

Hydrodynamic determination of the moving direction of an artificial fin by a harbour seal (*Phoca vitulina*)

S. Wieskotten¹, G. Dehnhardt¹, B. Mauck², L. Miersch¹ and W. Hanke^{1,*}

¹University of Rostock, Institute for Biosciences, Albert-Einstein-Strasse 3, 18059 Rostock, Germany and ²University of Southern Denmark, Institute of Biology, Campusvej 55, 5230 Odense M, Denmark

*Author for correspondence (wolf.hanke@uni-rostock.de)

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SUMMARY

Harbour seals can use their vibrissal system to detect and follow hydrodynamic trails left by moving objects. In this study we determined the maximum time after which a harbour seal could indicate the moving direction of an artificial fish tail and analysed the hydrodynamic parameters allowing the discrimination. Hydrodynamic trails were generated using a fin-like paddle moving from left to right or from right to left in the calm water of an experimental box. The blindfolded seal was able to recognise the direction of the paddle movement when the hydrodynamic trail was up to 35 s old. Particle Image Velocimetry (PIV) revealed that the seal might have perceived and used two different hydrodynamic parameters to determine the moving direction of the fin-like paddle. The structure and spatial arrangement of the vortices in the hydrodynamic trail and high water velocities between two counter-rotating vortices are characteristic of the movement direction and are within the sensory range of the seal.

Key words: harbour seal, vibrissae, hydrodynamic reception, PIV, vortex structure.

INTRODUCTION

While visual and auditory capabilities of pinnipeds have been studied quite intensively, little work has been done on their ability to perceive hydrodynamic stimuli. After some earlier studies have already shown that the vibrissae of harbour seals respond to vibrations mediated by a rod directly contacting the hair (Dykes, 1975; Mills and Renouf, 1986; Renouf, 1979), Dehnhardt et al. (Dehnhardt et al., 1998) demonstrated their function as a hydrodynamic receptor system using dipole water movements generated by a vibrating sphere, a technique commonly used to test lateral line function in fish (Bleckmann, 1994). In terms of particle displacement, absolute thresholds of the harbour seal (0.8 µm at 50 Hz) were in the same order of magnitude as those determined for the piscivorous sea snake *Lapemis curtus* (Westhoff et al., 2005), while thresholds of a California sea lion (*Zalophus californianus*) for hydrodynamic dipole stimuli of 20 Hz and 30 Hz were even lower (Dehnhardt et al., 2004). Further experiments with hydrodynamic dipole stimuli revealed that a harbour seal not only can detect but also can discriminate such water movements (Dehnhardt and Mauck, 2008). Presented with a stimulus amplitude of 3 µm at 40 Hz, the animal could discriminate a change in amplitude of 0.8 µm. In a sensory ecology approach, Dehnhardt et al. (Dehnhardt et al., 2001) demonstrated that harbour seals can use their mystacial vibrissae to detect and track hydrodynamic trails and thus most likely follow the hydrodynamic trails of fish, which can persist for up to several minutes (Hanke and Bleckmann, 2004; Hanke et al., 2000). To approximate the wakes of fishes, an autonomously running miniature submarine was applied to generate hydrodynamic trails. The blindfolded seals were able to track hydrodynamic trails as long as 40 m. However, when a stocking mask covered the seal's muzzle so that coupling of the whiskers to the water movements in the trail was impeded, the seals failed to detect the hydrodynamic trails. Recently, it has been shown that the subcarangiform or thunniform swimming style of phocid seals (Fish et al., 1988; Williams and

Kooyman, 1985) generates a hydrodynamic trail similar in structure to that left by fishes and that harbour seals can also follow such biogenic hydrodynamic trails (Schulte-Pelkum et al., 2007). Although the basic knowledge regarding this sensory system is now well established, further studies are needed to better understand the function and efficiency of hydrodynamic reception in seals.

Even the wake behind a small swimming goldfish (*Carassius auratus*) of 10 cm body length can contain water velocities significantly higher than background noise several minutes after its passage; thus, representing trackable hydrodynamic trails of considerable length (Hanke et al., 2000). Although fish trails are generally described to consist of vortices arranged in a highly complex, ladder-like three-dimensional pattern (Blickhan et al., 1992), their structure depends on the body shape and the swimming style of the species (Drucker and Lauder, 2002; Hanke and Bleckmann, 2004; Hanke et al., 2000; Nauen and Lauder, 2002b; Standen and Lauder, 2007; Tytell et al., 2008). According to flow measurements using Particle Image Velocimetry (PIV), the swimming direction of a fish is suggested to be derived from the velocity gradient in its wake and from the direction of gross water flow in the wake (Hanke et al., 2000). While there is already evidence that harbour seals can determine the direction of a moving miniature submarine from its wake (Dehnhardt et al., 2001), the main objective of this study was to investigate how the ageing of a hydrodynamic trail affects this ability, specifically with an artificial fish fin as the trail generator. Stimulus quantification using PIV allows the characterisation of the hydrodynamic parameters used by a seal to decide about the moving direction.

