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# Visual fields and eye movements in a harbor seal (*Phoca vitulina*)

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## Abstract

The boundaries of the visual fields of a harbor seal were measured using static perimetry. In the seal lying on a plane surface (fixation point “0°” straight ahead at eye-level), the visual field with fixed eyes extended over 208° horizontally and reached from –12° to +69° vertically. The binocular visual field amounted to 67°. Eye movements of 12° ( $\pm 2^\circ$ ) to both sides and 64° upwards could be induced. In the seal performing eye movements, a visual field of 210° in the horizontal plane and 121° to the dorsal side was determined. From the measured eye movements, a visual field of 232° in the horizontal plane appears possible.

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*Keywords:* Harbor seal; *Phoca vitulina*; Visual field; Eye motility; Perimetry

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## 1. Introduction

Harbor seals (*Phoca vitulina*) are amphibious carnivores that feed on pelagic and benthic fishes, mollusks, and crustaceans. Although water conditions may frequently limit vision in foraging seals (Dehnhardt, Mauck, & Bleckmann, 1998; Dehnhardt, Mauck, Hanke, & Bleckmann, 2001; Schusterman & Balliet, 1970; Weiffen, Möller, Mauck, & Dehnhardt, 2006), their large and highly sensitive eyes give evidence that vision might play an important role in orientation (Dehnhardt, 2002; Levenson & Schusterman, 1997, 1999). The visual spatial resolution of harbor seals underwater was found to lie between 5 and 13 min of arc (Schusterman & Balliet, 1970; Weiffen et al., 2006) and compares well with that of land-living carnivores in air. There are, however, no data on the size of the visual fields and eye movements of harbor seals or any other marine mammal.

Visual fields comprise the cyclopean visual field, the monocular visual fields, the binocular visual field and the dynamic visual field. The first three refer to the space that the animal can survey without moving its eyes, head or body. Under these conditions, the cyclopean visual field

is the whole space from where visual stimuli can be perceived; the right (left) monocular visual field is the space from where stimuli can be perceived using the right (left) eye only, and the binocular visual field is the intersection of the two monocular visual fields. The dynamic visual field, also known as the combined field of fixation and field of view, is the space that an animal can survey without moving its head or body, but with the help of eye movements.

The visual fields of an animal can be assessed by directly viewing the ocular fundus and the extent of the retina, e.g., with an ophthalmoscope mounted to a perimeter (Martin, 1984, 1986; Martin & Young, 1983), or in behavioral experiments (e.g., Harwerth, Smith, & DeSantis, 1993). While measurements with an ophthalmoscope are the most accurate method to determine the absolute boundaries of the visual field (Hughes, 1977), i.e., the maximum angles under which some kind of visual stimulus can be perceived, they provide no information about differences in sensitivity or resolution across the retina. A detailed description of the effective visual field and the thresholds of perception can only be obtained in a psychophysical experiment (Timney & Macuda, 2001).

While Walls (1963) stated that harbor seals have only “little eye mobility,” we observed significant lateral and especially dorsal eye movements in harbor seals kept in

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our research facilities. As the visual fields of an animal are important parameters of its visual orientation, we determined the boundaries of the visual fields of a harbor seal using static perimetry. Maximum eye movements that could be induced were calculated from video recordings by the change in the pupil's position or the flattened area of the cornea, respectively.

## 2. Materials and methods

### 2.1. Experimental animal

The experiments were carried out with an eleven-year-old male harbor seal ("Sam") kept in our Marine Mammal Research Laboratory at Zoo Cologne, Germany. Prior to this study the seal served as subject in experiments on visual acuity, eccentric photorefractive, and auditory sensitivity. The experiments were in accordance with the guidelines for treatment of experimental animals established by the German animal protection law.

### 2.2. Experimental chamber

To guarantee a reproducible background illumination, all experiments were carried out in an experimental chamber (380 × 180 cm, 140 cm high) built on the land part adjacent to the experimental pool. The experimenter and the test animal could enter this chamber through a folding-door at its front side. In addition, the entrance was equipped with an opaque plastic curtain that allowed darkening of the experimental chamber while the doors were open, so that the animal could retreat to the pool at any time.

The walls and the ceiling of that half of the chamber where the animal placed its head were fit out with white linen in a way that the corners were rounded, thus approximating a half sphere. In the experiments for the assessment of the ventral visual field (perimeter B, see Section 2.3), the whole chamber was fit out with white linen.

The experimental chamber was illuminated with three halogen lamps (20 W each) and one electric bulb (60 W). These light sources could be dimmed and were used in different combinations for the two perimeter setups (see below) to achieve an appropriate uniform illumination of the linen on the walls. The illumination was measured using a luminance meter (Konica Minolta LS-110). The luminance of the white linen measured in six positions around the animal's head was in a range of 7–11 cd/m<sup>2</sup> (average 9 cd/m<sup>2</sup>).

### 2.3. Perimeters

Two perimeters were built: perimeter A to assess the upper and lateral visual field, and perimeter B to assess the lower visual field (Figs. 1A and B). In each perimeter, a vertical perimeter bow (a semicircle with a radius of 50 cm) was mounted to a plank on which the seal lay during the experiments. The part of the plank on which the seal's body rested from shoulders to tail was broadened to 40–50 cm. In perimeter B, the part of the plank where the seal laid its head was chosen as narrow as not to impair the seal's ventral field of view. Also mounted on each plank was a stationing target (A: plastic sphere equipped with a nose clamp and a chin cup, B: small piece of plastic equipped with a nose stopper) where the animal positioned its snout ('stationed'). At the side of the animal's head was a plastic sphere that served as a response target. The seal was trained to touch this response target with its snout when it perceived a visual stimulus (go-response, cf. experimental procedure). In each perimeter, the animal's shoulders were fixed by a frame in a way that the seal had to stretch its neck for stationing with its muzzle at the target. In this way a reproducible position of the seal's head was guaranteed.

