The vision of marine mammals has a number of specific features associated with its ability to function in both water and air. Although many marine mammals (cetaceans, sirenians) spend their entire life in water, their aerial breathing confines them to a near-surface layer of water. Other marine mammals (pinnipeds, some sea otters) spend a significant part of their life on land. As a result, the organization of their visual system fits requirements of both these different media. Although some aspects of organization of the visual system of marine mammals still remain unstudied, many features of their vision are known already.

I. Visual Abilities of Marine Mammals

A. Cetaceans

It was long believed that dolphins—animals with excellent hearing and echolocation—have a poorly developed visual system playing a minor role in their life. However, observations of the visual activity of dolphins have demonstrated the opposite. The ability to catch fish in air, perform precisely aimed jumps to reach targets above the water, and recognize their trainers all show that vision in dolphins is well developed. In conditions of keeping in captivity, dolphins decrease their use of echolocation and, as their interest in events above the water increases, vision takes on a leading role.

Reviews of Madsen and Herman (1980) and Mobley and Helweg (1990) summarized observations of dolphins in captivity and experimental studies which provide a basis for regarding the vision of dolphins as playing an important role in various aspects of their life: in social interactions, discrimination between individuals and species based on their colors and individual marks, the search and discrimination of prey, orientation, reproductive activity, and defense. Only vision provides the ability for rapid and precise assessment of distances to objects in air where echolocation does not operate.

Apart from numerous observations, good visual abilities of cetaceans were demonstrated in behavioral experiments for assessing their visual acuity (Table 1). Precise behavioral measurements (Herman et al., 1975) on the bottlenose dolphin resulted in an estimate of underwater visual acuity of 8.2 arcmin (at the best distance of 1 m) and aerial visual acuity of 12.5 arcmin (at distances of 2.5 m and longer).

Dolphins are equally capable of the perception of complex configurations of objects using both vision and echolocation. Besides, there is also a possibility of intermodal transfer between these two modalities: objects known for a dolphin only by visual appearance can be discriminated and recognized by echolocation, and vice versa. The intermodal transfer is equally successful when visual experience is used for echolocation discrimination and when echolocation experience is used for visual discrimination (Mobley and Helweg, 1990).

Studies of color vision in cetaceans are very few in number. The sensitivity peaks of their photoreceptors are considerably blue-shifted as compared to those of many terrestrial mammals (Jacobs, 1995). Therefore, the dolphin lacks the common dichromatic vision typical of many terrestrial mammals. If color vision is present in dolphins, it is poorly developed and limited to a blue-green region of the spectrum (Peichl et al., 2001; Reuter and Peichl, 2008).

B. Pinnipeds

Because pinnipeds spend their life partially in water and partially on land, they use both underwater and aerial vision. On land, vision plays an important role during the reproductive period, during birth and feeding of pups, and for maintaining intrapopulation relationships, as well as for orientation. In water, vision is used for prey detection and recognition, avoiding predators, and spatial orientation during migrations.

Because of a great diversity of pinniped species in terms of systematic position and ecology, the role of vision diverges widely as well. Walruses (Odobenus rosmarus) rely mainly on their vibrissal sensitivity to identify objects during benthic foraging. Other pinnipeds also have a well-developed vibrissal apparatus; however,
in aquatic conditions, most otariids and phocids (seals and sea lions) use both visual and tactile modalities to search for food. Experiments demonstrated that seals are capable of distinguishing rather small objects visually, recognize the shape of figures, and perform a complex analysis of visual images. Seals are capable of quickly solving rather complex tasks of mental rotation of visually inspected objects and conceptualize complex visual information.

### C. Other Marine Mammals

1. **Sirenians.** Little is known of the visual capabilities in sirenians. A few observations summarized by Piggins et al. (1983) showed that the Amazon manatee (*Trichechus inunguis*) is capable of visually driven behavior, in particular, visual tracking of underwater objects, but has poor underwater visual acuity (Table 1). It remains unknown whether the manatee has an ability of good aerial vision.