MATERIALS AND METHODS

Experimental subject

The present study was conducted at the Marine Science Center (Zoo Cologne, but see www.msc-mv.de), Germany. The experimental animal (Henry) was a 6-year-old male harbour seal (*Phoca vitulina*

L.). It was housed outdoors with seven other harbour seals in two interconnected freshwater pools with a total volume of about 1000 m³ and a maximum depth of 1.7 m. Henry had previous experience in performing hydrodynamic perception tasks (Dehnhardt et al., 2001). The animal received approximately 90% of its daily diet (3–5 kg of cut herring) during experimental sessions. Tests were carried out twice a day, on five days per week. During experiments, the seven other seals were separated from the test animal.

Experimental setup and stimuli

To achieve calm water conditions, experiments were performed in a closed experimental box (1.8 m × 2.0 m × 1.3 m, L × W × H) fixed on the bottom of the pool at a depth of 1.1 m (Fig. 1). A circular gate (40 cm in diameter) in the centre of the front wall of the box allowed the seal to swim into the box up to its pectoral flippers. Outside the box, two underwater response targets (small plastic spheres, Fig. 1) were mounted on both sides of the gate. Between the two response targets, a station target was fixed 20 cm above the water surface.

As the trail of a miniature submarine, like those used in our former studies, lacks the characteristic vorticity found in fish trails, fin-like paddles were used to generate the hydrodynamic trails. Two identical fin-like paddles were used for trail generation. Each trail generator consisted of a steel rod ending with a flexible plastic fin (2 mm thick, 227 mm², see Fig. 2). The paddle was moved parallel to the front wall of the experimental box. To control for the plane of movement the respective steel rod was moved along a horizontal guide rail fixed on top of the box. The artificial fin was at a depth of 0.8 m, 30 cm in front of the gate. The experimenter moved the paddle at a constant speed of approximately 0.2 m s⁻¹. The speed was verified using a camera above the experimental box (see Data recording and analysis section below). While moving, the fin pointed towards the seal at an angle of 45 ± 10 deg with the plane defined by the vertical steel rod and the direction of movement.

In order to avoid secondary cues from the final position of the trail generators, two identical paddles were inserted at the same side of the experimental box and only one of them was moved to the other side. Consequently, there was always one paddle on each side of the box during the decision process of the seal.

Experimental procedure

The animal was trained to discriminate the two possible moving directions of the artificial fin (from right to left or from left to right) using only the fin's hydrodynamic trail. Experiments were conducted according to a left/right forced choice procedure. A trial started with blindfolding the seal by an opaque stocking mask, leaving its mystacial vibrissae uncovered. The blindfolded seal pressed its muzzle on the station target, so that its head and vibrissae were above the water surface. In this position the seal was supplied with headphones, which transmitted pink noise for acoustical masking. Then the fin-like paddle was drawn from one side of the experimental box to the other. After completion of the hydrodynamic trail, the headphones were removed from the animal's head, indicating the start of a trial. Between trail generation and the start of a trial there was a minimum delay of 5 s. During a delay, the seal remained at the station target. As soon as the headphones were removed, the seal submerged immediately and entered the box through the gate up to its pectoral flippers. After trail detection the animal was required to respond by leaving the box and touching the left (moving direction of the fin from right to left) or right (moving direction of the fin from left to right) response target, respectively. Each correct directional reference was rewarded by a

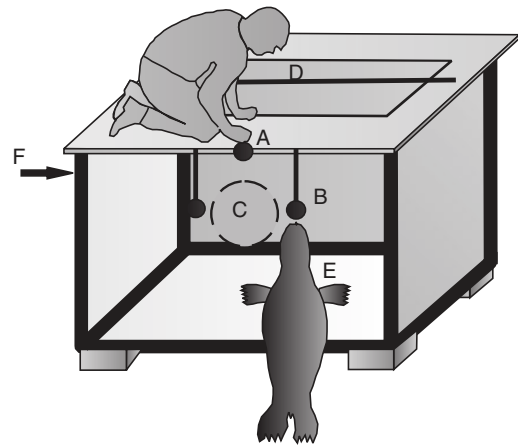


Fig. 1. Schematic drawing of the experimental box. A, station target; B, underwater response targets; C, circular gate; D, horizontal guide rail; E, experimental animal pushing the right response target; F, water level.

piece of cut herring. During the training phase, before delays longer than 5 s (10 s, 20 s, 25 s, 30 s) between trail generation and start of the trial were introduced, the seal was required to demonstrate its ability to perform the task by responding correctly in at least 90% of the trials for three consecutive sessions.

During the testing phase, 20 experimental sessions, each consisting of up to 30 trials, were conducted. In a session the direction of the moving fin and the delays were presented pseudorandomly (Gellermann, 1933). In order to obtain calm water conditions for every new trail generation, an inter-trial interval of at least 3 min was introduced.

As aquatic animals may also use chemosensory and/or acoustic input for the perception of hydrodynamic stimuli (Enger et al., 1989; Ferner and Weissburg, 2005; Pohlmann et al., 2001; Weissburg, 2000), control experiments were carried out during which the seal's mystacial vibrissae were covered by an elastic nylon stocking mask. This mask was permeable to water and allowed the animal to open its mouth for tasting water. The experimental procedure during control trials was identical to that of test trials.

Data recording and analysis

A total of 180 trials were recorded with a digital camera (Canon XL1S, Canon Inc., Tokyo, Japan) equipped with a wide-angle lens



Fig. 2. Artificial fin used for generation of hydrodynamic trails.

