

RESEARCH ARTICLE

Saccadic movement strategy in a semiaquatic species – the harbour seal (*Phoca vitulina*)

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ABSTRACT

Moving animals can estimate the distance of visual objects from image shift on their retina (optic flow) created during translational, but not rotational movements. To facilitate this distance estimation, many terrestrial and flying animals perform saccadic movements, thereby temporally separating translational and rotational movements, keeping rotation times short. In this study, we analysed whether a semiaquatic mammal, the harbour seal, also adopts a saccadic movement strategy. We recorded the seals' normal swimming pattern with video cameras and analysed head and body movements. The swimming seals indeed minimized rotation times by saccadic head and body turns, with top rotation speeds exceeding 350 deg s⁻¹ which leads to an increase of translational movements. Saccades occurred during both types of locomotion of the seals' intermittent swimming mode: active propulsion and gliding. In conclusion, harbour seals share the saccadic movement strategy of terrestrial animals. Whether this movement strategy is adopted to facilitate distance estimation from optic flow or serves a different function will be a topic of future research.

KEY WORDS: Optic flow, Vision, Pinnipeds

INTRODUCTION

Optic flow, the pattern of visual motion elicited on the retina of a moving observer (Gibson, 1950), has been shown to be involved in tasks including object avoidance, gap passing, goal-directed locomotion and navigation. The use of optic flow has been widely studied in terrestrial and aerial species (e.g. Baird et al., 2011; Bhagavatula et al., 2011; Britten and van Wezel, 1998, 2002; Gu et al., 2010; Krapp and Hengstenberg, 1996; Kress et al., 2015; Sherk and Fowler, 2000; Srinivasan et al., 1996). In contrast, the use of optic flow has only recently been considered in aquatic animals (Gläser et al., 2014; Scholtyssek et al., 2014), beyond fish optomotor studies (e.g. Neuhauss, 2003). The ability to perceive optic flow could provide aquatic animals, such as seals (Gläser et al., 2014), with valuable information, especially under turbid water conditions. Although particles in the water impair object detection and visual resolution in seals (Weiffen et al., 2006) or plunge-diving cormorants (Strod et al., 2004), the optic flow created by swimming through these particles could be exploited for distance information. Swimming through particle-rich water, but also swimming close to the water surface or the ground, generates optic flow information

that could be analysed to extract information for underwater odometry, the guidance of locomotion or orientation.

In the first optic flow study involving a harbour seal (Gläser et al., 2014), the seal was presented with a 2D simulation of a linear forward movement through a dot cloud on an underwater projection screen, which is a classic paradigm also used for analysing optic flow perception in human and non-human primates (Britten, 2008; Warren, 2004). The seal very accurately indicated whether a cross superimposed on the flow field deviated from or matched the focus of expansion, the point from which the flow pattern seems to emanate and that corresponds to the seal's heading during a translational movement. The seal's performance was comparable to the performance of humans (Warren and Hannon, 1988; Warren et al., 1988) and monkeys (Britten and van Wezel, 1998, 2002; Gu et al., 2010).

In the present study, we analysed whether harbour seals use a saccadic movement strategy comparable to that of terrestrial species that either walk (Blaj and van Hateren, 2004; Geurten et al., 2014; Kress and Egelhaaf, 2014a,b; Ribak et al., 2009) or fly (Boeddeker et al., 2010; Collett and Land, 1975; Eckmeier et al., 2008; Geurten et al., 2010; Tammero and Dickinson, 2002; Van Hateren and Schilstra, 1999). This strategy compresses rotations into short burst-like movements, called saccades. Pure rotational optic flow does not contain any depth information (Koenderink, 1986; Koenderink and van Doorn, 1987). Therefore, it is generally a valid strategy to reduce rotation durations to enhance 3D information in the optic flow field. Stabilizing movements of the eyes would reduce the rotational component of the optic flow even further by shortening the rotation period. Fast body turns were previously observed in aquatic species such as fish (Easter et al., 1974; Easter and Nicola, 1997; Fernald, 1975, 1985); however, whether they are part of a saccadic movement strategy was not analysed. Just recently, a saccadic movement strategy has been documented for common cuttlefish (*Sepia officinalis*; Helmer et al., 2017). The presence of a saccadic movement strategy in seals might indicate an optimization of optic flow information, which is essential for a fast-moving harbour seal that needs to estimate distances to objects to safely navigate through the environment. There are many other beneficial effects of brief rotation periods, such as optical blur minimization, fixation of objects, stabilization of vestibular sensory organs, fast evasive manoeuvres or optimization of search patterns.

