RESEARCH ARTICLE

Hydrodynamic discrimination of wakes caused by objects of different size or shape in a harbour seal (*Phoca vitulina*)

Sven Wieskotten[1], Björn Mauck[2], Lars Miersch[1], Guido Dehnhardt[1] and Wolf Hanke[1],*

[1]University of Rostock, Sensory and Cognitive Ecology, Albert-Einstein-Strasse 3, 18059 Rostock, Germany and [2]Institute of Biology, University of Southern Denmark, Campusvej 55, 5230 Odense M, Denmark

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

SUMMARY

Harbour seals can use their mystacial vibrissae to detect and track hydrodynamic wakes. We investigated the ability of a harbour seal to discriminate objects of different size or shape by their hydrodynamic signature and used particle image velocimetry to identify the hydrodynamic parameters that a seal may be using to do so. Hydrodynamic trails were generated by different sized or shaped paddles that were moved in the calm water of an experimental box to produce a characteristic signal. In a two-alternative forced-choice procedure the blindfolded subject was able to discriminate size differences of down to 3.6 cm (Weber fraction 0.6) when paddles were moved at the same speed. Furthermore the subject distinguished hydrodynamic signals generated by flat, cylindrical, triangular or undulated paddles of the same width. Particle image velocimetry measurements demonstrated that the seal could have used the highest velocities and the steepness of the gradients within the wake to discriminate object size, beside the size of counter-rotating vortices and the spatial extension of a wake. For shape discrimination the subject could have used the spatial extension of the whole wake, in addition to the arrangement of the vortices. We tested whether the seal used highest velocities, the steepness of the gradients and the spatial extension of the wake in a second set of experiments by varying moving speed and paddle size, respectively. The subject was still able to discriminate between the respective object sizes, but the minimum detectable size difference increased to 4.4 cm (Weber fraction 3.6). For the shape discrimination task, the seal was only able to distinguish flat from triangular paddles. Our results indicate that the seal's discrimination abilities depend on more than one hydrodynamic parameter.

Key words: harbour seal, vibrissae, hydrodynamic perception, size discrimination, shape discrimination, hydrodynamic signature.

INTRODUCTION

Most aquatic animals have developed hydrodynamic receptor systems for the detection of conspecifics, predators or prey, such as the lateral line organ in fishes (Dijkgraaf, 1963; Bleckmann, 1994; Coombs et al., 1989) and the diverse hydrodynamic receptor systems in many invertebrate phyla (Budelmann, 1996; Heinisch and Wiese, 1987; Laverack, 1962; Tautz and Sandemann, 1980; Wiese, 1976). In mammals, it has been demonstrated that harbour seals (*Phoca vitulina* L.) can use their vibrissae as a highly sensitive hydrodynamic receptor system, capable of detecting water velocities down to 245 μm s^{-1} (Dehnhardt et al., 1998). In a stationary California sea lion (*Zalophus californianus*) the thresholds for hydrodynamic dipole stimuli of 20 and 30 Hz were found to be even lower (Dehnhardt and Mauck, 2008).

Fishes swimming through the water column leave a trail of water disturbances that can be measured up to several minutes after its generation (Hanke et al., 2000; Hanke and Bleckmann, 2004). Under conditions where visibility is severely limited, e.g. by the abundance of plankton and other particulate matter (Aarup, 2002; Aksnes and Giske, 1993; Abrahams and Kattenfeld, 1997; Aksnes and Utne, 1997; Vogel and Beauchamp, 1999), hydrodynamic trails can aid piscivorous predators in capturing prey (Dehnhardt et al., 2001; Dehnhardt et al., 2004). Blindfolded harbour seals can reliably follow artificial hydrodynamic trails (Dehnhardt et al., 2001; Wieskotten et al., 2010a; Wieskotten et al., 2010b) and hydrodynamic trails

generated by conspecifics (Schulte-Pelkum et al., 2007). Harbour seals were able to track the abiotic trails of a remote-controlled miniature submarine as long as 40 m and to detect an artificial fish fin more than 30 s after its passage by means of their vibrissae, suggesting that hydrodynamic information can be used for long-distance location of moving objects, including fish.

However, natural hydrodynamic trails generated by swimming fish are quite diverse. Although the wake of fishes propelled by the caudal fin generally consists of vortices arranged in a highly complex, ladder-like three-dimensional pattern (e.g. Blickhan et al., 1992), their fine structure depends on a multitude of factors. Body shape, size, swimming style and velocity of each species all affect the temporal and spatial characteristics of fish wakes (Drucker and Lauder, 2002; Hanke et al., 2000; Hanke and Bleckmann, 2004; Nauen and Lauder, 2002a; Standen and Lauder, 2007; Tytell et al., 2008). Hence, a piscivorous predator capable of perceiving hydrodynamic stimuli could extract more information from a hydrodynamic trail than the mere presence of a fish. Several studies have described the capability of various aquatic animals, such as fishes and amphibians, to locate the sources of surface waves and subsurface water movements (e.g. Bleckmann et al., 1989; Coombs and Fay, 1993; Behrend et al., 2006; Görner, 1973) and to discriminate between parameters such as stimulus frequency (Bleckmann et al., 1981; Frühbeis, 1984; Elepfandt et al., 1985), amplitude (Waldner, 1981; Coombs and Fay, 1993) and object size

or shape (Vogel and Bleckmann, 2001). Furthermore, it has been shown that blind cave fishes are able to identify and discriminate the shape and spatial arrangement of stationary objects by means of lateral-line input (e.g. Campenhausen et al., 1981; Teyke, 1985; Hassan, 1986). For aquatic mammals, studies have shown that harbour seals are not only able to detect dipole water movements but also to discriminate a change in amplitude of 0.8 μm of such water movements (Dehnhardt and Mauck, 2008). In addition, the vibrissal system enables them to detect the direction of movement of a small object by its hydrodynamic trail 35 s after it was generated (Wieskotten et al., 2010a).

Although these findings indicate that seals are able to distinguish between different water movements such as different amplitudes of dipole stimuli and the direction of a hydrodynamic trail, nothing is known about the ability of seal to discriminate the hydrodynamic trails of different sizes and shapes. The objective of the present study was to investigate whether, and how accurately, a harbour seal was able to discriminate between hydrodynamic trails of different size or shape and to identify which hydrodynamic parameters harbour seals use to make this discrimination.

MATERIALS AND METHODS
Subject
The study was conducted at the Marine Science Center, Cologne and Rostock, Germany. A single 12-year-old male harbour seal [*Phoca vitulina* (Linnaeus 1758)] was used. This seal was familiar with psychophysical experiments and experienced in hydrodynamic trail detection (Dehnhardt et al., 2001; Wieskotten et al., 2010a). At the time of the experiments described here it was kept within a group of eight seals in two interconnected freshwater pools with a total volume of approximately 1000 m³ and an average depth of 1.3 m. During experiments the other seals of the group were separated within an enclosure located in a corner of the holding pool. Prior to data acquisition, training sessions were conducted once or twice a day, typically 5 days per week, for 26 weeks. Experimental sessions with data acquisition were conducted once or twice a day, typically 5 days per week, for 10 weeks. A session usually consisted of 40 trials. The subject received approximately 90% of its daily amount of food in the form of freshly thawed cut herring during these experiments.