Perimeter A was equipped with a vertical perimeter bow that comprised the dorsal visual field. At a vertical elevation of 0° or 20°, a horizontal perimeter bow was fixed to the vertical bow to assess the horizontal

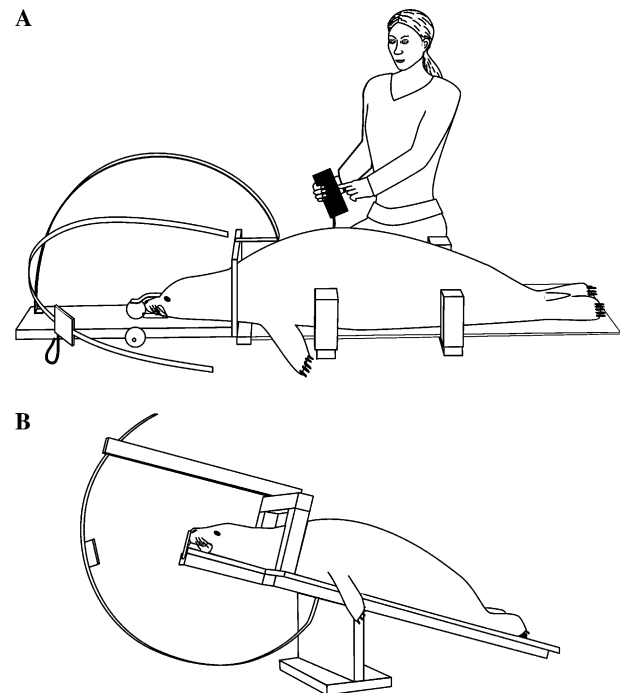


Fig. 1. Experimental setup. (A) Perimeter A for the assessment of the dorsal and horizontal field of view. (B) Perimeter B for the assessment of the ventral field of view.

visual field. Perimeter A was operated lying flat on the ground (Fig. 1A). Perimeter B was equipped with a vertical bow that comprised the ventral visual field. Therefore, perimeter B was propped up in a way that the plank was at an angle of 20° with the ground (Fig. 1B).

Visual stimuli were applied using a green LED (550 nm) that was mounted behind a small (10 × 15 cm) back-projection screen, termed the 'test stimulus screen.' The test stimulus screen was attached to the perimeter bows at varying positions. The back-projection screen served to reduce the angular dependency of the emitted light intensity and to generate a uniform background for the stimulus. Behind the test stimulus screen and the LED, an opaque white cardboard was mounted to prevent light from the walls from shining through the screen. This stimulus design was found to yield the best practicable constant background luminance for the stimulus when the test stimulus screen was moved to different positions on the perimeter bows.

In the experiments with fixed gaze (Experiment 2), a second stimulus screen was mounted straight ahead of the animal, termed the fixation stimulus screen. The fixation stimulus screen was almost identical to the test stimulus screen, but lacked the opaque cardboard as it was not necessary.

The stimulus positions on the perimeter bows were marked in 5° steps relative to the direction straight ahead at the seal's eye level (vertical and horizontal position of 0°) with an accuracy of ±1°. Dorsal positions of the stimulus were denoted with positive angles, ventral positions with negative angles. Horizontal stimulus positions were denoted with positive angles to the left or to the right. The position of the test stimulus screen was varied along the perimeter bows. During a given experimental session, the position of the test stimulus screen remained constant. The fixation stimulus screen was mounted at 0° horizontally. Its vertical position was 0° for the assessment of the ventral field of view and 20° else.

The luminance of the stimulus background, i.e., of the stimulus screen with the LED off, was measured using a luminance meter (Konica Minolta LS-110) for all stimulus positions. With the same luminance meter, a calibration curve was recorded that related the luminance of the LED shining through the screen to the electric current through the LED. Using this calibration curve, the brightness of the LED was adjusted via the

electric current to achieve a stimulus-to-background-ratio of  $2 \pm 0.2$  for all positions of the test stimulus. The fixation stimulus had a stimulus-to-background-ratio between 2.5 and 3.5.

The experimenter stayed at the right side of the animal, clearly out of the seal's field of view that had been roughly estimated during the initial training. Eye movements were filmed with a camera in front of the animal, viewed online on an LCD monitor and in most experiments recorded as S-VHS videos.

## 2.4. Experimental procedure

### 2.4.1. Perimetry

The seal was trained to respond to an LED stimulus from one of the stimulus screens on the perimeter bows by shifting its snout and touching the response target (go-response or positive response), and to remain in its original position when no LED stimulus was perceived (no-go-response or negative response). Correct responses, i.e., a go-response when a stimulus was present (hit) and a no-go-response when no stimulus was present (correct rejection), were reinforced with small pieces of herring. Incorrect responses, i.e., a no-go-response when a stimulus was present (miss) or a go-response when no stimulus was present (false alarm), were verbally indicated by the experimenter and were not reinforced.

At the beginning of an experimental session, the animal was required to position itself on the plank of the perimeter in the experimental chamber. Three to five minutes were taken to let the seal adapt to the light intensity in the chamber and to perform a couple of warm-up trials.

At the beginning of each trial, the experimenter produced a click sound with a mechanical clicker. Upon this signal, the seal usually immediately fixed its eyes on the stimulus screen (the test stimulus screen when eye movements were allowed, or the fixation stimulus screen in the experiments with fixed gaze) as far as possible (for problems with stimulus screen positions beyond the range of convenient eye movements, see results and discussion). Directly after the click sound, the experimenter pressed one of three switches: for a test stimulus or a fixation stimulus (see below), the test or fixation LED was lit, respectively; for a catch trial (see below), the switch was blind and neither LED was lit. After the click signal, the seal was given 5 s to perform a go-response, otherwise a no-go-response was scored.

**2.4.1.1. Experiment 1: Eye movements allowed (dynamic field of view).** In Experiment 1, the dynamic field of view was measured by using the test stimulus screen without a fixation stimulus screen. The animal was allowed to shift its gaze to the test stimulus screen and to use both eyes. Two types of trials were performed: (i) In a test trial, the LED behind the test stimulus screen was lit. The go-response or no-go-response of the seal was scored to determine the hit and miss rates. (ii) In a catch trial, no LED was lit. The go-response or no-go-response of the seal was scored to determine the false alarm and correct rejection rates. A session consisted of 30 test trials and 30 catch trials in random order.

**2.4.1.2. Experiment 2: Fixed gaze (cyclopean, monocular, and binocular fields of view).** In Experiment 2, the cyclopean visual field as well as both monocular visual fields with fixed gaze were determined. The animal was trained to fix its eyes on the fixation stimulus screen at the beginning of each trial. To achieve this behavior, fixation trials were interspersed between the test trials and the catch trials (which were the same as in Experiment 1, see above) in each session. In a fixation trial, only the LED behind the fixation stimulus screen was lit. The task for the seal was, like in a test trial, to move its snout to the response target upon a fixation stimulus.

For each position of the test stimulus screen, 30 test stimuli, 45 fixation stimuli, and 75 catch stimuli were given in a random order. Thus, the probability for a fixation stimulus to occur exceeded that for a test stimulus by a factor of 3:2. Together with the fact that the fixation stimulus occurred in a more convenient position than the test stimulus, this enhanced probability caused the animal to fix its eyes on the fixation stimulus screen, not the test stimulus screen, as soon as the click signal indicating the beginning of a trial was given.

The go-responses or no-go-responses of the seal in the test trials and catch trials were scored as in Experiment 1. The go-responses or no-go-responses in the fixation trials were also scored to estimate the animal's motivational state. They were, however, excluded from the analysis of the visual fields, as the fixation stimuli served only to direct the seal's gaze on the fixation stimulus screen.