<table>
<thead>
<tr>
<th>Species</th>
<th>Water</th>
<th>Air</th>
<th>Mode of measurement</th>
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</thead>
<tbody>
<tr>
<td><strong>CETACEANS (ODONTOCETES)</strong></td>
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<tr>
<td>Bottlenose dolphin <em>Tursiops truncatus</em></td>
<td>8–9</td>
<td>11–12</td>
<td>BR</td>
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<tr>
<td>Short beaked common dolphin <em>Delphinus delphis</em></td>
<td>8–11</td>
<td>15</td>
<td>R</td>
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<tr>
<td>Harbor porpoise <em>Phocoena phocoena</em></td>
<td>11</td>
<td>15</td>
<td>R</td>
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<tr>
<td>Tucuxi dolphin <em>Sotalia fluviatilis</em></td>
<td>25</td>
<td>33</td>
<td>R</td>
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<tr>
<td>Amazon river dolphin <em>Isla geoffrensis</em></td>
<td>40</td>
<td>53</td>
<td>R</td>
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<tr>
<td>Dall’s porpoise <em>Phocoenoides dalli</em></td>
<td>11</td>
<td></td>
<td>R</td>
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<tr>
<td>False killer whale <em>Pseudorca crassidens</em></td>
<td>9</td>
<td></td>
<td>R</td>
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<tr>
<td>Pacific white-sided dolphin <em>Lagenorhynchus obliquidens</em></td>
<td>11</td>
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<tr>
<td>Killer whale <em>Orcinus orca</em></td>
<td>10</td>
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<tr>
<td>Beluga whale <em>Delphinapterus leucas</em></td>
<td>14</td>
<td>19</td>
<td>R</td>
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<tr>
<td><strong>CETACEANS (MYSTICETES)</strong></td>
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<tr>
<td>Minke whale <em>Balaenoptera acutorostrata</em></td>
<td>7</td>
<td></td>
<td>R</td>
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<tr>
<td>Gray whale <em>Eschrichtius robustus</em></td>
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<td>11</td>
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<tr>
<td><strong>PINNIPEDS (PHOCIDS)</strong></td>
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<tr>
<td>Harbor seal <em>Phoca vitulina</em></td>
<td>8</td>
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</tr>
<tr>
<td>Harp seal <em>Pagophilus groenlandicus</em></td>
<td>3.6</td>
<td>4.4</td>
<td>R</td>
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<tr>
<td>Caspian seal <em>Pusa caspica</em></td>
<td>3.5</td>
<td>4.7</td>
<td>R</td>
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<tr>
<td>Baikal seal <em>Pusa sibirica</em></td>
<td>2.4</td>
<td>3.0</td>
<td>R</td>
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<tr>
<td>Largha seal <em>Phoca largha</em></td>
<td>3.5</td>
<td>4.7</td>
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<tr>
<td><strong>PINNIPEDS (OTARIIDS)</strong></td>
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<tr>
<td>Northern fur seal <em>Callorhinus ursinus</em></td>
<td>4–5</td>
<td>5–7</td>
<td>R</td>
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<tr>
<td>Steller’s sea lion <em>Eumetopias jubatus</em></td>
<td>6–7</td>
<td>5.5</td>
<td>R</td>
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<tr>
<td>California sea lion <em>Zalophus californianus</em></td>
<td>5–6</td>
<td>5–7</td>
<td>B</td>
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<tr>
<td>Cape fur seal <em>Arctocephalus pusillus</em></td>
<td></td>
<td>6–7</td>
<td>B</td>
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<tr>
<td>4.7</td>
<td>6.3</td>
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<tr>
<td>Southern fur seal <em>Arctocephalus australis</em></td>
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<tr>
<td>Walrus <em>Odobenus rosmarus</em></td>
<td>8</td>
<td>10</td>
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<tr>
<td><strong>SIRENIANS</strong></td>
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<tr>
<td>Caribbean manatee <em>Trichechus manatus</em></td>
<td>20</td>
<td></td>
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<td><strong>OTTERS</strong></td>
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<tr>
<td>Sea otter <em>Enhydra lutris</em></td>
<td>7</td>
<td></td>
<td>R</td>
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</tbody>
</table>

Visual acuity is presented as minimal resolvable distance in arc minutes. In some cases, a range of variation is indicated (e.g., 11–12 arcmin). Estimates of visual acuity are given for underwater (water) and aerial (air) vision. In the column air, data are not presented when none of the authors attempted to interpret their results in terms of aerial visual acuity. When several estimates of visual acuity in different conditions are available (e.g., in the nasal and temporal best-vision areas in cetaceans, at various illumination conditions, etc.), the best estimate (i.e., the minimal resolvable distance) is selected. Mode of measurement: B, behavioral data; R, data on retinal resolution.
2. Sea Otters. Little is known of the visual abilities of sea otters (*Enhydra lutris*). Inhabiting the coastal zone and feeding underwater, sea otters need to have good vision in both air and water. Observations showed that they actively use vision, and experiments have shown their capability to discriminate objects of different sizes. Quantitative behavioral measurements of their visual abilities are absent.

II. Eye Anatomy and Optics

A. Cetaceans

In all cetaceans, the eyes are positioned laterally, thus providing a visual field as wide as 120–130 degrees and panoramic vision. Although positioned laterally, the eyes are directed somewhat forward and downward (ventronasally). On viewing visual objects in air, the dolphin eyes can move forward by 10–15 mm, so that the visual fields of the two eyes overlap by 20–30 degrees in the frontal sector, giving a basis for binocular vision. However, uncrossed optic fibers have not yet been demonstrated in dolphins. Therefore, the existence of true binocular (stereoscopic) vision (based on interaction of crossed and uncrossed optic fibers) in dolphins still remains under question.