Test apparatus and stimuli
To provide nearly calm water conditions during the experimental trials, experiments were performed in a closed experimental box measuring 1.8×2.0×1.3 m (length×width×height) fixed on the bottom of the pool at a depth of 1.1 m (Fig. 1A). A circular gate (40 cm in diameter) in the centre of the front wall of the box allowed the subject to swim into the box up to its pectoral flippers. This experimental box was in principle the same as used by Wieskotten et al. (Wieskotten et al., 2010a), only differing in the position of the response targets. Outside the box, one response target (small plastic sphere) was mounted underwater at the right side of the gate. Another response target was fixed above the gate outside the box (Fig. 1A). The upper target also served as the station target for the seal.

To study the size discrimination ability, hydrodynamic trails were generated by means of thin rectangular steel paddles, oriented with their long axis vertically (see Fig. 1D). The paddles differed in size: the width ranged from 2 to 8 cm.; the height of the paddles was 30 cm. The paddles were attached *via* a thin rod to the tip of a rotor
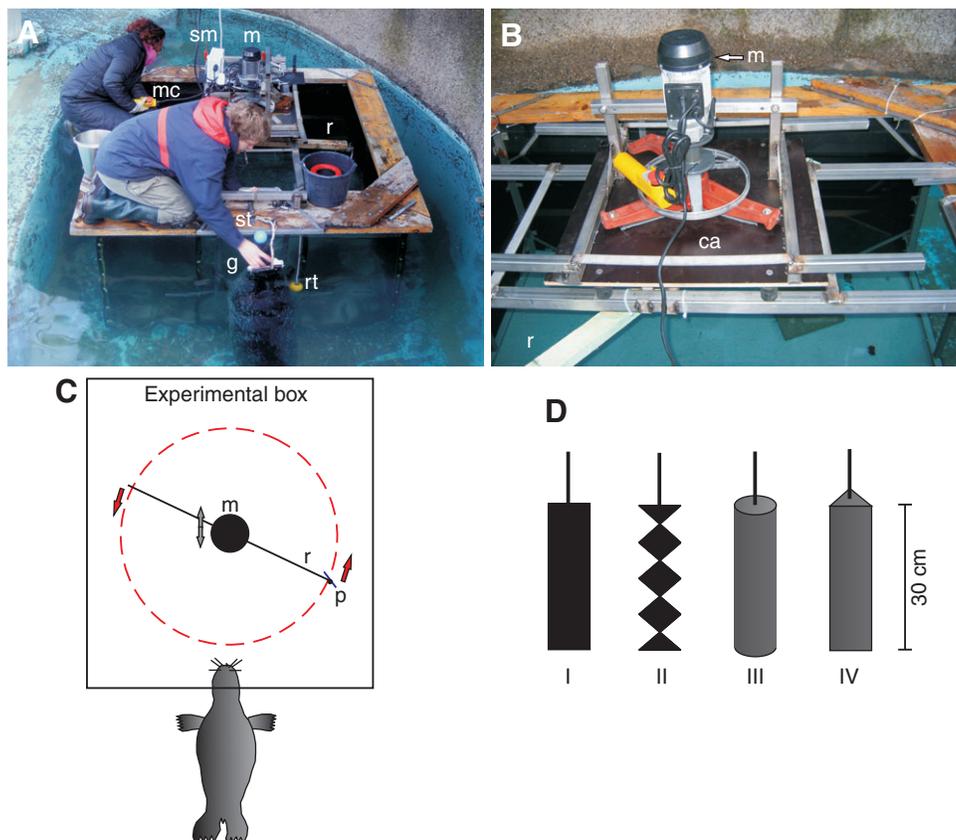

Fig. 1. (A) Experimental box providing calm water conditions. In this picture the seal is waiting blindfolded at its station (st) and response target (rt); g, gate; m, motor; sm, speedometer; mc, motor-controller; r, rotor system at which testing paddles are inserted. (B) Close-up of the motor (m) fixed onto the moveable carriage (ca). (C) Schematic drawing of the experimental box, viewed from above. The red dashed line indicates the circular path of the trail-generating paddle. After trail generation the subject is required to enter the box through the gate, up to its foreflippers, to analyse the hydrodynamic trail by its vibrissae. The position of the motor could be altered by moving the carriage (indicated by the double arrow), which allowed a change in distance between the paddle and the front side of the box. p, paddle for trail generation. (D) Paddles used for trail generation: (I) flat rectangular paddle, (II) flat undulated paddle, (III) cylindrical paddle and (IV) triangular paddle.

(1.4 m diameter), which was driven above the water surface anti-clockwise at a predetermined speed by an electric motor (Fig. 1B,C). The paddles were thus moved on a circular path of 1.4 m diameter in a fixed orientation to the direction of movement. The motor was mounted on a carriage attached to the experimental box, which allowed the distance between the paddles and the front side of the box to be changed (see Fig. 1B). The paddles were moved past the gate in the front side of the box on a circular path of radius 0.7 m (according to the rotor diameter of 1.4 m; see Fig. 1C), which guaranteed that the subject always encountered a hydrodynamic trail when entering the experimental box, even if it did not swim perfectly straight. Paddles were started at the rear part of the box and stopped on the right side, thus avoiding water disturbances in the area of trail detection caused by effects of the start and stop phases of the paddle. The motor system was damped against vibrations by several vibration absorbers. The rotation speed of the motor was adjusted by a variable transformer and continuously measured by an optical speedometer. Paddle size and paddle velocity were varied among trials. Because the hydrodynamic trails of the larger paddles expanded faster and reached the front of the box faster, the distance between the paddle and the gate of the experimental box was randomized by varying the position of the motor on its carriage. This prevented the subject from making a decision regarding trail size simply by recognizing how far it had to enter the box until it hit a hydrodynamic trail.

For the shape discrimination study, trails were generated by flat rectangular, cylindrical, triangular cross section and flat undulated paddles (see Fig. 1D). While the flat and undulated paddles pointed towards the seal at an angle of 85±1 deg to the plane defined by the vertical steel rod and the direction of movement, the triangular paddle was oriented with the baseline at 90 deg relative to its direction of motion and the tip of the triangle pointing in the direction of motion. The height of the paddle was 30 cm and in the first set of experiments the width was constant at 4 cm. In a second set of experiments the width of the paddles was varied randomly between 2, 4, 5 and 7 cm, while the height was kept constant at 30 cm.

To avoid any chemosensory cues, all paddles were made of chemically inert material such as stainless steel and polyethylene.

Experimental procedure

Experiments were conducted according to a modified two-alternative forced choice paradigm (limit of four consecutive tests of the same width difference or shape difference). A trial started with the blindfolded seal [opaque stocking mask (see also Dehnhardt et al., 2001; Wieskotten et al., 2010a; Wieskotten et al., 2010b)] placing its snout on the station target, where its vibrissae were above the water surface. For acoustical masking the seal was supplied with headphones transmitting pink noise, which provides masking in the relevant low to medium frequency range. Additionally a water inlet close to the experimental box produced underwater sound with a sound pressure level of approximately 80 dB. Hydrodynamic trails were then generated by moving the different sized (respectively shaped) paddles on a circular path by means of the rotor. The direction of movement was always the same (anti-clockwise when viewed from above, thus from left to right from the seal's perspective; Fig. 1C). After trail generation was completed and after an additional delay of 3 s, the headphones were removed from the seal's head, which served also as a start signal for the animal. As soon as the start signal was given, the seal submerged and entered the experimental box by the gate, up to its foreflippers.