The vertical position of the fixation stimulus screen was  $0^\circ$  for the assessment of the ventral visual field, but  $20^\circ$  for the assessment of the dorsal and horizontal visual field, because this was more convenient for the seal and resulted in a better resting position of the seal's eyes. For our summarized data set, we calculated the dorsal visual field as if the eyes had been fixed to a vertical position of  $0^\circ$  by subtracting  $20^\circ$ , because this can serve as a convenient standard for comparison with future studies.

Monocular visual fields were measured in the same way, but with one of the eyes blindfolded with an eye flap. The binocular visual field is the intersection of the two monocular visual fields.

### 2.4.2. Assessment of induced eye movements

In addition to the video recordings of the eyes that served to control eye movements during the perimetric measurements, close-up video sequences of one eye were recorded for quantitative evaluation in three separate sessions.

The seal lay on the plank of perimeter A in the experimental chamber, looking at the fixation stimulus screen at  $0^\circ$  horizontal/ $20^\circ$  vertical, where it expected a fixation stimulus. Eye movements were induced by hand movements and by tapping on the signal stimulus screen that was mounted in an ipsilateral, contralateral or dorsal position. Selected video sequences with high-amplitude eye movements were digitized (Cameo Grabster 200, Terratech, Nettetal, Germany) and analyzed using the software Scion Image Beta 4.0.2. for Windows (Scion Corporation, Frederick, Maryland, USA).

Lateral eye movements were estimated from the position of the pupil in frontal video recordings of the right eye. The change of the pupil position was then measured in pixels, corrected for minimal head movements that were measured from discernible fur structures and converted to millimeters using a scale recorded close to the eye. The shift of pupil position was then converted to an eye movement in degrees using the following geometrical relation: if  $v$  is the lateral displacement of the pupil and  $d$  is the distance between the pupil and the rotation center of the eye, it can be shown that the eye movement in degrees is  $\alpha = 90^\circ - \arccos(v/d)$ . This method requires making an assumption about the distance  $d$ . We set  $d$  to 15 mm, consistent with Fig. 2 in Jamieson and Fisher (1972). Errors were estimated by varying this value to 13 or 17 mm.

Lateral recordings of the left eye were taken to quantify dorsal eye movements by determining the angle of the flattened area of the cornea relative to the plank on which the seal rested.

## 2.5. Analysis of the boundaries of the visual fields

Correct positive responses to a test stimulus ('hits') and incorrect responses in the absence of a test stimulus ('false alarms') performed by the seal were transformed to hit rates and false alarm rates in percents of the test trials or catch trials, respectively, and plotted against the position of the test stimulus screen on the perimeter bow (in degrees). The boundaries of the visual fields were defined at a level of 50% correct responses to the test stimulus (i.e., a hit rate of 50%) and were determined by linear interpolation of the two neighboring values.

In addition, the boundaries of the visual fields were calculated using a 5% probability of chance criterion in Experiment 1 and a 1% probability of chance criterion in Experiment 2 (where a 5% level was not always reached). To do so, correct responses and correct rejections were added up and termed correct answers, while misses and false alarms were added up and termed wrong answers. The seal's probability of achieving correct answers by chance was derived from Bernoulli's distribution. In the experiments with a fixation stimulus screen, the 45 fixation stimuli for each stimulus screen position were excluded from the analysis. The numbers of responses to the catch trials, i.e., the number of false alarms and the number of correct rejections, were divided by 75:30 to estimate how many

responses of this type would have occurred if there had been only 30 catch trials. Since the chance levels calculated in this way allow to decide where the probability that the animal answered correctly by mere chance lies below 5% (1%) and the number of correct answers is thus statistically significant, they were also termed the 5% (1%) significance level.

### 3. Results

#### 3.1. Experiment 1: Dynamic visual field (eye movements allowed)

Fig. 2 shows the psychometric functions (hits and false alarms related to stimulus position) of Experiment 1 in which no fixation stimulus was presented. The boundaries of the visual field defined by the 50% threshold or by the  $p = 0.05$  significance level, are given in Table 1. Fig. 3 is a graphical representation of the 50% thresholds.

The visual field of the harbor seal with eye movements was remarkably wide on the dorsal side (121°). Ventrally, it appeared to be limited by the seal's snout. Laterally, the visual field was nearly equal to the right and to the left and comprised 210° in total.

#### 3.2. Experiment 2: Visual fields with fixed gaze

##### 3.2.1. Full visual fields (both eyes) with fixed gaze

Fig. 4 shows the psychometric functions of the cyclopean visual field obtained in Experiment 2. The vertical position of the fixation stimulus screen was 0° for the assessment of the ventral visual field, and 20° else (see Section 2.4.1).

The boundaries of the visual field defined by the 50% threshold or by the 1% significance level, respectively, are given in Table 2. Fig. 5 is a graphical representation of the 50%-thresholds from Table 2, but with 20° subtracted for the dorsal visual field, as if the eyes had been fixed on a vertical position of 0° (see Section 2.4.1). The dorsal visual field with fixed eyes was then 69°, thus 52° smaller than the visual field with eye movements. Ventrally, it was 12°, thus 5° smaller than the visual field with eye movements. To check for possible reasons for this difference in the ventral fields of view, additional experiments were performed with the fixation stimulus more dorsally at 60°, and the test stimulus at 50°, 40°, and 30°, respectively. In these experiments, the border

