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Ganglion Cell Topography and Retinal Resolution of the Steller Sea Lion (*Eumetopias jubatus*)

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Abstract

The total number, soma size, topographic distribution, and density of ganglion cells were studied in retinal wholemounts of the Steller sea lion (*Eumetopias jubatus*). Ganglion cell soma size varied from 6 to 37 μm, and the majority of cells were of a size from 10 to 25 μm. A distinct group were large ganglion cells of more than 25 to 37 μm, which were similar to the α-cells known in terrestrial mammals. The number of α-like cells constituted 8% of the total ganglion cell population. The topographic distribution of ganglion cells showed a definite area of high cell density similar to the area centralis of terrestrial carnivores. This area was located in the temporal retinal quadrant, 8 to 9 mm from the optic disk. In this area, the peak cell densities in six wholemounts ranged from 1,512 to 2,520 (mean 1,904) cells/mm^2. With a posterior nodal distance of 19 mm (underwater), these densities corresponded to 166 to 277 (mean 209) cells/deg^2. This predicts a mean retinal resolution of 4.15' of minimum visibility (7.2 cycle/deg) in water and 5.5' (5.5 cycle/deg) in air. Topographic distribution of α-like cells was qualitatively similar to that of the total ganglion cell population, but the density of α-like cells reached only 45 to 72 (mean 59) cells/mm^2.

Key Words: Steller sea lion, *Eumetopias jubatus*, mammals, retina, ganglion cells, retinal topograpy, area centralis, visual acuity, α-cells

Introduction

The visual system of pinnipeds, which is adapted to both aquatic and terrestrial habitats, features a remarkable morphological and functional organization (Jamieson & Fisher, 1972; Supin et al., 2001; Griebel & Peichl, 2003). On land, vision plays a significant role in reproductive behavior, intrapopulation communications, and spatial orientation. Since pinnipeds forage exclusively in water and do not echolocate (Schusterman, 1967; Schevill, 1968; Wartzok et al., 1984; Schusterman & Kastak, 2000), underwater vision is necessary for their hunting behavior. New experimental data concerning the functional abilities of the pinniped's eye support the hypothesis that underwater vision of pinnipeds is of importance to locate and capture prey while diving (Levenson & Schusterman, 1997, 1999).

Specific features of the pinniped's visual system include big eyes, very high light sensitivity, adaptation to low-light conditions, and variation of the pupil area (from 70 to 470 times among different species) when the animal dives (see Supin et al., 2001; Griebel & Peichl, 2003, for review). A flattened center region of the cornea serves as an "emmetropic window" in which refraction remains emmetropic in both air and water (Pütter, 1903; Dawson et al., 1987; Mass & Supin, 1992, 2003). Due to these adaptations, seals and sea lions have a rather good visual acuity (of an order of a few arc minutes) in both water and air (Busch & Dücker, 1987; Schusterman & Balliet, 1970a, 1970b; Mass & Supin, 1992, 2003); however, many aspects of the organization of pinniped's vision need further investigation.

Investigations of the retinal structure may be helpful to understand many features of the visual system: visual discrimination, color vision, visual field organization, mechanisms of adaptation, and visual acuity. Many of these features are more noticeable in the topography of the retina rather than in its laminar organization. Therefore, an effective approach to study some aspects of the organization of the visual system is the investigation of retinal topography, particularly the areas of high ganglion cell density. These areas of the retina feature the highest resolution, determine the visual acuity, and are responsible for fine visual discrimination. In terrestrial mammals, they are known as the area centralis and the visual streak. These areas were studied in many terrestrial mammals, and it was demonstrated that their organization varies from species to species and depends on the eye position and lifestyle (see reviews by

Hughes, 1977; Stone, 1983; Pettigrew et al., 1988; Peichl, 1992).

Until recently, presence of high-density areas in pinnipeds was considered questionable. Initial attempts to identify the area centralis in the retina of the California sea lion (*Zalopus californianus*, Landau & Dawson, 1970), the harp seal (*Pagophilus groenlandicus*, Nagy & Ronald, 1970), and the harbor seal (*Phoca vitulina*, Jamieson & Fisher, 1971) did not reveal any areas of high ganglion cell density. These authors studied transverse retinal sections. Later topographic mapping of ganglion cells in retinal wholemounts revealed high-density areas in some pinnipeds and demonstrated that their organization varies among species. At the present time, four pinniped species belonging to different families have been studied: the walrus (*Odobenus rosmarus*, Odobenidae) (Mass, 1992), the northern fur seal (*Callorhinus ursinus*, Otariidae) (Mass & Supin, 1992), the harp seal (Phocidae) (Mass & Supin, 2003), and Weddell seal (*Leptonychotes weddellii*, Phocidae) (Welsch et al., 2001). The northern fur seal, harp seal, and Weddell seal featured a high-density area similar to an area centralis. Quite different was the retinal topography in the walrus. The area of increased ganglion cell density is a horizontally extended oval, resembling the visual streak of terrestrial mammals. Thus, the pinniped's retina contains a high-resolution area, but its organization differs among species.