To determine the minimum size differences of objects that the seal is able to distinguish by their hydrodynamic trails, we used paddles of different sizes. Different paddle sizes were presented in a modified Gellermann series (Gellermann, 1933) and tested against the respective standard paddle. Size difference thresholds were determined for three standard paddles with a width of 2, 6 or 8 cm, by comparing them with test paddles of different sizes. Test paddle sizes were 2, 3, 4, 5, 6, 7 and 8 cm in width. The 2 cm wide standard paddle was tested 80 times against the 3, 4, 5, 6, 7 and 8 cm wide test paddles (upper difference threshold). The 6 cm wide standard paddle was tested 80 times against the 2, 3, 4 and 5 cm wide test paddles (lower difference threshold). The 8 cm wide standard paddle was tested 80 times against the 2, 3, 4, 5 and 6 cm wide test paddles (lower difference threshold). The subject was required to respond to the hydrodynamic trail generated by the standard paddle by leaving the experimental box and touching the response target to the right. By contrast, all paddles of other width had to be responded to by touching the response target above the gate. Correct responses were rewarded by pieces of cut herring. Between each trial a break of at least 2 min was introduced to avoid any influence from a previous trail on the following trail.

For shape discrimination, the same experimental procedure was used. To determine the seal's ability to distinguish between different shaped paddles by their hydrodynamic trails, the various paddles were again presented in a modified Gellermann series (Gellermann, 1933). Each paddle was tested 120 times against each other paddle (six paddle combinations). The subject was required to respond to the hydrodynamic trails by leaving the experimental box and touching the right or upper response target, respectively.

To ensure that the tested animal did not use other sensory cues to enable it to distinguish size or shape differences, control experiments were carried out during which the seal's mystacial vibrissae were covered by a water-permeable nylon stocking, still allowing the animal to perceive water in its mouth and nose. The experimental procedure during control trials was in accordance with that of the test trials.

Stimulus characterization

To visualize and analyse the hydrodynamic wakes generated by the different sized or shaped paddles, particle image velocimetry [PIV; compare Adrian (Adrian, 1991) and Westerweel (Westerweel, 1997)] was used. The PIV setup underwent some modifications in order to adapt it to our needs (see Wieskotten et al., 2010a). PIV measurements were carried out inside the experimental box, which provides nearly calm water conditions. Neutrally buoyant seeding particles (Vestosint 1101, Degussa-Hüls AG, Marl, Germany) were added to the water column and 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 approximately 2 mm thick. A CCD camera (DMK2001, The Imaging Source, Bremen, Germany) was mounted above the water surface, filming a section of 32×24, 44×33 or 30×22.5 cm of the illuminated area. The water surface was smoothed by a Perspex screen. The video signal was stored digitally into a DV camera (XL1S, Canon, Krefeld, Germany). Measurements of each trial included recordings of the background flow for 2 s. Hydrodynamic trails were recorded over 5 s. The video recordings were stored as single frames (25 frames s^{-1}; using Main Actor for Windows, v 3.65, MainConcept GmbH, Aachen, Germany) and analyzed using custom-made correlation programs in MATLAB 6.5 (MathWorks Inc., Natick, MA, USA) (see Hanke and Bleckmann, 2004), which followed the principles of digital PIV (Hart, 2000; Willert and Gharib, 1991).

RESULTS
Stimulus characterization

Hydrodynamic trails of all paddles showed water velocities higher than background noise and were within the sensory range of the vibrissal system (Dehnhardt et al., 1998).

All the rectangular paddles used for both the size and shape discrimination experiments generated water disturbances including characteristic counter-rotating vortices that spread slowly laterally in one branch. A laminar jet flow directed towards the paddle movement was found between these vortices, including the highest velocities of the wake (see Fig. 2).

At constant speed ($55\,\mathrm{cm\,s^{-1}}$), hydrodynamic trails generated by different sized paddles could be distinguished by four different wake characteristics: (1) the diameter of vortices; (2) the lateral spread of the whole wake (W_{10}; which was defined as the width of the area where velocities exceeded $10\,\mathrm{cm\,s^{-1}}$ and were thus clearly distinguishable from background noise); (3) the highest detected velocities; and (4) the size of the area where water velocities exceeded $25\,\mathrm{cm\,s^{-1}}$ (W_{25}; the deep red area in Fig. 3). The relationship between W_{10} and W_{25} can also be expressed by the steepness of the gradient between W_{10} and W_{25}. Wakes with a wider W_{25} area (e.g. wakes of 8 cm wide paddles) are characterized by a steeper gradient from high velocities in their centre to lower velocities at their periphery, in contrast to the flatter gradient found in wakes of smaller paddles.

Within the first 5 s, the trails of the 2 cm wide paddle could exceed 25 cm in lateral spread (W_{10}), whereas the areas of highest velocities (W_{25}) within such a wake were relatively small, resulting in a flat gradient from highest to lower velocities. Highest velocities within these wakes were greater than $25\,\mathrm{cm\,s^{-1}}$. In comparison, the W_{10} of the 8 cm wide paddle often exceeded 40 cm, whereas W_{25} had a remarkably wide spread, resulting in a steeper gradient from high to low velocities. Highest velocities in the wake could reach more than $40\,\mathrm{cm\,s^{-1}}$.

In order to avoid an association of the maximum water velocities and W_{25} with paddle size, which could be used as a cue by the subject, paddle speed was randomized between 31 and $85\,\mathrm{cm\,s^{-1}}$.

For instance, trails of the smallest paddle at a velocity of $85\,\mathrm{cm\,s^{-1}}$ had a wider W_{25} and a steeper gradient from high to low water velocities than the 8 cm wide paddles at lower velocity. Additionally, the highest water velocities of the small, fast moving paddle were on average greater than those found for the largest, but slow moving paddle ($>25\,\mathrm{cm\,s^{-1}}$ for the 2 cm paddle moving at 85 *vs* $14\,\mathrm{cm\,s^{-1}}$ for the 8 cm paddle at a velocity of $31\,\mathrm{cm\,s^{-1}}$). By contrast, the averaged W_{10} could still be related to paddle size (compare the images in Fig. 3), even though the width of the trail could be influenced by the paddle velocity. In some cases we measured a maximum W_{10} of approximately 35 cm for a small 2 cm wide paddle moving at high speed ($85\,\mathrm{cm\,s^{-1}}$) compared with 34 cm obtained for an 8 cm wide paddle at low speed. However, the diameter of single vortices within the wake was found to be much more constant, even when paddle speed was randomized. The measurements showed that even vortices generated by slow moving 8 cm wide paddles have a clearly wider diameter (14.5 ± 2.1 cm; mean $\pm$ s.d.; minimum 13 cm) than those of a 2 cm wide paddle moving at high speed (9.7 ± 2.3 cm; maximum 11 cm).

Also when comparing the different shaped paddles, all paddles generated water disturbances including characteristic counter-rotating vortices. With the technical means available, the PIV measurements and visualizations of the hydrodynamic trails yielded quantitative data on flow velocities and the spread of the wake and qualitative descriptions of the vortex patterns. At constant size the different shaped paddles generated hydrodynamic trails that could be clearly distinguished by the spatial arrangement of the vortices.

The flat rectangular paddles generated water disturbances including characteristic counter-rotating vortices. Because these paddles were drawn through the water at an angle of approximately 85 deg relative to the direction of movement, vortices slowly spread laterally in one branch from the outer edge of the paddles. The highest velocities of the wake were found in the jet flow between these vortices.