In general, aquatic animals show an intermittent locomotion pattern with phases of gliding and active propulsion. The interspersed gliding phases reduces the costs of locomotion drastically, which is crucial for a breath-hold diver (Gleiss et al., 2010; Kramer and McLaughlin, 2001; Weihs, 1973; Williams, 2001; Williams et al., 2000). As intermittent swimming and saccadic movement strategies segregate locomotion into distinct phases, their interconnection was additionally analysed.

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MATERIALS AND METHODS

Subjects

Nine harbour seals (*Phoca vitulina* Linnaeus 1758) served as experimental subjects. They were housed in seawater enclosures, netpockets made out of black net with a mesh size of 5×5 cm that are attached to black floating elements and directly inserted into the Baltic Sea, at the Marine Science Center Rostock, Germany. The experiments were carried out in accordance with the European Communities Council Directive of 24 November 1986 (86/609/EEC). According to Section 8 of the German Animal Welfare Act of 18 May 2006 (BGB I. S. 1206, 1313), we did not need approval or notification for experiments conducted in this study as they did not cause pain, suffering or injury to the animals.

Filming and analysis of swimming behaviour

Harbour seals were filmed with a hand-held digital video camera (30 Hz, Sony HDR-CX116, Sony Corporation, Tokyo, Japan). To minimize camera movements, only video sequences with a stable camera were used. Therefore, we analysed image movements by image registration algorithms with subpixel acuity (Guizar-Sicairos et al., 2008). The maximal image movement from frame to frame was 0.6%, whereas the cumulative sum of image movement of a whole sequence was 2.1% on average. The seals were filmed swimming within two enclosures. In the large enclosure (60 m×30 m×1.5–6 m), the camera was not fixed in position, and the camera axis was slightly tilted towards the water surface. This allowed for detailed analysis of the body orientation of the animals, but it should be noted that we could not record depth or roll information. Additionally, a careful analysis of head movements or translational velocities was impossible. In order to achieve better spatial resolution and to address these additional aspects of our analysis, harbour seals' movements were also recorded in a small enclosure (6 m×3 m×1 m) with a fixed video camera (15 Hz, B&S XC229SR) perpendicular to the water surface. The quality of these recordings allowed an analysis of head and body movements. Position and orientation of the seals' bodies and heads were obtained manually by marking the centre of mass of the body and head using ivTrace Image Analysis (<https://opensource.cit-ec.de/projects/ivtools>). The position and orientation information obtained for each single frame was further analysed in Matlab (The MathWorks, Natick, MA, USA). The peak velocities of saccades

were detected using a speed threshold of 80 deg s⁻¹, which was empirically determined. The start and end of a saccade were determined by searching for an inflection point in the velocity–time curve or when the yaw velocity reached 0 deg s⁻¹. We calculated triggered averages of the saccades using their peak velocity as a trigger. The angle between body long axis and movement direction (ψ) was calculated as in Collet and Land (1975) and Geurten et al. (2010).

We also analysed the occurrence of saccades during the two modes of intermittent swimming: active propulsion and gliding. If the seals were moving their hind-flippers, the seal was said to be engaged in active propulsion. In contrast, gliding phases were characterized by an absence of hind-flipper movements.

Statistical analysis was done using Fisher's exact permutation test and a *t*-test in Matlab. *P*-values were corrected with Benjamini–Hochberg's false discovery rate correction, if needed.

