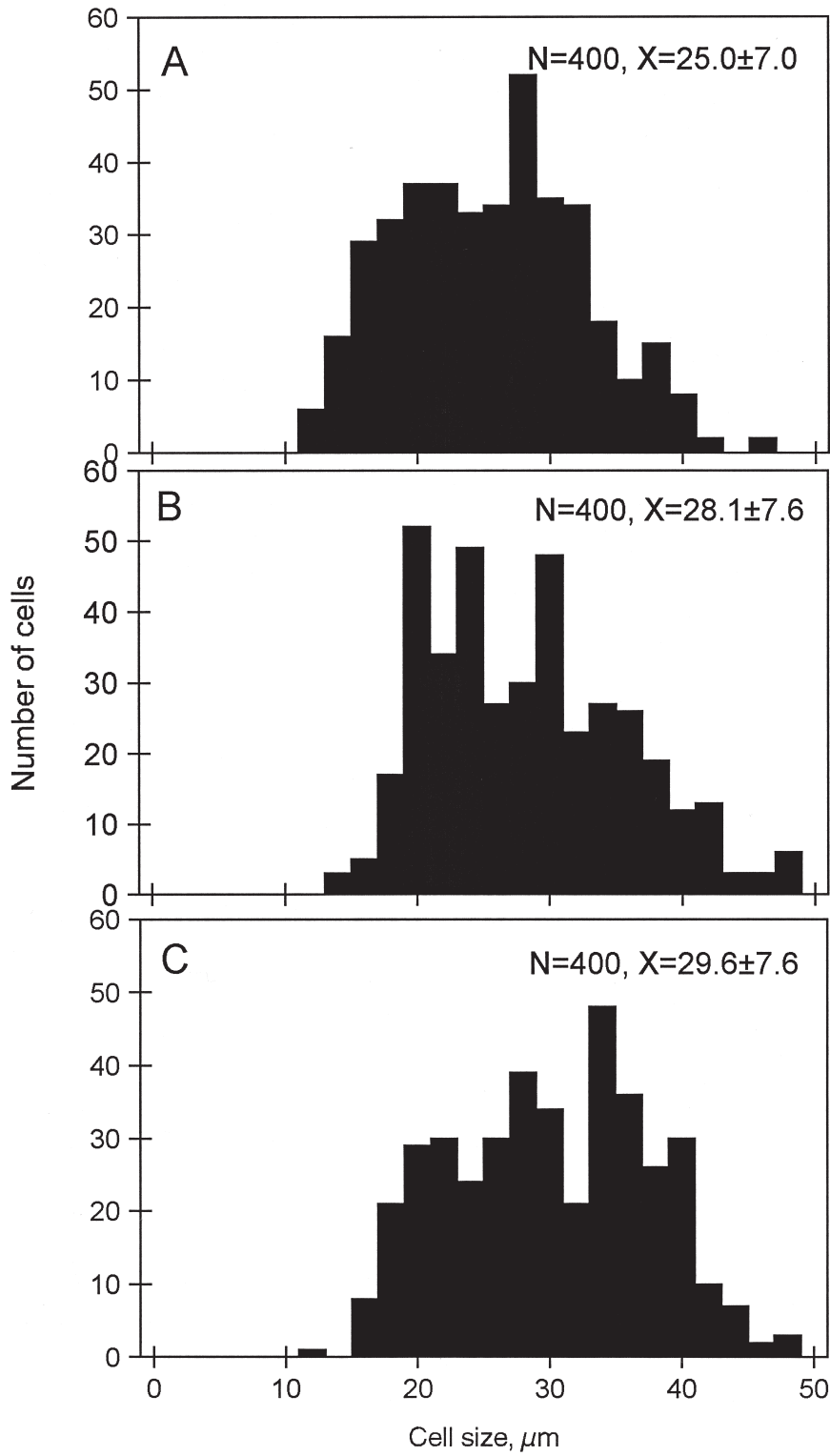
*A. M. Mass and A. Ya. Supin*

**Table 2.** Retinal-topography based estimates of visual acuity in some cetaceans.

| Species | Visual acuity | Reference |
|---|---|---|
| *Delphinus delphis* | 8–9.5′ | Dral, 1983 |
| *Phocoena phocoena* | 11–14′ | Mass, Supin, 1986 |
| *Tursiops truncatus* | 8–12′ | Mass, Supin, 1995 |
| *Phocoenoides dalli* | 11.5′ | Murayama *et al.* (1995) |
| *Lagenorhynchus obliquidens* | 11.2′ | Murayama & Somiya (1998) |
| *Pseudorca crassidens* | 9.3′ | Murayama & Somiya (1998) |
| *Eschrichtius gibbosus* | 10–11′ | Mass & Supin (1997) |
| *Delphinapterus leucas* | 11.8′ | Murayama & Somiya (1998) |
| *Delphinapterus leucas* | 14.4′ | Present study |

*Eschrichtius gibbosus, Balaenoptera acutorostrata* (Mass & Supin, 1997; Murayama *et al.*, 1992). The only exception was the Amazon River dolphin, *Inia geoffrensis*, (family Iniidae) (Mass & Supin, 1989). Thus, data presented herein confirm that the retinal topography with two high-resolution areas is a common property of most cetaceans, independent of their family.