The wake of the cylindrical paddles was a Kármán street, i.e. large counter-rotating vortices were generated behind the paddles that were shed alternately from the right and the left side.
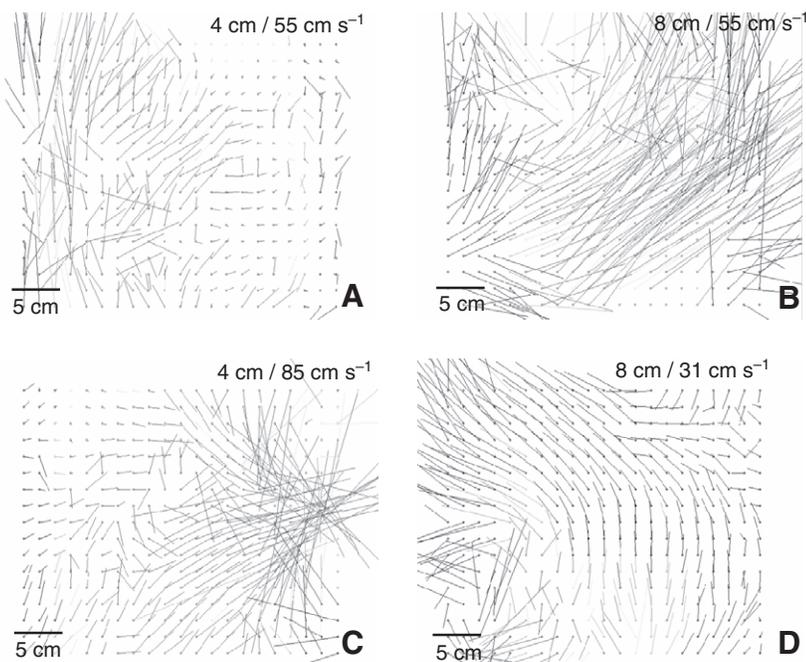

Fig. 2. Water velocities shown as vector fields. Upper row: vector field after 3 s of a 4 cm wide paddle (A) and the 8 cm wide paddle (B) at the same speed. Lower row: vector field after 3 s of a 4 cm paddle (C) and the 8 cm paddle (D) at different speeds. In each example the paddle passed the field of view at the left side in the upwards direction.

The triangular paddles generated a hydrodynamic trail in which smaller vortices detached symmetrically from both edges of the paddle. The laminar jet flow between these counter-rotating vortices contained the highest velocities. The undulated paddle stimuli were measured in the plane just below the thickest part of the paddles. Owing to the slight angle at which these paddles were drawn through the water, the occurring vortices spread slowly laterally in one branch from the paddles. Because of the undulated shape, vortices probably interacted and partly extinguished each other after generation (Bearman and Owen, 1998) (see also Hanke et al., 2010).

Besides the spatial arrangement of the wake, the hydrodynamic trails of the different shaped paddles could also be distinguished by the W_{10} of the whole wake. Flat paddles generated wakes with the widest lateral extension (27.8±3.9 cm; mean ± s.d.). The trails of the other stimuli had a smaller lateral extension (cylindrical paddle: 18.5±4.9 cm; triangular paddle: 22±4.2 cm; undulated paddle: 20.25±3.6 cm).

By randomizing paddle size between 2, 4, 5 and 7 cm, the lateral extension of the trails could no longer be associated with a particular paddle shape.

Behavioural experiments: size discrimination

Before data acquisition started, a modified 'go/no-go' procedure was used to ensure that the subject was able to detect the weakest hydrodynamic trails that were presented during the experiments. We tested the seal's ability to detect the 2-cm wide paddle moving with a velocity of 31 cm s^{-1}, which is the smallest paddle at the lowest velocity. Since the animal was able to respond correctly with high reliability (≥95%) in this task, data acquisition was started.

In the first part of the experiments we tested the 6 and 8 cm wide standard paddles against smaller paddles (ranging from 2 to 5 cm, and 2 to 6 cm in width, respectively), and the 2 cm wide standard against larger paddles (ranging from 4 to 8 cm in width) at a constant speed of 55 cm s^{-1}. As soon as the headphones were removed from

the animal's head, it immediately left the stationing target, submerged quickly and moved its head through the gate into the experimental box for trail detection. The hydrodynamic trail at this point in time was approximately 4 to 5 s old.

Psychometric functions allowing the determination of size discrimination thresholds were obtained for all three standard paddles (Fig. 4). When presented with test paddles at the same speed, the seal was able to distinguish between these and the standard paddles with high reliability when size differences were maximal (8 vs 2 cm: 92.5%; 6 vs 2 cm: 77.5%; 2 vs 8 cm: 88.8%). A decrease in width difference between the standard and the comparative paddles was accompanied by a decrease in performance (8 vs 3 cm: 88.75%; 8 vs 4 cm: 83.75%; 8 vs 5 cm: 72.5%; 8 vs 6 cm: 56.25%). The exact size discrimination threshold was determined by a linear regression. The threshold was defined as 75% correct choices, which was statistically highly significant ($P<0.001$, χ^2-test). Minimum size differences were found at 2.8 cm for the 2 cm wide standard paddle and 3.6 cm for the 6 and 8 cm wide standards, resulting in Weber fractions of 1.4 for the 2 cm standard paddle, 0.6 for the 6 cm and 0.45 for the 8 cm standard paddle. (The Weber fraction is the ratio of the size difference at threshold ΔD to the size of the comparison paddle D.) Because PIV measurements demonstrated that larger paddles generated hydrodynamic trails with the highest spatial extension (W_{10}) and the largest single vortices, higher velocities and a wider extension of the highest water velocities within the wake (W_{25}) than found in the smaller paddles (compare Figs 2 and 3), the seal could have used the size of the vortices, the maximal flow velocity or the extension of the area of high velocities within the wake as a cue to distinguish between different paddle sizes. We tested the hypothesis that the discrimination performance did not solely depend on maximal flow velocity or the extension of the area of high velocities in a second set of experiments by varying the velocity of the paddles randomly, such that larger paddles did not always cause the greatest velocities and a larger W_{25}. Paddle
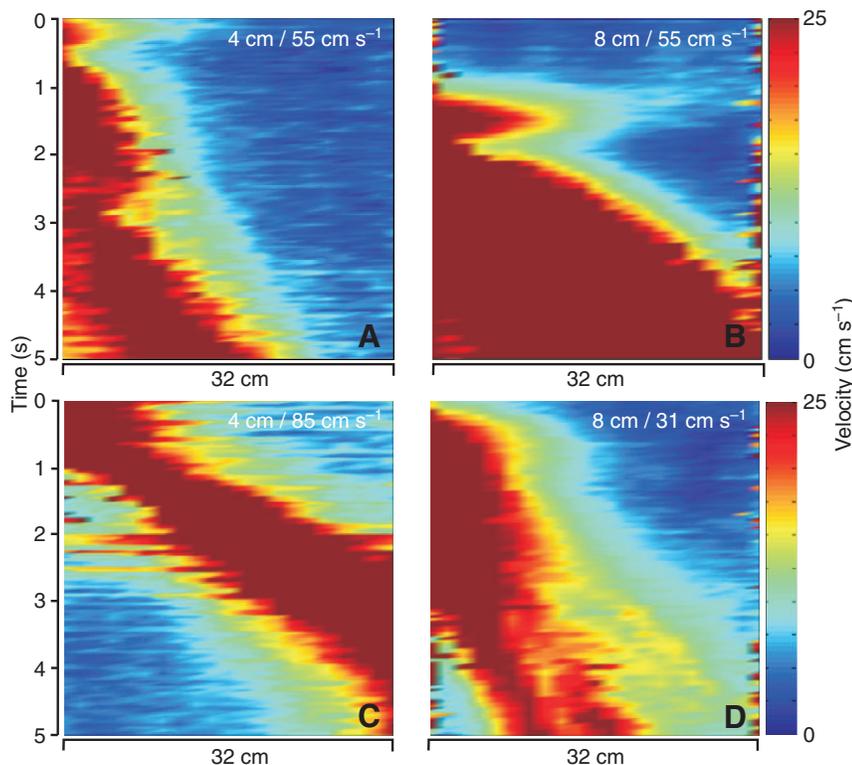