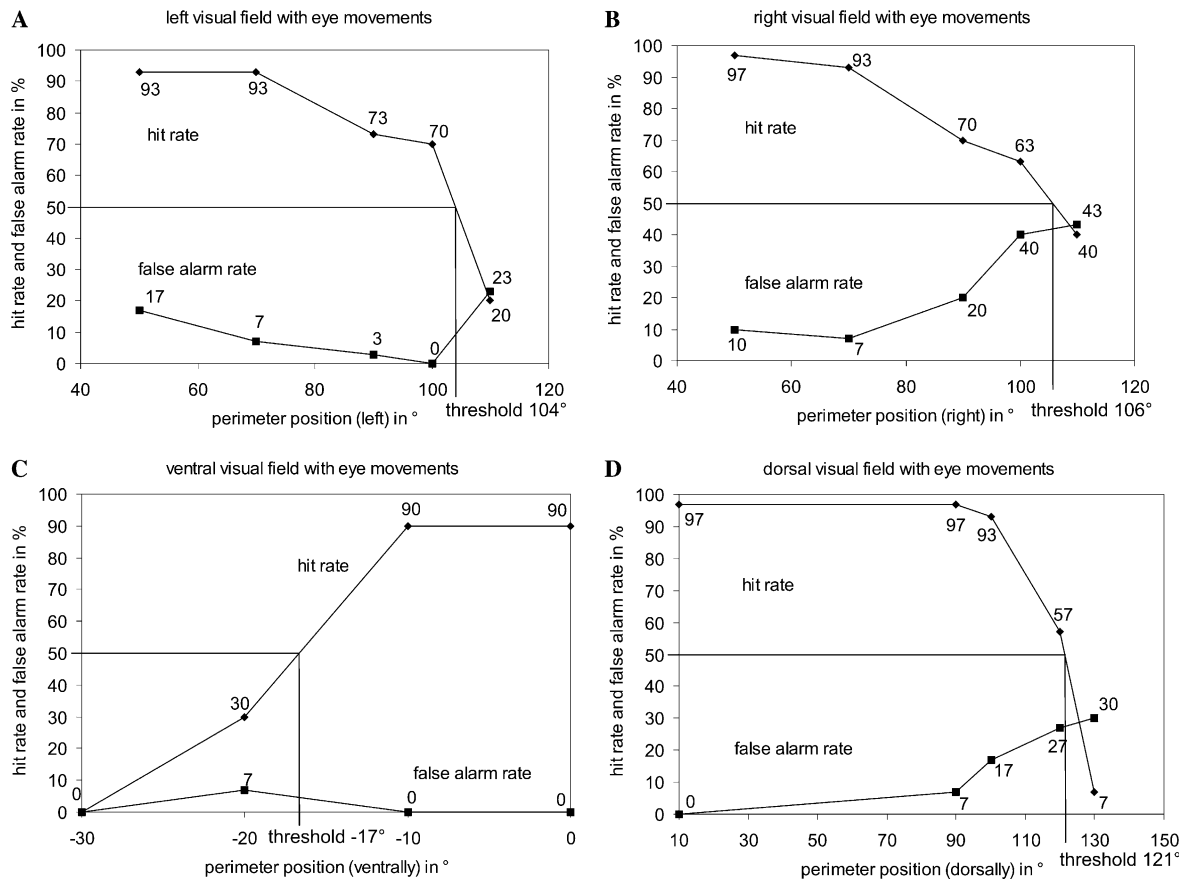


Fig. 2. Psychometric functions for the assessment of the boundaries of the visual field with eye movements (Experiment 1). The perimeter position 0° vertically and 0° horizontally is straight ahead at eye level of the animal resting on a plank. Left and right positions on the perimeter bow are both denoted with positive angles from this direction, the dorsal positions are denoted positive, and the ventral positions negative. Thresholds for the perception of the visual stimulus are defined by a hit rate of 50% and are calculated by linear interpolation of the two neighboring values as shown. (A) Left visual field; (B) right visual field; (C) ventral visual field; (D) dorsal visual field.

Table 1  
The borders of the field of view with eye movements allowed (Experiment 1)

|                           | Ventral field of view (°) | Dorsal field of view (°) | Right lateral field of view (°) | Left lateral field of view (°) |
|---------------------------|---------------------------|--------------------------|---------------------------------|--------------------------------|
| 50% Perception threshold  | -17                       | 121                      | 106                             | 104                            |
| 5% Significance threshold | -20.1                     | 120.4                    | 100.1                           | 100.5                          |

Lateral eye movements were scarcely performed. Thresholds were calculated by linear interpolation. The 50% perception threshold is the perimeter position where 50% of the test stimuli were answered correctly (50% hits, 50% misses). The 5% significance threshold is the perimeter position, where the probability for the seal to reach an equally good result by mere guessing dropped below 5%.

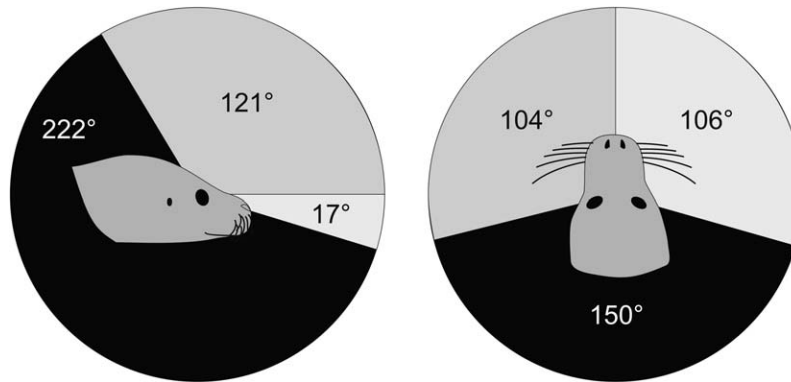


Fig. 3. Survey of the dynamic visual field (Experiment 1) obtained from the psychometric functions using the 50% hit rate as shown in Fig 2.

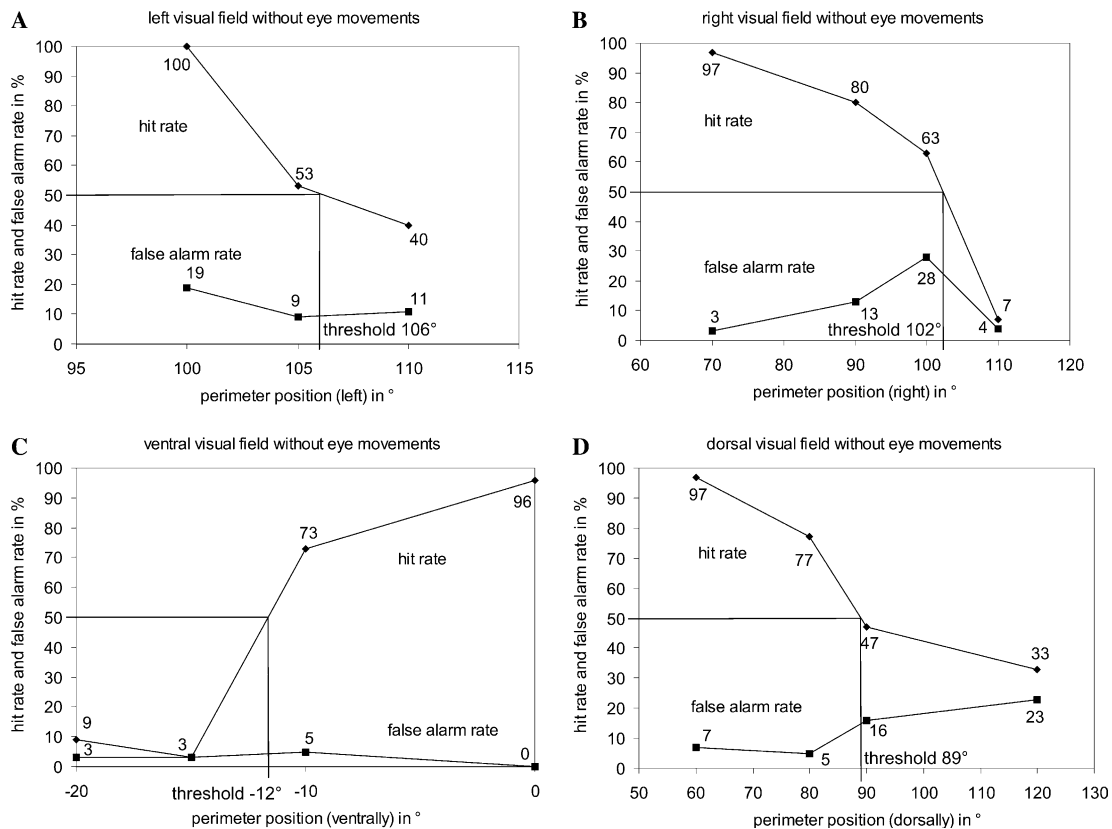


Fig. 4. Psychometric functions for the cyclopean visual field (Experiment 2), i.e., the visual field with fixed eyes. In the same manner as in Fig. 2 (dynamic visual field), the hit rates and false alarm rates (in percent) are given for the left (A), right (B), ventral (C), and dorsal visual field (D) for all angles tested. Horizontal and vertical lines indicate the 50% hit rate and the boundary of the visual field (perception threshold) derived from it.



