

## Tracking of biogenic hydrodynamic trails in harbour seals (*Phoca vitulina*)

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### Summary

**For seals hunting in dark and murky waters one source of sensory information for locating prey consists of fish-generated water movements, which they can detect using their highly sensitive mystacial vibrissae. As water movements in the wake of fishes can persist for several minutes, hydrodynamic trails of considerable length are generated. It has been demonstrated that seals can use their vibrissae to detect and track hydrodynamic trails generated artificially by miniature submarines. In the present study, we trained a harbour seal to swim predefined courses, thus generating biogenic hydrodynamic trails. The structure of these trails was**

**measured using Particle Image Velocimetry. A second seal was trained to search for and track the trail after the trail-generating seal had left the water. Our trail-following seal was able to detect and accurately track the hydrodynamic trail, showing search patterns either mostly congruent with the trail or crossing the trail repeatedly in an undulatory way. The undulatory trail-following search pattern might allow a seal to relocate a lost trail or successfully track a fleeing, zigzagging prey fish.**

Key words: natural hydrodynamic trails, trail-following, harbour seal, vibrissae.

### Introduction

Medium disturbances in the sense of vibration or flow events convey information about the environment in aerial, terrestrial and aquatic habitats. In the aquatic environment, hydrodynamic stimuli of both biotic and abiotic origin can be valuable sources of information for orientation, hunting and predator avoidance. Hence, it is not surprising that many of the aquatic and semiaquatic phyla have developed specialized sensory systems for the reception of such stimuli. Well-studied examples are the fish lateral line (Bleckmann, 1994; Coombs et al., 1989) and diverse hydrodynamic receptor systems in many invertebrate phyla (Heinisch and Wiese, 1987; Laverack, 1962; Tautz and Sandemann, 1980; Wiese, 1976). In mammals, the vibrissae of harbour seals were demonstrated to respond to vibrations mediated by a rod contacting the hair in earlier studies (Dykes, 1975; Mills and Renouf, 1986; Renouf, 1979), but their function as a hydrodynamic receptor system was demonstrated only a few years ago using a technique commonly used to study the fish lateral line (Dehnhardt et al., 1998). The tuning curve of detection thresholds for dipole water movements (10–100 Hz) determined in a psychophysical experiment characterized the vibrissae of harbour seals as a highly sensitive hydrodynamic receptor system.

Concerning the ecological significance of seal vibrissae as a hydrodynamic receptor system, however, it was pointed out that even the deep-diving pinnipeds are adequately adapted for

visual functioning under dark conditions in the depth and thus there might be no need for compensatory non-visual explanations of their underwater sensory orientation (Levenson and Schusterman, 1999). Furthermore, probably because the initial characterization of the pinniped hydrodynamic receptor system was done using an oscillating dipole (Dehnhardt et al., 1998) and water velocities attenuate rapidly with distance from a flow-field generating dipole source, it was assumed for underwater orientation of hunting seals that prey is detected mainly visually, and hydrodynamic information may be used only during the last stage of prey pursuit (Davis et al., 1999). Concerning the first argument our recent results show that in pinnipeds, even though darkness might not impair underwater vision, it clearly is impaired by even moderate levels of turbidity (Weiffen et al., 2006). Thus, there is good reason to assume that underwater orientation cannot rely on vision alone but is in fact a multimodal sensory process. Furthermore, the assumption that hydrodynamic events might be important only in the vicinity of potential prey seems obsolete, since it has been demonstrated that water movements in the wake of fishes show a complex vortex structure (Blickhan et al., 1992) with water velocities persisting for up to several minutes above the threshold of most hydrodynamic receptor systems (Hanke et al., 2000). Thus, the wakes of fishes constitute hydrodynamic trails that could be tracked by a piscivorous predator equipped with a suitable receptor system.