Ocular anatomy in cetaceans is markedly different from that in terrestrial mammals by being adjusted to optical properties of water and to a number of other factors: possibility of eye damage because of high density of water and presence of suspended particles, low temperature and low illumination deep in water, significant light scatter, etc. Characteristic examples of eye structure in cetaceans are shown in Fig. 1. Remarkable features are a thick sclera (especially so in whales, Fig. 1C), a thickened cornea, a highly developed vascular network forming a typical vascular *rete mirabili* which fills a significant part of the orbit behind the eyeball, and massive ocular muscles. All these structures take part in protecting the eye from underwater cooling and mechanical damage.

Unlike terrestrial mammals that have an almost spherical eyeball, in cetaceans the anterior part of the eye is flattened, so that the anterior chamber is small and the eyecup is of almost a hemispherical shape. More precisely, the eyecup shape approximates a segment of a sphere of about 150 degrees of arc (Fig. 1A and B), and its naso-temporal diameter slightly exceeds the dorso-ventral one.

The corneal surface plays very little part in underwater light refraction. Therefore, in cetaceans, light refraction and focusing of an image on the retina are almost entirely performed by the almost spherical lens which provides sufficiently high refractive power. These optics are similar to those in fish, which is not surprising given that in both cases the eye is adjusted to optical properties of the same medium.

In the cetacean eye, the spherical lens is located in such a way that its center almost coincides with the center of the spherical segment of the eyecup. Therefore, light rays coming from any direction are focused almost identically on the retina. This is significantly different from the case in terrestrial mammals, which provides the best focusing on the eye axis.

In terrestrial mammal eyes, accommodation (refraction adjustment to the distance to the object) is performed by change in the shape of the lens due to contraction and relaxation of the ciliary muscle. In cetaceans, spherical lens shape and poorly developed ciliary muscle imply that that accommodation cannot be achieved by changing the lens shape. It has been suggested that accommodation in cetaceans is performed by axial displacement of the lens due to changes in intraocular pressure. Intraocular pressure can change because of contraction of the retractor muscle (*M. retractor bulbi*).

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**Figure 1**  
Schematic presentation of eye anatomy and optics in some cetaceans: (A) the bottlenose dolphin, (B) beluga, (C) gray whale, and (D) Amazon river dolphin. Co, cornea; L, lens; Ir, iris; O, operculum; S, sclera; Ch, choroids; R, retina; ON, optic nerve. Arrows delimit a part of the eyecup that can be approximated by a spherical segment of about 150 degrees.
When the eyeball is pulled back into the orbit, intraocular pressure increases, thus shifting the lens forward; when the eyeball is moved forward, the pressure decreases, shifting the lens backward.

The cornea in cetaceans is thicker than in many terrestrial mammals, and this thickness is not uniform: the cornea is thinner in the center and thicker in the periphery. 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; i.e., the cornea has a shape of a divergent lens. Under water, this lens makes a minor contribution to the total refraction power, as the media on both sides of the cornea (water outside and the anterior chamber liquid inside) have refractive indices rather close to that of the cornea. However, some difference between the refractive indices of water (1.33) and the cornea (from 1.37 in the central part to 1.55 in the periphery) does exist. Thus, the cornea acts as a weak but nonetheless divergent lens (Kröger and Katzir, 2008).

Because most cetacean corneas are similar in shape it is likely that negative refractive power residing in the cornea is a feature typical of cetacean eyes. A negative lens (cornea) combined with a positive lens (crystalline lens) increases the visual field, a feature that may be of importance for cetaceans because the eyes are positioned laterally and deeply inserted into the body.

Adaptation to underwater vision also affects the cetacean iris and pupil. The cetacean vision functions in conditions of wide and rapid changes of illumination when the animal dives from the well-illuminated water surface into the depth where illumination is low. This requires the pupil to react in a wide range of illuminations and to have a wide range of sizes. The cetacean pupil is of an unusual shape. The upper part of the iris has a characteristic protuberance, the operculum. At low illumination, the operculum is contracted (raised), so the pupil, similarly to other mammals, is of a round or slightly oval shape; its horizontal diameter in dolphins is of about 10 mm (Fig. 2A). With illumination increase, the operculum advances downward, turning the pupil into a U-shaped slit (Fig. 2B). At high illumination, the operculum advances so far that the slit becomes closed, leaving only two narrow holes in the temporal and nasal parts of the iris (Fig. 2C). This pupil shape is characteristic of many dolphins and whales, although in several whales the operculum is small. A known exception is the Amazon river dolphin which has a round pupil even when it is constricted.

Another adaptation of the cetacean eye to low underwater illumination is the well-developed reflective layer, the tapetum (Tapetum lucidum). It lies behind the retinal pigment epithelium within the choroid. In cetaceans, the tapetum is formed with extracellular collagen fibrils (Tapetum fibrosum). Multiple reflection of light from 50 to 70 layers of fibrils results in significant light reflection back to the retina, thus increasing visual sensitivity in scotopic conditions. The tapetum is present in all cetaceans. In most of the investigated cetaceans, particularly in mysticete whales, it covers all of the fundus (although varies in coloration), or at least it covers a large dorsal part of the fundus.