In this context, an interesting object of study is the Steller sea lion (*Eumetopias jubatus*, Otariidae). The Steller sea lion is the largest of the otariids. This species is more land-based than the northern fur seal investigated previously; it seasonally migrates not far from the breeding places and does not migrate for long distances.

Visual capabilities of the Steller sea lion were studied in only one psychophysical investigation (Schusterman & Balliet, 1970b). Data on its retina's morphology are limited by a single investigation (Pütter, 1903). Retinal wholemounts of this species have not yet been described.

The present study is an attempt to topographically map the ganglion cells in the retina of the Steller sea lion, with the aim to locate areas of the highest cell density. The topographic data also were used to assess the retinal resolution.

Materials and Methods

Five 3- to 4-month-old animals and one yearling from rookeries at the Kuril Islands were the source for the specimens. Seven of the eyes collected were good enough for further processing. The specimens were fixed in 10% buffered formalin. Six eyes were used to prepare retinal wholemounts; small pieces of two of them also were used to prepare transverse sections; and one eye was sectioned to determine its macromorphological characteristics and to estimate the main optic dimensions.

For a macromorphological investigation, external dimensions (axial length and equatorial diameter) of all the eyes were measured. One eye was frozen and longitudinally sectioned. Sections near the eye axis were digitally photographed, and these pictures were used to diagram the eye and to measure the main dimensions.

Retinal wholemounts were prepared as described in detail by Mass & Supin (2003). The iris, lens, and vitreous body of the eye were removed. After noting its orientation, the retina was separated from the pigment epithelium and excised from the eyecup. Several radial cuts were made in the retina to flatten it. The retina was flatmounted on a slide with the ganglion cell layer upward, weighted in 10% buffered formalin solution for several hours, and air-dried. Then, the retina was stained by the Nissl method with 0.1% cresyl-violet, monitored visually, dehydrated in graduated ethanol, cleared with xylene, and mounted in Permount.

For ganglion cell mapping, they were counted in 0.078 mm^2 samples on a 1-mm square grid over the whole retina in one wholemount. Five other wholemounts were not complete enough and were used to count ganglion cells in the high-density areas only. The counts were converted to cells/mm^2. The data obtained were used for mapping the distribution of ganglion cells (a complete map from one wholemount and fragmental maps from the others). The data from the complete wholemount were used as well for calculating the total number of ganglion cells. In the topographic maps, 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.

Ganglion cell soma size was measured across two perpendicular axes of the cell—the long and short ones—and the mean was taken as the cell size.

To study retinal laminar organization, a series of transverse sections were prepared. For that, small retinal samples fixed in 10% buffered formalin were dehydrated, embedded in Paraplast, serially sectioned by 6 to 10 μm, stained with Hematoxylin and phloxine, and embedded in balsam.

Results

Eye Dimensions

External dimensions of all the Steller sea lions' eyes were as follows: axial length, 32 to 33 (mean 32.5) mm; and equatorial diameter, 35 to 39 (mean 36.7) mm.

Figure 1 presents diagramatically a longitudinal section of the frozen eye. The eyeball shape

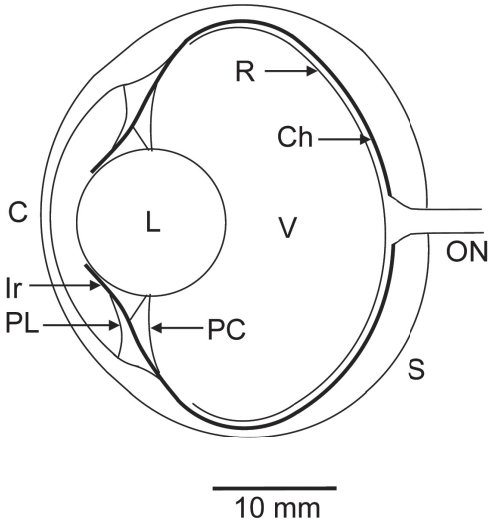

Figure 1. A diagram of the longitudinal section of a Steller sea lion's eye (drawn from photographs): C – cornea, Ir – iris, PL – pectinate ligament, L – lens, PC – processus ciliares, S – sclera, Ch – choroid, R – retina, V – vitreous body, ON – optic nerve

was almost spherical: outer horizontal diameter was approximately equal to the vertical diameter (36.5 mm), and only a slight degree of flattening was observed in the axial direction (32.5 mm). The steel blue tapetum was well-developed and covered most of the eyecup. The lower ventral third and equatorial area of the eyecup were covered with dark pigment.

The optic nerve was 2 to 2.5 mm in diameter and entered the eyecup at a point slightly temporal of the eyecup center.

The cornea was about 26 mm in diameter; its thickness was about 1 mm in the center and increased up to 2 mm at the edges. The quality of formalin-fixed specimens did not allow us to determine the presence or absence of a flattened center region of the corneal surface.

