

Optokinetic nystagmus in harbor seals (*Phoca vitulina*)

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Abstract

Harbor seals experience motion due to self-motion and to movement in the external world. However, motion vision has not been studied yet in marine mammals moving in the underwater world. To open up this research, optokinetic nystagmus (OKN) as a basic motion sensing and retinal image stabilizing reflex was studied in four harbor seals during stimulation with moving black-and-white stripe patterns. All seals responded with optokinetic eye movements. Detailed measurements obtained with one animal revealed a moderate gain for horizontal binocular OKN. Monocularly stimulated, the seal displayed a symmetrical OKN with slightly stronger responses to leftward moving stimuli, and, surprisingly, a symmetrical OKN was found in the vertical domain.

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1. Introduction

The origin of perceived motion can lie in the subject itself, in the external world or in a combination of both. If an object is in motion, the observer's eyes usually move in pursuit of it in order to stabilize the object's image on the retina and, therefore, to retain a high level of resolving power (Yarbus, 1967). When a large portion of the visual field moves, the eyes move smoothly with the field (slow phase) interrupted by saccades (fast phase) in the opposite direction. This rhythmic oscillation of the eye is called optokinetic nystagmus (OKN). In concert with other mechanisms like the smooth pursuit system or the vestibular-ocular reflex (VOR), the OKN nullifies or at least reduces the slip of the retinal image (Collewijn, 1985; Schor, 1993) caused by rotations of eye, head or body. Consequently, images on the retina are stabilized (Walls, 1942, 1962) and conditions for clear and unblurred vision maintained.

Optokinetic nystagmus (OKN) has been studied in detail in a variety of organisms. But so far, no studies have analyzed motion vision including basic principles, e.g. the ability to perform optokinetic eye movements, in marine mammals. This field of research is of great interest especially in marine mammals, as, on the one hand, they move in the low structured, three-dimensional underwater world, and, on the other hand, their own locomotion involves, beside translation, rotations along all axis. Thus, visual perception might be different from that of terrestrial mammals (Schusterman & Thomas, 1966), and general features of the optokinetic nystagmus found in terrestrial species could also be different in marine mammals.

It appears highly probable that marine mammals in general and harbor seals in particular possess the ability of seeing motion. Harbor seals are amphibious mammals. Under water, they prey on diverse vertebrate and invertebrate species which are normally moving. The ability to see motion would imply that the predator can see the moving object from a significantly greater distance than if it was static. Furthermore, motion provides the predator with important information about direction and distance, because near features move faster across the

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retina than distant ones (Miles, 1998). Motion vision also helps to separate figure from background, and motion information helps to detect and assess self-motion (Nakayama, 1985). The OKN stabilizes the eye with respect to whole-field motion which enhances the sensitivity to individual moving objects, e.g. prey, in the visual field (Schor, 1993). This is of high importance concerning the detection of prey and the onset of smooth pursuit to successfully hunt it.

In line with these considerations, we show in this study that a marine mammal, the harbor seal, shows optokinetic responses under water. On the one hand, we tested under water because harbor seals are nearly emmetropic in water (Hanke, Dehnhardt, Schaeffel, & Hanke, 2006), and all essential activities requiring high level performance of the sensory organs are displayed in this medium. On the other hand, we tested under water because we wanted to reveal possible adaptations to the underwater environment harbor seals share with fully aquatic species, as e.g. fish. The optokinetic systems of fish have been studied already (see e.g. Dieringer, Reichenberger, & Graf, 1992; Easter, 1972; Marsh & Baker, 1997). However, only results for horizontal OKN are reported, and these are very variable among (and within) species. Dieringer et al. (1992) propose that the optokinetic responses may reflect species specific differences in the movement of the organism or in the environment.

We tried to assess the nature of optokinetic eye movements in the horizontal domain under binocular and monocular viewing conditions to compare them to results obtained in fish and to theoretical predictions from the visual consequences of forward locomotion and eye placement (Grasse & Cynader, 1988) which have been discussed for several terrestrial species. During forward movement, flow fields in frontally eyed terrestrial animals are composed of flow lines with the predominant asymmetries in the vertical and no significant asymmetry between naso-temporal and temporal-nasal. Frontal eye placement therefore leads to symmetrical binocular OKN as a response to a leftward and rightward horizontal stimulus movement. As harbor seals are frontally eyed, one could expect to find a symmetric horizontal OKN.

The vertical OKN in terrestrial species investigated so far shows a remarkable asymmetry with higher gain for upward moving stimuli (Grasse & Cynader, 1988; Matsuo & Cohen, 1984; Takahashi & Igarashi, 1977). The reduced sensitivity to a downward moving stimulus has been explained in terms of preventing the eye from rotating downwards while walking over a highly-textured ground (Schor, 1993). In the swimming harbor seal, such a textured ground does not play a prominent role because the seal frequently experiences the ground, the water surface, both, or none of them. The orientation to the ground and the surface can change when the seal rolls its body. With respect to its aquatic lifestyle, we considered it interesting to investigate the vertical OKN in the harbor seal.

Under monocular viewing conditions, frontal-eyed vertebrates with an area of high resolution in the retina display a symmetric response to horizontally moving stimuli. The question whether there is a high resolution area (area centralis) in the retina of the harbor seal is not yet answered. According to Jamieson and Fisher (1971), harbor seals do not possess any kind of area centralis. In contrast to this finding, recent studies on retinal topography in other seals (Stellar sea lion, Mass and Supin, 2005; Harp seal, Mass & Supin, 2003; Fur seal, Mass & Supin, 1992) have always assessed a definite area of high ganglion cell density similar to the area centralis in terrestrial carnivores. Therefore, we would expect to find a high resolution area in the retina of harbor seals with modern techniques as well, which, together with frontal eye placement, make a symmetric monocular OKN in harbor seals likely.

2. Material and methods

2.1. Experimental animals

Harbor seals were studied in our Marine Mammal Laboratory in the Zoo of Cologne, Germany. The optokinetic response (OKN) was tested in four male animals between 7 and 12 years of age (maximum age of harbor seals in captivity and in the wild up to 35 yrs, cited after King (1983) and our own records). All animals had previous experience with visual tasks. The data of the velocity tuning of horizontal binocular OKN presented in this study represent measurements of one animal (“Henry”, 9 yrs old). Three additional seals (“Sam”, “Bill”, “Nick”) were tested for the presence or absence of optokinetic responses under binocular viewing conditions but were not quantified further. Vertical binocular and monocular OKN was examined in one seal (“Henry”).

The experiments were conducted according to the guidelines of the German animal protection law.