In air, refraction on the outer convex corneal surface adds to the lens refraction. The difference of refractive indices of air and the cornea results in significant refractive power of the central, the most convex part of the corneal surface: about 20 diopters. The addition of this refraction to the emmetropic lens refraction should make the cetacean eye catastrophically myopic (near-seeing) in air. Nonetheless, dolphins have good visual acuity in both water and air (Table 1). The solution of the problem is in the presence of flattened (low-curvature) regions of the cornea. A flat corneal surface does not produce additional refraction in air. Even if the surface is not truly flat but a little convex, its refractive power is low enough and may be compensated by some additional mechanisms. Keratoscopic studies in common and bottlenose dolphins showed a “spoon” shape of the cornea with lower curvature in its ventro-nasal and ventro-temporal regions (Dawson et al., 1987).

Aerial myopia can also be partially compensated by accommodative displacements of the lens. For aerial vision, the dolphin eye moves forward thus producing decrease of intraocular pressure; this results in shifting the lens backward and reduced myopia. Additionally, reduction of intraocular pressure decreases the curvature of the cornea. Under water, the eye is retracted into the orbit, which results in increased intraocular pressure and a shift of the lens forward to a position providing underwater emmetropia.

An additional mechanism for the correction of aerial myopia is pupil constriction. Above water, high illumination results in strong pupil constriction; the latter corrects all errors of refraction, including aerial myopia, and provides fairly good depth of focus.

The river dolphins feature additional adaptations to inhabiting turbid low-transparent water. In the Amazon river dolphin (Inia geoffrensis), the lens is yellow, the tapetum lucidum is almost absent. The eyes are more frontally directed than in any other cetacean species. The eyes are small, however fully functional. In the Chinese river dolphin (Lipotes vexillifer, Lipotidae), eyes feature signs of reduction, but seem to be functional.

B. Pinnipeds

Seals and sea lions. In otariid and phocid pinnipeds (seals and sea lions), both the absolute and the relative sizes of the eyeball are large. Eye structure in seals (Fig. 3A and B) and sea lions, despite significant differences from cetaceans, has some common features arising from adaptation to underwater vision (Jamieson and Fisher, 1972). A characteristic feature is an almost spherical or slightly
elliptical lens. Although the eyeball does not appear as shortened in the axial direction, a major part of the eyecup has a shape close to a hemisphere, so a significant part of the retina is almost constantly distant from the lens center. Thus, the eye optics, like in cetaceans, is almost centrally symmetrical. The difference between the eyeball shape in cetaceans and pinnipeds (shorter axial length in cetaceans and longer in pinnipeds) is mainly due to larger size of the anterior chamber in pinnipeds.

The iris in seals and sea lions is very muscular and heavily vascularized. The dilator is well developed. Pupil size can change over a very wide range. Most seals and sea lions have a pupil which being constricted becomes pear-shaped; at bright illumination, it constricts to a very small vertical slit. In shallow-diving species, the range of pupillary area variation is rather small: 26–70.5 times. In a deep diver, the northern elephant seal \(\text{Mirounga angustirostris}\), the pupil area varied within an extremely wide range, from \(422 \text{ mm}^2\) in dark-adapted conditions to a pinhole of \(0.9 \text{ mm}^2\) in light-adapted conditions, i.e., almost 470 times.

The ciliary muscle in pinnipeds is well developed, although accommodation is either absent or weak. However, harbor seal \(\text{Phoca vitulina}\) lenses have been shown to possess multiple focal lengths, which could serve to focus objects at various distances therefore reducing the need for a broad range of accommodation (Hanke et al., 2009).

Unlike cetaceans, the central part of the cornea has a clearly delimited region (6–10 mm in diameter) of almost a flat surface. It is located near the center of the cornea, slightly shifted to the nasal direction (FC region in Fig. 3A and B). Such a flat region of the cornea was found in a number of both seals and sea lions and was demonstrated by precise measurements on the Californian sea lion \(\text{Zalophus californianus}\), Dawson et al., 1987) and harbor seal \(\text{P. vitulina}\), Hanke et al., 2009). The flat region of the cornea serves as an emmetropic “window” in which refraction remains almost equal in both water and air. In the hooded seal \(\text{Cystophora cristata}\), the flattened part of the cornea does not look like a delimited region but arises because of low curvature of the cornea of the extremely large eyeball.

The presence of a flat region in the central part of the cornea indicates a specific principle of eye construction in seals and sea lions. Indeed, the convex shape of the cornea in most vertebrates is a consequence of excessive intraocular pressure, which is necessary for maintaining the shape and size of the eyeball. Direct data on intraocular pressure in pinnipeds are absent, but their flat cornea suggests that this pressure is very low, perhaps about zero.