RESULTS

More than 5 h of video material from seals swimming freely in the large and small enclosure were collected. Through manual tracking and subsequent analysis, it became apparent that the seals performed saccadic body movements (Fig. 1). Their movement pattern could be split into two major categories: short saccades during which the body rotates and long periods of translational movements in between the saccades. All in all, 136 body saccades defined by rotation velocities of more than 80 deg s⁻¹ were detected. Subthreshold rotations were analysed in respect to their direction and duration. They do not represent prolonged bank turns as their duration was 320±120 ms. Furthermore, their direction was continuously alternating, which indicates that these subthreshold rotations were probably residual effects of the undulation of the body or digitization noise. The saccade threshold is in line with the harbour seal eye responding to stimulus velocities exceeding 80 deg s⁻¹ with only very low gain during optokinetic stimulation (Hanke et al., 2008). A saccade was completed within 412±40 ms on average, with the duration of single saccades varying between 200 and 900 ms (Fig. 2A). During a body saccade, the body reached rotation velocities between 96.4 and 388.7 deg s⁻¹ with an average velocity of 138.2±11.2 deg s⁻¹ (median±95% confidence interval; Fig. 2B) and a mean rotation angle of up to 30 deg (Fig. 2C). During free swimming, the seals were predominantly gliding (64%);

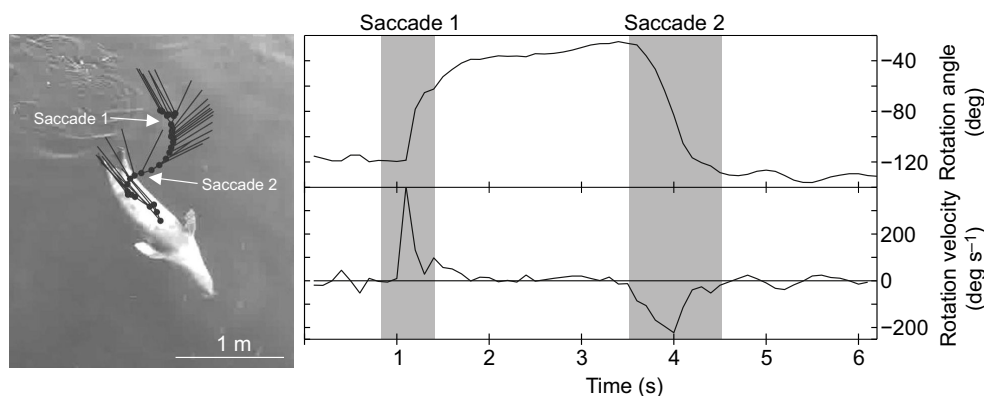


Fig. 1. Swimming path of a harbour seal showing body saccades. Left: the dots indicate the trajectory of the centre of mass of the seal body over a period of 6 s during which the seal was swimming in the large enclosure on an S-shaped path from the top to the centre of the field of view of the camera. Line segments indicate the yaw orientation of the body every 33 ms. The white arrows mark two body saccades, the first to the right and the second to the left of the seal body. Right: the rotation angle (top) and the rotation velocity (bottom) as a function of time for the movement of the seal depicted on the left. Rotations refer to yaw body rotations. Saccades (shaded in grey) are characterized as brief intervals during which the body drastically changes its orientation with high rotation velocities. In between the saccades, the seal showed almost constant body orientation.