2.2. Optokinetic measurements

2.2.1. Experimental set-up

Experiments were carried out in a projection chamber which allowed to present stimuli to the animals on a projection screen underwater (Fig. 1). For this purpose, light coming from a beamer (Epson EMP-9100) was reflected by one mirror, passed an acrylic frame that lay on the water to calm the surface, and was reflected by a second mirror onto the projection screen from behind. The animal’s compartment (A, Fig. 1) was on the front side of the projection screen which was closed against the daylight by the chamber’s front door (Fig. 1). The experimental animals put their heads through a 40 cm diameter aperture in the front door and placed their snouts on a target 65 cm in front of the projection screen. This unrestrained positioning allowed for small head movements. A camera (C-MOS camera module in an underwater housing made of plexiglass) was mounted approximately 20 cm above (horizontal optokinetic nystagmus; Fig. 1) or to the side (vertical optokinetic nystagmus) of the animal’s head and continuously recorded eye movements in the direction of the stimulus motion. A digital camera (Canon MV-XL1s) served as a recorder. For the determination of the relationship between stimulus and gaze velocity, a close-up of one eye was filmed, whereas for clarifying the question concerning the symmetry of the optokinetic response, the camera filmed both eyes (distance of the camera above the eye approximately 40 cm). Eye movements were surveyed real time via a control monitor in the experimenter’s compartment of the projection chamber (E, Fig. 1) to allow for rewarding the animal according to its behavior. The animals were not able to see the actions taking place in the experimenter’s compartment. All stationary objects except of the camera and the stationing

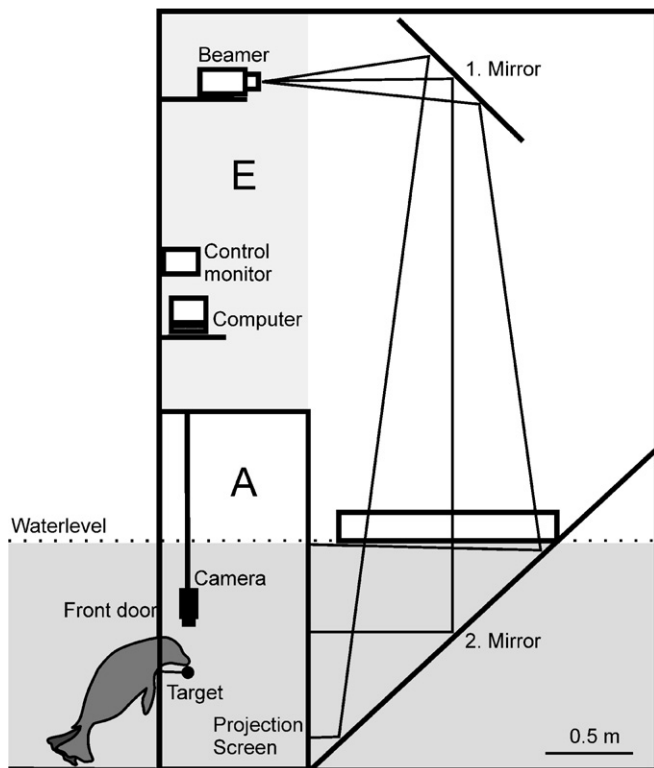


Fig. 1. Experimental set up to measure optokinetic nystagmus in harbor seals under water (side view). In the animal's compartment (A), the seal is voluntarily stationing at a target 65 cm in front of a projection screen on which optokinetic stimuli (black-and-white stripe pattern produced real time on a portable computer) are back projected with the help of a beamer and a mirror system. The water surface is calmed by an acrylic frame. The image from the camera continuously filming the animal's head is displayed on a control monitor and recorded at the same time in the experimenter's compartment (E).

target were removed from the animal's compartment in order to avoid a suppression of OKN by the animal directing its attention towards stationary objects.

2.2.2. Optokinetic stimuli

Optokinetic nystagmus was elicited by a black-and-white stripe pattern generated in Matlab 6.5 (The Mathworks, Natick, Massachusetts, USA) with the help of the Psychophysics Toolbox (Brainard, 1997). This pattern

was increased to the maximum (limited by the projection screen's size) covering $98^\circ \times 108^\circ$ (vertical \times horizontal) of the animals' visual fields. During experiments, stimuli were generated real time on a portable computer (Dell Inspiron 8200). Nine black and nine white bars with a contrast (defined as $(L_{\max} - L_{\min}) / (L_{\max} + L_{\min})$) of 0.5 were presented on the projection screen. The full range of stimulus velocities which were possible to generate with the experimental devices without artefacts (minimum 5 deg/s, maximum 80 deg/s) was used for measurements. Stimulus orientation was varied between 180° (pattern moving from the animals' left to right side) and 0° (pattern moving from the animals' right to left side) as well as 90° (pattern moving upwards) and 270° (pattern moving downwards). The brightness of the stimulus measured without water (dry pool) with a luminance meter (Konika-Minolta LS 110) was 50 cd/m^2 (dark stripes) and 150 cd/m^2 (bright stripes). The brightness of the beamer (set to -15 of total -30 in the beamer's brightness function) was adjusted as a compromise between optimizing stimulus environment and optimizing video recordings for analysis. The duration of stimulus presentation was varied between 30 s and 120 s.

2.2.3. Experimental procedure

The respective experimental animal placed its snout on a target in the animal's compartment (Fig. 1) and remained there watching the stimulus throughout the stimulus presentation. As the presentation of optokinetic responses was discontinuous at the beginning of the training, the animals were reinforced for paying attention to the stimulus and, therefore, showing optokinetic responses. The amount of optokinetic responses necessary for a reward was then increased, and during data collection, reinforcement could be shifted to the end of the stimulus presentation after the animals had remained at the target and had shown optokinetic eye movements. Between stimulus presentations, the animal could swim for some time or was trained on an easy task to maintain a high level of alertness. For monocular testing, the animal was equipped with a mask. This mask covers one eye with neither placing pressure on the covered nor on the uncovered eye. During data collection, we randomly presented stimuli with different velocities and orientations.

2.2.4. Analysis

All video recordings were digitized. Video sequences were converted into single frames (sampling rate 25 Hz). In order to assess the start- and endpoint of the optokinetic slow phase eye movement, we scanned all frames visually. Two frames were extracted: the start of the slow phase eye movement which could be detected after the saccade (fast phase; Fig. 2A) and the end of the slow phase eye movement which was clearly defined by the onset of the saccade (Fig. 2B). These two frames were further analyzed in Scion Image 4.0.2 for Windows (Scion Corporation, Frederick, MD, USA) and Corel Draw Graphics Suite 12 (Corel Corporation, Ottawa, Canada). To obtain the amplitude of the slow phase gaze movement, a circle with a diameter of 40 mm (value represents mean hor-

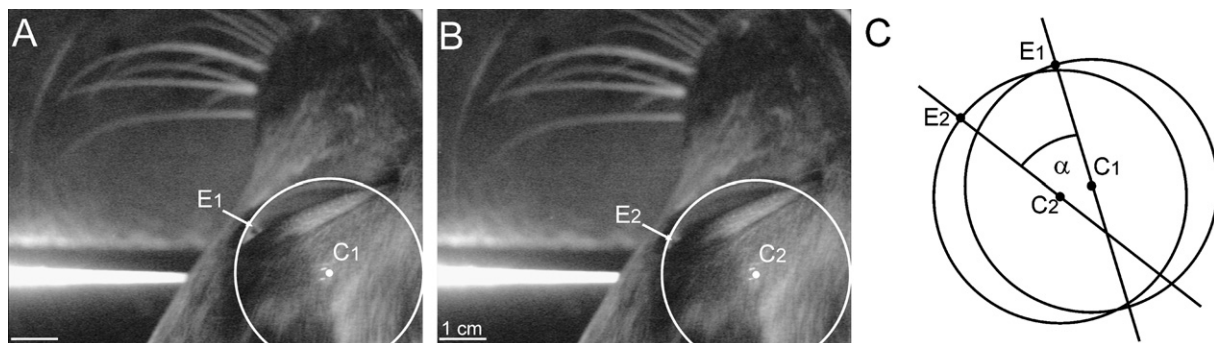


Fig. 2. Examples for start frame (A) and end frame (B) of one slow phase movement in naso-temporal direction. Arrows point on the point of reference (E_1 on start frame, E_2 on end frame) on the animal's conjunctiva. C_1 (on start frame) and C_2 (on end frame) represent the eye's assumed center of rotation which was determined by fitting a circle of 40 mm diameter to the visible part of the eye. (C) Slow phase amplitude was calculated as the angle of intersection α between line E_1C_1 on the start frame and line E_2C_2 on the end frame.