The tapetum in seals and sea lions is one of the best developed among both terrestrial and aquatic mammals. Contrary to the tapetum fibrosum in cetacean, the tapetum in pinnipeds is formed with intracellular reflective rodlets (tapetum cellulosum). It consists of a large number (20–30 or more) of cell layers and extends from the center of the retina to about the equator of the eye (Jamieson and Fisher, 1972).

C. Other Marine Mammals

1. Sirensians. Both in \textit{Trichechus manatus} and in \textit{T. inunguis} the eye is rather small (15–19 mm in diameter) and is set deeply within the ocular fascia. Its general morphology resembles more that
of terrestrial mammals than the cetacean eye (Fig. 3C). The eyeball is almost spherical (the axial length differs little from the equatorial diameter), the anterior chamber is shallow, and the lens is set forward and is not true spherical: its axial dimension is shorter than the diameter. The nictitating membrane is present. The tear gland is absent, but Harderian gland is well developed. The ciliary muscle is rudimentary such that accommodative changes in focal length of the eye seem not to be possible. A distinctive feature of the manatee’s eye is the vascularized cornea which in all other mammals is pathology. The sclera is rather thin. Thus, despite the completely aquatic mode of life of the manatee, its eye anatomy exhibits a number of conservative features (Piggins et al., 1983). Underwater, the eye is almost emmetropic or slightly hyperopic, but in air it is strongly myopic. It remains unknown whether the manatee has some mechanisms to compensate for aerial myopia; thus, its capability to aerial vision remains unknown.

2. Sea otters. To a large extent, the eyeball of the sea otter E. lutris is similar to those of terrestrial mammals (Fig. 3D): it is almost spherical, axial length is only a little shorter than the diameter. Contrary to spherical lenses of cetaceans and pinnipeds, the sea otter’s lens is lenticular, like that of terrestrial mammals with a comparable sized eye. However, the front surface of the lens has a protuberance of increased curvature. A characteristic feature of the eye anatomy is that the iris is fastened to the frontal lens surface. Therefore, contraction of the iris muscles influences the curvature of the frontal lens surface. This mechanism is capable of providing an accommodation range of up to 60 diopters, thus compensating for the appearance of refraction at the corneal surface in air and its disappearance in water. This accommodation mechanism in the sea otter eye is capable to preserve emmetropia in both air and water.

III. Eye Movements

All dolphins and whales have mobile eyes. However, measurements in the bottlenose dolphin indicated that eye mobility is less than in humans, and eye movements are slower.

Oculomotor muscles are well developed in dolphins and whales; an exception is the Ganges river dolphin P. gangetica, which has reduced eyes and no oculomotor muscles. Other cetaceans have a complete set of muscles known in mammals: four straight and two oblique muscles. These muscles allow eye movements in both the horizontal and the vertical directions. In addition, unlike terrestrial mammals, cetaceans have a retractor muscle (M. retractor bulbi), which produces axial (in/out) movements of the eye in the orbit. The bottlenose dolphin is capable of moving its eye forward to 10–15 mm and pulling it back. As a rule, forward eye movements (protraction) appear when the dolphin visually examines an object in air. These eye movements may be used for binocular examination of objects. As mentioned earlier, the eye protraction in air can also provide accommodation to avoid the aerial myopia.

Another intriguing feature of oculomotor activity in dolphins is the ability to move the left and right eyes independently. Quantitative measurements in dolphins have shown that correlation of movements of the left and the right eyes are very low; i.e., independent eye movements in dolphins are a rule rather than exception.

In addition to independent eye movements, cetaceans have rather independent pupil reflexes of the two eyes. Moreover, eyelids of the left and the right eyes can also function independently, so one eye can be open while the other is closed. Such observations were made during sleep in dolphins, although similar behavior is also possible in wakefulness: dolphins can swim for long periods with one eye open and the other one closed, with the left and the right eye alternating. As to pinnipeds and sea otters, there is no significant difference from terrestrial mammals in their oculomotor muscle anatomy and the character of eye.

IV. The Retina and Optic Nerve

A. Features of the Retina in Cetaceans

The histological structure of the retina has been investigated in a number of both odontocetes and mysticetes (Dral, 1977; Dawson, 1980) and its laminar structure is fully developed in all cetaceans. Even in the Ganges river dolphin with strongly reduced eyes, the retina contains all the layers. Being basically similar in cetaceans and terrestrial mammals, the retina has a number of specific features in cetaceans. It is markedly thicker than in terrestrial mammals, ranging from 370 to 425 μm, whereas in terrestrial mammals, the retina is 110–240 μm thick.