Table 2  
The borders of the cyclopean field of view with eyes fixed upon a fixation stimulus (Experiment 2)

|  | Ventral field of view (°) | Dorsal field of view (°) | Right lateral field of view (°) | Left lateral field of view (°) |
|--|---------------------------|--------------------------|---------------------------------|--------------------------------|
| 50% Perception threshold               | -12                       | 89                       | 102                             | 106                            |
| 1% Significance threshold              | -10.1                     | 87.3                     | 100.2                           | 108.6                          |
| Vertical position of fixation stimulus | 0                         | 20                       | 20                              | 20                             |

Thresholds were calculated by linear interpolation. The 50% perception threshold is the perimeter position where 50% of the test stimuli were answered correctly (50% hits, 50% misses). The 1% significance threshold is the perimeter position up to which the probability for the seal to reach an equally good result by mere guessing remained below 1%.

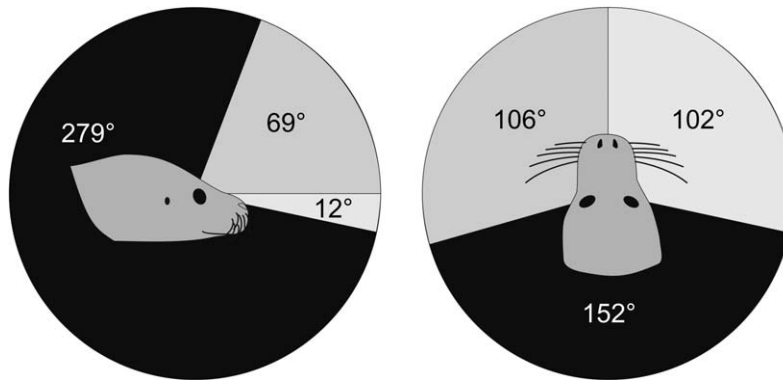


Fig. 5. Survey of the cyclopean visual field (Experiment 2) obtained from the psychometric functions using the 50% hit rate as shown in Fig. 4. For the dorsal visual field, 20° were subtracted from the value from Fig. 4 and Table 2 to relate the field of view to a fixation point at 0° vertically.

of the visual field was not reached. Laterally, the visual field with fixed eyes was similar to the right and to the left and comprised 208° in total, thus only 2° less than the visual field with eye movements. The reason for not finding a larger difference is that in Experiment 1 the seal did not turn its eyes towards the stimulus screen if it was situated more than 40° to either side, but looked more or less straight ahead. Implications for the comparison of the visual field with and without eye movements are given in the discussion.

3.2.2. Monocular and binocular visual fields with fixed gaze

Fig. 6 shows the psychometric functions for the horizontal extent of the right and the left monocular visual field, i.e., the visual fields assessed while one eye was blindfolded with an eye flap. Both the fixation stimulus screen and the horizontal perimeter bow were fixed on the vertical perimeter bow at an elevation of 20°.

Defined by the 50% threshold of correct responses, the left boundary of the visual field of the right eye was 34° to the left of the seal, and the right boundary of the visual field of the left eye was 33° to the right. Thus, the binocular visual field extended over 67°.

Fig. 7 represents a graphical summary of the total, the binocular and the monocular horizontal visual fields of the harbor seal, under the assumption that they were precisely symmetrical to the mediosagittal plane.

3.3. Amplitudes of induced eye movements

3.3.1. Lateral eye movements

Fig. 8 shows four example pictures of the frontal video recordings used to estimate lateral eye movements with the pupil clearly discernible. Table 3 lists the horizontal positions where the stimuli for inducing an eye movement

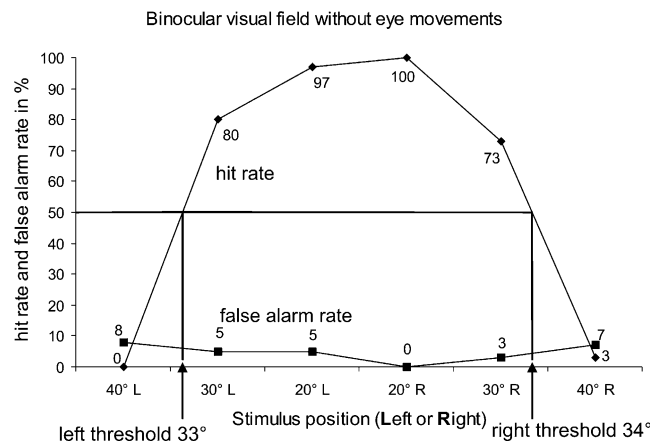


Fig. 6. Psychometric functions for both monocular visual fields (eyes fixed). Their intersection is the binocular visual field. Defined by the 50% hit threshold (indicated in the figure), the binocular visual field reached from 33° on the left to 34° on the right. The symmetrical form of the binocular field of view is clearly discernible.

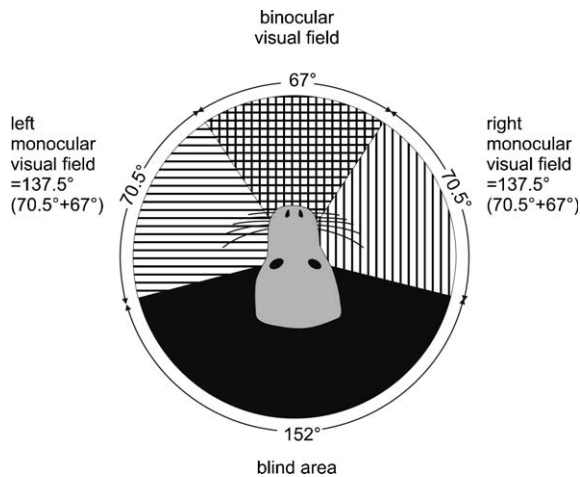


Fig. 7. Survey of the monocular and binocular visual fields obtained from the psychometric functions using the 50% hit rate as shown in Fig. 6.

were given, together with the calculated eye movement in degrees (Section 2.4.2). Induced eye movements did not closely follow the position of the stimulus, but reached at most  $(11 \pm 2)^\circ$  ipsilaterally and  $(12 \pm 2)^\circ$  contralaterally. Errors of these estimated eye movements are dominated by the uncertainty in the distance  $d$  between the pupil and the center of rotation of the eye. Assuming  $d = 15$  mm with an error of  $\pm 2$  mm leads to errors of up to  $1.9^\circ$ , so an error of  $2^\circ$  can be assumed.