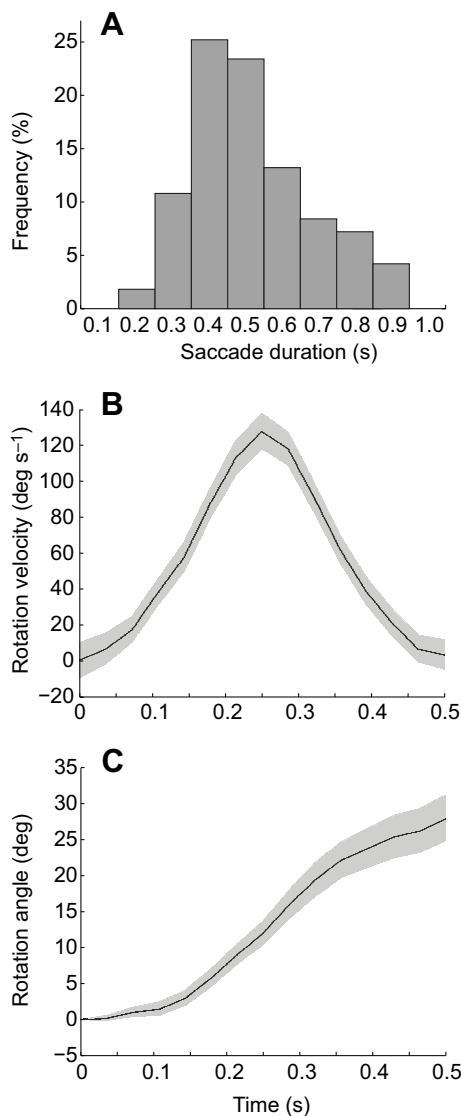


Fig. 2. Characterization of the seals' body movements. (A) The frequency of saccades of a specific duration (in bins of 100 ms), plotted as percentage of the total number of saccades ($N=136$). The majority of the saccades were completed within 400–500 ms. (B) Average rotation velocity and (C) average rotation angle during saccades ($N=136$). The solid line marks the median velocity (B) or angle (C), whereas the shaded area denotes its 95% confidence interval. Saccades to the right and left were similar and were thus pooled by mirroring. During a saccade, the seal body reached a mean rotation velocity of 138.2 deg s^{-1} and covered a mean rotation angle of up to 30 deg. Rotations refer to yaw body rotations.

however, saccades occurred irrespective of the mode of locomotion ($P>0.05$, Kruskal–Wallis; Fig. S1). In contrast, prolonged banked body turns (Fig. S2) were observed when a blindfolded seal followed the hydrodynamic trail left behind by a remote-controlled submarine (Dehnhardt et al., 2001; Schulte-Pelkum et al., 2007; Wieskotten et al., 2010). Thus, generally, seals can perform banked body turns; however, they do not perform these smooth rotations during free swimming but instead move in a saccadic fashion.

To analyse head and body movements, we had to increase the spatial resolution of the scenery and, therefore, had to film the seals in a smaller enclosure. Here, the seals' rotational speeds were reduced by 27% in comparison to their swimming behaviour in the large enclosure. We observed a similar trend in translational

velocities, which is probably due to the limited amount of space they had to accelerate in. Analysing head and body movements revealed that the seals are able to move their heads and bodies independently, and the respective movement patterns of both are saccadic. During 150 body and head saccades, the head reached its peak velocity on average 733 ms before the body's point of peak velocity (Fig. 3A). The time difference between the peak yaw velocity of the head and body saccades showed that in 80% of cases the head movement precedes movement of the body (Fig. 3B). While the body was still rotating, the head showed a counter-rotation, which ultimately stabilizes head orientation. Head saccades were found to be approximately 200 ms shorter than body saccades ($P<0.01$, Fisher's exact permutation test), and saccades of both head and body were significantly shorter than translational movements ($P<0.01$, Fisher's exact permutation test; Fig. 3C). Additionally, head saccades reached higher peak rotation velocities than body saccades ($P<0.05$, Fisher's exact permutation test; Fig. 3D). Rotation velocities of the head amounted to $80.6\text{--}196.7 \text{ deg s}^{-1}$ or $100.9\pm 3.2 \text{ deg s}^{-1}$ on average, whereas rotation velocities of $30.5\text{--}134.8 \text{ deg s}^{-1}$ with an average of $51.1\pm 7.4 \text{ deg s}^{-1}$ were obtained for the body. During translational bouts, the head was more stabilized against residual rotation than the body. On average, the residual body yaw velocity was $15\pm 3.8 \text{ deg s}^{-1}$ whereas the head moved at a slower yaw velocity of $9.6\pm 0.6 \text{ deg s}^{-1}$ ($P<0.001$, Fisher's exact permutation test). Although the angle between head and body (ψ) occasionally exceeded 100 deg, the orientation of the head and body only differed by approximately 10 deg during the intersaccadic interval, probably as a result of the undulatory swimming mode (Fig. 4). We calculated the cross-correlation of head and body yaw and normalized the coefficient to the autocorrelation (Fig. S3). This revealed that the angular velocities of the head and body were highly correlated and that the body followed the head with a lag of 600 ms, which is consistent with the timing difference in peak velocity during saccades. In conclusion, seals perform body saccades, which are accommodated by head saccades, thus massively reducing the time spent in rotations.