The pupil was almost circular and slightly oval when constricted.

The sclera thickness was not uniform. It was 1 to 1.5 mm thick in the equatorial belt, with a thickness increase of up to 3 to 3.5 mm towards the optic nerve. In the region of corneo-scleral junction, there was a thicker belt. Much of the space between the sclera and iris was occupied by a profuse fiber network—the pectinate ligament.

The lens was almost spherical, with a diameter of 13 to 14 mm, and was almost in the center of the eyecup. The distance from the lens center to the retina was 19 mm.

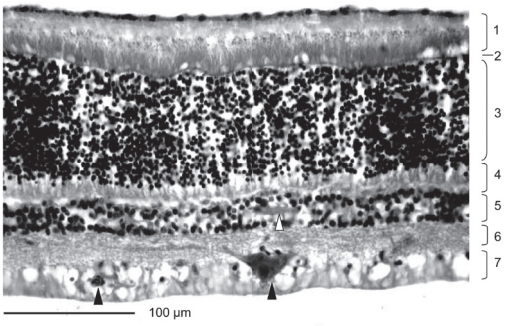

Figure 2. Vertical cross section of the periferal area of the Steller sea lion's retina: 1 – receptor layer, 2 – outer limiting membrane, 3 – outer nuclear layer, 4 – outer plexiform layer, 5 – inner nuclear layer, 6 – inner plexiform layer, 7 – ganglion cell layer. Dark arrowheads point to ganglion cells (one of them is giant); light arrowhead points to a horizontal cell.

Laminar Organization of the Retina

Laminar organization of the sea lion's retina was investigated in transverse sections (Figure 2). The retinas thickness was from 200 to 230 μm. In general, the laminar structure of the retina was the same as in terrestrial mammals. All retinal layers were present: the receptor layer, outer nuclear layer, outer plexiform layer, inner nuclear layer, inner plexiform layer, ganglion cell layer, and, finally, the optic-fiber layer.

The photoreceptor layer contained densely packed, slender, nearly cylindrical, long outer segments of rods. Near the outer limiting membrane, profiles of another type could be discerned, but we have no criteria to say that these cone-like profiles are really cones.

The photoreceptor layer showed two zones: (1) a lightly staining outer segment layer and (2) a darker staining inner segment layer. The outer limiting membrane was clearly discernible between the photoreceptor and the outer nuclear layers.

The outer nuclear layer was composed of receptor pericarya arranged in a multilevel manner. This layer was the thickest of all the layers, being 22 to 24 pericarya deep and ordered in transverse strings.

The inner nuclear layer was thin and rather chaotically organized. The bipolar and amacrine cells were diffusely distributed. Only slight ordering could be seen near the outer and inner plexiform layers. There were giant horizontal cells within the layer.

The ganglion layer was only one cell row thick. Cell soma sizes varied from 6 to 37 μm (for more detailed information about cell size, see below). Within the single row of ganglion cells, there was some number of giant (30 to 37 μm) ganglion cells. These neurons had a huge soma with abundant cytoplasm in which large clumps of a Nissl substance were clearly discernible. Their large

nuclei were stained lighter than the surrounding cytoplasm. Occasionally, large dendrites were found to originate from the soma.

Characteristics of Ganglion Cells in Wholemounts

Ganglion cells were identified according to the criteria described earlier (Nagy & Ronald, 1970; Mass & Supin, 1992, 2003). Ganglion cells looked like typical neurons in the superficial retinal layer. Most of them were polygonal neurons, larger than 6 μm in size, with abundant cytoplasm in which intensely stained Nissl granules were clearly discernible (Figure 3). The large nucleus with a prominent nucleolus was stained lighter than the surrounding cytoplasm. Throughout the retina (except for the high-density area), ganglion cells were separated by wide intercellular spaces. Conglomerations composed by two or three neurons can be distinguished. The majority of the cells' somas were 10 to 25 μm in size; however, a distinct small population of large and giant cells (30 to 37 μm) could be identified. Large and giant cells were regularly spaced.

Apart from typical ganglion cells, small cells (typically < 5 to 6 μm in size) were discernible in the ganglion layer. Their pale nucleus with a distinct nucleolus was surrounded with a thin rim of cytoplasm without Nissl granules. These cells looked translucent. They could be discriminated easily from intensely stained ganglion cells. They were observed mostly at the periphery of the retina and were tentatively classified as amacrine cells. Small (about 5 μm), rounded, deeply stained cells were considered neuroglia and were very rare. Cells categorized as both amacrine and neuroglial were not included in counting ganglion cells nor in the analysis of their distribution.