In a pilot study presenting the first evidence for hydrodynamic trail-following in seals, a miniature submarine was used to generate reproducible hydrodynamic trails (Dehnhardt et al., 2001). By visualizing and measuring the submarine's trail using Particle Image Velocimetry (PIV), a narrow jet flow of turbulent water was found containing velocities in the same order of magnitude as those calculated for the wake of a fish of 30 cm body length. Blindfolded harbour seals were perfectly able to follow the submarine's course exclusively by using their mystacial vibrissae. The seals also detected the swimming direction of the submarine when perpendicularly encountering its trail and were able to follow distinct changes in the course of a trail. Control tests with a stocking mask covering the seal's muzzle, thereby impeding whisker movements, showed that the seal failed even to detect the hydrodynamic trail without vibrissae.

However, although these experiments showed that seals in principle can detect and follow hydrodynamic trails, the artificial hydrodynamic trail left by a miniature submarine certainly differs from biogenic trails, concerning both the three-dimensional structure and the ageing of available information. The submarine used by Dehnhardt et al. generated a trail of turbulent structure with a jet flow mainly in the opposite direction of the submarine's motion (Dehnhardt et al., 2001). This trail decayed within approximately 30 s. In contrast, hydrodynamic trails generated by fish consist of vortices arranged in a highly complex, ladder-like three-dimensional pattern (Bleckmann et al., 1991; Blickhan et al., 1992). The trail of a goldfish of 10 cm body length has been shown to last for more than 3 min under laboratory conditions (Hanke et al., 2000).

Given these differences, the objective of the present study was to investigate if a harbour seal is also able to follow natural hydrodynamic trails. The subcarangiform or thunniform swimming style of seals (Fish et al., 1988; Williams and Kooyman, 1985) generates a hydrodynamic trail similar in structure to that left by respective fishes and thus can serve as an easy-to-perceive adequate stimulus for predators hunting by hydrodynamic cues. We therefore trained a harbour seal to swim predefined courses and measured its hydrodynamic trail by Particle Image Velocimetry. The test seal was trained to follow the predefined hydrodynamic trails of its conspecific.

## Materials and methods

### *Experimental subjects*

The test animal was a 3-year-old male harbour seal *Phoca vitulina* L. named Nick, which had already participated in the experiment on hydrodynamic trail-following (Dehnhardt et al., 2001) mentioned in the Introduction. The trail-generating animal was a 3-year-old experimentally naive male harbour seal named Malte which, however, was already accustomed to basic training tasks. Both seals were born in captivity and were housed with seven other harbour seals in a spacious enclosure consisting of two interconnected outdoor pools with a total volume of about 1000 m<sup>3</sup> of freshwater and adjacent land parts

at our 'Marine Science Center' at Cologne Zoo, Germany. The seals were fed 2–5 kg of freshly thawed cut herring supplemented with vitamins; about half of the seals' daily diet was fed during the experiments. Typically experiments were conducted over 5 days per week. There was a routine food deprivation of 12–18 h between the last feeding in the late afternoon and the experiments on the next day. During experiments the two subjects were separated from the other seals.

### *Experimental setup*

The experiments were conducted in a kidney-shaped pool (Fig. 1). We used half of this pool for conducting the actual trail-following experiments in an almost semi-circular area; the other half was used to station the trail generator outside the water on a platform after a hydrodynamic trail had been generated. The test seal's start position was a stationing hoop attached just above the water surface next to the experimenter's platform at the edge of the pool's experimental area. At the opposite side of the pool nine positions near the pool edge were defined as end points for the trail-following. The position directly facing the seal's start position was defined as 0°; to the left and right of this position, respectively, another four end points were defined in terms of the angle with the 0° position in steps of 10° (i.e. –10° to –40° and 10° to 40°). Due to the shape of the pool the distances between the start position and the end points varied between 10.5 m and 15 m.

