SOME COMMENTS ON THE OPTICAL SYSTEM OF PINNIPEDIA AS A RESULT OF OBSERVATIONS ON THE WEDDELL SEAL (*Leptonychotes weddelli*)

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ABSTRACT. Clear vision in air and water requires special adaptations in the optical system of the eye. The cornea of the seal is flattened in the meridian corresponding to the long axis of the slit pupil, and it is believed this allows a sharp retinal image to be formed when the eye is in air. The Weddell seal was examined by means of measurements of refractive error and corneal moulds, and it is concluded from the results that the original explanation for astigmatism in seals applies equally to the Antarctic species.

RECENT studies in the visual ability of marine mammals (Schustermann and others, 1965; Baldwin, 1966; Hobson, 1966) have indicated a dearth of information on anatomical and physiological aspects of their optical system. None of the Antarctic Pinnipedia have been studied from this aspect and it is with the refractive mechanism of the Weddell seal eye that the experimental side of this paper is concerned.

It is to be expected that the eyes of seals will show some adaptation to the aquatic environment in keeping with changes in other parts of the body. The naso-lacrimal canal, which in a wholly terrestrial mammal would prevent tears from spilling over the edge of the lids, has disappeared. The similarity in refractive index of water and corneal tissue has occasioned the development of an almost spherical lens to compensate the optical loss of the cornea underwater. But perhaps the most interesting adaptation is that of astigmatism, first mentioned by Johnson (1893). He found that the eye of the common seal (*Phoca vitulina*) had a refractive error (from an anthropomorphic viewpoint) in air of −4·0 dioptres in the vertical meridian and −13·0 dioptres in the horizontal meridian, that is to say that the eye is myopic in all meridians, but least so in the vertical and most in the horizontal. With the seal immersed in water, however, the refractive error disappeared and it was justifiably assumed that the cornea was responsible for the astigmatism. Later, Johnson (1901) reported that astigmatism of the same type was found in *Otaria jubata* (= *Eumetopias jubatus*) and, as Matthiesen (1893) had already found a lower degree in the whales, he concluded that this must be a characteristic of marine mammals.

Walls (1942) enlarged on earlier interpretations of this refractive error, pointing out that the meridian in which it is lowest corresponds to the direction of the very narrow slit-pupil. The optical properties of this pupil can be related to those of a pinhole or, more exactly, what is known as a stenopaic aperture. The stenopaic aperture is a thin slit sometimes used in the investigation of astigmatism or irregular errors in refraction in the human eye. If it is rotated while the eye looks through it, objects might be found to appear sharper at one position than any other, and obviously this position would represent the meridian in which the refractive error was lowest. In the seal the slit-pupil corresponds to the stenopaic slit and its axis lies along the meridian of the eye where the refractive error is least, and therefore prevents rays from passing through which are likely to interfere with the quality of the retinal image.

The slit-pupil in conjunction with the corneal astigmatism were considered as adaptations to produce useful vision in air; in water there was no refractive error and the size of the pupil would be determined by conditions of illumination.

The purposes of this investigation were: first, to confirm the presence of astigmatism in the Weddell seal; secondly, to examine the curvature of the cornea and hence the power by means of corneal moulds; thirdly, in the light of these experiments, to re-assess the significance of the unusual characteristics of the optical system.

METHOD AND RESULTS

All measurements were made as soon as possible after the death of the animal, usually within 30 min. The cause of death was an overdose of Sernylan, nicotine or succinylcholine chloride, the drug being administered with a "Cap-Chur" pistol. Measurement in life was not found to be practicable, particularly in the case of corneal moulds where access to the large cornea is hindered by the nictitating membrane and small palpebral aperture.

Several hours after death the cornea lost its turgidity due to seepage of aqueous humour away from the eye. Care was therefore taken to transport the head to the laboratory quickly so that measurements could be completed before the onset of this *post-mortem* change. The eyes were not excised, but small parts of the lids and nictitating membrane were removed to expose the pupil for retinoscopy and ensure a means of approach to the cornea for moulding.