Topographic Distribution of Ganglion Cells

In one wholemount (#1 in Table 1), ganglion cell distribution was mapped over the whole retina. The total area of the wholemount was 1,522 mm^2, and the total number of ganglion cells was estimated as 177,500. Even by visual inspection, the distribution of ganglion cells over the retinal wholemount appeared non-uniform. Figure 4 shows the topographic mapping results of the total ganglion cell population in the wholemount. The map illustrates significant variations in ganglion cell density across the retina. A local high-density area was easily discernible in the temporal quadrant. It looked like an oval spot slightly elongated in the naso-temporal direction. The density peak was 8 to 9 mm away from the optic disk. The highest density in this wholemount was 1,512 cells/mm^2. The high-density area was quite local: at a distance of 3 to 4 mm away from its center, the cell density fell to about one-

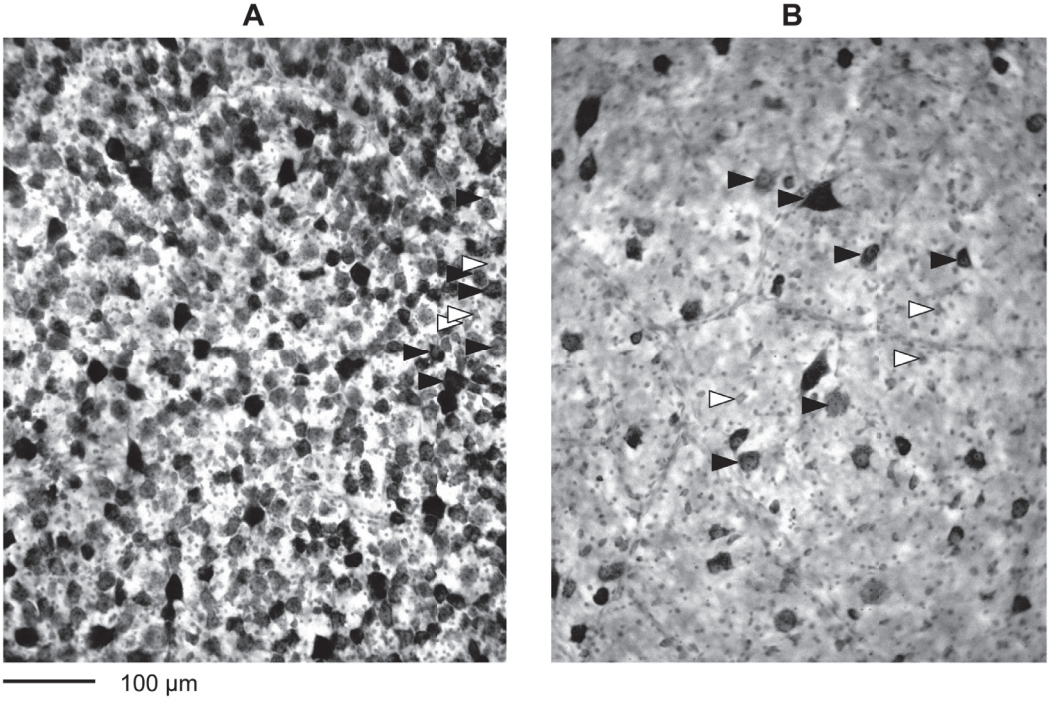

Figure 3. Light micrographs from a ganglion cell layer of a Nissl-stained retinal wholemount of a Steller sea lion; A – high-density area; B – low-density area. Dark arrowheads exemplify a few cells identified as ganglion cells; light arrowheads exemplify those identified as amacrine cells.

Table 1. Ganglion cell density (cells/mm^2) in the highest-density area of wholemounts of a Steller sea lion

Wholemount #	1*	2**	3	4	5**	6	Mean
Total cells	1,512	2,000	1,512	1,700	2,180	2,520	1,904
Large cells	60	60	45	72	67	50	59

*Complete wholemount used for mapping and measurement of the total area and number of cells
**Wholemounts used for cell size measurements

third of the peak value. Over the major part of the retina, cell density did not exceed 250 cells/mm^2.

Because of the incompleteness of the other five wholemounts, ganglion cell density was not measured over the entire retinal area and was measured only in the region of the highest cell density. The results are presented in Table 1. The peak densities varied from preparation to preparation, from 1,512 to 2,520 cells/mm^2. The mean peak density of six wholemounts was 1,904 cells/mm^2.

The topographic distribution of large and giant (more than 20 to 25 μm in size) ganglion cells also was studied. In the complete wholemount, the number of these cells was 14,340 (8% of the total population). The topographic map of their distribution is presented in Figure 5. This map also contained a high-density area, which coincided with that of the entire ganglion cell population (see Figure 4) in location and peak position; however, large cell density was much lower than that of the total ganglion cell population—the peak density varied from 45 to 72 (mean 59) cells/mm^2 (Table 1). The density decreased with the distance from the peak point, however, though less steeply than the density of the total population (note wider spread of isodensity lines in Figure 5 as compared to those in Figure 4). Thus, the proportion of large cells is higher in the retinal periphery than in the high-density area.