### *Experimental procedure*

The test seal was blindfolded by an opaque elastic mask that was pulled over the animal's head, leaving its mystacial vibrissae uncovered. The blindfolded seal was then led to the hoop station, facing the 0° end point. In this position, the animal's head and vibrissae were completely above the water surface. Headphones transmitting pink noise were applied for masking all acoustical cues. Meanwhile, the trail generator was stationed in a shallow-water area close to the stationing hoop of the test seal (area marked B in Fig. 1). The actual experimental procedure had to meet two conditions: it was necessary to control the trail generator's swimming direction and it was mandatory to have the trail generator removed from the pool after trail generation to avoid unintentional cues. Therefore, we trained the trail generator to pick up an object (a neutrally buoyant plastic ring) placed at the respective end point of the trail to be generated and let the trail generator retrieve this object from the pool by placing it on a dry platform in a part of the pool well outside the test area (marked C in Fig. 1). From the edge of the pool opposite to the test seal's hoop station, the plastic ring was silently placed in the water at a pseudorandomly chosen end point of a trail (Gellermann, 1933). Now the trail generator was sent to this position to pick up the ring floating in mid-water and to make a sharp turn towards the platform in the other half of the pool. The trail generator, still carrying the ring, jumped onto the platform and remained silently in this position until the end of the trial. After the trail generator had left the water, the headphones were

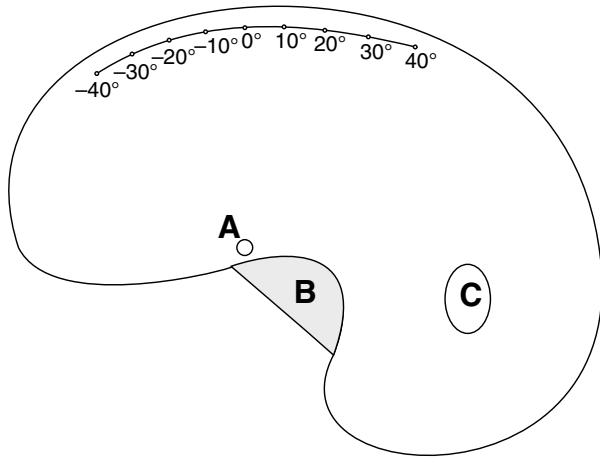


Fig. 1. Schematic drawing of the experimental pool. (A) Stationing hoop for the test seal. (B) Shallow-water area in which the trail generator was stationed before each trial. (C) Platform on which the trail generator awaited the end of the trial after having generated the trail. The positions marked as  $-40^{\circ}$  to  $40^{\circ}$  represent the end points of the nine courses of the hydrodynamic trails.

removed from the test seal's head, which was the signal to start the search for the hydrodynamic trail. The trial was considered successful when the test seal followed the trail to the end point where the trail generator had picked up the plastic ring, or when it reached an area of one body length radius (1.5 m) around this point. Successful trials were rewarded with pieces of herring; the trail generator was rewarded for retrieving the plastic ring to the experimenter.

The probability that the test seal reached the correct end point by mere chance can be calculated as follows. The area in which the end points were defined spanned a distance of 21 m. Since all trials in which the seal reached an area of one body length radius ( $\sim 1.5$  m) around the actual end point of the trail were evaluated as hits, the probability that the animal reached this area by chance was  $P=(2 \times 1.5)/21=0.14$ .

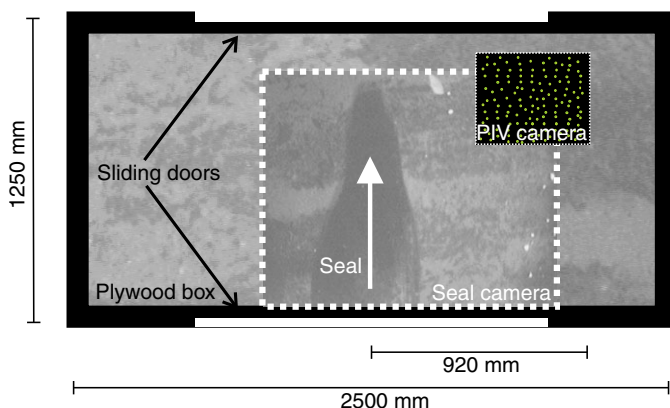


Fig. 2. The set-up for the PIV measurements of the seal's wake.

Control experiments were carried out during which the test seal's mystacial vibrissae were covered by an elastic nylon stocking. The experimental procedure in control trials was the same as in test trials.