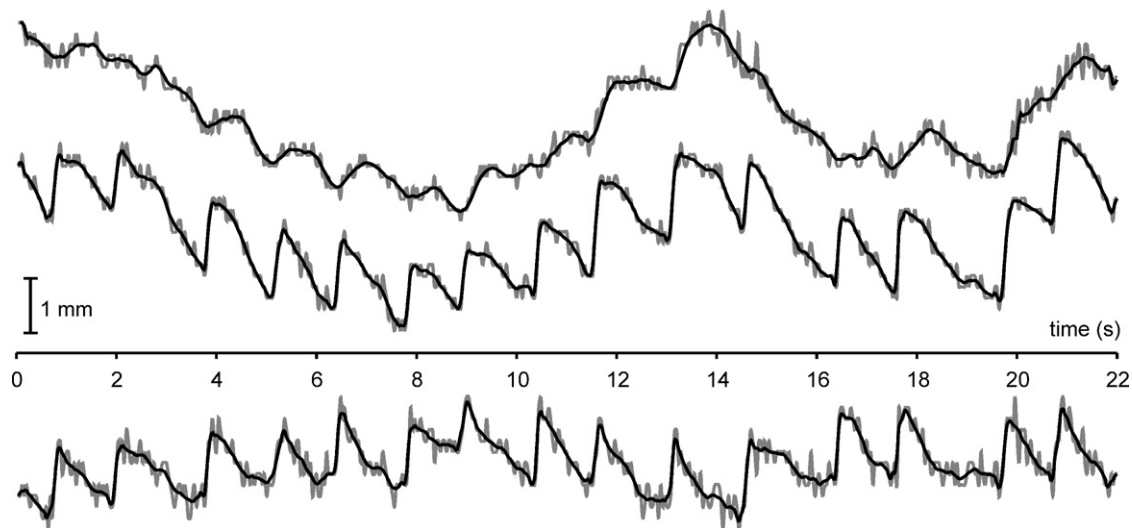


Fig. 3. Example optokinetic traces of one harbor seal. From top to bottom: head movement (measured), eye in space (gaze; measured), and eye in head (calculated). Downward deflection corresponds to a movement to the left side (scale 1 mm). Stimulus velocity was 10 deg/s, and stimulus movement was from the animal's right to its left. Lines in grey represent the tracing of the respective points, remaining noise is due to measurement errors in tracing the points of reference and does not represent a real movement. In order to approach the real movement of head, gaze, and eye in head, we smoothed our data by a moving average filter (black lines).

horizontal eye diameter of four dissected adult harbor seals' eyes) was fit to the visible part of the eye (Fig. 2). The center of this circle was defined as the center of rotation (C; Fig. 2) of the eye. In both the start and end frame of the slow phase movement, the coordinates of the center of rotation as well as the coordinates of the pigmented spot on the conjunctiva (point of reference) was extracted. Slow phase amplitude was determined as the angle of intersection α between line 1 on the start frame and line 2 on the end frame (lines defined by the point of reference and the center of rotation; Fig. 2C). Clearly discernable fur pigmentation on the forehead served as a scale. Slow phase gaze velocity was calculated as the quotient of the amplitude (in degrees) and the duration (sum of frames in seconds) of the eye movement.

In order to illustrate the movement of head, gaze (eye in space), and eye in head (Fig. 3), we traced the point of reference on the head close to the eye and the point of reference on the conjunctiva and recorded the coordinates of these two points in every frame for 550 frames (22 s). These coordinates were plotted as a function of time. The trace of the eye in head was derived by subtracting the movement of head from the movement of gaze.

Furthermore, we analyzed all intersaccadic intervals occurring during a stimulus presentation of 1 min per stimulus configuration (Fig. 5). The time between consecutive saccades was calculated by the number of frames (sampling rate 25 Hz). This way, we analyzed the results of both eyes of one animal as responses to both stimulus directions (naso-temporal, temporo-nasal) and summarized all results for each of the 8 stimulus velocities. One histogram was created for every stimulus velocity. For each histogram, the number of intersaccadic intervals within a 0.25 s-interval are counted and plotted as a function of time (Fig. 5).

We tested for significant differences ($p < 0.05$) using an univariate 2-way ANOVA with one dependent (gaze velocity) and two independent (stimulus velocity and stimulus orientation) variables.

2.2.5. Analysis of possible errors

The accuracy of the determination of the coordinates of the point of reference on the conjunctiva highly influenced the result. To estimate the error, we analyzed six randomly chosen slow phases twice without knowing the results and the coordinates of the first measurement. This way, errors occurring while tracing the point of reference were estimated as being 0.1–0.6 pixels. This inaccuracy produced errors of 0.5–10.8% con-

cerning typical gaze velocities of approximately 5 deg/s. The error in determining the coordinates of the eye's center of rotation also affected the result and was estimated as 0.1–0.7 pixels (1.6–7.2%).

When watching the stimulus on the tangent screen under different angles, the animal experienced different velocities which is another factor influencing the result. The whole projection is seen under an angle of 108 deg (see Section 2.2.2), so the harbor seal sees the projection's edge at a lateral angle of 54 deg to the left or right side. Under this viewing angle, the distance over which the stimulus moves seems shorter, by a factor of $\cos(54 \text{ deg}) \approx 0.6$, than it actually is. Therefore, while looking on the edge of the tangent projection compared to looking on the center, the animal would have experienced a 40% lower velocity. The mean stimulus velocity averaged over the field of view was 86% of the maximal velocity straight ahead.

Furthermore, the experienced stimulus velocity decreases with translational following head movements. Considering a translational head movement of 5 mm in stimulus direction lasting 1.5 s measured for a stimulus moving 5 deg/s, the seal would have actually experienced a 6% slower stimulus.

3. Results

3.1. General observations

All tested animals showed optokinetic eye movements as a response to a presented black-and-white bar pattern. An illustration of the rhythmic movements of head, gaze, and eye over time is given in Fig. 3. Remaining noise (grey lines; Fig. 3) is due to the measurement errors while tracing the point of reference on the eye's conjunctiva and does not reflect real head, gaze or eye movement. Real head, gaze or eye movement is approximated by smoothing the original data with a moving average filter (black lines; Fig. 3). As can be seen in Fig. 3, the main experimental animal ("Henry") moved its head in small amplitudes. After several experimental sessions, it positioned itself in a very

constant way in front of the screen with the body axis perpendicular to the projection showing pronounced eye movements accompanied by small head movements.