Fig. 3. Colour representation of water velocity distribution in the hydrodynamic wakes of two of the paddles used. The examples compare the temporal and spatial development of the lateral spread in a horizontal plane. Velocity is encoded by colour, where dark red indicates highest and dark blue the lowest velocity. Upper row: trail of a 4 cm wide paddle (A) and the 8 cm wide paddle at the same speed (B). Lower row: vector field of a 4 cm paddle (C) and the 8 cm paddle (D) at different speeds.
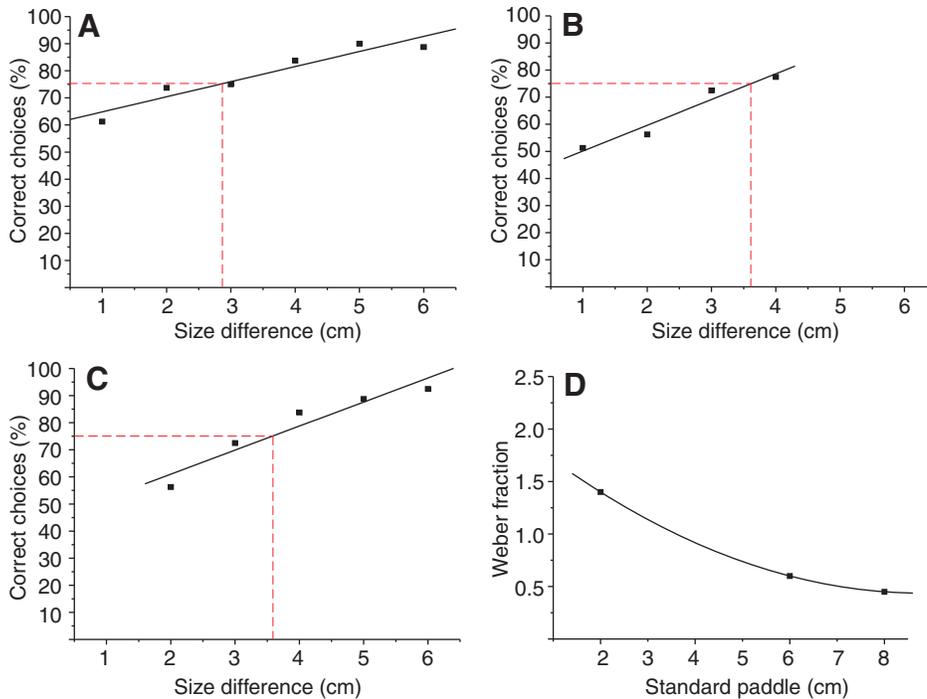
Fig. 4. Psychometric functions of the subject's performance in discriminating different sized paddles all moving at 55 cm s⁻¹.
(A–C) Percentage of correct choices *vs* difference in size between the standard and test paddle. The red dashed lines at 75% correct choices mark the difference thresholds. Each datum point represents the result of 80 single trials. (A) Determination of the upper difference threshold for the standard paddle of 2 cm width. (B) Determination of the upper difference threshold for the 6 cm wide standard paddle. (C) Determination of the lower difference threshold for the standard paddle of 2 cm width. (D) Weber functions showing the relationship between Weber fractions (the ratio of the size difference at threshold ΔD to the size of the test paddle D) and test paddle size (D).

speed was varied between 31, 43, 55, 69 and 85 cm s⁻¹. Psychometric functions allowing the determination of size discrimination thresholds were again obtained for all three standard paddles (Fig. 5). When paddles were presented at randomized speed, the seal was still able to distinguish between different sized paddles and the standard paddles with high reliability when size differences were maximal (8 *vs* 2 cm: 93.8%; 6 *vs* 2 cm: 75.0% and 2 *vs* 8 cm: 92.5%). Also the general run of the psychometric function was found to be similar to that obtained in experiments with constant

speed. However, a further decrease in width difference was accompanied by a slightly faster decrease in performance (i.e. 8 *vs* 3 cm: 77.5%; 8 *vs* 4 cm: 73.8%; 8 *vs* 5 cm: 66.3%; 8 *vs* 6 cm: 45.0%). The achieved Weber fractions, determined by a linear regression, increased slightly to 2.05 for the 2 cm, 0.73 for the 6 cm and 0.54 for the 8 cm wide standard paddle. In other words, the subject now needed minimum size differences of 4.1, 4.4 and 4.3 cm to distinguish the different sized comparative paddles from the respective standard.
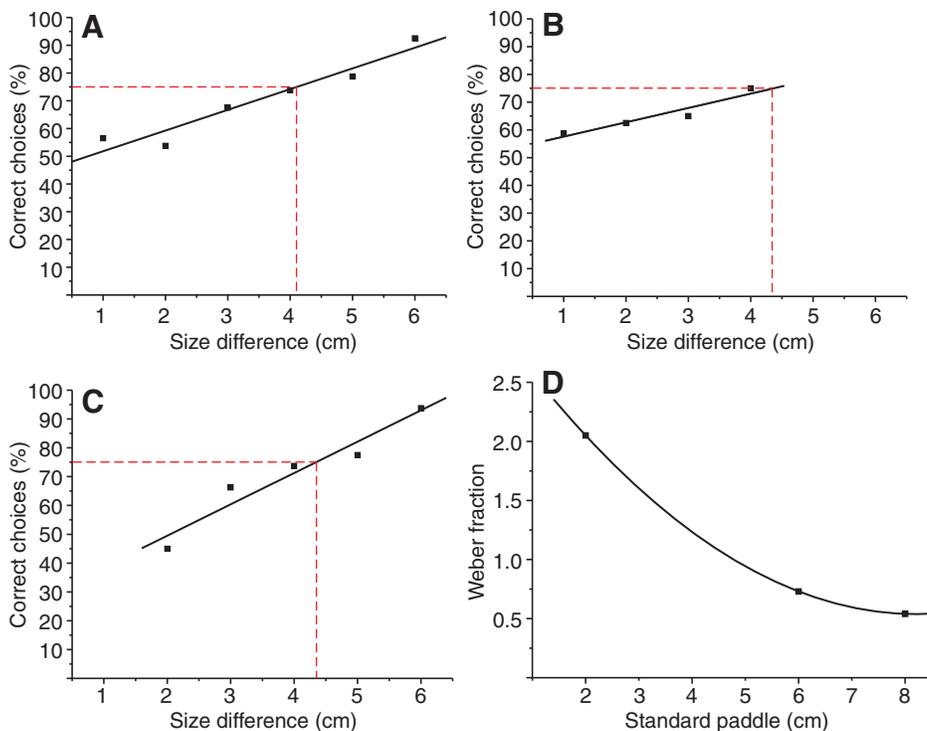

