The Distribution of Ganglion Cells in the Retina and Visual Acuity of Minke Whale

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In order to understand the visual ability of baleen whale, the distribution of ganglion cells in the retina of minke whale Balaenoptera acutorostrata was examined. The mean diameter of ganglion cells in the retina of minke whale was 42.9 μm, which was greater than those of terrestrial mammals. The distribution of the ganglion cells in the retina was irregular and two high density areas existed in the temporal and rostral sectors. The rostral and temporal areas of high density seem to be related to side vision and frontal vision, respectively. Cell density measurement gave a visual acuity value of 4 cycles/degree (7 min of arc). This value for the minke whale did not differ greatly from those of other cetaceans and was similar to some terrestrial herbivorous mammals.

Cetaceans spend their lives in water, and they have specifically adapted their visual sense to such an environment. The vision of cetaceans has been studied by several investigators, including Madsen and Herman,13) Pilleri,23) Nachti- gall.3) These studies suggest that the visual sense of cetaceans plays an important role both in the water and in the air during their life. However, there is not as much information available on their visual system as on their auditory system.

The visual ability of the eye is considered to be related to the distribution of ganglion cells in the retina,4) and examination of the distribution of ganglion cells is valuable in comparing visual specialization (e.g. visual streak and area centralis) among different animal species.5) Since the retinal ganglion cells link the eye with the behavioral output, the spatial distribution of the ganglion cells in the retina provides the upper limit of spatial resolving power of the whole animal, that is, the upper limit of spatial resolving power of the eye can be obtained from the interganglion cell distance.6) Based on this theory, studies on the topographic distribution of the retinal ganglion cells and on the estimation of visual acuity have been conducted on a variety of species.4)–13) In the baleen whale, however, little is known concerning the distribution of ganglion cells in the retina, although some morphological studies have been carried out. In order to understand the visual ability of the baleen whale, we examined the distribution of ganglion cells in the retina of minke whale Balaenoptera acutorostrata and estimated the upper limits of visual acuity in the present study.

Material and Methods

We examined two individuals of minke whale (body length: 8.0 and 8.4 m) which had been caught by the Japanese research take in 1989/90.

The right eyes of the individuals were fixed in 10% formalin. After the elimination of the cornea, iris, lens and vitreous humor, the retinae were excised gently from each eyecup in water. Wholemount preparations were made following the protocol of Stone,16) Stone and Halasz4) and Mass and Supin,14) which have generally been used for the investigation of ganglion cells in the retina. Radial cuts were performed near the periphery so that the retinal preparations might lie flat on the object slides. These preparations were glued to slides with the ganglion cell layer upward, and stained with cresyl violet.

The ganglion cells were identified according to generally accepted morphological criteria.8,14,16) The diameters of 120 ganglion cells were measured in 4 regions (Fig. 2) in the retina with an eyepiece micrometer under a light microscope. The number of ganglion cells was counted over the surface area of the retina.

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of the retina at 3 mm intervals in 0.50 mm² squares (Fig. 2), and these counts were converted into the number of cells per 1 mm² square. In analyzing the size and density of the ganglion cells, we did not distinguish the types of ganglion cells as Dral¹⁰ did.

Results

Figure 1 shows the eye extracted from a minke whale. The structure of the eye was similar to that of other mammals. The cornea was transparent and the lens was colorless and slightly elliptical. The retina was observed through the vitreous humor which was transparent and gelatinous.

**Cell Size Distribution of Ganglion Cells**

The diameter of the ganglion cells in the retina of minke whale ranged from 12 to 80 µm and the mean cell diameter for the two whales was 42.9 µm. Figure 3 shows the histograms of ganglion cell size combined from the two whales at each region. The histograms differed slightly from region to region; the histogram for region 1 had a bimodal form while those for regions 3 and 4 had unimodal forms, and that for region 2 was intermediate between the other two forms. The mean diameter varied slightly among regions, for example, the value for region 3 is smaller than the others.

**Topographic Distribution of Ganglion Cells in the Retina**

Figure 4 shows photographs of ganglion cells taken in different areas of the retina. These photographs indicate that the distribution of ganglion cells is irregular in the retina of the minke whale. Isodensity maps of ganglion cells (Fig. 5)
were made on the basis of the density of ganglion cells per 1 mm² area. These maps show that two high density areas (Figs. 5-A, B) existed in the temporal and rostral sectors. In the two individuals examined in this study, the maximum densities of the ganglion cells were 118 and 161 cells/mm² as observed in the temporal area of the retina. This area is considered to be homologous with the “area centralis”. On the other hand, there were few ganglion cells around the optic disk.