The retinal receptor layer consists predominantly of rods (receptors for achromatic vision). The question of the existence of cones (chromatic-vision receptors) in cetaceans remained debatable for some time. Studies of visual pigments have shown that the cetacean retina does contain cone receptors; however, rods dominate: cone proportion is in the range of 1%–2% (Peichl et al., 2001, Meredith et al., 2013).

Contrary to the majority of terrestrial mammals which have two types of cones with different pigments providing color vision (short-wave sensitive S-opsin and middle-to-long-wave sensitive L-opsin), only cones containing L-opsin with the best sensitivity at 525 nm were found in the cetacean retina (Peichl et al., 2001). S-opsin has not been reported. Rods are best sensitive to 488 nm. These sensitivity peaks are considerably blue-shifted as compared to those of many terrestrial mammals (Jacobs, 1993). Therefore, dolphins lack the common dichromatic vision typical of many terrestrial mammals, which is based on two cone types with different chromatic sensitivity. However, residual color vision limited to a blue-green region of the spectrum may be present in dolphins based on comparison of signals from rods and cones (Griebel and Peichl, 2003). This corresponds to behavioral data showing poor color vision in dolphins.

The inner plexiform layer and the ganglion layer of the cetacean retina feature a marked difference from terrestrial mammals. The ganglion layer looks as a single row of large, sparsely distributed neurons separated by large intercellular spaces. These neurons have large cell bodies with a clearly defined cell membrane, large amount of cytoplasm, a well visible nucleus up to 15 μm in diameter, and clearly defined nucleolus 4–5 μm in diameter. Cell bodies contain clearly visible, well stained Nissl granules.

A remarkable feature of the cetacean retina is large size of ganglion cells, particularly, the presence of giant ganglion cells. Bodies of such cells reach 75–80 μm, sometimes more. Giant ganglion cells were described in a number of odontocetes and in a few mysticetes. In some dolphins, retinal ganglion cells do not feature giant sizes: in the Amazon river dolphin and the Indian river dolphin, they do not exceed 40–42 and 20 μm, respectively. However, even these cells are large as compared to those in many other mammals. The smallest ganglion cells in cetaceans are as large as 10 μm.

There is presently no satisfactory explanation why ganglion cells in the cetacean retina are so large. One of possible explanations is that large ganglion cells have thick axons with high velocity of conduction; in a large body, it may be helpful for fast transmission of
B. Features of the Retina in Pinnipeds

In general, the retinal structure in pinnipeds is the same as in terrestrial mammals. All layers are present in the pinniped retina, although there are a number of specific features, mainly of the outer nuclear, inner nuclear, and ganglion layers (Jamieon and Fisher, 1972). The very thick outer nuclear layer is characteristic of many pinnipeds. The inner nuclear layer does not have clear margins, in contrast to terrestrial mammals, where this layer is strictly ordered. There are large horizontal cells with very long processes within this layer. The giant horizontal cells are located irregularly among bipolar and amacrine cells, which are also distributed chaotically. Bipolar cells are located mostly in the outer part of the inner nuclear layer while large amacrine cells are located close to the inner plexiform layer.

The ganglion layer in pinnipeds consists of a single row of ganglion cells separated by wide intercellular distances. Ganglion cells have large pericaria, a large amount of Nissl substance in the cytoplasm and long dendrites. Most of these cells are of intermediate size (10–30 μm), although large cells (up to 50 μm) are also encountered.

All pinnipeds have a predominately rod retina. The question of existence of cones has been a matter of discussion for a long time. However, light and electron microscopy have shown the presence of cones in the harbor seal and harp seal, although photoreceptors of this type are not numerous. Immunohistochemical studies in a few pinniped species demonstrated that their retinas contained sparse populations of cones, constituting 1%–2% of photoreceptors (Peichl et al., 2001). However, these studies revealed only one opsin type in the cone receptors, the middle-to-long-wave sensitive L-opsin and did not reveal the short-wave sensitive S-opsin. This feature is common with cetaceans and distinguishes pinnipeds from the majority of terrestrial mammals that have at least two spectrally sensitive cone types (middle- and short-wave sensitive) or three cone types in primates. The existence of some amount of cones corresponds to behavioral data showing a limited capability of color discrimination in pinnipeds.

The best rod sensitivity in the harbor seal (P. vitulina) was found at 495 nm, and cone sensitivity at 501 nm; i.e., similarly to dolphins, the spectral sensitivity is blue-shifted as compared to terrestrial mammals.

C. Optic Nerve Structure in Cetaceans

Retinal ganglion cells send their axons into the optic nerve. Consistent with the large sizes of ganglion cell bodies, the axon diameters in cetaceans are also greater than in terrestrial mammals. In a variety of dolphin species, a significant proportion of optic fibers exceed 15 μm in diameter. For comparison, the maximum fiber diameter in cats and in monkeys is no more than 8 μm. The only exception is the Chinese river dolphin L. vexillifer, which has thin optic fibers, although its retina contains ganglion cells as large as 75 μm.