The establishment of the stimulus condition proved to be difficult. Our main experimental animal did neither react with optokinetic eye movements when presented with a small sized ($0.7\text{ m} \times 1.5\text{ m}$) random dot display nor with the projection of a swarm of herring (comparable size as the finally used black-and-white stripe pattern). Very fast, bright, and high contrast stripe patterns did not lead to an optokinetic nystagmus either. Under these circumstances, the animal just showed saccades or no eye movements at all. The same observation was made when the animal's head was further fixed with a lower jaw station. Without any head fixation, head movements were performed against the stimulus direction coupled with eye movements compensating head movements (vestibulo-ocular reflex, VOR) or the animal was swimming vigorously against the front door of the projection chamber in direction to the screen. Reducing the overall illumination in the animal's compartment and using a black-and-white stripe pattern with reduced contrast (contrast = 0.5) finally proved to be an appropriate optokinetic stimulus configuration.

After the establishment of the stimulus condition with our main experimental animal, the other animals showed optokinetic responses when presented with the stimulus configuration for the first time. However, the rhythmic pattern was often interrupted by fixation phases.

During detailed measurements with our main experimental animal, all stimulus velocities resulted in the presentation of optokinetic responses. With the onset of the stimulus, the eyes always made a saccade against the stimulus orientation. The following eye movements rarely led to the very temporal or nasal corner of the orbit, but instead a saccade repositioned the eye more centrally before the following eye movement led to the maximal

angle of rotation. Especially with stimuli moving temporo-nasally, the saccades did not reposition the eye in the original starting position but the eyes continuously drifted to very temporal positions over the complete stimulus presentation time. Thus, the average eye position (the "Schlagfeld", Jung & Mittermaier, 1939) is shifted against the direction of stimulus motion. Velocities up to 20–25 deg/s were followed by an unbroken stream of optokinetic nystagmus, but with higher velocities, the optokinetic response was more and more discontinuous, and sometimes saccades were elicited in direction of the stimulus and against it.

3.2. Binocular optokinetic nystagmus

3.2.1. Horizontal optokinetic nystagmus

During binocular stimulation both stimulus directions elicited optokinetic responses in all tested animals ($N = 4$). Fig. 4 shows the relation between gaze gain and stimulus velocity (gain 1.0 corresponds to perfect image stabilization). Each data point represents the mean gaze velocity of 10–109 analyzed slow phases obtained during several sessions. Gain, defined as the angular velocity of the eye divided by the angular velocity of the stimulus, is generally low. Gain decreases with increasing stimulus velocity. The univariate 2-way ANOVA tests of between-subject effects revealed a significant relation between gaze velocity and stimulus velocity for both eyes (left eye: $F = 16.371$, $p < 0.001$; right eye: $F = 47.114$, $p < 0.001$).

The shape of the curve is not comparable to curves obtained from e.g. the cat (Collewijn, 1985; Donaghy, 1980; Schweigart & Hoffmann, 1988). While in cats unity tracking occurs until a certain stimulus velocity is reached (cut-off frequency) beyond which gain drops drastically, we observe a more linear relation between gaze velocity and the logarithmic values of stimulus velocity. Interestingly, the curves resemble more those of goldfish (Dieringer

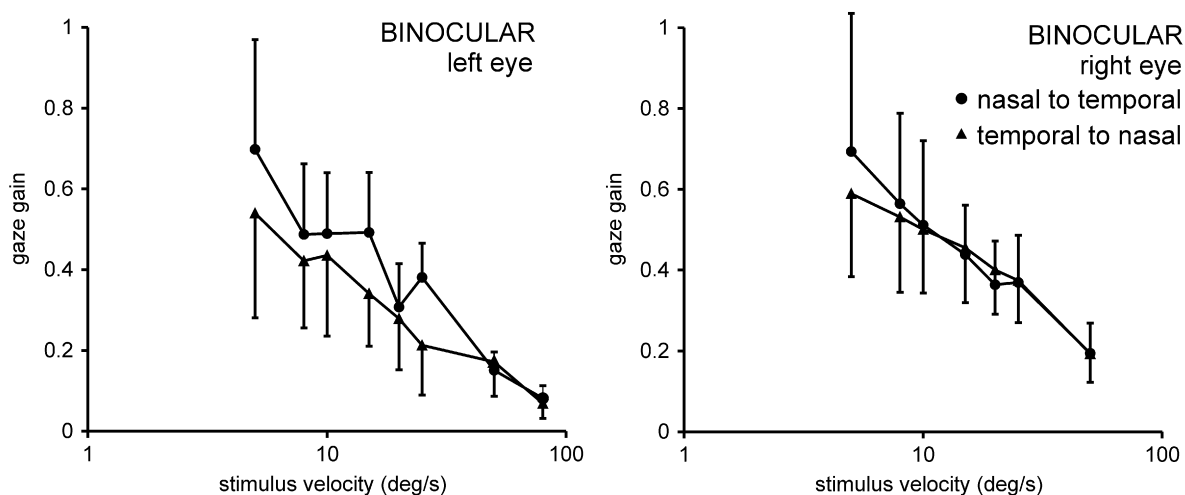


Fig. 4. Results of binocular horizontal optokinetic measurements of one harbor seal. OKN gain (gaze velocity/stimulus velocity; mean value with SD) is plotted versus stimulus velocity for binocular viewing conditions for the left (left panel) and right eye (right panel). Each panel shows two curves illustrating the optokinetic response of the respective eye to temporo-nasally (triangles) and naso-temporally (circles) moving stimuli.

et al., 1992; Schairer & Bennett, 1986) and of several other ostariophysan species (Dieringer et al., 1992) regarding their shape and relatively low gain values.

Mean gaze velocity never approaches stimulus velocity. Even for a stimulus velocity of 5 deg/s, mean gain for all measured eyes maximally reaches only 0.7. Presented with other stimulus velocities, mean gain for all measured eyes is always below 0.56. No significant difference occurs for the gaze velocities of the right eye comparing the two tested stimulus directions ($F = 0.700$, $p > 0.05$). However, for the left eye, gaze follows preferably a naso-temporally moving stimulus ($F = 8.921$, $p < 0.05$).

As the two eyes appeared to possess slightly different response characteristics, we recorded both eyes simultaneously during the same stimulus configuration to reveal possible asymmetries or disjunct movements of the left and right eye. We measured gaze velocities of the left and right eye recorded simultaneously for 50 slow phases at eight different stimulus velocities. Correlating all single measurements of the left with all the single measurements of the right eye, we found conjugate eye movements ($R^2 = 0.79$, $N = 50$). Symmetry indices defined as the ratio of gain of the eye moving naso-temporally to gain of the eye moving temporo-nasally ranged between 0.72 and 1 for the measured stimulus velocities. These data were obtained in one experimental session.

Gaze amplitude maximally reached 19.2 deg. Gaze velocities during the slow following motion never exceeded 20.8 deg/s. For a leftward stimulus movement, gaze velocities during the slow phase of OKN with maximal values of 13.3 deg/s (left eye) and 18.1 deg/s (right eye) were present whereas the reverse stimulus movement elicited maximal gaze velocities of 19 deg/s (left eye) and 20.8 deg/s (right eye).

Analyzing the intersaccadic intervals, we found that at high stimulus velocities, the intersaccadic interval histograms show narrow, symmetric peaks at approximately 0.75–1 s, whereas at low stimulus velocities, intersaccadic intervals are broadly distributed (Fig. 5). The interval between consecutive saccades can change by a factor of four and more while the animal is presented with a slowly moving stimulus. As we plotted the absolute frequency of OKN, Fig. 5 also shows that the intensity of OKN (number of OKN movements per time) increased with increasing stimulus velocity. The OKN becomes more and more regular with increasing stimulus velocity, however, at 80 deg/s stimulus velocity, the regular nystagmic pattern was interrupted by staring phases. The animal just occasionally showed OKN movements, and the intensity of OKN movements dropped (see Section 3.1).