Refractive error

Method. A Hamblin Streak retinoscope was used to assess the refractive error; this technique is well known in its general application in ophthalmic optics and ophthalmology and will not be discussed here in detail. Standard lenses of values +10·0, +8·0, +4·0, +2·0, +1·0, +0·5, +0·25, and −10·0, −8·0, −4·0, −2·0, −1·0, −0·5, and −0·25 dioptres were mounted singly or sometimes in pairs close to the eye being measured. When a value near to the refractive error was obtained, fine adjustments were made by the observer moving the retinoscope and his eye towards or away from that of the seal. The recognition of astigmatism required measurement of the error along the two principal axes and the recording of the orientation of these axes. The magnitude of the refractive error was calculated from the power of the lenses mounted in front of the eye being tested, and the distance of the eye of the observer from these lenses.

The head was then immersed in sea-water so that the cornea was just covered and the procedure was repeated.

Results. In Table I the refractive error when the eye is in air is shown on the left, and that when immersed in water on the right. Measurements are in dioptres. The error is given along the two principal meridians "A" and "B", which are always at right-angles. The orientation of the meridian "B" is shown in brackets and it is referred to the slit-pupil so that an axis of 90° represents the direction of the long axis of the pupil, that is, almost vertical. A direction of 0° would represent the short axis of the pupil, that is, almost horizontal. Following the practice used in studies of the human eye, these angles are measured in an anti-clockwise direction facing the eye (Fig. 1). Where the error is given only for "A", it is to be understood as spherical in nature, and hence equal in all meridians. In the cases where no reading is shown in air the cornea had deteriorated, making the measurement impossible.

TABLE I

	Left or right eye	*Air*		*Water*	
		"A" (dioptres)	*"B"* (dioptres)	*"A"* (dioptres)	*"B"* (dioptres)
1	L			+1·0	
	R			+0·5	
2	L	−19·5	−13·0 (90°)	0·0	+0·5 (135°)
3	L	−14·5	−10·0 (90°)	−0·5	
	R	−13·0	− 7·0 (60°)	+1·0	+2·5 (90°)
4	L	−15·5	− 8·0 (90°)	−1·0	
	R	−20·0	−11·0 (90°)	−1·5	0·0 (135°)
5	L	−15·0	− 3·0 (90°)	0·0	+1·0 (180°)
	R	−14·0	− 2·5 (90°)	0·0	+2·0 (180°)

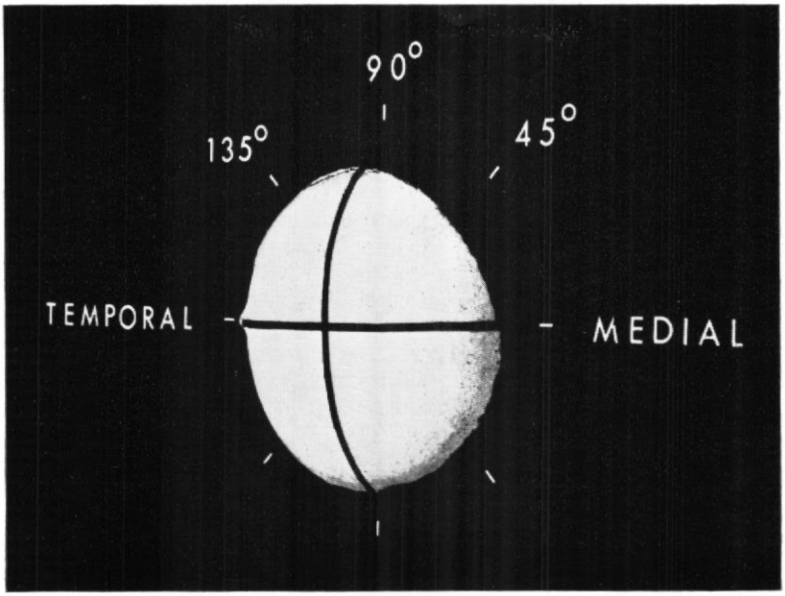

Fig. 1. Mould of the cornea (right eye) showing the axes corresponding to the profiles in Fig. 2.

Casts of the cornea

Method. After the measurements of refractive error had been completed an impression was made of the cornea. A moulding technique was chosen as being the most suitable for study of the cornea in the Antarctic, since it allowed a permanent record to be preserved for study at a later date. The materials employed are in current use in contact lens practice and no change was made in their method of preparation. The impression material was contained in a watch-glass and while still fairly soft inverted over the eye. Once set, the mould was removed and a permanent positive cast prepared with "K.D." plaster.