#### Data recording and analysis

The experiments were filmed with a digital video camera (Canon XL1s, Krefeld, Germany) mounted on a mast above the pool. The recordings were digitally cut into single pictures at a frequency of  $5 \text{ frames s}^{-1}$ . The swimming paths of both animals were then marked on subsequent pictures and fitted into a diagram for evaluation.

#### Flow measurements

To investigate the flow in the seal's wake, we set up a PIV (Particle Image Velocimetry) system (cf. Adrian, 1991; Westerweel, 1997) that we specially designed for this application. A wooden box ( $125 \text{ cm} \times 245 \text{ cm} \times 125 \text{ cm}$ ,  $L \times W \times H$ ) with sliding doors in its broad sides was installed in the water (Fig. 2). A horizontal plane of laser light was fanned out in the box using an optical fibre and a cylinder lens (light source: 500 mW-DPSS-Laser, Entertainer 500, Quantum Physics, Newcastle, UK; optical fibre: Laserlight Showdesign, Berlin, Germany). The energy density of the fanned-out laser light was in the order of magnitude of a commercial laser pointer. A CCD Camera (DMK 2001, The Imaging Source, Bremen, Germany) above the box filmed a section of  $48 \text{ cm} \times 36 \text{ cm}$  of the illuminated layer. Another CCD camera (DMK 803, The Imaging Source) was used to film the movements of the seal. An 11 W lamp illuminated the scene as long as the seal was in the field of view.

Tracer particles (Vestosint 1101, Degussa-Hüls AG, Marl, Germany) were seeded into the water within the box with the sliding doors shut. After the water had calmed down, the sliding doors were opened, and after another delay of 5 min the measurements started. Each measurement started with recording the background flow in the box for 15 s with the seal waiting outside the box. With the laser switched off, the seal was then gestured to swim through the box; as soon as the first half of its body had passed the box, the laser was switched on. Video images of the flowing illuminated tracer particles were recorded for 1–3 min on digital tape (Canon XL1s used as recording device) with  $50 \text{ fields s}^{-1}$ . Analysis of the recorded images was done in MatLab 6.5 (The Mathworks, Natick, MA, USA) following the principles of digital Particle Image Velocimetry (Hart, 2000; Willert and Gharib, 1991).

## Results

### Trail-following experiments

Trail generation took a mean period of 13.42 s. In this time the trail generator dived to the respective end point of the trail, picked up the plastic ring and took it to the platform. When the headphones were removed from the test animal's head, it immediately left the stationing hoop, quickly

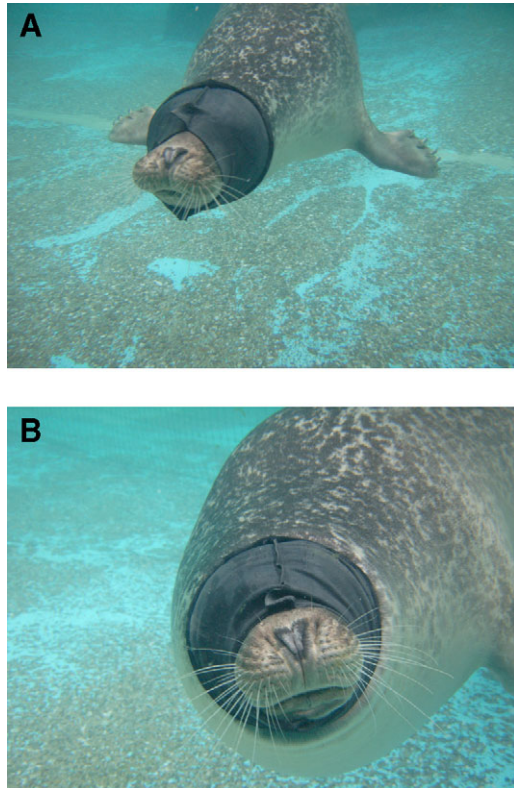


Fig. 3. (A) A blindfolded harbour seal starting to track a hydrodynamic trail. Note that the mystacial vibrissae are protracted to the most forward position. (B) A harbour seal correcting its course while tracking a hydrodynamic trail. The seal bends its whole body to swim a curve rather than performing slight lateral scanning movements with its head.

submerged and searched for the hydrodynamic trail with the mystacial vibrissae protracted to the most forward position (see Fig. 3A). The blindfolded seal followed the trails accurately, never deviating by more than a body length from the swim path of the trail generator. When correcting its course, the seal bent its whole body to swim a curve without performing lateral head movements for additional scanning (see Fig. 3B).