Apart from presenting ganglion cell density per retinal area unit (cells/mm^2), another way is to present it per visual sphere unit (cells/deg^2). Cell density as cells/mm^2 was converted to cells/deg^2 as

$d = D(\pi r/180)^2$,

where, d is the cell density as cells/deg^2, D is the density as cells/mm^2, and r is the posterior nodal distance (PND). Under water, where refraction at the corneal surface is negligible and the lens is the main refractive structure, the nodal point coincides with the center of the spheical lens. So, PND is the distance from the lens center to the retinal surface, which was estimated as 19 mm. With this PND, values from 1,512 to 2,520 (mean 1,904) cells/mm^2 correspond to 166 to 277 (mean 209) cells/deg^2. Large cell densities of 45 to 72 (mean 59) cells/mm^2 corresponded to 4.9 to 7.9 (mean 6.5) cells/deg^2.

The distribution of ganglion cells in the sea lion retina can be demonstrated by profiles across the horizontal diameter of the retina (Figure 6). The plots present data for the whole ganglion cell population (1) and for large cell population (2). Note 10-times difference of scales for the whole ganglion and large cell populations. The plots illustrate the cell density peaks (more than 1,500 cells/mm^2 for the whole population and 60 cells/

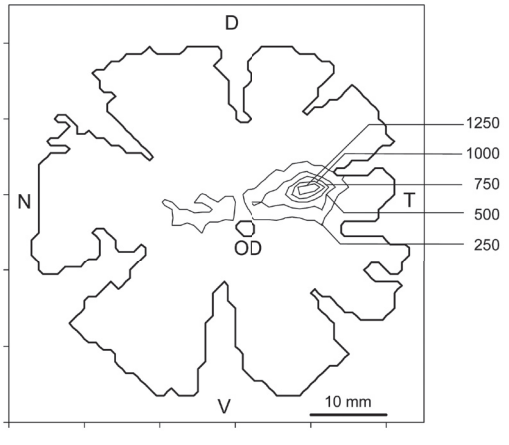

Figure 4. A topographic map of ganglion cell density of a Steller sea lion (total cell population); cell density (cells/mm^2) is indicated by isodensity lines. N, T, D, V – nasal, temporal, dorsal, and ventral poles of the retina, respectively; OD – optic disk.

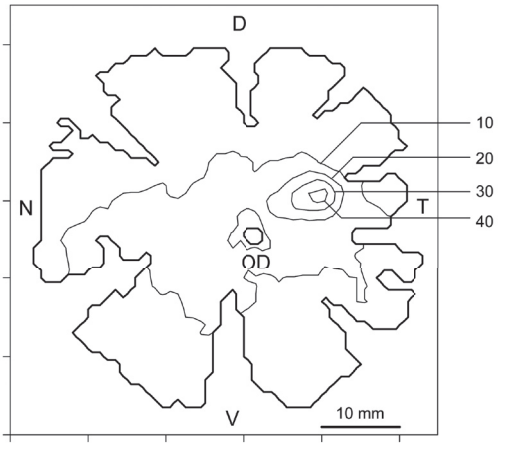

Figure 5. A topographic map of ganglion cell density of a Steller sea lion (large cell population); designations as in Figure 4.

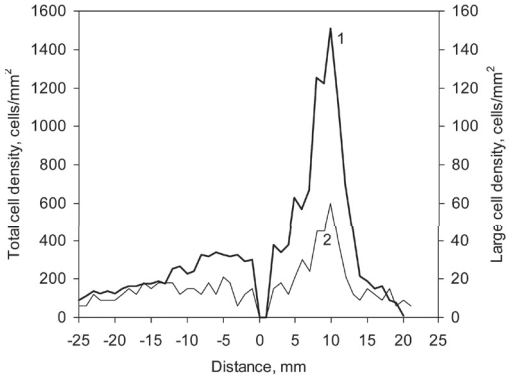

Figure 6. Profile of ganglion cell density distribution across a Steller sea lion's retina; cell density as a function of distance along the horizontal diameter: 1 – total cell population (left ordinate scale), 2 – large cell population (right ordinate scale). Abscissa zero corresponds to the optic disk, negative values – nasal direction; positive values – temporal direction.

mm² for the large cell population). For both populations, the peak positions coincided and were 8 to 9 mm from the optic disk. The plots demonstrate a little higher proportion of large cells at the retinal periphery (around 1:10 of the total population) than in the high-density area (around 1:25).

Ganglion Cell Sizes

A total of 2,100 ganglion cells were measured in two wholemounts (#2 and #5, see Table 1) in several regions of the retina: (1) in a region of the highest cell density in the temporal quadrant, where cell density was about 2,000 cells/mm²; (2) in the temporal quadrant, in a region where cell density was 700 to 800 cells/mm²; and (3) in the same quadrant, in a region were cell density was about 200 to 300 cells/mm².

Figure 7 presents frequency vs. size histograms for ganglion cells in these three regions (combined data from two wholemounts; 700 cells for each histogram). In high- and low-density regions, the majority of cell somas were of a size ranging from 10 to 20 μm and from 10 to 25 μm, respectively.