3.2.2. Vertical optokinetic nystagmus

Concerning vertically orientated stimulus movements, the tested animal responded with OKN movements to both upward and downward directions. The gaze amplitudes for upward stimulus movement were significantly larger than for downward movement ($F = 5023.462$, $p < 0.05$) in our

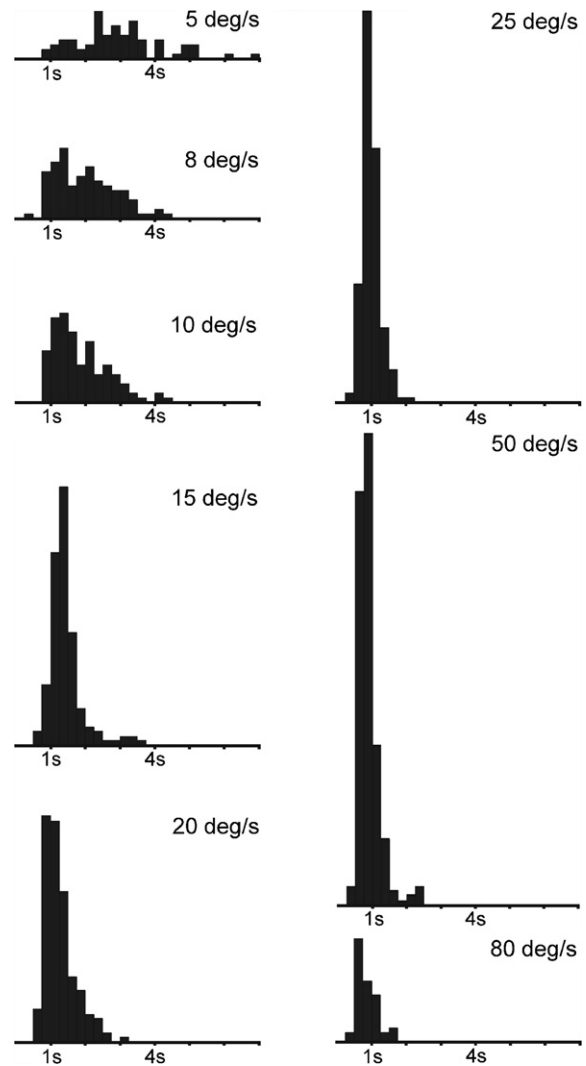


Fig. 5. Intersaccadic interval histograms of horizontal OKN. The absolute frequency of OKN movement is plotted. The intervals between OKN movements were binned into 0.25 s-segments. For each of the eight stimulus velocities, data for 1 min viewing for four configurations (two eyes, two horizontal stimulus directions), resulting in 4 min of data for each histogram, were pooled. The histograms are composed of 52–250 samples.

exemplary measurements (Fig. 6A). For a stimulus moving upwards, mean gaze amplitudes of 15.7 ± 6.7 deg (stimulus velocity 5 deg/s; $N = 6$) and 16.7 ± 8.7 deg (stimulus velocity 10 deg/s; $N = 11$) were recorded. The maximal gaze amplitude measured for an upward motion extended over 34.7 deg. In contrast, mean gaze amplitudes of 5.9 ± 2.2 deg ($N = 11$) and 7.1 ± 2.5 deg ($N = 13$) occurred for a downward stimulus movement of 5 deg/s and 10 deg/s, respectively. Mean gain was not significantly higher in one stimulus direction ($F = 5.376$, $p > 0.05$; Fig. 6B). Thus, the frequency of OKN movements was 2–3 times higher for downward compared to upward OKN. During vertical optokinetic stimulation, horizontal movements were observed as occasional features without a consistent amplitude or direction.

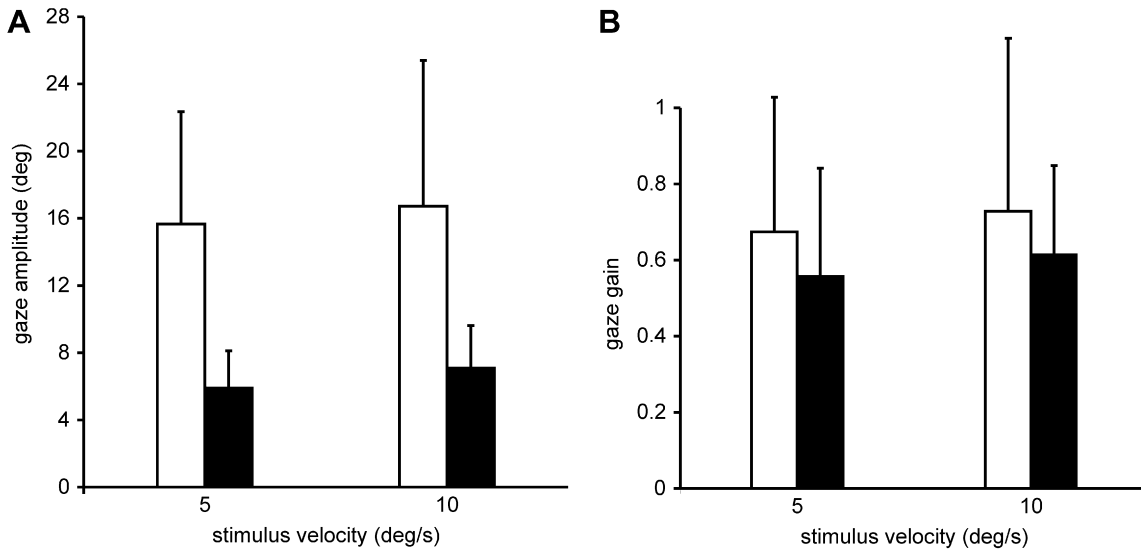


Fig. 6. Results of binocular vertical optokinetic measurements of one harbor seal. (A) Mean gaze amplitude (with SD) is plotted versus stimulus velocity. (B) Mean OKN gain (error bars indicating SD) is shown as a function of stimulus velocity. White bars indicate the responses to an upward, black bars to a downward moving stimulus.

3.3. Monocular optokinetic nystagmus

Under monocular viewing conditions, the tested harbor seal showed optokinetic responses for both stimulus directions (naso-temporally, and temporo-nasally). However, slow phase movements were often completely absent and just saccades in stimulus and against stimulus direction were shown. Furthermore, the animal tried to avoid watching the stimulus by e.g. directing its attention towards the non-moving part of the projection screen or seemed to stare on the projection screen without showing optokinetic responses.