DISCUSSION

We have presented evidence that a mammal, the semiaquatic harbour seal, shows saccadic head and body movements. In our study, head and body movements of the seals were analysed as a first approximation for gaze movements (see Eckmeier et al., 2008; Kress and Egelhaaf, 2012; Kress and Egelhaaf, 2014b) because eye movements could not be resolved in our video recordings. Seals have mobile eyes (Hanke et al., 2006; Hanke et al., 2008), so saccadic eye movements might add to the saccadic head and body shifts, as was reported for goldfish (Easter et al., 1974) and cichlid fish (Fernald, 1975, 1985). Taking those active eye movements into account, it would be possible to extract 3D information even during mild rotations, e.g. during subthreshold rotations. It is, however, unlikely that the seal is actively prolonging the saccade duration by extra rotations of the eye, but this study cannot exclude this possibility. The analysis of eye movements in free-swimming seals will be a topic of future research.

Saccades in seals were of low rotation velocity, almost 14 times slower than the fastest body saccades documented so far, which are performed by fruit flies during escape (Muijres et al., 2014). However, in this context, it is remarkable that seals are able to perform body saccades in the first place as (1) they possess very large and heavy bodies, and (2) water is more dense and viscous than air. For birds with much smaller bodies flying through air, it has been speculated that the high inertia of their bodies explains the absence of