There was some difference between cell size distributions and mean sizes in areas of high and low cell densities. The cells were, on average, smaller in the high-density area (mean 15.2 μm) than in the peripheral low-density areas (mean 18.4 μm). The difference between mean sizes is statistically significant (3.3 ± 0.25 μm SE). The low-density histograms (Figure 7C) featured a main peak and a "tail" of sizes 25 to 37 μm, indicative of a distinct population of large neurons. The high-density histogram was monomodal. Here, the population of large neurons did not manifest itself because of the small number of such cells (Figure 7A).

Discussion

Laminar Organization of the Retina

Laminar organization of the retina in the Steller sea lion basically corresponds to that of terrestrial mammals. Similar to terrestrial carnivores with nocturnal vision, the photoreceptor layer contained predominantly rods; the outer nuclear layer is thick; and the ganglion cell layer contains many small, displaced amacrine cells. On the other hand, there are several specific features similar to that of aquatic mammals—mainly the

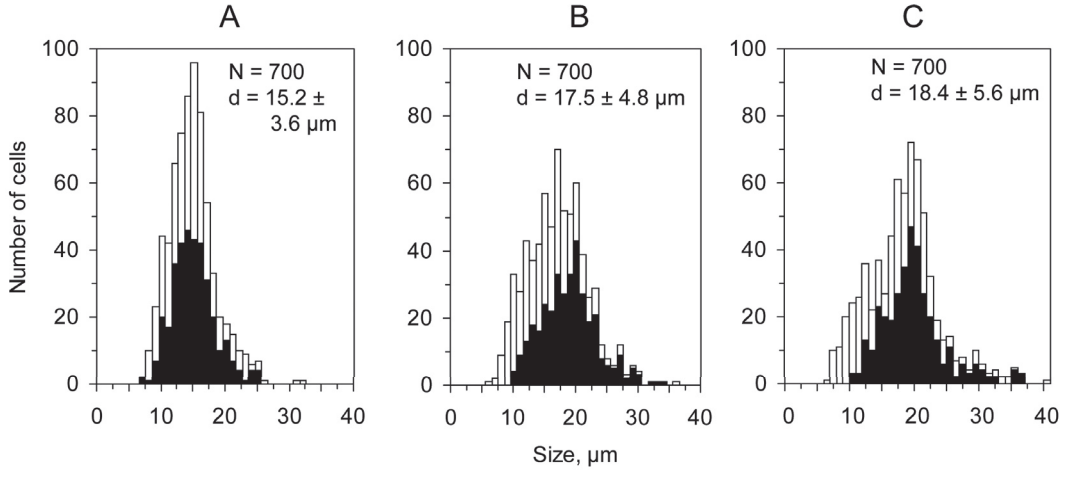

Figure 7. Ganglion cell size distributions in different areas of a Steller sea lion's retina: A – in a high-density area, B – in a middle-density area (temporal quadrant), C – in a low-density area (temporal quadrant); data from wholemounts #2 and #5 are arranged in stacks. Total number of measured cells (N) and means (d) ± SD for the combined histogram are indicated for each of the histograms.

outer nuclear, inner nuclear, and ganglion layers. Chaotic organization of the inner nuclear layer contrasts with terrestrial mammals and is similar to previously studied pinnipeds. Organization of the ganglion cell layer as a single row of rather large, loosely distributed ganglion cells is similar to that of the harp seal (Nagy & Ronald, 1970), fur seal (Mass & Supin, 1992), harbor seal (Jamieson & Fisher, 1971), and Weddell seal (Welsch et al., 2001). All of these species and the sea lion have giant ganglion cells.

Identification of Ganglion Cells in Retinal Wholemounts

Apart from ganglion cells, the ganglion layer of the sea lion's retina contained a significant number of small cells, presumably displaced amacrine and neuroglial cells. To discriminate small ganglion cells from amacrine ones in Nissl-stained wholemounts, we adopted commonly used criteria (Hughes, 1981; Wong et al., 1986; Wong & Hughes, 1987; Wässle et al., 1987). With the use of these criteria, the total number of ganglion cells in the Steller sea lion was estimated at 177,500. This value is a little higher than the 140,000 optic fibers found by Pütter (1903); however, that optic fiber count was not done by electron microscopy and may be an underestimate. We conclude, therefore, that the criteria we used provided satisfactory discrimination of ganglion cells from displaced amacrine and neuroglial cells.

Ganglion Cell Topography

The data presented above demonstrate the presence of a definite area of high ganglion cell density in the retina of another pinniped species, the Steller sea lion. In total, ganglion cell topography has been studied in five pinniped species: the walrus (Mass, 1992), the northern fur seal (Mass & Supin, 1992), the Weddell seal (Welsch et al., 2001), the harp seal (Mass & Supin, 2003), and the Steller sea lion (this study). In all these species, a certain area of high ganglion cell density has been found. It may be suggested that the presence of such an area is a feature of many, if not all, pinniped species.