The test animal performed successful trail-following in 90% of the trials (444 out of 495 trials). With respect to the nine courses of the hydrodynamic trails the seal's performance was never less than 80% successful trail-following (hit-rates:  $-40^{\circ}$ : 87.2%;  $-30^{\circ}$ : 83.7%;  $-20^{\circ}$ : 90.9%;  $-10^{\circ}$ : 94.5%;  $0^{\circ}$ : 92.7%;  $10^{\circ}$ : 94.5%;  $20^{\circ}$ : 85.5%;  $30^{\circ}$ : 90.9%;  $40^{\circ}$ : 87.2%) A  $\chi^2$ -test did not reveal a correlation between the nine courses and hit- and miss-rates ( $\chi^2=7.48$ , d.f.=8,  $P=0.49$ ) (Fig. 4).

Two different patterns of trail-following were mainly observed. In 278 (63%) of the successful trials, the seal followed the trail and hardly ever diverged from it; we call this the 'linear pattern' (see Fig. 5A). In 150 (34%) of the successful trials, the seal repeatedly criss-crossed the trail (see Fig. 5B), which we call the 'undulatory pattern'. Sixteen (4%) of the successful trials could not be classified into either of

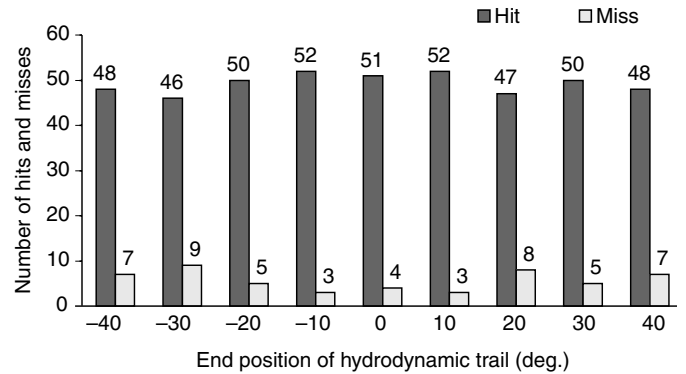


Fig. 4. The seal's performance plotted against the nine courses of the hydrodynamic trails.

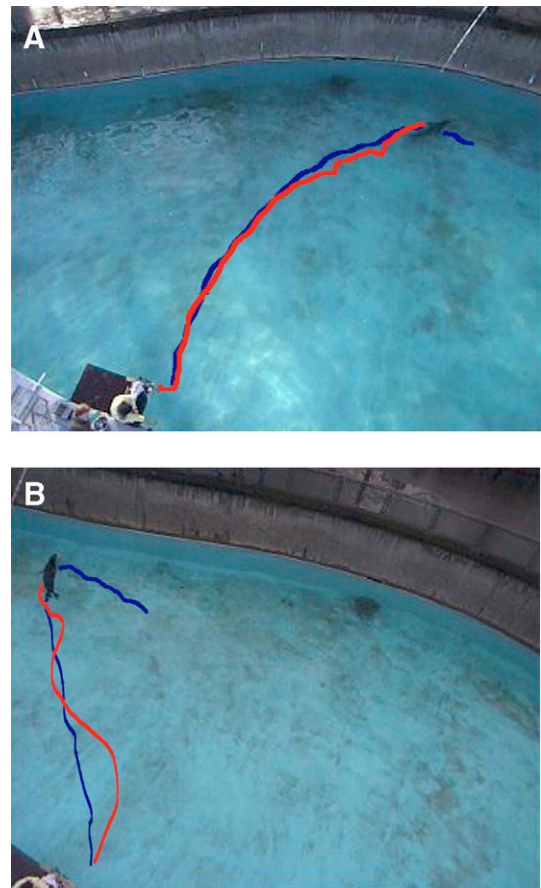


Fig. 5. (A) An exemplary trial showing the seal following a hydrodynamic trail (blue) by a linear pattern (red line). (B) An exemplary trial of hydrodynamic trail-following with an undulatory pattern.