The low density of ganglion cells in the retina of cetaceans corresponds to the low density of fibers in the optic nerve. In cross sections of the optic nerve of dolphins, the density of fibers is less than 50,000/mm², whereas in monkeys it exceeds 220,000/mm². Although the optic nerve in cetaceans is of a large diameter, the total number of optic fibers does not exceed that in many terrestrial mammals. More than 50% of the cross-section area of the cetacean optic nerve is occupied by intercellular space (contrary to 12%–20% in terrestrial mammals), not by glia. The smallest number of fibers (14,000–16,000) was found in the Indian river dolphin, P. gangetica, and the Amazon river dolphin, I. geoffrensis; the number of optic fibers in the Chinese river dolphin L. vexillifer is a little higher, more than 20,000. In the bottlenose dolphin, the number of optic fibers is 150,000–180,000. Other odontocetes have a number of optic fibers similar to that in the bottlenose dolphin. In mysticetes, the number of optic fibers is within a range of 250,000–420,000. The pygmy sperm whale Kogia breviceps seems to be a special case. It has more than 1 million axons in the optic nerve.

D. Optic Nerve Structure in Pinnipeds

The studied pinniped species—four species of seal and one species of sea lion—have 100,000–200,000 nerve fibers in the optic nerve (Putter, 1903). For comparison: the domestic cat also falls in this range. An exception among pinnipeds is the southern elephant seal M. leonina. It has about 750,000 fibers in optic nerve, which is in the same range as in humans.

In the walrus, the number of optic fibers is close to 100,000 (Putter, 1903).

E. The Retina of Other Marine Mammals

Sireniens. The retina of the manatees also features the common laminar organization. In contrast to cetaceans and pinnipeds, the herbivorous sirenians have diurnal retinas: receptors are presented by mostly rods and a significant proportion of cones, which provide for dichromatic color vision. Among specific features, the large size of ganglion cells can be mentioned: up to 60 μm, mostly 15–30 μm, and not less than 10 μm. Thus, the large size of ganglion cells seems to be a common feature of several groups of marine mammals.

Sea Otters. In the sea otter, the retina has many features similar to those in terrestrial rather than in aquatic mammals. Rods, middle/long-wavelength sensitive (M/L) cones, and short-wavelength sensitive (S) cones are present in the retina of sea otter. The majority of ganglion cells are not of large size: 7–30 μm, mostly 11–15 μm. The retina of the sea otter contains a large number of small amacrine and neuroglial cells.

V. Retinal Topography and Visual Field Organization

A. Retinal Topography in Cetaceans

The cetacean retina does not have avascular areas that would indicate the presence of fovea or area centralis. Therefore, visual examinations of the eye fundus are not capable of revealing such regions. Studies of retinal wholemounts have shown that different regions of the cetacean retina have different densities of ganglion cells (Fig. 4A and B). Beginning from the pioneering studies by Dral (1977), studies of cetacean retinal wholemounts were performed in a number of dolphin species (see detail Supin, et al., 2001). These complement work on terrestrial mammals, reviewed by Hughes (1977), that show high densities of ganglion cells in one central area, the fovea, or in a narrow horizontal strip, the visual streak.

Unlike terrestrial mammals, all marine dolphins have not a single area of high ganglion cell density but two such areas. These areas are located near the horizontal diameter of the retina, one in the nasal and the other in the temporal sector (Fig. 4A). In the bottlenose dolphin, both these areas are located at a distance of 50–55 degrees of the visual field from the optic disk. Ganglion cell density in each of these areas is 700–800 cells/mm², which corresponds to 40–50 cells per squared degree of the visual field (cells/deg²).
The two high-density areas are connected by an elongated zone of increased, although somewhat lower, cell density, which runs below the optic disk; this zone looks like a visual streak. In other dolphin species, the retinal topography is basically similar to that described above: there are two areas of high ganglion cell density. Even at low cell density in some cetaceans inhabiting turbid and low-transparent water (the tucuxi), the retinal topography looks the same (Fig. 4B). However, some quantitative differences do exist. In the bottlenose dolphin, the ganglion cell density is almost equal in the two areas, the nasal and the temporal ones, whereas in the harbor porpoise, the cell density in the temporal area (i.e., the region serving the frontal visual field) is higher than in the nasal region: 28 and 20 cells/deg², respectively.

The retinal topography of ganglion cells was studied in two mysticete species: the gray whale (Eschrichtius robustus) and minke whale (Balaenoptera acutorostrata). Both of them also have ganglion cell distributions with two areas of high cell density, in the nasal and temporal segments (Fig. 4C). Again, the cell density in the temporal area is slightly higher than in the nasal one: 28 and 21 cells/deg² in the gray whale.