A match stick, if rested on the crest of the jugal bone and directed towards the centre of the pupil, was found to be parallel to the upper palate, and also at right-angles to the long axis of the pupil when the eye is viewed from in front. It was convenient to define this as the horizontal meridian (0°) of the eye. Thus, a match stick positioned on the eye before commencing the moulding procedure, served as a guide to the orientation of the mould, and of the eye in relation to the bone structure.

Results. The casts were interpreted using a shadowgraph—an instrument which projects a magnified profile of an object on to a screen. Profiles were obtained at 15° intervals, from 0° to 165°; 180° would repeat the same meridian as 0°, and 195° the same as 15° and so forth, there being no necessity to duplicate these. These profiles were drawn on a large sheet of paper at a magnification of ×10 and from them the corneal curvature was estimated using templates of various radii specially made for the purpose.

As would be expected from knowledge of the human eye, a section of the seal cornea is not a perfect arc of a circle, the curve being flattened towards the periphery. In this case it was only possible to fit the circular templates to a central region of the cornea approximately 15 mm. long. As the pupil would be considerably less than this in aerial vision in normal illumination, no other part need be considered. The average radius of curvature of nine eyes, each with 12 meridians measured, was 25·6 mm. In any one eye the greatest difference in radius, from maximum to minimum, was 6 mm. (23 mm. to 29 mm.) and the average difference in nine eyes was only 1·9 mm. The significance of this will be discussed later.

Refractive index

The refractive index of the cornea was measured using a Bellingham & Stanley pocket refractometer in conjunction with a sodium light source. This was found to be 1·376, the same as that given by Gullstrand for the human eye. This field of investigation was not pursued further as the results were not unique, although it can be noted that the aqueous and vitreous humours were also the same as in Man (1·336).

Discussion

The refractive error results demonstrate astigmatism and myopia in the Weddell seal. This astigmatism varies between 4·5 and 12 dioptres and, in six of the seven eyes examined, it was such that the lowest refractive error was in the vertical meridian. Immersed in water, the eye shows low hypermetropia or myopia, with low astigmatism of variable axis, suggesting that in water the average condition is close to emmetropia.

If the astigmatism is calculated from the radii of the cornea and the refractive index, it is seen that the variation in radius is not enough to account for the high astigmatism measured with the retinoscope. With a refractive index of 1·376 for the cornea, the power of this surface for various radii is given in Table II.

Table II

Radius (mm.)	*Power* (dioptres)
22	15·0
23	14·5
24	14·0
25	13·5
26	12·8
27	12·3
28	11·9
29	11·5
30	11·1
31	10·7
32	10·4

It will be recalled that the greatest variation in radius in any eye was from 23 to 29 mm., and it can be seen that this will only produce a difference in power of 3·0 dioptres, not enough to explain the 4·5 to 12 dioptres encountered with the retinoscope. Yet, as has been pointed out by other writers, the astigmatism almost disappears on immersing the eye in water and therefore resides in the cornea. Fig. 2 shows the presence of a flattened area in the upper temporal region, which, although small, would have a marked effect on the optical system if rays passing through it were to reach the retina. A flattening of this nature was found on several of the moulds, but not always in the same region of the cornea. The small area covered by this flattening, and the critical juxtaposition of it and the pupil, make it difficult to establish a quantitative relation between calculated refractive error and that obtained from the retinoscope. It does seem possible, however, that the astigmatism is not due to a systematic variation in radius involving the whole cornea, but rather to a small local flattening.

Although expressed in greater detail, these results agree with the findings of Johnson working with the common seal and the Californian sea lion. Using a net, muzzle and several

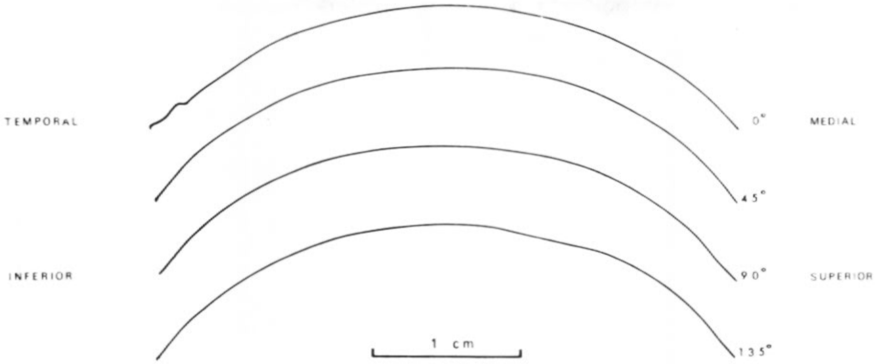

Fig. 2. Profiles obtained from a corneal mould using a shadowgraph.

helpers, he managed to get close enough to assess the refractive error with an ophthalmoscope and a retinoscope. Out of water, he found this to be −4·0 dioptres in the vertical and −13·0 dioptres in the horizontal, but unfortunately we are not told whether he found similar individual variation to that described in this paper.