these two patterns; these were trials in which the seal had lost the trail but retrieved it obviously more or less by chance, or simply swam into the correct direction and might have found the end point by chance. The linear search pattern was the more accurate strategy. Only 6.8% of the trials with the linear pattern

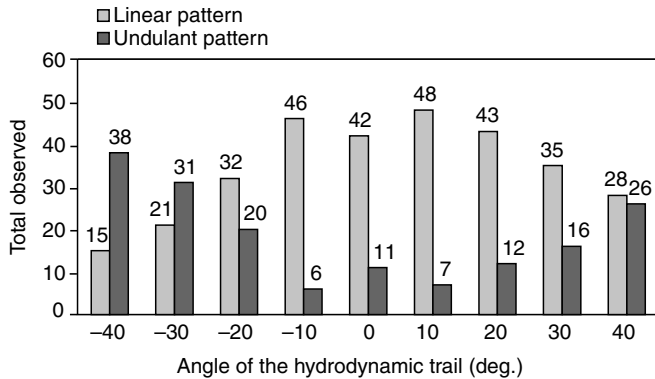


Fig. 6. The distribution of the linear and undulatory trail-following patterns over the nine courses of the hydrodynamic trails.

were unsuccessful, whereas 17.4% of the trials with the undulatory pattern were not successful. Fig. 6 shows a distribution of the two search patterns over the nine courses. The abundance of the undulatory search pattern increases and that of the linear pattern decreases with increasing angles between the 0°-position and the end point of the course for both directions. Two separate Cochran–Armitage tests for trends found significant respective correlations ( $Q=49.07$  (d.f.=4) for 0° to -40° and  $Q=14.90$  (d.f.=4) for 0° to 40°;  $P<0.005$ ).

In the control experiments with the vibrissae covered, no successful trail-following was observed. In fact, the test animal refused to start its search for the trail at all, not leaving its hoop station even though the start signal had been given. When manually pulled out of the hoop station and pushed in the direction where the hydrodynamic trail could be found, the seal was clearly irritated, never moved further away than approximately 1 m from the experimenter and tried to shake off the stocking mask from its muzzle.

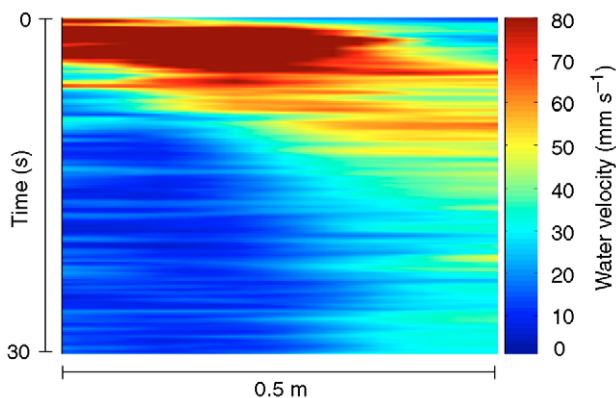


Fig. 7. Visualisation of the spatial extent of one of two lateral branches of the trail generator's wake. Each vector field in this figure was reduced to a row by averaging over the columns of the vector field, and the rows resulting from this procedure were assembled in temporal order. Velocities of  $80 \text{ mm s}^{-1}$  or higher are dark red.