Fig. 5. Psychometric functions of the subject's performance in discriminating different sized paddles moving at different (randomized) speeds ranging from 31 to 85 cm s⁻¹.
(A–C) Percentage of correct choices *vs* difference in size between standard and test paddles. The red dashed lines at 75% correct choices mark difference thresholds. Each datum point represents the result of 80 single trials. (A) Determination of the upper difference threshold for the standard paddle of 2 cm width. (B) Determination of the upper difference threshold for the 6 cm wide standard paddle. (C) Determination of the lower difference threshold for the standard paddle of 2 cm width. (D) Weber functions showing the relationship between Weber fractions and test paddle size.
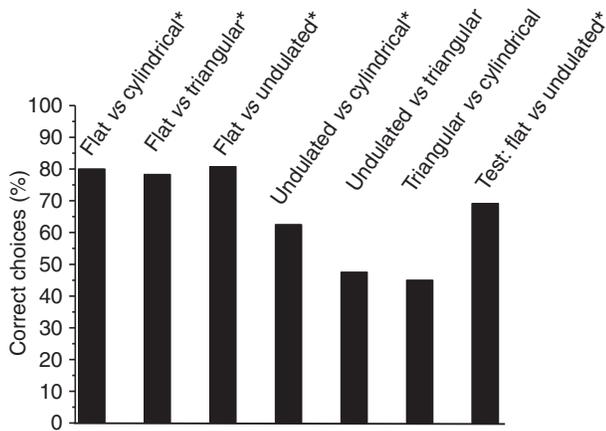
Fig. 6. The seal's performance in discriminating shape differences of paddles that were all 4 cm wide. Each bar represents the result of 120 single trials. *Significant ability to distinguish the different shapes.
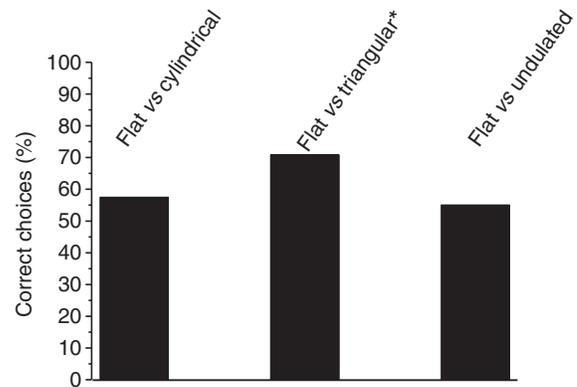

Fig. 7. The seal's performance in discriminating shape differences of paddles when the width was varied randomly. The width of the paddles was randomized between 2, 4, 5 and 7 cm. Each bar represents the result of 120 single trials. *Significant ability to distinguish the different shapes.

Behavioural experiments: shape discrimination

Before data of a new discrimination task were collected, several training sessions with the respective comparative paddles were conducted. As the animal learned a new task usually within four sessions, no more than 12 training sessions were ever conducted before the tests started (except for the first shape comparison task, which included the whole pre-training for this experiment).

In the first set of shape discrimination experiments, all paddle shapes were tested against each other at a constant speed of 55 cm s^{-1} (± 2 cm s^{-1}) and constant paddle width of 4 cm. The results are shown in Fig. 6. When paddles of constant width were presented, the seal was able to discriminate the flat paddle from the cylindrical paddles in 80% of cases (χ^2-test, $P \le 0.001$). It was also able to discriminate the flat paddles from the triangular paddles (81.3%; χ^2-test, $P \le 0.001$), the flat from the undulated paddles (80.8%; χ^2-test, $P \le 0.001$) and the undulated from the cylindrical paddle (62.5%; χ^2-test, $P < 0.01$). However, it was unable to distinguish the undulated from the triangular paddle (47.5%; χ^2-test, $P > 0.1$), or the cylindrical from the triangular paddle (45%; χ^2-test, $P > 0.1$). To exclude motivational reasons for not discriminating between these shapes, the flat paddle was tested against the undulated paddle once more, directly after the test of cylindrical vs triangular. The tested animal was immediately successful in discriminating these two shapes (69.2%; χ^2-test, $P < 0.001$).

PIV measurements demonstrated that the generated hydrodynamic trails differed not only in their spatial arrangement but also in their spatial extension (particularly for the flat paddles, whose wakes had the highest lateral extension), so the seal could have used the spatial extension as a cue to distinguish between different shaped paddles. This hypothesis was tested in a second set of experiments by varying the width of the paddles randomly, so that the spatial extension of the trails alone did not provide the seal with a cue to solve this discrimination task. Since the subject was successful in discriminating the cylindrical, the triangular and the undulated paddle vs the flat paddle most reliably, the second set of experiments was conducted with these three comparative tasks. Paddle with widths of 2, 4, 5 and 7 cm were varied randomly. As shown in Fig. 7, the seal was no longer able to discriminate between the flat paddles and the cylindrical paddles (57.5% correct choices; χ^2-test, $P = 0.1$). The subject also failed to distinguish the flat paddle from the undulated paddles (55% correct choices; χ^2-test, $P > 0.1$), but it was still able to discriminate between the flat paddle and the

triangular paddle (70.8%; χ^2-test, $P < 0.001$). The slight decrease in the percentage of correct responses does not represent a significant difference (χ^2 homogeneity test: $P > 0.01$).

Control experiments

When the seal's mystacial vibrissae were covered by a water-permeable nylon stocking in addition to its eye cover, the animal failed to accomplish the experimental procedure. Even after several training sessions where the seal's muzzle was completely covered, it was not able to find the gate and consequently to perform successful trail detection; it usually did not attempt to give any answer by touching a response target, demonstrating that no cues were available without encountering the hydrodynamic trail.

DISCUSSION

The results of the present study show that harbour seals can discriminate between different sized or shaped objects by means of the water disturbances that they cause. This is similar to what was found in goldfish (*Carassius auratus*) except that they use their lateral line (Vogel and Bleckmann, 2001). However, unlike the goldfish in the study of Vogel and Bleckmann (Vogel and Bleckmann, 2001), the subject in our study was only allowed to use the hydrodynamic trail behind the object.

To exclude other relevant sensory input during the discrimination task, the animal was blindfolded by an opaque stocking mask and acoustically masked by headphones transmitting pink noise. Although the paddles were made of chemically inert material, control experiments for chemical cues were conducted, in which the vibrissae were covered by a water-permeable nylon stocking, still allowing the animal to perceive water in its mouth (the nose is closed under water). Blocking the vibrissal system in our controls always caused the seal to abort the trial, strongly indicating that the animal did not rely on other sensory input to solve the task. Even though it cannot be completely excluded that the subject waiting in front of the gate while the paddle passed by could have felt the water movements on its body at the moment of the passage, these controls demonstrated that it is highly likely that any sensation on the body surface is negligible compared with the specialized vibrissal system.