Successful measurements have also been recorded for other aquatic mammals; Cetacea have 3·9 to 4·5 dioptres of astigmatism (Matthiesen, 1893), that is, less than in the Pinnipedia, and they differ also in that the meridian of least power and the long axis of the slit-pupil are in the horizontal. Both the seal and whale cornea when viewed from in front are elliptical with the major diameter in the horizontal, though the difference between the horizontal and vertical diameters is more pronounced in the whale. Considering the form of the cornea, it is to be expected that where the cornea is broadest its radius of curvature will be large, and conversely where the cornea is narrow the radius of curvature will be less. This would result in the vertical meridian being the most steeply curved and hence the most powerful optically, which is the condition as it obtains in the whale. In the seal, as has been shown, the horizontal is the most powerful and for this reversal to occur in a cornea which is horizontally elliptical must require local architectural adjustments to the curvature. The constant relation in seals and whales of the slit-pupil to the flattest corneal meridian suggests that the interdependence of these two structures plays an important role in the optics of the eye. As the optical function of the cornea is negligible in water, it is tempting to consider these adaptations in terms of aerial vision, but caution must be observed in pronouncing any one characteristic as an adaptation to air when so many gross morphological and physiological changes are obviously referable to an aquatic environment.

The otter (*Lutra*), in vision and other aspects, shows fewer adaptations to water. It is emmetropic in air and compensates for the loss of power of the cornea underwater by means of a large amplitude of accommodation. Nevertheless, in this technique it would not appear to be fully successful (Gentry and Peterson, 1967) as the sea otter (*Enhydra lutris*) has been found to have less effective underwater vision than the seal or porpoise. Thus the problem of precise vision in both air and water has not been solved in the same manner by all the aquatic mammals; the otter is emmetropic in air and a strong ciliary muscle enables the eye to increase in power sufficiently to compensate the optical loss of the cornea when the eye is in water. On the other hand, the seal and probably the whale are emmetropic in water and modifications of the corneal curvature and pupil reduce the increase in power which would normally occur when the eyes are brought out of water thus preserving to some extent the quality of the retinal image.

If the sharpness of the retinal image influences visual acuity, it is not the only factor and the quality of the mechanism available for the interpretation of this image must also play a part. Observations have demonstrated that generally the two types of photoceptor, rods and cones, are concerned with vision under different conditions. Cones are associated usually with colour vision and perception of detail in good illumination, whereas rods are associated with perception in low illumination, particularly of movement. The seal retina is believed to be rod-dominated (Walls, 1942) but there is scope for further verification of this as the whale was held to be without cones until this belief was challenged (Mann, 1946). Certainly, consideration of the habits of the seal would not suggest a necessity for well-developed cone vision, and attempts to elicit colour awareness have been unsuccessful (Baldwin, 1966). A reflecting structure, called the tapetum, which increases sensitivity in low illumination, is prominent in seals and must be particularly useful in the case of the Weddell seal which feeds in deep water and must spend much of the winter in the gloom beneath the Antarctic sea ice.

In regions other than certain parts of the Arctic at least, there are no land predators and the demands on vision in air are probably not great: the reconnaissance of possible landing places, the avoidance of obstacles between the sea and breeding sites, and perhaps some contribution to the organization of breeding colonies. Probably social breeding demands recognition of some visual as well as auditory signals, though this varies widely throughout otariids and phocids, and in the grey seal for example successful mating, parturition and lactation has been observed in totally blind cows (personal communication from E. A. Smith). An adequate optical system is therefore provided by a slit-pupil in connection with corneal flattening to reduce myopia. Nonetheless, the main function of the pupil must be the protection of the sensitive retina made doubly vulnerable to strong illumination by the addition of a tapetum.

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