### Measurements of the trail generator's hydrodynamic trail

The structure of our harbour seal's wake resembles that of a fish with thunniform or subcarangiform swimming style (cf. Hanke et al., 2000; Hanke and Bleckmann, 2004). It spreads laterally in two branches (one of which was measured here, Fig. 7). During the first 5 s the trail contained water velocities that could exceed  $200 \text{ mm s}^{-1}$  and spread laterally mainly to about 80 cm to each side. While the lateral spread of the trail increased further during the next 5 s, water velocities decreased to about  $45\text{--}60 \text{ mm s}^{-1}$ . After 30 s water velocities of about  $30 \text{ mm s}^{-1}$  were measured in the outer areas of the box while the areas between the two branches of the trail consisted of comparatively calm water. The wake was then at least 2 m wide. The wake's vertical extent was probably much smaller as our harbour seal swam at a depth of approximately 0.5–1 m and there was no indication of the wake disturbing the water surface.

## Discussion

### The seal's performance

Our results show for the first time that a harbour seal can follow hydrodynamic trails of biological origin, and that it does so with high accuracy. Even small deviations from a straight course can be precisely followed (see Fig. 5A). Usage of the vibrissae for trail-following was vividly demonstrated by the fact that the seal was obviously quite comfortable with visual deprivation during normal experiments, while the temporary deprivation of its vibrissae during the control experiments had a strongly irritating effect.

The seal's overall performance in locating the biological trail's end point was not affected by the direction in which the trail led and was even slightly higher (ranging from 83.7% to 94.5%) than the performance of our two seals tested with the miniature submarine's trail (Henry: 78.5%; Nick: 82.2%) (Dehnhardt et al., 2001).

The reasons for the slightly better overall performance can be speculated on. One aspect might be variable motivation of a test animal, resulting in differing performance both within a study and between studies using the same task. In addition, as Nick took part in both studies but was experimentally naive in the first study, he might have learned to follow hydrodynamic trails more effectively. Nevertheless, it might be also possible that the hydrodynamic trail to be followed in the present study represented a stimulus very easy to detect and to track, at least in comparison with the hydrodynamic trail of the miniature submarine we used earlier (Dehnhardt et al., 2001).

In contrast to biological trails such as those left by swimming fishes, the submarine's trail does not consist of several branches, but mainly of a rapidly decaying backward streaming jet of rather round cross-sectional shape. Although the earlier results with the submarine stimuli unequivocally demonstrated the capability of harbour seals to track hydrodynamic trails in general, these stimuli are only a rather rough approach to trails encountered in the natural habitat. The use of a harbour seal as a trail generator in the present study combined the advantage

of being able to generate highly reproducible trails due to the reliable training of the seal with generating easy-to-detect, high-intensity hydrodynamic trails assumed to resemble those left by a carangiform or thunniform swimming fish (Fish et al., 1988; Lighthill, 1969), concerning both the complex three-dimensional structure and the slow ageing of the hydrodynamic information. It seems plausible that this kind of trail represents a more adequate hydrodynamic stimulus for the vibrissal system. Therefore, the present results open the door towards a more sensory-ecologically oriented research using natural hydrodynamic stimuli.

#### *Some ecological implications of the results*

Underwater orientation in marine mammals is certainly a multimodal process that may involve vision (e.g. Davis et al., 1999; Levenson and Schusterman, 1999) (but see Weiffen et al., 2006), echolocation and/or passive audition (Au, 1993; Bodson et al., 2006), taste (e.g. Sticken and Dehnhardt, 2000) and active touch (e.g. Dehnhardt and Dücker, 1996; Dehnhardt and Kaminski, 1995), as well as hydrodynamic perception, to compose a complex representation of the environment. Which of the various senses of a seal predominates in a given situation, however, probably depends on the information available at a certain time and place. In the case of hydrodynamic information, this means that trails of water movements could supplement or even temporarily substitute other types of information if these are currently not available.