(3.4–10.2 mm, camera aperture: 1.8–2.2). This camera was mounted vertically over the experimental box at a height of 1.5 m. The recordings were digitally cut into single frames at a frequency of 5 frames s⁻¹. Frame-by-frame analyses were conducted to document the seal's behaviour during the trials ('Main Actor for Windows', V 3.65, MainConcept GmbH, Aachen, Germany, and 'Scion Image for Windows', Beta 4.02, Scion Corporation, Frederick, MD, USA, allowing the measurement of the *x*-*y*-coordinates in single frames).

Flow measurements

To determine the crucial hydrodynamic parameters providing a seal with information about the moving direction, hydrodynamic trails up to 60 s old were analysed by PIV. Neutrally buoyant polyamide seeding particles (Vestosint 1101, Degussa-Hüls AG, Marl, Germany) were added to the water and were illuminated in a horizontal plane by a fanned-out diode-pumped solid-state laser (500-mW-DPSS-Laser, Entertainer 500, Quantum Physics, Newcastle, UK; optical fibre: Laserlight Showdesign, Berlin, Germany). The horizontal light sheet was about 2 mm thick. A CCD camera (DMK2001, The Imaging Source, Bremen, Germany) was mounted above the water surface filming the layer of illuminated particles. The water surface was smoothed by a plate of Perspex (40 cm × 40 cm). The video signal was stored digitally by a DV camera (Canon XL1S). Initially, the background flow was recorded in each PIV measurement for 5 s. Then the hydrodynamic trails of the fin were recorded for 60 s. The video recordings were cut into single frames (25 frames s⁻¹, 'Main Actor for Windows') and analysed using self-designed correlation programs in MatLab 6.5 (MathWorks, Inc., Natick, MA, USA) (Hanke and Bleckmann, 2004), which followed the principles of digital PIV (Hart, 2000; Willert and Gharib, 1991).

PIV measurements were conducted in two different ways. First, to obtain high-resolution measurements of the temporal and spatial changes in the hydrodynamic stimuli, PIV was conducted under controlled conditions in a round water tank (220 cm in diameter, 45 cm water depth). Second, PIV was set up in the experimental box during two sessions with the seal performing the task. These measurements served to visualise those parts of the trail the animal used during the decision process and to assess the time required from striking the hydrodynamic trail until making a decision. As the seal wore a visually opaque stocking mask during these measurements, the laser illumination could not harm its eyes.

RESULTS

Animal's performance

Video recordings documented the behaviour of the seal during the experiments. When the headphones were removed from the animal's head, it immediately left the station target, submerged quickly, passed its head through the gate into the experimental box and started searching for the hydrodynamic trail with the mystacial vibrissae protracted to the most forward position. After locating a trail, the blindfolded seal performed a minute lateral head movement, in most cases anticipating its subsequent choice of one of the response targets.

Fig. 3 shows the percentage of correct decisions as a function of the delay. The general run of the curve shows that the seal's performance decreased with increasing delay. For a delay of 5 s the seal indicated the correct moving direction of the artificial fin in 93.7% of the trials. Delays of 10 s and 20 s still allowed the seal to determine the moving direction in 91.3% and 87.5% of the trials, respectively. A further increase of the delay was accompanied by a faster decrease of correct decisions to 73.8% (25 s delay), 75%

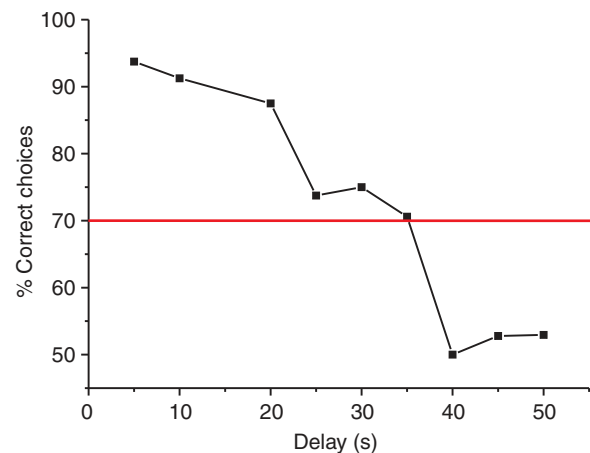


Fig. 3. The seal's ability to determine the moving direction of a hydrodynamic trail as a function of the delay. Data points above the red bar represent significant percentage of correct choices. The longest delay after which Henry was still able to determine the correct direction of an artificial fin was found to be 35 s.

(30 s delay) and 70.6% (35 s delay). According to the Bernoulli distribution the animal's performance was significantly higher than chance for delays ranging from 5 s to 35 s ($P < 0.01$ for 5–30 s, and $P = 0.012$ for a delay of 35 s) but not for delays of 40 s and longer.

During control experiments, with the mystacial vibrissae of the blindfolded seal covered by a stocking mask, the seal was not able to find the gate and thus failed to accomplish the experimental procedure even after several sessions. These trials were often abandoned by the seal by removing its stocking mask.