### 3.3.2. Vertical eye movements

Figs. 9A and B show two example pictures of the lateral video recordings used to estimate dorsal eye movements. In these pictures, the flattened area of the cornea can be seen

clearly. Eye movements were induced by the fixation stimulus at  $20^\circ$  (Fig. 9A), hand movements or tapping on the stimulus screen at  $80^\circ$  (Fig. 9B).

Table 4 lists seven measurements of the angle between the flattened area of the cornea and the horizontal (a) when the seal watched the fixation stimulus screen at  $20^\circ$  elevation prior to an induced eye movement, and (b) after an eye movement had been induced by a visual and acoustic stimulus at  $80^\circ$  elevation. The difference between these orientations is the induced eye movement. Measurements in each picture were accurate to  $2^\circ$ . The mean induced eye movement was  $(44.4 \pm 6.1)^\circ$  upwards from the fixation stimulus screen that was mounted at  $20^\circ$ , so the seal was capable of turning its eyes approximately  $64^\circ$  upwards relative to a 'normal' gaze direction of  $0^\circ$ . Eye orientations in the seal observing the fixation stimulus screen and when a dorsal eye movement had been induced by a stimulus at  $+80^\circ$  had both standard deviations of  $\pm 4^\circ$ .

## 4. Discussion

### 4.1. Visual fields

It must be noted that because of time constraints only one animal could be used in this study. We cannot be sure if the obtained results are representative for the species. However, harbor seal 'Sam' has a normal physiognomy and shows no behavioral deficits. This and the symmetric shape of the visual fields make us confident that the measured values are not extreme in any way.

The dynamic field of view with eye movements allowed (Experiment 1) reached from  $-17^\circ$  to  $121^\circ$  (total  $138^\circ$ )

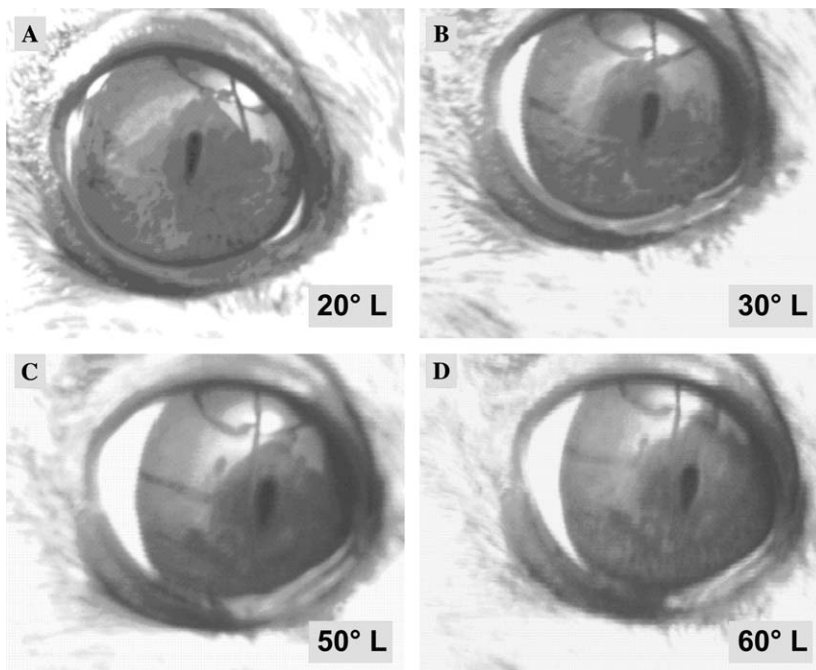


Fig. 8. Four examples of the pictures of the right eye that were used to assess lateral eye movements. The shift in pupil position was measured (Table 3). The angle at which the stimulus to induce an eye movement was given is indicated in each picture.

Table 3  
Lateral eye movements as calculated according to Section 2.4.1 from video recordings of the right eye in frontal view (cf. Fig. 8)

| Position of the lateral stimulus to induce eye movements (l, left; r, right) | Calculated eye movement $\alpha$ ( $\pm 2^\circ$ ) |
|--|--|
| 20° r  | 6.8°   |
| 30° r  | 8.4°   |
| 40° r  | 9.2°   |
| 50° r  | 9.2°   |
| 60° r  | 7.5°   |
| 70° r  | 11.3°  |
| 20° l  | 7.7°   |
| 30° l  | 11.9°  |
| 40° l  | 11.9°  |
| 50° l  | 11.9°  |
| 60° l  | 10.4°  |

The error of  $\pm 2^\circ$  results from the uncertainty in  $d$  (cf. Section 2.4.1).

vertically with the lower visual field probably limited by the seal's snout. The vertical field of view with fixed eyes (Experiment 2) extended from  $-12^\circ$  to  $+69^\circ$  and was thus smaller than the dynamic visual field with eye movements (Experiment 1) by an amount of  $5^\circ$  ventrally and  $52^\circ$  dorsally. The dorsal difference can be explained by the eye movements. The seal could turn its eyes  $64^\circ$  upwards, i.e.,  $12^\circ$  more than necessary to explain the difference in the fields of view. This means, on the other hand, that the dorsal field of view measured in Experiment 1 was  $12^\circ$  smaller than could be expected from eye movements. This can be due to different motivational states of the animal in the course of the experiments, resulting in different response criteria or different eye movements. It is also possible that the skin on the seal's forehead starts to cover the rim of the visual field in these extreme eye positions, which is consistent with Fig. 9B when it is taken into account that the pupil lies several millimeters behind the corneal surface.

The difference of  $5^\circ$  in the ventral field of view determined in Experiments 1 and 2 cannot be explained by eye movements, as additional tests of the ventral field of view

with a fixation stimulus at  $+60^\circ$  showed no defects of the visual field within  $30^\circ$  ventrally of the gaze direction (see Section 3.2.1). Again, motivational changes resulting in different response criteria may have caused this effect.

In humans, the vertical cyclopean and the vertical dynamic field of view are essentially the same size ( $-76^\circ$  to  $55^\circ$ ; Schober, 1960). They are limited by the eyebrows and lids. Vertical eye movements serve only to improve the image quality at the margins of the visual field. In contrast, vertical eye movements in the harbor seal are very effective for enhancing the size of the visual field. With fixed eyes, the seal's vertical visual field was smaller than the human's by  $50^\circ$ ; with vertical eye movements, it was wider than the human's by  $8^\circ$ . In both cases, the visual field of the harbor seal was shifted to the dorsal side as compared to a human. This is caused by the facial structures, i.e., the long snout and the missing supraorbital bones in the seal, and by the seal's high ability to turn its eyes upwards. We do not know if eye movements serve to improve image quality at the margins of the visual field in the seal as they do in humans, because there is no indication for a fovea in the harbor seal's retina (Jamieson & Fisher, 1970).