The measurements (Fig. 7) obtained from one animal show a higher gain of OKN for a stimulus moving from

the animal's right to its left for both eyes except at the lowest stimulus velocity of 5 deg/s. For this velocity, a higher gain is elicited in both eyes for a stimulus moving rightward. For this rightward stimulus direction, the animal did not markedly change gaze velocity in relation to stimulus velocity (correlation between mean gaze velocity and stimulus velocity: left eye $R^2 = 0.59$, right eye $R^2 = -0.01$). However, for a leftward moving stimulus, mean gaze velocity increased by approximately a factor of three for both eyes. Maximum gaze velocities also show a pronounced difference for the two stimulus directions. During responses to a rightward stimulus movement, gaze velocities maximally reached 8.0 deg/s (left eye) and 7.2 deg/s (right eye). But a stimulus moving in the opposite direction

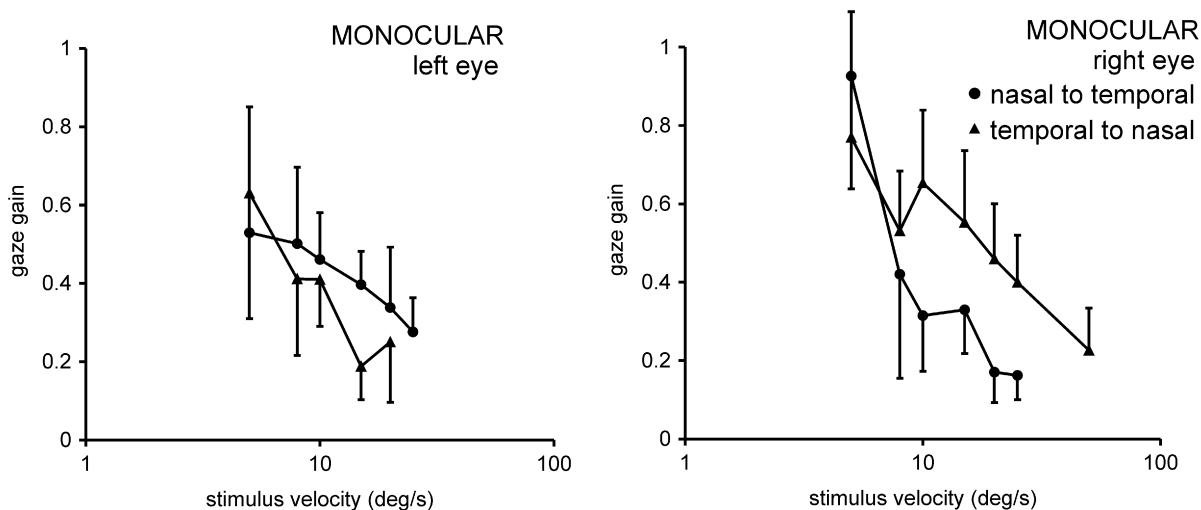


Fig. 7. Results of monocular optokinetic measurements of one harbor seal. OKN gain (gaze velocity/stimulus velocity; mean value with SD) is plotted versus stimulus velocity for monocular viewing conditions for the left (left panel) and right eye (right panel). As in Fig. 4, two curves illustrating the optokinetic response of the respective eye to temporo-nasally (triangles) and naso-temporally (circles) moving stimuli are shown for each eye.

(from the animal's right to its left) elicited maximal gaze velocities of 11.6 deg/s (left eye) and 24.1 deg/s (right eye), respectively.

4. Discussion

4.1. Characteristics of optokinetic measurements in the harbor seal

4.1.1. Methodological problems

One major limitation of this study is the fact that the presented data are measurements of just one animal which was available for extended measurements. The other animals could only be tested occasionally. Therefore, we cannot assess whether the detailed data obtained in one animal are representative for the species. However, the main experimental animal ("Henry") behaves normally, is experimentally highly experienced and does not show any visual deficits during daily tasks which make our data concerning this individual reliable.

In our study, slow phase gain is generally low. The question arises whether unity-tracking would have occurred with stimulus velocities below 5 deg/s. Unfortunately, we could not present these slow velocities due to artefacts in projection. However, in a variety of species, high gain values are only found at low stimulus velocities. Mice e.g. display gains of 0.7–0.8 constantly as a response to stimulus velocities not exceeding 8 deg/s, whereas gain decreased at higher stimulus velocities (Van Alphen, Stahl, & De Zeeuw, 2001).

If unity-tracking was found below 5 deg/s, our measurements would have been beyond the cut-off frequency at which gaze gain falls below one half its maximum (Ariel, 1990; Donaghy, 1980). The low cut-off frequency could be due to an ineffective stimulus configuration using a projected black-and-white bar pattern on a tangent screen. Collewijn (1985) reports that a real rotating drum is more effective than a projected pattern, and a random dot pattern is a better stimulus than a regular pattern in rabbits and cats. The effect of the stimulus configuration is also easily seen by comparing the results of optomotor studies in the cat. Donaghy (1980) used sinusoidally modulated gratings, Schweigart and Hoffmann (1988) used a random dot pattern projected on a tangent screen, and Collewijn (1985) used an optokinetic drum lined with a random dot pattern. Despite the fact that all studies found high gain values at stimulus velocities lower than the cut-off frequency, the estimated cut-off frequencies varied. While Donaghy (1980) reports a cut-off frequency of 4–8 deg/s, the break of the gain curve seems to occur above 20 deg/s (Schweigart & Hoffmann, 1988) or at 60 deg/s according to Collewijn (1985). Testing harbor seals under various stimulus conditions could clarify whether comparable effects would occur.

Generally, various factors could have negatively influenced gain as well as the overall optokinetic reaction. These

factors need to be considered concerning their effect on not only binocular but also on monocular OKN.

One of these factors influencing gain might be a change in alertness and attention of the animal during the course of the experiment. A reduced level of motivation could lower the overall optokinetic response (see Collewijn, 1985 for review; for saccades: Crommelinck & Roucoux, 1976). To maintain alertness in "head-fixed" situations, Schweigart and Hoffmann (1988) injected Met-amphetamine-hydrochloride subcutaneously. In their study, this was not necessary in "head-free" conditions in which the animal had to perform a special task. Our experimental situation also involved a training situation which forced the animal to maintain alertness and concentration to receive a fish reward. In addition, the soft training or pauses made after each stimulus presentation should have assured high responsiveness of the animal. We could not observe any obvious loss of motivation during an experimental session and during the whole time of data collection but it could have occurred unnoticed. Besides applying medication, another experimental approach to assure a high level of alertness could be in line with experiments in pigeons (Bilo & Bilo, 1978; Gioanni, 1988; Gioanni & Sansonetti, 1999; Maurice, Gioanni, & Abourachid, 2006). Pigeons experiencing frontal airflow in a flying posture displayed higher optokinetic, optocollic and vestibular gain. This can be due to the pigeon's increased attention induced by the airflow in flying condition or might indicate that the sensing of self-motion is crucial for a high level performance of optokinetic, optocollic and vestibular reflexes. Harbor seals could show a comparable effect according to the behavioral context, e.g. as a response to water flow mimicking swimming behavior.

The tangent projection could also lead to a reduction in gain. Due to the tangent projection screen, the stimulus velocity was 40% slower at the periphery compared to the center (see Section 2.2.5). The mean velocity of the whole projection amounted to 86% of the maximum velocity in the center. This change in velocity can account for some of the variation observed concerning slow phase gain even if it is unclear which velocity information—central, peripheral or an average over the whole or central field of view—the animal used.