Flow measurements

Results from the PIV revealed that the structure of the hydrodynamic trail generated by the artificial fin was similar to that found in fish wakes [compare Blickhan et al. (Blickhan et al., 1992) and Hanke et al. (Hanke et al., 2000)]. The fin generated water disturbances including characteristic vortices spreading slowly laterally in one branch (Fig. 4). Two different vortex structures turning in opposite directions were found. When the fin was moved from left to right (viewed from the seal's perspective), vortices were turning clockwise (viewed from above), initiating new vortices turning in the opposite direction. When moving the fin from right to left, the vortices turned *vice versa*. Between these counter-rotating vortices a laminar jet flow directed towards the fin was observed. The highest velocities of the wake were found in this laminar jet flow exceeding values of 60 mm s⁻¹ after 5 s. Even after a delay of 50 s velocities of more than 10 mm s⁻¹ were found in the jet flow. The pairs of counter-rotating vortices can be interpreted, according to the second proposition of Helmholtz (Shariff and Leonard, 1992), as transverse sections through vortex rings with central jet flow. Finally, weak water streams (<10 mm s⁻¹ after 5 s) directed towards the fin were found on the path of the fin.

After a delay of 5 s, the hydrodynamic trail could contain mean water velocities exceeding 6.0 mm s⁻¹ (see Fig. 5A). During the first 5 s, absolute values of mean water vorticities could exceed 0.04 s⁻¹ (see Fig. 5B). After this delay, the lateral spread of the wake was about 20 cm. While the lateral dimension of the trail increased to about 30 cm during the next 15 s (see Fig. 4), mean water velocities as well as absolute values of water vorticity decreased further to about 3 mm s⁻¹ and below 0.02 s⁻¹, respectively. After a delay of 35 s, the lateral spread of the trail increased to about 50 cm,

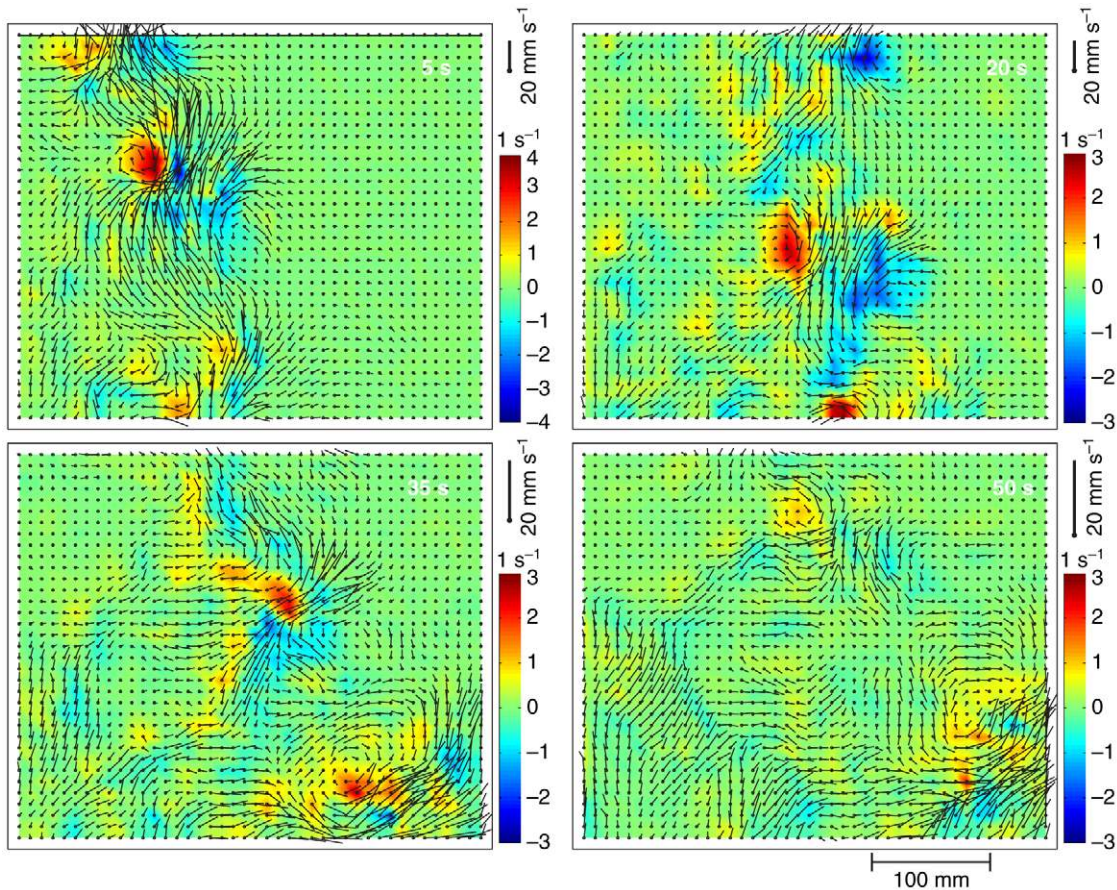


Fig. 4. Water velocities and vorticities after different delays for a typical hydrodynamic trail. In this example the paddle was moved to the right (path of the paddle is shown by dark blue arrow). Vorticities are coded by colour, i.e. red encodes the highest positive vorticity values, and dark blue the lowest negative vorticity values. Water velocities are represented as vectors. The generated trail includes characteristic counter-rotating vortices, which spread slowly in one branch. Highest velocities (up to $>60 \text{ mm s}^{-1}$ after 5 s) are found in the central jet flow between the counter-rotating vortices. In the plane of the paddle path only weak water streams are found. With increasing delay the lateral spread of the trail increases, while maximum vorticities, as well as the maximum velocities, decrease and reach values of 2 s^{-1} (from 4 s^{-1}) and less than 20 mm s^{-1} , respectively.

accompanied by a decrease in mean water velocities and absolute values of water vorticity to about 2 mm s^{-1} and less than 0.02 s^{-1} , respectively. After 50 s, the hydrodynamic trail had a dimension of about 60 cm with mean water velocities of less than 2 mm s^{-1} and a vorticity of less than 0.02 s^{-1} . As the generated hydrodynamic wake

consisted of closed vortex structures travelling laterally, the vertical extent of the wake can be expected to be in the order of the height of the fin.