Several types of this area of high ganglion cell density are known in mammals. Mammals with frontal vision (primates and carnivores) have the fovea or area centralis, respectively. In terrestrial mammals with laterally located eyes, the region of high cell density is shaped as a narrow horizontal strip—the visual streak (Hughes, 1977). The retina of cetaceans has two such areas—one in the nasal and the other in the temporal quadrant of the retina (Dral, 1977, 1983; Gao & Zhou, 1987; Mass & Supin, 1995, 1997, 2002; Murayama et al., 1992, 1995; Murayama & Somiya, 1998). A semiaquatic mammal, the sea otter (*Enhydra lutris*) has a combined area containing both the area centralis and the visual streak (Mass & Supin, 2000). The manatee (*Trichechus manatus*, Sirenia) has no definite area centralis or visual streak (Mass et al., 1997). Previously studied Otariidae and Phocidae pinnipeds, the northern fur seal and harp seal, have a high cell density area similar to the area centralis of terrestrial mammals (Mass & Supin, 1992, 2003), although in the walrus, this area appears as a visual streak (Mass, 1992).

The organization of the high cell density area of the Steller sea lion in terms of location on the retina, shape, and size is similar to the area centralis described in the northern fur seal and the harp seal. Peak cell density in the Steller sea lion's retina (around 2,000 cells/mm^2) is lower than in many terrestrial carnivores—for example, about 4,000 cells/mm^2 in the hyena (Calderone et al., 2003), 7,000 to 10,000 cells/mm^2 in the domestic cat (Stone, 1983; Wong & Hughes, 1987; Williams et al., 1993), up to 16,000 cells/mm^2 in a wild cat (Williams et al., 1993), 6,000 to 14,000 cells/mm^2 in the dog, and 12,000 to 14,000 cells/mm^2 in the wolf (Peichl, 1992). It is probable that the difference in cell density between terrestrial and aquatic carnivores is associated with different eye sizes. The Steller sea lion's eyeball is larger than those of many terrestrial mammals. Therefore, the difference in ganglion cell density is less prominent if it is presented as cells/deg^2, not cells/mm^2: 209 cells/deg^2 in the sea lion versus, for example, 333 to 475 cells/deg^2 in the domestic cat, based on a retinal magnification factor of 218 μm/deg (Pettigrew et al., 1988). These values also are comparable with those in other pinnipeds: the fur seal (125 to 205 cells/deg^2, Mass & Supin, 1992) and harp seal (327 to 495 cells/deg^2, Mass & Supin, 2003).

At the fronto-lateral eye position of the sea lion's eyes, the high cell density area may be located at the vertical meridian (naso-temporal decussation line) of the visual field. This position is characteristic of the area centralis in all terrestrial carnivores (Stone, 1983).

Thus, it may be suggested that the area of high ganglion cell density in the retina of the Steller sea lion in terms of the shape, location, and density of ganglion cells is the true area centralis.

Ganglion Cell Soma Size and Cell Types

In general, ganglion cells in the retina of the Steller sea lion are large. The majority of cells are 10 to 25 μm, and some cells are as large as 37 μm. Similar or larger sizes were found in other pinniped species: in the northern fur seal, ganglion cells were mostly 14 to 28 μm, with the largest cells up to 50 μm (Mass & Supin, 1992); in the harp seal, typical cells were 20 to 30 μm, and some cells were as large as 60 μm (Mass & Supin, 2003). Such cell sizes are not typical of terrestrial carnivores,

which have very few ganglion cells larger than 25 to 30 μm (Fukuda & Stone, 1974; Hughes, 1981; Wong & Hughes, 1987).

The large size of ganglion cells is a distinctive feature of other aquatic mammals—cetaceans, for example. In both odontocetes and mysticetes, cell sizes of 20 to 35 μm are typical, and some cells are as large as 60 μm (Dawson et al., 1982; Supin et al., 2001; Mass & Supin, 2002). There was an opinion that the large size of ganglion cells is associated in a certain way with the aquatic mode of life (Dawson et al., 1983); however, there has been no proof of the nature of this association.

The population of very large ganglion cells (larger than 25 to 30 μm) in pinnipeds deserves special attention. Giant ganglion cells were noticed long before in some pinnipeds—the harp seal (Nagy & Ronald, 1970; Mass & Supin, 2003), harbor seal (Jamieson & Fisher, 1971), and northern fur seal (Mass & Supin, 1992). Their similarity to ganglion α-cells described in the retinas of terrestrial mammals is obvious. The percentage of these cells in the sea lion (8%) is close to corresponding proportions of α-cells described in other mammals (from 1 to 10% in different mammals; Peichl, 1991). The distribution of large cells across the retina (in parallel with that of the total ganglion cell population) in the sea lion is similar to the distribution of α-cell populations in other mammals. So, we intended to estimate the large cells in the Steller sea lion (as well as in other pinnipeds) as typical α-cells.