In addition to hydrodynamic trails generated by swimming prey fish, trails left by conspecifics can gain significance for harbour seals in certain situations. For example, lactating harbour seals and their pups equipped with time-depth-recorders at Sable Island, Nova Scotia, spent about 40% of their time together at sea and tended to dive together (Bowen et al., 1999). Pups appeared to descend with their mother at the beginning of a dive, returned to the surface to load oxygen if the dive exceeded about 1.5 min, and then dived again, presumably to rejoin their mother (Bowen et al., 1999). The authors hypothesize that on these dives, in addition to maintaining contact to the mother, the pups may also learn where and on what the mother is feeding. Furthermore, a young harbour seal could benefit from following a more experienced conspecific while exploring safe routes and feeding grounds. Harbour seal pups have to cope with an abrupt transition from milk to food they obtain themselves (cf. Frost et al., 2006). They increase their vertical operating range continuously (Bekkby and Bjorge, 2000; Frost et al., 2006) and can undertake excursions of more than 75 km from their natal area in their first summer (Small et al., 2005). Even older harbour seals may encounter situations when it pays to follow a conspecific with deeper knowledge of the respective area. Following another seal by its hydrodynamic trail could be of great importance in these cases if water or light conditions limit vision.

While hunting, seals may use hydrodynamic information not just during the last stage of prey pursuit after having detected prey visually, as assumed by Davis et al. (Davis et al., 1999). We

suppose that it might be rather the other way round: seals may detect and possibly even identify prey when encountering a hydrodynamic trail, and trail-following might bring the seal close to its prey where it can be hunted down visually. In the light of this hypothesis our results also provide a first important step to our understanding of how hydrodynamic events are used by seals in terms of search strategies for prey. Our seal employed at least two different search patterns, probably depending on the way it encountered the hydrodynamic trail. When the seal encountered the trail at an acute angle it mostly stayed in the main channel of water turbulences (compare Fig. 5A), between the two branches of the trail or touching these on both sides while following the trail. Although the structure of the harbour seal trails used in the present study was different, this linear pattern of trail-following corresponds well to the way our seals tracked hydrodynamic trails generated by the miniature submarine used in earlier work (Dehnhardt et al., 2001). As it accounted for 63% of the successful trials of the present study, the linear pattern is a fairly reliable way of trail-following and thus can be assumed to be preferably used in the wild whenever possible, e.g. to stalk travelling prey fish. However, our present results also reveal that when the seal encountered the trail generator's hydrodynamic trail at a more obtuse angle – the probability of which was higher the further the trail's end point deviated from the 0° direction – it was obviously often moving so fast that on missing it seemed to overshoot the trail (or at least the first lateral branch of the trail) and subsequently corrected its course. This resulted in the undulatory pattern of trail-following consisting of a course that repetitively crossed the trail (or one of its branches), and only by gradually narrowing led the seal to the end point. In the wild, this trail-following pattern might be used to track prey fish the trail of which has been newly encountered and subsequently missed for some reason, or to track down fleeing prey fish trying to escape by repetitive protean manoeuvres (rapidly turning away from the predator's attack path at unpredictable times and turning angles).

The question of how hydrodynamic information could support or even substitute vision remains, however. In contrast to terrestrial habitats where some of the large predator species are frequently observed to attack their prey over rather large distances [e.g. 50–200 m for cheetah (Eaton, 1970)], most fish predator pursuits and corresponding prey escapes examined up to now are obviously rather brief and occur over relatively short distances [(Godin, 1997) and references therein]. This might be related to the fact that many fish predator attacks seem to be guided visually and thus terminated as soon as the fleeing prey gets out of sight. Given that visibility is often drastically reduced in the marine environment (Aarup, 2002), a fleeing prey fish might simply vanish in the haze after a short fast start or some protean manoeuvres and then stop fleeing to save the costs associated with continued flight (e.g. energy expenditure, lost opportunities). In contrast to fish predators, which have not been shown yet to be capable of hydrodynamic trail-following bridging a large distance between predator and prey (but see Pohlmann et al., 2001; Pohlmann et al., 2004), harbour seals and probably some other pinnipeds capable of tracking the trail

left by a prey fish would be able to bridge this distance using hydrodynamic information until vision is of some use again. This multimodal use of available information while hunting could represent a fitness advantage and might have favoured the evolution of vibrissae as a hydrodynamic receptor system.

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