The significance of the two areas of high ganglion cell density (i.e., of high retinal resolution) is supposed to be associated with the cetacean’s capability of good vision both above and under water, in particular, with preventing aerial myopia. The high-resolution areas are located just opposite the two small pupil holes formed when the pupil is constricted in air (see Fig. 2). Because of the centrally symmetric optics of the cetacean eye, light falls onto each of these areas through the opposite hole of the pupil. The areas of the cornea with minimal curvature are located across from these narrow pupil holes. Both the pinhole pupils and the low cornea curvature are devices to prevent aerial myopia. Thus, images are projected onto the high-resolution areas of the retina with minimal distortions.

The two high-resolution retinal areas in cetaceans may be used differently for underwater and aerial vision (Supin et al., 2001). When a dolphin looks at an underwater object, it takes a position lateral to the object; i.e., the object is placed into the posterolateral part of the visual field, which projects onto the nasal high-resolution area of the retina. On the contrary, when a dolphin looks at an object above water, it places the object into the ventronasal part of the visual field, which projects onto the temporal high-resolution area of the retina. Of course, the temporal high-resolution area of the retina also participates in underwater vision. This area serves the frontal part of the visual field, which is important for forward-moving animals. The existence of two high-resolution areas of the retina can also compensate for limited head mobility in many cetaceans. At low head mobility, even at high mobility of the eyes, a single high-resolution area allows the animal to inspect only a

![Figure 4](image-url)
limited part of the surrounding space, whereas two such areas can provide almost panoramic vision.

The retina of the Amazon river dolphin is a special case. The visual system of this species is adapted to inhabiting low-transparent turbid water where vision is possible only at short distances. Contrary to all other investigated cetaceans, the retina of the Amazon river dolphin has only one area of higher ganglion cell density. However, this single area is located not in the center or temporal sector, but in the lower part of the retina, i.e., in the region responsible for the upper part of the visual field (Fig. 4D). In turbid low-transparent water, significant illumination exists only near the water surface, i.e., in the upper part of the visual field of a normally oriented animal. Just this part of the visual field is served by the ventral part of the retina where the Amazon river dolphin has higher retinal resolution. The density of ganglion cells in this region reaches 500 cells/mm², with the small size of the eyeball, this corresponds to a cell density of about 2 cells/deg².

B. Retinal Topography in Pinnipeds

Several otariid and phocid species have been subjects of studying the ganglion cell topography in retinal wholemounts (Mass and Supin, 2007; Supin et al., 2001). The shape and position of the high-density area in the retinas of all investigated pinniped species indicate its close similarity to the area centralis of terrestrial carnivores. The area centralis is located at a distance of 35–40 degrees from the visual field center (Fig. 5A); at the frontal position of the eye in orbit, this place is a projection of the vertical meridian of the visual field. Thus, the position of the area in otariids is similar to that in terrestrial carnivores. Cell density in this area reaches 1000–3800 cells/mm², which corresponds to 160–630 cells/deg².

Among otariids, a definite area centralis was found in the fur seal (C. ursinus) and Steller sea lion E. jubatus; among phocids, it was found in the harp seal (P. groenlandicus) and Baikal seal (P. sibirica). The harbor seal (P. vitulina) and Caspian seal (P. caspica) have the high-density area as a naso-temporal streak with a well-defined spot of the highest cells density (the area centralis) within the temporal part of this streak.

Quite different is the retinal topography in the walrus. The area of increased ganglion cell density is not defined as clearly as in otariids and phocids. It looks like a horizontally extended oval, resembling the visual streak of terrestrial mammals (Fig. 5B). Within this streak, the highest cell density in its temporal part exceeds 1000 cells/mm²; because of a smaller size of the walrus eye, this cell density corresponds to about 50 cells/deg².

C. Retinal Topography in Other Marine Mammals

Sireniens. Ganglion cell distribution in the manatee retina presents an example of low specialization. There is no sharply restricted spot of cell concentration. Ganglion cell distribution is not uniform but varies smoothly across the retina: cell density is higher in a central part of the retina (except the nearest vicinity of the optic disk) and diminishes toward edges (Fig. 5C). The highest
cell density is about 250–300 cells/mm²; for a rather small manatee eye, this corresponds to 6–7 cells/deg².

Sea otters. In the sea otter retina, ganglion cell topography (Fig. 3D) has a number of features similar to those of terrestrial mammals. The high-density area resembles a naso-temporal streak which in its temporal part contains a narrow and well-defined spot of the highest cells density which is similar to the area centralis in terrestrial mammals. The highest ganglion cell density in the sea otter exceeds 4000 cells/mm²; in the rather small eye of the sea otter, this corresponds to 50–60 cells/deg².

VI. Conclusions

In general, the visual system of marine mammals demonstrates a high degree of development and performance; in particular, good visual acuity, capabilities to precisely aim visually driven behavior and intermodal transfer, and well-developed visual brain centers. This system also exhibits a number of specific features associated with adaptation to both aquatic and aerial environment; in particular, specific retinal topography (positions of best-vision areas) along with pupil and cornea structure which provide emmetropia in both air and water.

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References