Thus, the retinal organization of the Steller sea lion exhibits many properties in common with both terrestrial and aquatic mammals in terms of both ganglion cell characteristics and their topographic distribution.

Retinal Resolution and Visual Acuity of the Sea Lion

Data on ganglion cell density expressed in terms of cells per angular unit allow the assessment of the retinal resolution as the angular spacing between ganglion cells.

The mean angular spacing of ganglion cells is $\alpha = 1/\sqrt{d}$, where, α is the angular spacing (deg), and d is the cell's density (cells/deg^2). For d = 209 cells/deg^2 (mean density for all wholemounts in the high-density area), α = 0.069° (4.15'). This value predicts the "minimum visible" measure of the retinal resolution of the Steller sea lion.

Another measure of retinal resolution is the resolvable spatial frequency (cycle/deg):

$F = 1/2\alpha$ (the factor of 2 is because, according to the Nyquist limit, at least two samples are necessary to resolve one cycle of spatial frequency), with α = 0.069°, F = 7.2 cycle/deg.

These values can be adopted as the retinal resolution in the highest-density area. They may be used as an estimate of the visual acuity in water since the angular cell density was calculated for underwater conditions when the nodal point is in the lens center (see "Results"). In air, refraction by the air/cornea surface is added to the refraction by lens. If the eye refraction remains emmetropic (which is possible when either the air/cornea surface is flat or its curvature is compensated by a shorter postero-nodal distance), the retinal image in air should be smaller than in water proportionally to the air-to-water refraction index ratio. This ratio is 1.00 : 1.33 = 0.75. Hence, a retinal image in air should be 0.75 of that in water. Therefore, the angular retinal resolution in air may be estimated as 4.15 / 0.75 = 5.5' or 7.2 × 0.75 = 5.5 cycle/deg.

It should be noted that the calculation presented above is done based on the total ganglion cell population. A possibility cannot be excluded that only a part of the cells really determine the retinal resolution; however, except large α-cells, which constitute a small proportion of the ganglion cell population, we could not separate any other ganglion cell types in the Steller sea lion's retina. So, using the total cell population may be accepted as a preliminary approach that makes possible comparison with other marine mammals.

The obtained estimates of retinal resolution may be considered as estimates of the visual acuity of the Steller sea lion because the retinal resolution is a good predictor of the visual acuity. These estimates are rather similar to those of other pinnipeds—both sea lions and seals. In behavioral studies, underwater visual acuity in Steller sea lions was estimated as 7.5' to 6.5', an average around 7'; in harbor seals, it was 8.3' (Schusterman & Balliet, 1970a). In another sea lion, *Zalophus californianus*, the visual acuity was estimated as 4.7 to 7.0', with an average around 5.5' (Schusterman & Balliet, 1970b). Aerial visual acuity of southern fur seals (*Arctocephalus pusillus* and *A. australis*) was estimated as 6.6' and 7.2', respectively (Busch & Dücker, 1987). Based on ganglion cell density, we estimated the visual acuity of the northern fur seal (*Callorchinus ursinus*) as 4.8' in water and 6.4' in air (Supin et al., 2001). Among the studied pinniped species, only the harp seal has markedly higher visual acuity—3' under water (Mass & Supin, 2003). In the walrus, the visual acuity is worse than in seals—around 8' in water and 10' in air (Mass, 1992). Comparative data on pinnipeds' visual acuity are summarized in Table 2.

Thus, the Steller sea lion has a rather good visual acuity similar to that of most pinnipeds. This acuity also is close to that of terrestrial carnivores: the cat (6 to 9 cycle/deg; Hall & Mitchell, 1991), the dog (6 to 11 cycle/deg; Murphy et al., 1997), and the hyena (8.4 cycle/deg; Calderone et al., 2003). The visual system of the sea lion can be estimated as rather well-developed.

Table 2. Estimates of visual acuity of some pinnipeds (arc minutes)

Species	Water	Air	Mode of measurement	References
Phocidae				
Harbor seal (*Phoca vitulina*)	8.3		B	4
Harp seal (*Pagophilus groenlandicus*)	3.1	4.1	R	3
Otariidae				
Northern fur seal (*Callorhinus ursinus*)	4.8	6.4	R	2
Steller sea lion (*Eumetopias jubatus*)	7.1		B	4
	4.1	5.5	R	6
California sea lion (*Zalophus californianus*)	5.5	5.5	B	5
Southern fur seal (*Arctocephalus pusillus*)		6.6	B	1
Southern fur seal (*Arctocephalus australis*)		7.2	B	1
Odobenidae				
Walrus (*Odobenus rosmarus*)	7.8	10.4	R	2

Modes of measurement: B – behavioral, R – retinal topography

References: 1 – Busch & Dücker, 1987, 2 – Mass, 1992, 3 – Mass & Supin, 2003, 4 – Schusterman & Balliet, 1970a, 5 – Schusterman & Balliet, 1970b, 6 – this study

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