PIV conducted during the psychophysical experiments showed that while scanning the hydrodynamic trails with its vibrissae, the

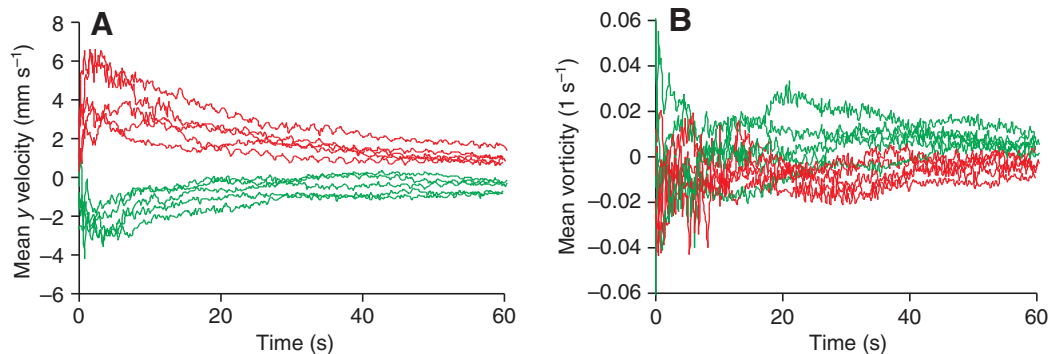


Fig. 5. Mean y velocities (A) and mean vorticities (B) as a function of time ($t=0$ s indicates the time of trail generation by the paddle) for 10 typical examples. The y -axis (defining the y velocity) is the axis along which the paddle moved. Red curves represent data for a movement to the right, viewed by the seal (positive y direction); green curves represent data for a movement to the left. The mean velocity and vorticity values were obtained by averaging over the whole field of view.

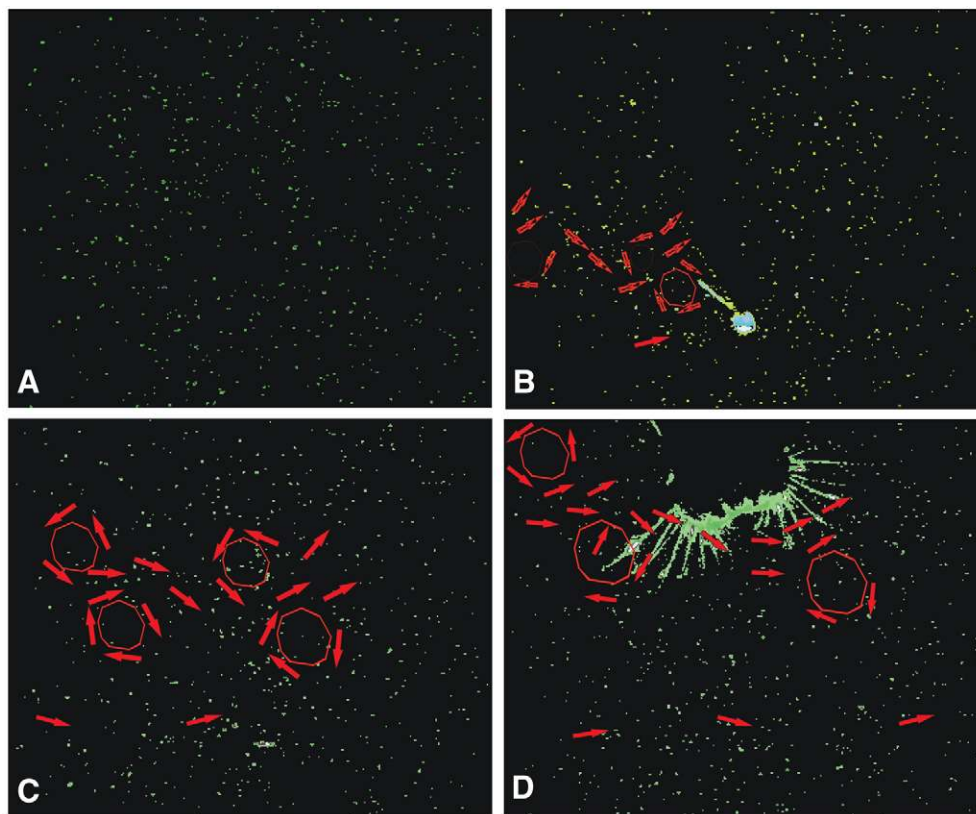


Fig. 6. Local and temporal changes in water flow during a behavioural trial. The generated vortices and water velocities are illustrated by red arrows. The arrows are not to scale, for values see Figs 4 and 5. (A) Calm water before the trial; (B) generation of the hydrodynamic trail by the fin-like paddle; (C) temporal and spatial changes of vortices; (D) the seal detects the vortices with its vibrissae. Note that the protracted, fanned-out vibrissae have contact with the vortices as well as with the central jet flow.