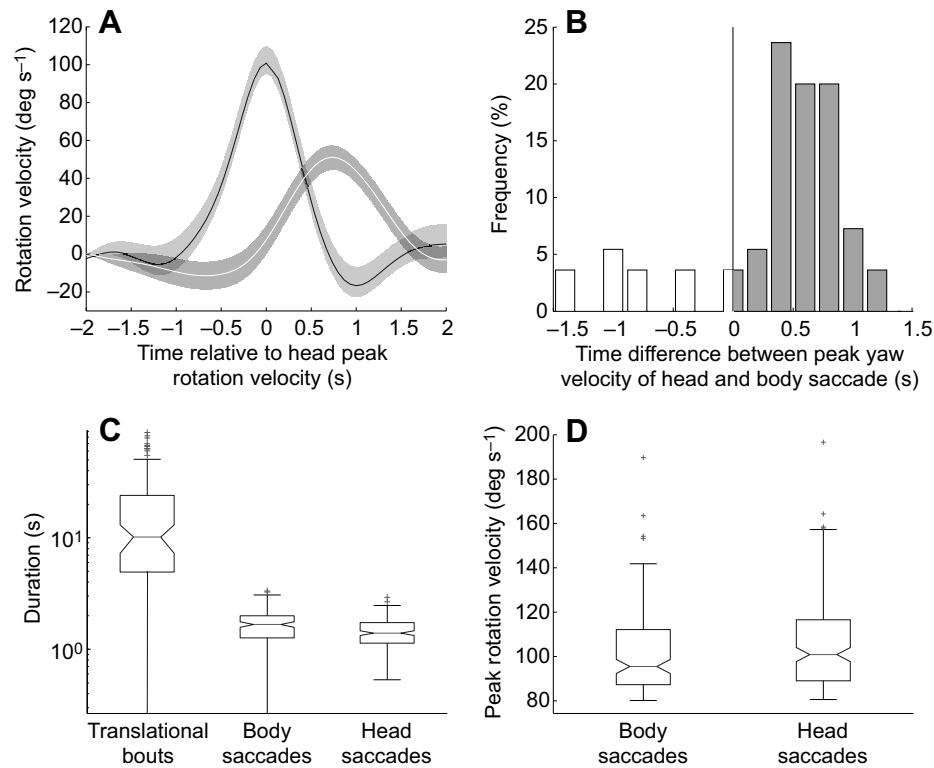


Fig. 3. Characterization of the seals' head and body movements. (A) Average rotation velocity of the head (black line) and body (white line) during saccadic movements as a function of time based on 150 head and body saccades. The head moves on average 733 ± 95.3 ms before the body and reaches a higher rotation velocity. (B) Frequency with which a specific time difference value between the peak yaw velocity of the head and body saccade occurs as a function of total events. In most instances, the head moved faster than the body (grey bars; $P > 0.01$, t -test) and only rarely the body moved faster than the head (white bars). (C) Boxplots for the duration (logarithmic scale) of translational bouts, and body and head saccades. The median is shown as the central horizontal line. Boxes indicate the 25% and 74% quantile. The notches inside the boxes denote the 95% confidence interval of the median. Non-overlapping notches indicate that the median of two datasets is significantly different. The whiskers show 1.5 times the interquartile range; crosses are outliers. Translations are significantly longer events than body and head saccades, and head saccades are the fastest events ($P < 0.01$, Fisher's exact permutation test). (D) Boxplots for the peak rotation velocity for body and head saccades. Conventions as in C. During head saccades, higher peak rotation velocities are reached in comparison to those during body saccades ($P < 0.05$, Fisher's exact permutation test). Rotations refer to yaw body rotations.

saccadic body turns (Eckmeier et al., 2008). An additional factor that was suggested to explain the bird's inability to perform body saccades is their high flight velocity (see e.g. Eckmeier et al., 2008), which is much higher than the flight velocities reached by insects. In contrast, harbour seals typically swim at a velocity of 2 m s^{-1} (e.g. Bodson et al., 2006), thus they move at an intermediate speed to birds, at the upper end, and insects, at the lower end. The seals' moderate velocity of movement might make body saccades possible in the first place. In common cuttlefish, saccades are performed depending on the type and, thus, also depending on the speed of movement; if they are swimming at high velocity propelled by their siphons, they abolish saccadic movements (Helmer et al., 2017).

In seals, head saccades reach higher velocities and are shorter than the corresponding body saccades. This pattern has also been found in walking and flying species (e.g. Blaj and van Hateren, 2004). The fact that the head rotates faster is easily explained by (1) the head being much lighter than the body, and thus less force has to be overcome, and (2) the head saccade being performed together with the body saccade. As their heads are able to turn faster than their bodies, seals can further reduce the rotation time. Compensating eye rotations would reduce the rotational duration even further and are likely to occur. Furthermore, it is also highly possible that the eyes rotate to fixate to new objects of interest. However, unfortunately, our data do not encompass eye movements, which must be the subject of future studies.

The head saccades of seals also start earlier than the body saccades; the body begins to rotate when the head reaches its peak velocity ($P < 0.01$, t -test). This pattern contrasts with what has previously been documented for insects, for which either head and body saccades start at the same time (Blaj and van Hateren, 2004), are aligned by their peak in rotation velocity (Blaj and van Hateren, 2004; Geurten et al., 2014) and end at the same time (Geurten et al., 2010) or the body saccade starts earlier and ends later than the corresponding head saccade (Boeddeker et al., 2015; Schilstra and van Hateren, 1998). As in walking insects (Blaj and van Hateren, 2004), the mechanical destabilization of the body induced by an earlier initiation of the saccade of the head in comparison to the body and a corresponding counter-yaw of the body might be minimal in swimming animals.

The presence of saccadic movements in harbour seals, together with the dataset obtained in common cuttlefish (Helmer et al., 2017), seems to corroborate the idea that this movement strategy is universal in the animal kingdom (Eckmeier et al., 2008). A saccadic movement strategy has now been documented in invertebrates and vertebrates, terrestrial and aquatic, irrespective of eye type and type of locomotion. Regarding the type of locomotion, we can add that, in seals, saccades occur regardless of the mode of forward swimming, be it active propulsion or gliding. It needs to be stressed that the seals' saccadic movement strategy does not ultimately result from an inability of seals to perform banked turns.