Size discrimination

When paddles moved at the same speed, the blindfolded seal was able to discriminate paddles differing in size by 3.6 cm (when tested

against the 6 and 8 cm wide standard paddles, resulting in Weber fractions of 0.6 for the 6 cm and 0.45 for the 8 cm wide standard) and 2.8 cm in width (when tested against the 2 cm standard paddle, resulting in a Weber fraction of 1.4) by means of their hydrodynamic wakes only. However, when the speed of the paddles were altered randomly, such that the larger paddles did not always cause the greatest water velocities and the widest extension of the area of high velocities within the wake, the threshold for size discrimination slightly increased to 4.1 cm (2 cm standard; Weber fraction 2.05), 4.4 cm (6 cm standard; Weber fraction 0.73) and 4.3 cm (8 cm standard; Weber fraction 0.54). These results are generally in accordance with results obtained in goldfish (Vogel and Bleckmann, 2001), indicating that size discrimination by the harbour seal is not dependent on just one hydrodynamic parameter. PIV measurements demonstrated that the mean spatial extension of the trail and the size of a single vortex can be related to different paddle sizes. This suggests that paddle size discrimination might be based primarily on these two characteristics. Since the average is not available to the animal and the W_{10} varied more from trial to trial than the size of single vortices did, we expect a higher relevance of the counter-rotating vortices within the wakes. Also W_{25} and the mean velocity gradient between W_{10} and W_{25} were less reproducible from trial to trial than the size of the vortices was. However, these parameters and/or the maximum water velocity in the wake apparently aided the seal in its decision, as the seal's performance dropped slightly when these cues were removed by randomizing paddle velocity.

Shape discrimination

When paddle width was constant, the subject was able to discriminate between the flat and the cylindrical paddle, between the flat and the triangular paddle and between the flat and undulated paddle by means of their hydrodynamic trails, as well as, with slightly lower reliability, the undulated from the cylindrical paddle. However, the subject failed to discriminate all other stimulus combinations. PIV measurements demonstrated that, in addition to the spatial arrangement of the vortices within the wake, the seal could have used the lateral extension of the trails, because this parameter was conspicuously different among the stimuli. Indeed, when the width of the paddles was altered randomly, so that the lateral extension of the wake did not provide an unequivocal cue anymore, the subject was not able to distinguish flat *vs* cylindrical, or flat *vs* undulated paddles, as in the previous experiments. These findings are in contrast to the results obtained in goldfishes (Vogel and Bleckmann, 2001). However, the subject was successful in discriminating the flat *vs* the triangular paddles even when paddle sizes were randomized. Although the percentage of correct choices decreased slightly, no significant difference was found. This suggests that for these two objects, shape discrimination was mainly based on the spatial arrangement of the wake. PIV measurements demonstrated that the spatial arrangements of vortices of these two paddle shapes differed the most. Although all other tested shapes generated trails containing vortices detaching asymmetrically from the objects, the vortices of the triangular paddle shed symmetrically from both edges of the paddle. The subject was capable of true shape discrimination by means of different shaped hydrodynamic trails in one out of six comparative tasks.

An interesting finding of this study is that the counter-rotating single vortices might be highly relevant to the seal's discrimination ability, consistent with the findings of Wieskotten et al. (Wieskotten et al., 2010a). Vortices are usually characteristic features of animal (fish)-generated trails (e.g. Blickhan et al., 1992; Müller et al., 1997; Nauen and Lauder, 2002a). In addition to the role of the arrangement of multiple vortices, another question is what information is encoded within a single vortex that is usable for a tracking seal. Therefore we are pursuing behavioural experiments to understand the relevance of various parameters of single vortices for the discrimination abilities of harbour seals.

Ecological implications

Our experiments show that the subject was able to distinguish the hydrodynamic trails generated by paddles of different size or shape to a certain degree even when two presumably strong cues, the absolute water velocity and the position of the hydrodynamic trail, were not available for the decision. Although the study is based on one experimental subject and the obtained thresholds represent only one example out of the population of harbour seals, it shows that the sensory basis and the learning abilities for this discrimination task are, in principle, present.

Hydrodynamic trails can differ strongly between species (Hanke and Bleckmann, 2004). Trails of pelagic fish that use their caudal fin for propulsion generally produce a trail of alternating vortices (Blickhan et al., 1992, Nauen and Lauder, 2002a; Nauen and Lauder, 2002b), in this regard being similar to the cylindrical paddles used in our experiments. Even within one species, the appearance of a fish trail is considerably influenced by swimming style or fish size (e.g. Hanke et al., 2000; Hanke and Bleckmann, 2004; Nauen and Lauder, 2002a; Nauen and Lauder, 2002b).

Harbour seals are known to be generalists that prey mainly on abundant and easily available species, with diets varying by season and region (e.g. King, 1983; Bowen and Siniff, 1999). At first glance, a discrimination of fish species by the spatial arrangement of their hydrodynamic trails do not seem to be a crucial capability for harbour seals. However, energy contents of fish vary greatly between species (Anthony et al., 2000), resulting in a potentially high adaptive value of the ability to discriminate prey species while foraging on pelagic fish. Given that prey profitability varies with prey size in several species of fish, it is also crucial for a seal to adapt its hunting behaviour to fish size.

The sensitivity thresholds for size discrimination in our harbour seal are higher than those determined in fishes. For example, goldfishes presented with square objects moving at 5 cm s^{-1} were able to indicate size differences down to 0.4 cm, corresponding to a Weber fraction of 0.4 (Vogel and Bleckmann, 2001). However, harbour seals feed on a range of fish sizes, typically in the order of 10 to 65 cm (Bowen et al., 2002; Hauksson and Bogason, 1997; Sharples et al., 2009), and would benefit from being able to distinguish these fish from each other as well as from fish that are outside their range. So the fish of interest for a seal differ by several hundred percent in length. The vibrissal system of seals is clearly sensitive enough to solve these tasks. Measurements by Williams et al. (Williams et al., 2004) have shown that the energy requirement of a swimming seal is correlated with dive depth, dive time and the number of flipper strokes. Provided that small fishes provide less calorie intake than big ones (a rule of thumb that does not always apply), a seal hunting small fish has to catch more fishes than a seal hunting bigger fish in order to obtain an equivalent calorie intake. However, this results in more hunting attempts and requires more energy. The capability to identify certain hydrodynamic signatures encoding information about prey size should be of high significance for optimal foraging, as a hunting seal could decide if it is worth following a fish of a certain size.

Studies on hydrodynamic trail following in harbour seals have shown that perception is not reduced to the last few meters of the hunt, but also suitable to detect far away prey (Dehnhardt et al.,

2001; Schulte-Pelkum et al., 2007; Wieskotten et al., 2010a; Wieskotten et al., 2010b). From the results of these previous studies and those of the present study it is likely that harbour seals can obtain more information from a hydrodynamic trail than the mere presence of a fish, and discriminate their prey from a distance to a certain degree.

REFERENCES

Aarup, T. (2002). Transparency of the North Sea and Baltic Sea – a Secchi depth data mining study. *Oceanologia* **44**, 323-337.

Abrahams, M. and Kattenfeld, M. (1997). The role of turbidity as a constraint on predator-prey interactions in aquatic environments. *Behav. Ecol. Sociobiol.* **40**, 169-174.

Adrian, R. J. (1991). Particle imaging techniques for experimental fluid mechanics. *Annu. Rev. Fluid Mech.* **23**, 261-304.

Aksnes, D. L. and Giske, J. (1993). A theoretical model of aquatic visual feeding. *Ecol. Modell.* **67**, 233-250.

Aksnes, D. L. and Utne, A. C. W. (1997). A revised model of visual range in fish. *Sarsia* **82**, 137-147.

Anthony, J. A., Roby, D. D. and Turco, K. R. (2000). Lipid content and energy density of forage fishes from the northern Gulf of Alaska. *J. Exp. Mar. Biol. Ecol.* **248**, 53-78.

Bearman, P. W. and Owen, J. C. (1998). Reduction of bluff-body drag and suppression of vortex shedding by the introduction of wavy separation lines. *J. Fluids Struct.* **12**, 123-130.