Gaze velocity is also affected by the projection size. Goldfish e.g. display slow tracking velocities if the target size is reduced (Easter, 1972). In humans, pursuit velocity only reaches high values with full-field stimulation (Schor, 1993). It was speculated that smaller stimulus fields restrict the velocity range because of the proximity of stationary edges to the fovea (Schor & Narayan, 1981). So far, it is not known whether harbor seals possess an area centralis, but they probably do (see Section 1). However, the stimulus, covering $98^\circ \times 108^\circ$, is completely filling the binocular visual field of harbor seals which extends over 67° measured in air, leading to a binocular visual field of at least 42° calculated for underwater conditions (Hanke, Römer, & Dehnhardt, 2006). Thus, the animal should not have

experienced the borders of the projection within its assumed region of high resolution. Therefore, the projection size does not seem to be a factor lowering pursuit velocity in our case.

We tested optokinetic responses for just one set of black-and-white bars (nine black and nine white bars) and one contrast. These parameters might have been sub-optimal to elicit high gain values in harbor seals constantly. Our own observations (not quantified) reveal no consistent difference in OKN gain when the number of black and white bars was changed. Contrast as well as brightness used in our experiment was adjusted during the establishment of the stimulus environment because optokinetic responses were absent with high contrast pattern and very bright stimuli. However, we did not systematically change these values. The low contrast could have reduced gain in harbor seals analogous to the reduction found in cats (Donaghy, 1980) or goldfish (Easter, 1972). More data on contrast affecting OKN gain are needed in order to assess the influence of this parameter on slow phase gain in harbor seals.

The low gain could also be due to a deficit in the smooth pursuit system. Smooth pursuit could have come into play if the animal had paid attention to a single stripe and followed it across the projection screen. However, in our daily work with the animals, we observe that gaze is mainly saccadically redirected, and following of small sized objects is also saccadic. A poorly or not developed smooth pursuit system could lower gain below unity, as has been already discussed for cats (Godeaux, Gobert, & Halleux, 1983).

In general, it must be noted that the performance of the optokinetic system and the integrative performance of all fundamental visual or vestibulo-ocular reflexes in real life can only be assessed in a freely behaving subject (Collewijn, 1977). They may be much better during active behaviour when spatial orientation is essential compared to a laboratory test situation. Therefore, it would be interesting to e.g. mount a camera on a freely moving harbor seal comparable to the approach of Davies et al. (1999) continuously filming the eye. Corresponding experiments are currently developed in our lab.

4.1.2. Binocular horizontal OKN

Measuring our main experimental animal revealed an equally sensitive optokinetic response to naso-temporal and temporo-nasal stimulus motion for the right eye. However, a significant difference between the left eye's responses to the two stimulus movements (naso-temporal, temporo-nasal) is present. We think that these differences have to be mainly discussed considering the measurement errors. The overall pronounced variability of our optokinetic measurements accompanied by the measured high level of conjunction of left and right eye let us expect that extended optokinetic measurements in harbor seals would reveal symmetric optokinetic responses for horizontal stimulus movements for both eyes.

This assumed symmetry is in accordance with general considerations concerning eye placement and forward loco-

motion (Grasse & Cynader, 1988). Harbor seals are frontal-eyed animals. For them, movement ahead will not predominantly lead to a temporo-nasal movement of the retinal image (Carpenter, 1988) but rather to an expansion of the optic flow field from a focus straight ahead, and the optokinetic reflex can be equally sensitive to both horizontal directions of motion. If eye position is indeed also decisive for predicting optokinetic characteristics in marine mammals, a comparison of our data to optokinetic data of e.g. the California sea lion would be interesting as the sea lion's eyes are positioned more laterally. An aquatic species with lateral eyes is the goldfish. The properties of the OKN in goldfish have been studied extensively. However, the question concerning symmetric or asymmetric binocular horizontal OKN in goldfish cannot be answered with certainty as on the one hand, asymmetric OKN at low stimulus velocities (Dieringer et al., 1992; Easter 1972; Keng & Anastasio, 1997) is reported but on the other hand, a conjugate and symmetrical OKN was found (Marsh & Baker, 1997). In one study, even differences between individuals are reported (Easter, 1972). Further work is needed in order to better understand the relationship between eye placement and horizontal OKN in animals with amphibious or aquatic lifestyle.

Our harbor seal only occasionally followed the stimulus with the exact stimulus velocity (gain was usually smaller than 1). On the one hand, this has to be discussed in terms of methodological problems (see Section 4.1.1). But on the other hand, it could also reflect a tolerance to retinal slip velocities in harbor seals. During active head movements, humans can tolerate retinal image motion up to 4 deg/s without that vision is seriously affected (Steinman & Collewijn, 1980).

Furthermore, van der Steen and Collewijn (1984) discuss that perfect gaze stabilization might not be necessary during locomotion. But the harbor seals' predatory nature could require that gaze is redirected under oculomotor control relatively precisely corresponding to a high resolution area in the retina in order to hunt successfully. Assuming the presence of a specialized area in the retina as has been discussed in the introduction, it could have a streak-like appearance which makes the retina more tolerant to horizontal displacement. In harp seals (Mass & Supin, 2003), which are phocid seals with eye sizes comparable to harbor seals, the area possessing ganglion cell densities equal or greater than 60% of the greatest ganglion cell density extends over 6.5 deg horizontally. An area centralis of this kind would be 6.5 times wider compared to the human fovea which is supposed to cover 1 deg on the horizon and could explain a higher tolerance to retinal slip velocities.

Many studies have been conducted with the head completely stationary which does not reflect natural behaviour (Leigh & Zee, 1999). Most organisms use a combination of eye and head movements to visually track targets, stabilize moving objects or whole-field motion. Our setup allowed for small head movements. Analyzing gaze velocity under

voluntary positioning of the head, both eyes showed maximal gaze amplitudes of 18–20 deg for stimuli moving from left to right, for the reverse stimulus direction gaze amplitudes of 15–19 deg occurred. Hanke et al. (2006) showed that a harbor seal was able to rotate its eyes up to 12 deg in the head horizontally. Considering this amount of eye movement, the head would have contributed 33–44% (stimulus moving from left to right), 20–37% (stimulus moving from right to left), respectively. However, our observations suggest that head movements were less pronounced in our experiments (see Section 3.1). Under completely free conditions without fixation, gaze changes could be mainly performed by the head comparable to cats in which the head contributes 40–80% to gaze slow phase (Schweigart & Hoffmann, 1988) because harbor seals possess highly flexible necks. But considering streamlining underwater, it would be advantageous for seals to move only their eyes (eye-in-head-strategy) instead of the whole head (head-on-body-strategy). The large visual field of harbor seals (Hanke et al., 2006) might support the eye-in-head-strategy allowing the seal to scan a large part of the scene without a need of significant head movements. However, even if under natural conditions the contribution of the head was higher than in our experimental situation, slow phase velocities would not necessarily increase as has been shown in cats in a comparison between “head-fixed” and “head-free” conditions (Schweigart & Hoffmann, 1988).

Generally, the optokinetic nystagmus in harbor seals is very rhythmic. This is especially evident with stimulus velocities between 15 and 50 deg/s. With very fast stimulus velocities, the OKN turns irregular and discontinuous as has been described for humans as well (Cheng & Outerbridge, 1974). Below 15 deg/s, the analysis of intersaccadic intervals showed that, also comparable to humans (Cheng & Outerbridge, 1974), the nystagmus becomes more irregular and its intensity decreases. The distribution of intersaccadic intervals is very broad with low stimulus velocities but we could not observe a distinctive multimodal pattern as described by Cheng and Outerbridge (1974).