Horizontally, the seal's field of view determined in Experiment 1 was only  $2^\circ$  broader than that determined in Experiment 2. A difference of  $24^\circ$  would have been expected from the measurements of lateral eye movements that could broaden the visual field up to  $12^\circ$ . This discrepancy arises from the fact that the seal, as we became aware after Experiment 1 had been completed, hardly moved its eyes to the sides if the stimulus screen was mounted more than  $60^\circ$  laterally, but instead kept on looking straight ahead. We had the impression that lateral eye movements were hard and fatiguing for the seal, and therefore the results of Experiment 1 reflect a practical field of view that is relevant in most cases. This practical field of view can be expanded by approximately  $22^\circ$  ( $11^\circ$  to each side) by eye movements if necessary.

The horizontal cyclopean field of the harbor seal with fixed eyes was very similar to that of a human, which is also estimated to be  $208^\circ$  by Hughes (1977) or  $200^\circ$  by Schober (1960). It was wider than that of a cat by  $22^\circ$

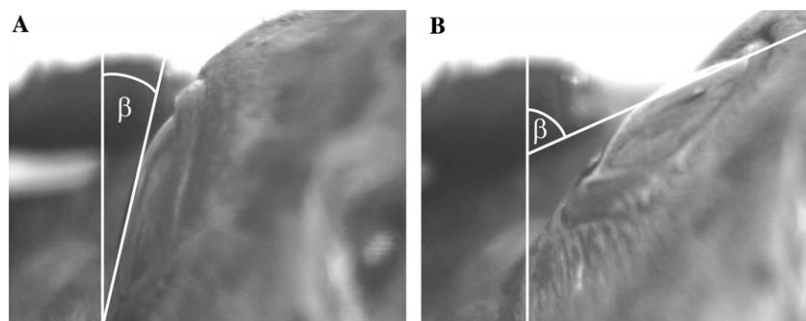


Fig. 9. Two examples of the pictures of the left eye that were used to assess dorsal eye movements. The angle  $\beta$  between the vertical and the flattened part of the cornea was measured (Table 4).



Table 4  
Dorsal eye movements as measured from video recordings of the left eye in lateral view (cf. Fig. 9)

|             | $\beta$ When the seal was watching the fixation screen at 20° vertically (°) | $\beta$ When the seal was encouraged to look at a stimulus at 80° vertically (°) | Difference (°) |
|-------------|--|--|----------------|
| Recording 1 | 14   | 66   | 52             |
| Recording 2 | 19   | 59   | 40             |
| Recording 3 | 13   | 66   | 53             |
| Recording 4 | 23   | 60   | 37             |
| Recording 5 | 20   | 61   | 41             |
| Recording 6 | 19   | 65   | 46             |
| Recording 7 | 13   | 55   | 42             |
| Mean        | 17.3 ± 3.9   | 61.7 ± 4.2   | 44.4 ± 6.1     |

The angle  $\beta$  between the vertical and the flattened area of the cornea was measured to an accuracy of  $\pm 2^\circ$ .

(186° was measured in the cat by Hughes (1976)), but 32–42° smaller than that of a dog (240° was measured by Sherman and Wilson (1975), 250° calculated by Walls (1963)). So, the horizontal cyclopean field of view in the harbor seal lies within the range known for carnivores, which have generally smaller panoramic fields of view than herbivores do (Duke-Elder, 1958; Hughes, 1977; Walls, 1963).

Since the eyes in the harbor seal are positioned more frontally than laterally, their optical axes deviating only 15° from the forward direction (Johnson, 1901), their typical carnivore horizontal field of view is associated with a considerably large monocular field of view. The two main factors that influence the unocular field of view are the corneal curvature and the extent of the retina, while the diameter of the pupil can also have some effect (Duke-Elder, 1958). Contrary to Johnson (1893), the harbor seal's cornea shows a large radius of curvature in the central part (Hanke, Dehnhardt, Schaeffel, & Hanke, 2006) i.e., it is flattened. The cornea is thus of little help to enlarge the field of view. Probably the considerable unocular field of view in the harbor seal is achieved by a relatively extensive retina.

The binocular visual field in the harbor seal was 67° and thus narrower than in the cat (100°, Hughes, 1976) or in the dog (70–80°, Hughes, 1976), but well within the limits known for terrestrial carnivores (60–130°, Hughes, 1976). It was clearly narrower than the binocular field of primates (130–140°, Duke-Elder, 1958). Binocular vision not only enables stereopsis, but also enhances the sensitivity to light (Hughes, 1977; Schober, 1960). Both functions are relevant to the seal that hunts agile prey, frequently under low light conditions.

It has been proposed that the size of an animal's binocular field is related to the space within which it manipulates objects in its environment (Hughes, 1977; Trevarthen, 1968). The visual field associated with this space has been termed the 'praxic field' (Trevarthen, 1968). According to this hypothesis, the larger binocular field of the cat as compared to the dog is a result of the fact that a cat catches its prey with its well abductable forelimbs, while a dog uses mainly its jaws with only little help of the forelimbs. A harbor seal does not use its foreflippers, but exclusively its jaws to capture prey. The fact that the harbor seal's binocular

field is slightly smaller than the dog's fits well into the hypothesis that the extent of the praxic field of a species influences the degree of its binocular vision.

We believe that the main reason for the carnivore-like features of the horizontal and binocular visual fields in the harbor seals lies in their predatory mode of foraging rather than their ancestry from land-living carnivores. Eye position is a relatively plastic feature in the course of evolution, as can be seen for example in the shift of the eyes from a dorsal to a lateral position in the whales. Within the pinnipedia, we would predict that the walrus (*Odobenus rosmarus*) has the smallest binocular visual field, as it combines laterally oriented eyes with a large, bulky snout. This would be consistent with the interpretation that, in the time scale of pinniped evolution, life-style has a stronger effect on eye position than ancestry, as the walrus feeds mainly on mussels.

It must be noted that the visual fields in air reported here might be larger than those under water, because the difference in refractive indices between air and the eye helps directing light into the pupil. From the geometrical considerations explained in Appendix A (Fig. A1) follows that the binocular field under water should still be at least 42°, the horizontal cyclopean field at least 144° and the dorsal visual field at least 46° with the eyes fixed straight ahead (or 98° with eye movements). These values are lower boundaries for the true visual fields, as they were obtained under the pessimistic assumptions that the dilatation of the pupil under water does not significantly widen the field of view, and that the margins of the field of view measured in-air in this study were caused by the extent of the retina. In fact, the pupil dilates to a large circle under water even under bright light conditions, and the binocular and dorsal field may be restricted more by the seal's snout and forehead than by the margins of the retina.