Behrend, O., Branoner, F., Zhivkov, Z. and Ziehm, U. (2006). Neural responses to water surface waves in the midbrain of the aquatic predator *Xenopus laevis*. *Eur. J. Neurosci.* **23**, 729-744.

Bleckmann, H. (1994). *Reception of Hydrodynamic Stimuli in Aquatic and Semiaquatic Animals*. Stuttgart, Jena and New York: Fischer.

Bleckmann, H., Waldner, I. and Schwartz, E. (1981). Frequency discrimination of the surface-feeding fish *Aplocheilus lineatus* – a prerequisite for prey localization? *J. Comp. Physiol. A* **143**, 485-490.

Bleckmann, H., Tittel, G. and Blübaum-Gronau, E. (1989). The lateral line system of surface-feeding fish: anatomy, physiology and behaviour. In *Sensory Biology of Aquatic Animals* (ed. J. Atema, R. R. Fay, A. N. Popper and W. N. Tavolga), pp. 501-526. Berlin, Heidelberg and New York: Springer.

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.

Bowen, D. and Siniff, D. (1999). Distribution, population biology, and feeding ecology of marine mammals. In *Biology of Marine Mammals* (ed. J. E. Reynolds and S. A. Rommel), pp. 423-484. New York: Smithsonian Press.

Bowen, W. D., Tully, D., Boness, D. J., Bulheier, B. M. and Marshall, G. J. (2002). Prey-dependent foraging tactics and prey profitability in a marine mammal. *Mar. Ecol. Prog. Ser.* **244**, 235-245.

Budelmann, B. U. (1996). Active marine predators: the sensory world of cephalopods. In *Mar. Freshwater Behav. Physiol.* **27**, 59-75.

Campenhausen, C. von, Riess, I. and Weissert, R. (1981). Detection of stationary objects in the blind cave fish *Anoptichthys jordani* (Characidae). *J. Comp. Physiol. A* **143**, 369-374.

Coombs, S. and Fay, R. R. (1993). Source level discrimination by the lateral line system of the mottled sculpin, *Cottus bairdi*. *J. Acoust. Soc. Am.* **93**, 2116-2123.

Coombs, S., Görner, P. and Münz, H. (1989). *The Mechanosensory Lateral Line. Neurobiology and Evolution*. New York, Berlin, Heidelberg and London: Springer.

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. Berkely: 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 harbour seals (*Phoca vitulina*). *Science* **293**, 102-104.

Dehnhardt, G., Mauck, B. and Hanke, W. (2004). Hydrodynamic perception in seals. In *Dynamic Perception* (ed. U. Ilg, H. H. Bülthoff and A. Mallot), pp. 27-32. Berlin: Akademische Verlagsgesellschaft Aka GmbH.

Dijkgraaf, S. (1963). The functioning and significance of the lateral-line organs. *Biol. Rev.* **38**, 51-105.

Drucker, E. G. and Lauder, G. V. (2002). Experimental hydrodynamics of fish locomotion: functional insights from wake visualization. *Integr. Comp. Biol.* **42**, 243-257.

Elepfandt, A., Seiler, B. and Aicher, B. (1985). Water wave frequency discrimination in the clawed frog, *Xenopus laevis*. *J. Comp. Physiol. A* **157**, 255-261.

Frühbeis, B. (1984). Verhaltensphysiologische Untersuchungen zur Frequenzunterscheidung und Empfindlichkeit durch das Seitenlinienorgan des blinden Höhlenfisches *Anoptichtyus jordani*. PhD Thesis, Universität Mainz, Mainz, Germany.

Gellermann, L. W. (1933). Chance orders of alternating stimuli in visual discrimination experiments. *J. Genet. Psychol.* **42**, 206-208.

Görner, P. (1973). The importance of the lateral line system for the perception of surface waves in the clawed toad, *Xenopus laevis*. *Experientia* **9**, 295-296.

Hanke, W. and Bleckmann, H. (2004). The hydrodynamic trails of *Lepomis gibbosus* (Centrarchidae), *Colomesus psittacus* (Tetraodontidae) and *Thysochromis ansorgii* (Cichlidae) investigated 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.

Hanke, W., Witte, M., Miersch, L., Brede, M., Oeffner, J., Michael, M., Hanke, F., Leder, A. and Dehnhardt, G. (2010). Harbour seal vibrissa morphology suppresses vortex-induced vibrations. *J. Exp. Biol.* **213**, 2665-2672.

Hart, D. P. (2000). PIV error correction. *Exp. Fluids* **29**, 13-22.

Hassan, E.-S. (1986). On the discrimination of spatial intervals by the blind cave fish (*Anoptichthys jordani*). *J. Comp. Physiol. A* **159**, 701-710.

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.

Heinisch, P. and Wiese, K. (1987). Sensitivity to movement and vibration of water in the north-sea shrimp *Crangon crangon*. *J. Crust. Biol.* **7**, 401-413.

King, J. E. (1983). *Seals of the World*, 82 pp. Ithaca: Cornell University Press.

Laverack, M. S. (1962). Responses of cuticular sense organs of the lobster *Homarus vulgaris* (Crustacea): I. Hair-peg organs as water current receptors. *Comp. Biochem. Physiol.* **5**, 319-325.

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.

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.

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.

Tautz, J. and Sandemann, D. C. (1980). The detection of waterborne vibration by sensory hairs on the chelae of the crayfish. *J. Exp. Biol.* **88**, 351-356.

Teyke, T. (1985). Collision with an avoidance of obstacles by blind cave fish *Anoptichthys jordani* (Characidae). *J. Comp. Physiol. A* **157**, 837-843.

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.

Vogel, D. and Bleckmann, H. (2001). Behavioral discrimination of water motions caused by moving objects. *J. Comp. Physiol. A* **186**, 1107-1117.

Vogel, J. L. and Beauchamp, D. A. (1999). Effects of light, prey size, and turbidity on the reaction distances of lake trout (*Salvelinus namaycush*) to salmoid prey. *Can. J. Fish. Aquat. Sci.* **56**, 1293-1297.

Waldner, I. (1981). Habituation von *Aplocheilus lineatus* auf Oberflächenwellen des Wassers. PhD Thesis, University of Gießen, Gießen, Germany.

Westerweel, J. (1997). Fundamentals of digital particle image velocimetry. *Meas. Sci. Technol.* **8**, 1379-1392.

Wiese, K. (1976). Mechanoreceptors for near-field water displacements in crayfish. *J. Neurophysiol.* **39**, 816-833.

Wieskotten, S., Dehnhardt, G., Mauck, B., Miersch, L. and Hanke, W. (2010a). Hydrodynamic determination of the moving direction of an artificial fin by a harbour seal (*Phoca vitulina*). *J. Exp. Biol.* **213**, 2194-2200.

Wieskotten, S., Dehnhardt, G., Mauck, B., Miersch, L. and Hanke, W. (2010b). The Impact of glide phases on the trackability of hydrodynamic trails in harbour seals (*Phoca vitulina*). *J. Exp. Biol.* **213**, 3734-3740.

Willert, C. E. and Gharib, M. (1991). Digital particle image velocimetry. *Exp. Fluids* **10**, 181-193.

Williams, T. M., Fuiman, L. A., Horning, M. and Davis, R. W. (2004). The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddellii*: pricing by the stroke. *J. Exp. Biol.* **207**, 973-982.