The two high-resolution retinal areas in cetaceans may be differently used for underwater and aerial vision. Presumably in the underwater vision, both areas are used, whereas the aerial vision relies mostly on one of the two (Supin *et al.*, 2001). Our observations of beluga whales in captivity show that when beluga whales look at an object above water, it places the object into the ventronasal part of the visual field that projects onto the temporal high-resolution retinal area. When belugas look at an underwater objects, they take a position beside the object i.e., the object is placed into the postero-lateral part of the visual field that projects onto the nasal high-resolution retinal area. However, the temporal high-resolution retinal area also partici-pates in underwater vision serving the frontal part of the visual field. Such a use of two high-resolution retinal areas may compensate for limited head mobility in many cetaceans. However, compared with dolphins or mysticetes, the beluga whale is less limited in the range of head movements; neverthe-less, its retina contains the same two high-resolution area.

The retinal topography with two high-resolution areas correlates with the shape of the pupil that becomes a U-shaped slit and then two narrow holes in the temporal and nasal parts of the iris with illumination increase. With such a pupil, light reaches the high-resolution retinal areas through peripheral parts of the cornea and then through side slits or holes of the pupil. This pupil shape is characteristic of many dolphins, including the bottlenose dolphin (*Tursiops truncatus*), harbour porpoise (*Phocoena phocoena*), common dolphin (*Delphinus delphis*), tucuxi dolphin (*Sotalia fluviatilis*), and also for gray whales (*Eschrichtius gibbosus*) (Dawson, 1980; Mass & Supin, 1997, 1999).

Taking that light reaches the high-resolution retinal areas through the corneal periphery, the shape of the cornea in the beluga whale deserves attention. It is non-uniform with peripheral thicker ridge. Pütter (1903) first described this ridge unique to the beluga whale eye. However, in a later study by Pilleri (1964) the scheme of the beluga whale eye was drawn without indicating this remarkable structure of the cornea. Unfortunately, it was Pilleri's scheme that was cited thereafter by others (Yablokov *et al.*, 1972; Von W. Neuhaus, 1986). A more or less prominent peripheral thickening of the cornea is typical of many whales: *Balaena mysticetus* (Putter, 1903; Zhu *et al.*, 2000), *Hyperoodon rostratus* (Putter, 1903), *Physeter macrocephalus, Megaptera novaeangliae* (Rochon-Duvigneaud, 1940), *Eschrichtius gibbosus* (Mass & Supin, 1997), *Physeter macrocephalus* (Mann, 1946), although it is less clearly visible in some dolphins: *Delphinus delphis, Phocoena phocoena* (Rochon-Duvigneaud, 1940; Kröger & Kirschfeld, 1994), *Phocoena communis* (Putter, 1903). This peripheral corneal ridge may be of importance for eye optics. Although major refraction in the cetacean eye is performed by the lens, the refractive role of the cornea is not negligible. Its outer surface is of lower curvature than the inner one, and some difference between the refractive indices of water (1.33) and the cornea (from 1.37 in the central part to 1.53 in the periphery) does exist. Therefore,

**Figure 5.** Histograms of ganglion-cell size distribution in a few areas of the retina. A—in the temporal high-density zone; B—in the nasal high-density zone; C—in a peripheral low-density zone. In each panel, the number of measured cells (N), and mean size (X) ± SD in μm are indicated.

the cornea has a shape of a divergent lens. Supposedly, the corneal peripheral thickening serves as a corrective lens (Kröger & Kirschfeld, 1994).

As to the estimate of visual acuity of the beluga whale in present study, it should be noted that the same method was used to assess the visual acuity in some marine dolphins and whales (Table 2). In the beluga whale, our data suggest slightly poorer visual acuity, mean 14.4′ in the temporal high-resolution area and 16.9′ in the nasal area (under water). This estimate does not coincide with that of Murayama & Somiya (1998); however, that estimate was obtained in a single retinal preparation.

### Acknowledgments

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