It is well understood why the seal's pupil constricts to a small pinhole in air under daylight conditions, while there is no need for such a constriction under water. The harbor seal's eye is strongly myopic and astigmatic in air, which can be partly compensated by the constriction of the pupil, but it is close to emmetropic under water, where therefore a small pupil is not necessary (Hanke et al., 2006). On the other hand, it is remarkable to what extent the pupil of this highly sensitive eye dilates under water even under an

illumination that causes a small pinhole in air (Walls, 1963, and own observations). This has the disadvantage that the pupil helps little in light regulation, and the depth of focus decreases. It is conceivable that the large pupil serves to maintain a wide field of view when the refractive power of the cornea is lost. Measurements of the visual fields of harbor seals underwater are needed to clarify this further.

#### 4.2. Eye movements

The seal's ability to turn its eyes dorsally was most striking. In addition, no signs of fatigue were observed when the seal had to turn its eyes dorsally, even in extended sessions. When the seal observed the fixation stimulus screen at  $+20^\circ$ ,  $\alpha$  was  $(17.3 \pm 4)^\circ$ . A similar variability in eye orientation probably occurred during perimetry and constitutes an error source for Experiment 2, but should there be mitigated by the higher number of measurements.

Lateral eye movements were less pronounced than vertical eye movements, but still significant. They could be estimated only with a larger relative error, since the calculation of the angle of eye movement from the frontal camera view requires an assumption about the distance  $d$  between the pupil and the center of rotation of the eye. From Fig. 2 in Jamieson and Fisher (1972),  $d$  was estimated to be  $(15 \pm 2)$  mm, assuming that the center of rotation should be close to the center of the eye. At any rate, it appears safe to assume that  $d$  is not longer than 20 mm. Consequently, the maximum lateral eye movements observed in this study were at least  $8.5^\circ$ . From observations of the seals in our research facilities, we have the impression that intraspecific variability in lateral eye motility is high and the highest values within the error range discussed here ( $14^\circ$ , see Table 3) appear realistic at least in some individuals.

Eye movements in carnivores are generally more vivid and extensive than in other mammalian orders like the rodentia or the ungulata, surpassed only by the primates (Duke-Elder, 1958). Harbor seals are no exception from this rule, contrary to Walls (Walls (1963)), who stated that '[the seals] roll and wiggle so much ... that they were probably hard to approach unseen even if they ... lacked what little eye mobility they do have.' In humans, eye movements of  $55^\circ$  dorsally,  $45^\circ$  ventrally, and  $30^\circ$  to each side are possible, but in practice  $18\text{--}20^\circ$  are rarely exceeded (Schober, 1960). So in summary, the harbor seal's eye movements reach approximately 50% of a human's, with a preference for turning the eyes upwards.

#### 4.3. Ecological implications

The results of this study show that harbor seals have an extremely wide dorsal field of view. This design enables the seal to pursue at least two different foraging strategies. First, seals and predatory fish have been observed to approach prey from below, when it is silhouetted against the relatively light surface (Hobson, 1966; Watanabe, Baranov, Sato, Naito, & Miyazaki, 2004).

The dorsally oriented and highly sensitive eyes of harbor seals are well suited for the detection of prey in this situation. Second, harbor seals spend a significant amount of time swimming upside-down, with their backs oriented to the ground. The reason for this behavior is not quite clear, but taking the dorsally oriented visual field into account, it appears most likely that they visually scan the ground in this way. Harbor seals feed on many aquatic species, including benthic prey (Behrens, 1985; Bowen, Tully, Boness, Bulheier, & Marshall, 2004).

Visual fields or eye movements have not been studied in other marine mammal species. Taking the highly diverse morphologies of the heads and faces even within the group of the *Pinnipedia* into account, we believe that substantial interspecific differences exist. More data are needed to clarify the inter- and intraspecific variability of visual fields and eye movements in marine mammals.

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#### Appendix A

The geometrical considerations to estimate the minimum size of the underwater visual fields from the aerial visual fields measured in this study are shown in Fig. A1. Let  $R$ , the radius of curvature of the cornea (30 mm horizontally, 80 mm vertically);  $d$  the radius of the pupil (0.5 mm horizontally, 1.5 mm vertically);  $G$ , the point on the cornea where a light ray from the environment is refracted to the rim of the pupil;  $\alpha$ , the angle between the light ray from the cornea to the rim of the pupil and the line perpendicular to the cornea in point  $G$ ;  $\beta$ , the angle between the light ray from the environment that is refracted in point  $G$  to reach the rim of the pupil and the line perpendicular to the cornea in point  $G$ ;  $\alpha'$

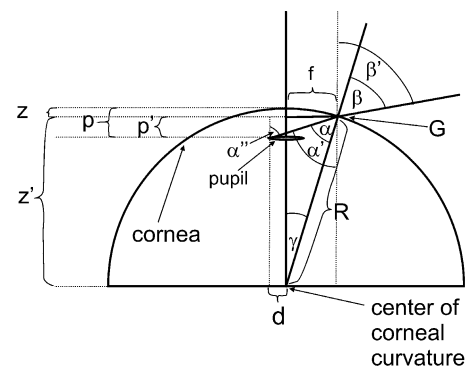


Fig. A1. Drawing of the geometrical considerations to estimate the visual field under water from the measured aerial visual fields. For explanation, see text of Appendix A.

and  $\beta'$ , the angles between these light rays and the optical axis of the eye.

The task is to find the corresponding  $\alpha'$  for the  $\beta'$  that was measured behaviorally in air, because under water the refractive power of the cornea is lost and only light rays that fall on the cornea in G under the angle  $\alpha'$ , not  $\beta'$ , will reach the rim of the pupil. To calculate  $\beta'$  from the measured margins of the visual field, recall that the optical axis of the eye points  $15^\circ$  outwards from the longitudinal axis of the animal (Johnson, 1901).

The following relations are found:

$$\begin{aligned} f &= R * \sin(\gamma), \\ z' &= R * \cos(\gamma), \\ p' &= p - z = p - (R - z') = p - R + R * \cos(\gamma), \\ \alpha' &= \alpha'' = \arctan((f + d)/p'), \\ \alpha &= \alpha' - \gamma. \end{aligned} \quad (1)$$

The refraction law of Snellius yields  $\sin(\alpha)/\sin(\beta) = (\text{refractive index of air})/(\text{refractive index of eye}) = 1/1.333$  or

$$\beta = \arcsin(1.333 * \sin(\alpha))$$

Further,

$$\beta' = \beta + \gamma \quad (2)$$

$\alpha'$  and  $\beta'$  were calculated numerically for a suitable set of angles  $\gamma$  using Eqs. (1) and (2), and the angle  $\alpha'$  that was associated to the  $\beta'$  measured in the seal (tolerance of  $\beta'$   $0.5^\circ$ ) was taken to be the direction of the incident light ray that reaches the rim of the pupil when refraction is lost under water.

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