Estimation of the Upper Limits of Visual Acuity

We estimated visual acuity according to an earlier protocol as follows.

As the minke whale seems to belong to arrhythmic and crepuscular species that are partially diurnal in their activity patterns and operate in a wider range of luminance than purely nocturnal species, the PND (Posterior Nodal Distance of the eye) is 57% of its axial length, i.e.

\[ \text{PND} = (\text{axial length of the eye}) \times 0.57 \]

The angle (θ) subtending 1 mm on the retina is calculated by

\[ \tan \theta = \frac{1 \text{ mm}}{\text{PND}} \]

\[ \theta = \arctan \left( \frac{1}{\text{PND}} \right)^\circ \]

When the density at area centralis is \( D \) (cells/mm²), linear density is \( \sqrt{D} \) (cells/mm). The spatial resolution can be calculated by obtaining the number of cells subtended by one degree of visual arc,

\[ \text{cells per degree} = \frac{\sqrt{D}}{\theta} \]

The maximum spatial resolution is estimated in cycles/degree, which is half the number of ganglion cells per linear degree.

\[ \text{cycles per degree} = \frac{1}{2} \times \frac{\sqrt{D}}{\theta} \]

In the eyes of the two individuals examined, the axial lengths were 67.0 and 73.0 mm, suggesting PNDs of 38.2 and 41.6 mm. The angles (θ) were 1.50 and 1.38 degrees. Since the maxi-
mum densities (D) of the ganglion cells at "area centralis" were 161 and 118 cells/mm² (see above), the linear densities were calculated to be 12.7, 10.9 cells/mm. Therefore the cells per degree were 8.47 and 7.90 cells/degree, and resolving power values (visual acuity) in the "area centralis" of the two whales were calculated to be 4.24 and 3.95 cycles/degree, respectively. The visual acuity can be estimated also in terms of min of arc by

\[
\text{min of arc} = \frac{60}{2 \times (\text{cycles per degree})}
\]

that is, 7.08 and 7.59 min of arc.

Discussion

The ganglion cells of the minke whale are apparently larger than those of terrestrial mammals such as the cat⁴ (max, 35 μm), rabbit⁵ (7–32 μm), and elephant⁶ (17–37 μm). It is also reported in other cetaceans⁷,⁸,¹¹,¹³,¹⁵ that large ganglion cells are abundant in comparison with terrestrial mammals. It is not clear from the results obtained in the present study whether the difference in the cells size between the minke whale and other animals is due to the difference in the function of the ganglion cells. The histograms for regions 3 and 4 (and perhaps 2) (Fig. 3) have a unimodal form while that for region 1 shows a bimodal form. Dra¹⁰ indicated that there are different types of ganglion cells in the retina. Furthermore, it is reported in several dolphins¹¹,¹⁴,¹⁵ that the cell size histograms of each type of ganglion cell have essentially different but close modes,
while the histograms combined for both types take a unimodal form, which seems to be due to the difference in numbers of cell types. In the minke whale, it also seems that two different types of ganglion cells exist in the retina but that the ratio of abundance of each cell type is different from region to region, that is, the ratios are approximately equal in region 1 and biased to one type in regions 2, 3 and 4. However, it is impossible to decide this since the number of cells and individuals examined here are not sufficient. Further research will be required with a larger sample size.

The presence of two high density areas have been observed in other cetaceans such as the bottlenosed dolphin, common dolphin, harbor porpoise, Chinese river dolphin, and finless porpoise. These horizontally-arranged high-density areas are located at a distance from the geometric center of the eyecup. And in terms of the optic axis of the eye, the frontal part and side part of the visual field are projected on these two areas. Perhaps the rostral high density area is related to side vision and the temporal one to frontal vision. However, since the position of the eye of the minke whale relative to its body axis is unknown, it is not clear whether the temporal one is related to the binocular vision of the whale, as in dolphins and porpoises.

The visual acuity of the minke whale (approximately 7 min of arc) did not differ greatly from that of the bottlenosed dolphin (9.5 min of arc), common dolphin (8 min of arc) and harbor porpoise (11 min of arc), but was quite different from that of the Amazon river dolphin (40–45 min of arc), that is, the acuity is not different from those of oceanic cetaceans. Compared with terrestrial mammals, the visual acuity values obtained in this study are lower than that of the cat (9.1–9.8 cycles/degree) but close to those of the rabbit (4.3 cycles/degree) (reviewed in Pettigrew et al.). Variations in acuity reflect the various foraging strategies of the animals. Minke whale, like oceanic dolphins and some terrestrial herbivorous mammals, do not require a high resolving power in the retina for their lives.

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References