4.1.3. Binocular vertical OKN

We could show that both vertical stimulus movements elicited optokinetic responses with no significant difference in mean gaze gain for the two tested stimulus velocities. Although gaze amplitudes as a response to an upward moving stimulus were larger compared to those following a downward stimulus movement, gain was not significantly higher for one stimulus direction because the seal displayed downward OKN movements with a higher frequency.

The ability of our harbor seal to equally pursue vertical up- and down-stimuli is an interesting finding as this response symmetry has not been reported so far in any species. In the animal kingdom, e.g. cats (Grasse & Cynader, 1988), squirrel monkeys (Takahashi & Igarashi, 1977), and rhesus monkeys (Matsuo & Cohen, 1984) poorly respond to downward stimulus movement in the vertical

domain. However, this asymmetry observed in cats and monkeys was more obvious at higher stimulus velocities which we did not test in our experiments. The response characteristic of human vertical OKN is highly variable with e.g. different individuals showing different preferences. Furthermore, according to Murasugi and Howard (1989), the experiments dealing with human vertical OKN have to be discussed methodologically. Nevertheless, humans also seem to display higher OKN gain as a response to upward stimulus motion (Murasugi & Howard, 1989; van den Berg & Collewijn, 1988).

The reduced sensitivity to a downward moving stimulus has been explained in terms of preventing the eye from rotating downwards while walking over a highly-textured ground (Schor, 1993). This means that the OKN is largely insensitive to the main optic flow experienced during forward locomotion as has already been explained for horizontal OKN.

The difference between the response characteristics of organisms to vertical stimulus motion could be discussed in respect to differences in heights of eye level (Takahashi & Igarashi, 1977). They suggest that animals with low placed eyes do not respond well to a downward moving stimulus due to the direct vicinity to the plane of main optic flow. Harbor seals' eyes are placed more dorsally indicated by their vertical cyclopean visual field which extends over just 12 deg ventrally but 69 deg dorsally (Hanke et al., 2006). Forward locomotion should therefore induce mainly upward optic flow which could have turned the eyes less responsive to upward moving stimuli. However, this effect was not found in our harbor seal. One could speculate that the natural environment of harbor seals compared to that of terrestrial carnivores renders the eye equally sensitive to all vertical stimulus directions as it rarely exposes harbor seals directly to a horizontal plane. Harbor seals swimming in the water column can either refer to none, to one or to two horizontal planes, i.e. the water surface and the bottom. The position of these reference planes can also change when the seal rotates its body while swimming. Therefore, it could be the missing asymmetries in the optic flow in the vertical that render asymmetric vertical optokinetic responses normally found in terrestrial organisms symmetric (see Section 4.2).

In line with the extended dorsal visual field, vertical gaze amplitudes were larger for an upward than for a downward stimulus movement. However, they did not reach the dorsal eye movement amplitudes of 64 deg reported in Hanke et al. (2006). This cannot be explained by the extensions of the stimulus on the projection screen. Vertically, the projection extended over 98 deg of the animal's visual field. As the animal was positioned in the center of the projection, it could have raised the eyes by an amount of 49 deg before reaching the projection's edge which has not been achieved even with the largest gaze movements. It could be that the eye amplitudes shown by our experimental animal suit the eye muscles' actions best (Carpenter, 1988).

Larger amplitudes as a response to an upward moving stimulus are in line with observations on seals approaching prey from below (Davies et al., 1999; Hobson, 1966) and in line with our own observations that harbor seals are often swimming upside-down which might be explained in terms of scanning the water body below (Hanke et al., 2006).

4.1.4. Monocular horizontal OKN

Under monocular viewing conditions, the harbor seal showed optokinetic responses to both horizontal stimulus directions. However, for both eyes, gain was always higher for a stimulus moving leftward than for the reverse stimulus direction concerning stimulus velocities higher than 5 deg/s. Monocular asymmetries reported in other studies represent a complete lack of optokinetic responses (optokinetic unidirectionality) or minor responses to a stimulus moving from nasal to temporal. This asymmetry has been explained in terms of preventing especially laterally-eyed animals of responding to naso-temporal optic flow produced by forward locomotion (Gioanni, Rey, Villaboiss, & Dalbera, 1984; Howard & Gonzalez, 1987). However, this aspect could only explain the data presented for the right eye. The data for the left eye show an inversed asymmetry, i.e. a stronger OKN in the naso-temporal than in the temporo-nasal direction. As harbor seals possess a frontal eye position, we would have expected to measure a symmetrical monocular optokinetic response as has been found in, e.g. ferrets, cats, and primates. We therefore assume, in consistency with our data, that the harbor seal's response would have been symmetric in naso-temporal and in temporo-nasal direction in both eyes if it had not been superimposed by a general preference for right-to-left moving stimuli. We cannot assess whether the preference for a leftward stimulus movement is an adaptation to the changed requirements resulting in an increase in gain, a phenomenon reported, e.g. in humans (Collewijn, 1985) or goldfish (Easter, 1972; Marsh & Baker, 1997; Schairer & Bennett, 1986), as we presented mainly leftward moving stimuli during the establishment of the stimulus environment, or whether the animal showed a spontaneous preference for this stimulus direction.

4.2. General implications

This is the first study to show that a marine mammal, the harbor seal, shows an optokinetic nystagmus under water. It is thus demonstrated that harbor seals can perceive motion under water, making it likely that they can benefit from motion information concerning a wide variety of visual tasks, e.g. reconstructing the third dimension, segmenting the image, separation of figure and background, eliciting attention, encoding self-motion, mediating size constancy, and detecting moving objects (Nakayama, 1985).

Our study on the optokinetic nystagmus revealed equal sensitivity to all stimulus directions. This is surpris-

ing especially concerning the symmetric vertical OKN which has never been reported in any species before. In the underwater environment, the horizontal and vertical planes are both of importance. If we just considered translation for a swimming seal, the optic flow would consist of streams of images emerging from a focus of expansion straight ahead and disappearing into a focus of contraction behind (Miles, 1998). If the seal is also looking straight ahead, it experiences an expanding world with only the most distant objects in the visual scene being stable on the retina. When looking to one side, all objects seem to pivot about far, stable objects. To be able to fixate an object, e.g. moving or non-moving prey, while looking to a side, the seal would have to compensate for its own motion with the help of compensating head and eye movements. However, the horizontal plane does not necessarily remain the main plane of reference as it does for e.g. the cat, even if it is climbing a tree. The significance of the horizontal plane has already been questioned for marine mammals in studies dealing with mental rotation as a cognitive aspect of vision (Mauck & Dehnhardt, 1997; Stich, Dehnhardt, & Mauck, 2003). Underwater, harbor seals sometimes even experience two horizontal planes of reference, the water surface and the ground. However, swimming at any depth in the water column without directly seeing the ground or the water surface, seals cannot or can only indirectly refer visually to the horizontal plane by, e.g. comparing the brightness around the body. The brighter water surface can rotate around the animal depending on the own body tilt as self-motion in harbor seals not only involves linear displacement or translation but quite often also rotations of head and body. Thus, the degrees of freedom are numerous since the location of the eye as well as of a target can change by rotations around three orthogonal axes and translations in three dimensions (Collewijn, 1985).

In our opinion, an eye with the ability to stabilize whole-field motion equally well in any plane, as our experiments indicate, could be perfectly tuned for an animal operating in the low structured, three-dimensional underwater world.

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