seal carried out little lateral head movements to one side, which were correlated with its subsequent response (see Fig. 6). Frame-by-frame analysis was used to assess the time the seal needed from striking the trail until making its decision. The first frame showing a contact between vibrissae and the trail was defined as the striking point. The first frame indicating the start of a lateral head movement was defined as the moment the seal made its decision, provided that this movement was observed in three successive frames. In all trials where PIV recordings allowed to clearly discern a hydrodynamic trail from background flow, the reaction time measured was less than 0.5 s. Furthermore, PIV revealed that while encountering the trail, the protracted vibrissae touched the vortices as well as the central jet flow. In trials where no wake was discernible from the flow visualisation, it was not possible to determine the reaction time. This was the case especially after delays of 40 s and more.

DISCUSSION

The present study shows how the ageing of a hydrodynamic trail affects the seal's ability to decide about the moving direction of an object and characterises the hydrodynamic parameters used by the animal.

Ageing of a hydrodynamic trail clearly affected the seal's performance in determining trail direction. Henry was able to determine the direction of a hydrodynamic trail as old as 35 s significantly better than chance level. By the use of PIV we analysed the ageing wakes regarding five different hydrodynamic parameters, which are characteristic for the movement direction. The evaluation of these parameters in correlation with the seals performance have shown that it is unlikely that the water stream on the path of the paddle, the mean vorticity and the mean velocity within a trail are crucial for the seals capability to identify the moving direction of the fin. Velocities in the water stream directly on the path of the

fin are low in comparison with those found in other areas of the trail and it is most unlikely that a seal would exploit the lowest velocity of the trail to determine its direction. Furthermore, video recordings of the seal operating in the experimental box under PIV control showed that it did not swim up to these low velocity areas. Due to the counter-rotating character of the vortices, the mean vorticity of the trails was low (absolute values not higher than 0.06 s^{-1} directly after trail generation, and hardly reaching values of 0.02 s^{-1} after 10 s). The crossing of the red and green curves in Fig. 5B, especially during the leading 10–20 seconds, shows that mean vorticity was not a reliable indicator of the paddle movement direction.

Mean velocities measured in the trails over the whole measurement area are within the sensory range of a seal's vibrissal system (Dehnhardt et al., 1998) and are reliable indicators of the paddle movement direction (Fig. 5A). However, it would have been a rather time-consuming process for the seal to first detect all water disturbances within a defined area and then to calculate the mean velocity. Furthermore, video recordings showed that the seal swam straight into the wake without any scanning movements and decided immediately after striking it. This strongly suggests that the seal did not use the mean velocity as a cue to determine the direction of the trail.

By contrast, the two remaining hydrodynamic parameters identified by PIV might play an important role for the seal's decision. The structure and spatial arrangement of the vortices in the hydrodynamic trail as well as the high water velocities between two counter-rotating vortices are characteristic of the movement direction and are within the sensory range of the seal. As vortices travel diagonally out of the path of generation, those generated during the onset of the trail reach the front side of the box earlier than those generated at the end of the trail. Given that the seal strikes the trail

in a rectangular way, it might try to detect the side where the vortices are farthest, which corresponds to the moving direction. The second parameter probably enabling the seal to sense the moving direction is the central jet flow between counter-rotating vortices. The highest velocities in a trail were measured within this flow and are directed towards the moving direction of the paddle, so that they could have been easily detected and interpreted by the seal. PIV measurements with the seal performing the task indeed demonstrated that its vibrissae always reached the areas where vortices as well as the central jet flow occurred. However, the present study does not allow determination of whether the seal primarily used one of these two parameters for its decision or a combination of them. The PIV under controlled conditions revealed that even after a delay of 35 s and more, velocities in the central jet flow were still significantly higher than the background noise (about 10 mm s^{-1} after 35 s, see Fig. 4) and vortex structures were clearly discernable. However, it must be noted that the background water disturbances in the experimental box caused by wind or by the seal itself were probably higher than those recorded under controlled conditions in the round water tank. These disturbances could have masked small water movements of the hydrodynamic trail, so that the delay of 35 s determined in this study must be interpreted as a conservative estimate (detection after longer time delays may be possible under less noisy conditions).