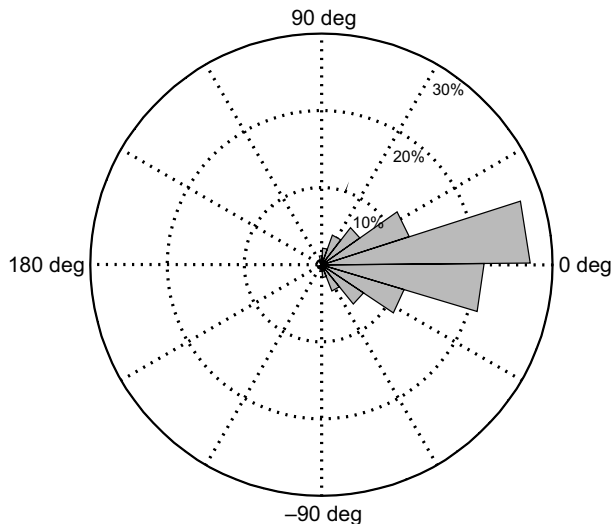


Fig. 4. Head/body coordination. Frequency depicted as percentage of total frames during translations ($N=31,833$) in which a specific angle between the animal's heading and its body long axis (ψ) occurred. If the body and heading are aligned, the angle is 0 deg, whereas angles are negative when the animal is looking to the left of its heading and angles are positive when it is looking to the right of its heading. In most instances, the seal's swimming direction and body were aligned within 30 deg to each side.

In contrast, seals move in banked turns under specific circumstances such as when following a hydrodynamic trail blindfolded.

There are various reasons why seals could perform fast rotational movements of the head and body (Boeddeker and Egelhaaf, 2005; Haselsteiner et al., 2014; Wagner, 1986). One explanation is that seals adopt a saccadic movement strategy to optimize the output from optic flow to gain distance information. A link between a saccadic movement strategy and distance estimation from optic flow has already been shown for numerous species (e.g. Eckmeier et al., 2008; Geurten et al., 2012; Kern et al., 2006; Tammero and Dickinson, 2002; van Hateren, 2005). If such a link is indeed revealed in future studies in seals, common cuttlefish (Helmer et al., 2017) and other (semi)aquatic animals, it would show that aquatic animals separate rotational from translational optic flow, complicated by optic flow being reduced to nearby regions underwater (Gläser et al., 2014; Koenderink and van Doorn, 1987; Lappe et al., 1999), in a comparable manner to terrestrial species, by reducing rotations to a minimum in the first place. Then, saccadic shifts would be a general solution to reduce the interference of rotational optic flow with visual perception. At the same time, the prolonged periods during which the animals perceive translational optic flow could enable distances to be estimated from optic flow as a vital outcome of visual scene analysis. Although seals also have the ability of stereopsis and might get 3D information for nearby objects via stereotriangulation, short rotations prove beneficial for other reasons as well: seals might be driven by rapid prey movement or during evasive behaviours to perform fast rotational movements of the head and body. Moreover, motion blur is reduced by fast rotations and vestibular sensation might be less influenced by a reduction of rotations.

In conclusion, harbour seals invest in a saccadic movement strategy. By moving their heads and bodies saccadically, comparable to the actions of many other species, they have the potential to use distance/depth information from the interpretation of the optic flow field mainly during translational phases, which will be addressed in future studies.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

All authors designed the study, B.R.H.G., B.N. and F.D.H. recorded the videos, B.R.H.G. and F.D.H. analysed the data, B.R.H.G. and F.D.H. wrote the manuscript, all authors edited the manuscript and gave final approval for publication.

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Data availability

The data can be downloaded from <http://cellneuro.uni-goettingen.de/downloads/sealsRawData.zip>

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.150763.supplemental>

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