Although there are still considerable differences between trails generated by our artificial fin and those of swimming fishes (e.g. the orientation of the jet flow), they are comparable with respect to the presence of the crucial hydrodynamic parameters. The wake of a swimming fish consists mainly of vortices with central jet flow arranged in a highly complex, ladder-like three-dimensional pattern (e.g. Blickhan et al., 1992; Müller et al., 1997; Nauen and Lauder, 2002a), suggesting that these trails provide a tracking predator with similar information as the trails in our experiments. In comparison with the artificial fish fin trails presented here, the wake of, e.g. a small pumpkinseed sunfish (*Lepomis gibbosus*) of 86 mm body length contained water velocities and vorticities that tend to be lower by a factor of two to three (Hanke and Bleckmann, 2004). Ten seconds after the passage of the sunfish, mean velocities dropped to about $1\text{--}1.5 \text{ mm s}^{-1}$, as opposed to $2\text{--}4 \text{ mm s}^{-1}$ in the present study. However, the sunfish measured was about two to five times smaller than typical prey fish of harbour seals, and water velocities should scale linearly with body length within a limited Reynolds number range. In addition, swimming speeds of fishes belonging to the natural prey of seals can be much higher, and thus the respective water disturbances within these wakes. Harbour seals are generalist predators and feed on a wide variety of prey (Andersen et al., 2004; Hauksson and Bogason, 1997; Sharples et al., 2009). To give a few examples of important prey species and their sustained swimming speeds, herring (*Clupea harengus*) of 25 cm body length can swim at a sustained speed of 1 m s^{-1} (He and Wardle, 1988), saithe (*Pollachius virens*) of 25 cm body length at 0.9 m s^{-1} (He and Wardle, 1988) and cod (*Gadus morhua*) of 35 cm body length at 0.9 m s^{-1} (Beamish, 1966). Maximum speeds are considerably higher than sustained speeds (Videler, 1996). It appears likely that harbour seals can detect the swimming direction of a fish after time delays similar to those found in the present study or longer under favourable conditions.

In olfactory tracking in dogs, deciding on the direction (*via* a chemosensory gradient) seems to be the most difficult and time-consuming phase (Thesen et al., 1993). By contrast, our results reveal that the phase during which the seal decided about the direction of the hydrodynamic trail was very short. Indeed, Henry swam straight onto the hydrodynamic trail and recognised immediately (less than

0.5 s) its direction. While the direction of chemical trails is only determinable by a gradient of the concentration, hydrodynamic trails contain additional information in the directional pattern of the water flow. Probably the arrangement of the vibrissal field fanned out over typically 200–300 mm aids in detecting the direction by enabling a comparison of water flow in multiple points (Dehnhardt, 2002; Dehnhardt et al., 2004).

As the structure of hydrodynamic trails produced by fishes depends on their size, shape and swimming style (Hanke and Bleckmann, 2004), our results lead to the hypothesis that the vibrissal system of seals could be a powerful tool not only to detect the direction and follow such wakes but also to distinguish between different trail generators. Current investigations in our lab will hopefully provide further insight into the ability of seals to discriminate trails of moving objects differing in size and shape by means of their vibrissae.

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REFERENCES

- Andersen, S. M., Lydersen, C., Grahl-Nielsen, O. and Kovacs, K. M. (2004). Autumn diet of harbour seals (*Phoca vitulina*) at Prins Karls Forland, Svalbard, assessed *via* scat and fatty-acid analyses. *Can. J. Zool.* **82**, 1230–1245.
- Beamish, F. W. H. (1966). Swimming endurance of some Northwest Atlantic fishes. *J. Fish. Res. Board Can.* **23**, 341–347.
- Bleckmann, H. (1994). *Reception of Hydrodynamic Stimuli in Aquatic and Semiaquatic Animals*. Stuttgart, Jena, New York: Fischer Verlag.
- Blickhan, R., Krick, C. M., Zehren, D. and Nachtigall, W. (1992). Generation of a vortex chain in the wake of a subundulatory swimmer. *Naturwissenschaften* **79**, 220–221.
- Dehnhardt, G. (2002). Sensory systems. In *Marine Mammal Biology* (ed. A. R. Hoelzel), pp. 116–141. Oxford: Blackwell Publishing.
- Dehnhardt, G. and Mauck, B. (2008). Mechanoreception in secondarily aquatic vertebrates. In *Sensory Evolution on the Threshold: Adaptations in Secondarily Aquatic Vertebrates* (ed. J. G. M. Thewissen and S. Nummela), pp. 295–314. Berkeley: University of California Press.
- Dehnhardt, G., Mauck, B. and Bleckmann, H. (1998). Seal whiskers detect water movements. *Nature* **394**, 235–236.
- Dehnhardt, G., Mauck, B., Hanke, W. and Bleckmann, H. (2001). Hydrodynamic trail following in harbor seals (*Phoca vitulina*). *Science* **293**, 102–104.
- Dehnhardt, G., Mauck, B. and Hanke, W. (2004). Hydrodynamic perception in seals. In *Dynamic Perception* (ed. U. J. Ilg, H. H. Bühlhoff and H. A. Mallot). Berlin: Akademische Verlagsgesellschaft Aka GmbH.
- Drucker, E. G. and Lauder, G. V. (2002). Experimental hydrodynamics of fish locomotion: functional insights from wake visualization. *Integr. Comp. Biol.* **42**, 243–257.
- Dykes, R. W. (1975). Afferent fibers from mystacial vibrissae of cats and seals. *J. Neurophysiol.* **38**, 650–662.
- Enger, P. S., Kalmijn, A. J. and Sand, O. (1989). Behavioral Investigations on the functions of the lateral line and inner ear in predation. In *The Mechanosensory Lateral Line-Neurobiology and Evolution* (ed. S. Coombs, P. Gömer and H. Münz), pp. 575–587. New York, Berlin, Heidelberg, London, Paris, Tokyo: Springer.
- Ferner, M. C. and Weissburg, M. J. (2005). Slow-moving predatory gastropods track prey odors in fast and turbulent flow. *J. Exp. Biol.* **208**, 809–819.
- Fish, F. E., Innes, S. and Ronald, K. (1988). Kinematics and estimated thrust production of swimming harp and ringed seals. *J. Exp. Biol.* **137**, 157–173.
- Gellermann, L. W. (1933). Chance orders of alternating stimuli in visual discrimination experiments. *J. Genet. Psychol.* **42**, 206–208.
- Hanke, W. and Bleckmann, H. (2004). The hydrodynamic trails of *Lepomis gibbosus* (Centrarchidae), *Colomesus psittacus* (Tetraodontidae) and *Thysochromis ansorgii* (Cichlidae) measured with Scanning Particle Image Velocimetry. *J. Exp. Biol.* **207**, 1585–1596.
- Hanke, W., Brücker, C. and Bleckmann, H. (2000). The ageing of the low-frequency water disturbances caused by swimming goldfish and its possible relevance to prey detection. *J. Exp. Biol.* **203**, 1193–1200.
- Hart, D. P. (2000). PIV error correction. *Exp. Fluids* **29**, 13–22.
- Hauksson, E. and Bogason, V. (1997). Comparative feeding of grey (*Halichoerus grypus*) and common seals (*Phoca vitulina*) in coastal waters of Iceland, with a note on the diet of hooded (*Cystophora cristata*) and harp seals (*Phoca groenlandica*). *J. Northwest Atl. Fish. Sci.* **22**, 125–135.
- He, P. and Wardle, C. S. (1988). Endurance at intermediate swimming speeds of Atlantic mackerel, *Scomber scombrus* L., herring, *Clupea harengus* L., and saithe, *Pollachius virens* L. *J. Fish Biol.* **33**, 255–266.

- Mills, F. H. J. and Renouf, D.** (1986). Determination of the vibration sensitivity of harbour seal *Phoca vitulina* (L.) vibrissae. *J. Exp. Mar. Biol. Ecol.* **100**, 3-9.
- Müller, U. K., van den Heuvel, B. L. E., Stamhuis, E. J. and Videler, J. J.** (1997). Fish foot prints: Morphology and energetics of the wake of a continuously swimming mullet. *J. Exp. Biol.* **200**, 2893-2906.
- Nauen, J. C. and Lauder, G. V.** (2002a). Hydrodynamics of caudal fin locomotion by chub mackerel, *Scomber japonicus* (Scombridae). *J. Exp. Biol.* **205**, 1709-1724.
- Nauen, J. C. and Lauder, G. V.** (2002b). Quantification of the wake of a rainbow trout using three-dimensional stereoscopic particle image velocimetry. *J. Exp. Biol.* **205**, 3271-3279.
- Pohlmann, K., Grasso, F. W. and Breithaupt, T.** (2001). Tracking wakes: the nocturnal predatory strategy of piscivorous catfish. *Proc. Natl. Acad. Sci. USA* **98**, 7371-7374.
- Renouf, D.** (1979). Preliminary measurements of the sensitivity of the vibrissae of Harbour seals (*Phoca vitulina*) to low frequency vibrations. *J. Zool.* **188**, 443-450.
- Schulte-Pelkum, N., Wieskotten, S., Hanke, W., Dehnhardt, G. and Mauck, B.** (2007). Tracking of biogenic hydrodynamic trails in a harbor seal (*Phoca vitulina*). *J. Exp. Biol.* **210**, 781-787.
- Shariff, K. and Leonard, A.** (1992). Vortex rings. *Annu. Rev. Fluid Mech.* **24**, 235-279.
- Sharples, R. J., Arrizabalaga, B. and Hammond, P. S.** (2009). Seals, sandeels and salmon: diet of harbour seals in St. Andrews Bay and the Tay Estuary, southeast Scotland. *Mar. Ecol. Prog. Ser.* **390**, 265-276.
- Standen, E. M. and Lauder, G. V.** (2007). Hydrodynamic function of dorsal and anal fins in brook trout (*Salvelinus fontinalis*). *J. Exp. Biol.* **210**, 325-339.
- Thesen, A., Steen, J. B. and Döving, K. B.** (1993). Behaviour of dogs during olfactory tracking. *J. Exp. Biol.* **180**, 247-251.
- Tytell, E. D., Standen, E. M. and Lauder, G. V.** (2008). Escaping Flatland: three-dimensional kinematics and hydrodynamics of median fins in fishes. *J. Exp. Biol.* **211**, 187-195.
- Videler, J. J.** (1996). *Fish Swimming*. London: Chapman and Hall.
- Weissburg, M. J.** (2000). The fluid dynamical context of chemosensory behavior. *Biol. Bull.* **198**, 188-202.
- Westhoff, G., Fry, B. G. and Bleckmann, H.** (2005). Sea snakes (*Lapemis curtus*) are sensitive to low-amplitude water motions. *Zoology* **108**, 195-200.
- Willert, C. E. and Gharib, M.** (1991). Digital particle image velocimetry. *Exp. Fluids* **10**, 181-193.
- Williams, T. M. and Kooyman, G. L.** (1985). Swimming performance and hydrodynamic characteristics of Harbor seals (*Phoca vitulina*). *Physiol. Zool.* **58**, 576-589.