

# Hydrodynamic Trail-Following in Harbor Seals (*Phoca vitulina*)

Guido Dehnhardt,<sup>1,2\*</sup> Björn Mauck,<sup>1,2</sup> Wolf Hanke,<sup>1</sup>  
Horst Bleckmann<sup>1</sup>

Marine mammals often forage in dark or turbid waters. Whereas dolphins use echolocation under such conditions, pinnipeds apparently lack this sensory ability. For seals hunting in the dark, one source of sensory information may consist of fish-generated water movements, which seals can detect with their highly sensitive whiskers. Water movements in the wake of fishes persist for several minutes. Here we show that blindfolded seals can use their whiskers to detect and accurately follow hydrodynamic trails generated by a miniature submarine. This shows that hydrodynamic information can be used for long-distance prey location.

Aquatic animals often have to cope with conditions where visibility is drastically reduced. Consequently, many aquatic species have sensory abilities that may supplement or even substitute vision, such as the active sonar system in toothed whales (1). However, although pinnipeds underlie similar ecological demands, corresponding sensory abilities have remained unknown in these marine mammals. As suggested by the wide distribution of hydrodynamic receptor systems, water movements generated by prey, predators, or conspecifics, as well as abiotic sources such as tides and currents, provide important sensory information (2). Like the fish lateral line (3), the whiskers of harbor seals are highly sensitive to water movements (4). However, the accepted view is that hydrodynamic object detection works only over short distances [for review, see (2)], as, for instance, during chemosensory mate search in marine copepods (5) or during the final stage of prey pursuit of seals (6). Particle velocities attenuate rapidly with distance from the flow field—generating source. Although this is true for stationary vibrating sphere stimuli usually used in laboratory studies on hydrodynamic receptor systems (3), the wake behind a swimming fish shows a vortex structure (7, 8) with particle velocities above threshold of most hydrodynamic receptors several minutes after the fish has passed by (9). Thus, a swimming fish can leave a hydrodynamic trail of considerable length that piscivorous predators might use for long-range prey detection.

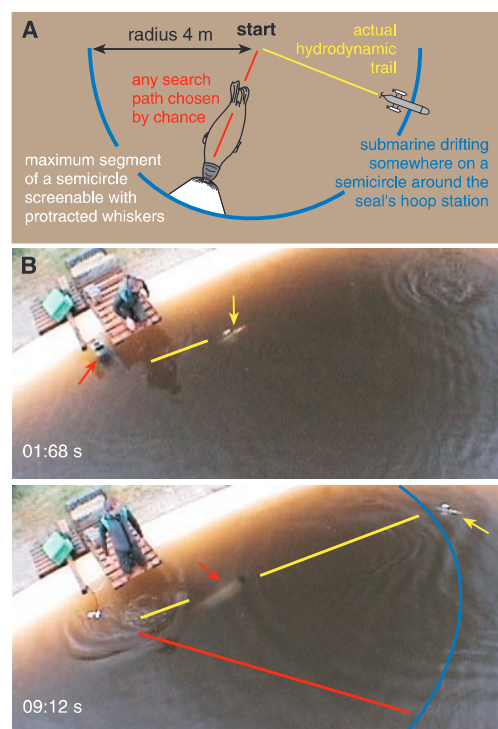
To find out whether seals can locate distant objects by hydrodynamic trail-following, trails were generated with a propeller-driven

miniature submarine (10, 11) and were visualized and measured using Particle Image Velocimetry (PIV) (10–12). Interpolation of overlapping measurements showed that similar to fish-generated hydrodynamic trails, the submarine's trail was a narrow street (width after ~20 s: <60 cm) of turbulent water movements. Compared with adjacent areas, it contained a change in the main direction of water flow (11, 13) and higher water velocities of >16 mm s<sup>-1</sup> after 20 s (11). This is the same order of magnitude as velocities calculated for the wake of a fish of 30-cm body length (extrapolated from goldfish-generated trails) (9). The submarine's trail differed from fish trails, however, in that the main water flow was opposite to its swimming direction and it consisted of a rather

unstructured pattern of turbulent water movements that broke down after ~20 s (13). In contrast, the fish-generated trails studied so far consist of stable, ladder-like chains of vortices (8, 14). Vortices in the wake of a small goldfish persist for >30 s and water velocities were, under laboratory conditions, significantly higher than background noise for at least 3 min (9). Although decaying faster, the submarine's trail represents a trackable continuum of turbulence and velocities deviating from the surrounding (11, 13).

The first block of experiments were conducted at the "Seehundstation Friedrichskoog" (Germany) with an experimentally naïve male harbor seal ("Henry") kept in an outdoor pool filled with naturally turbid seawater. The seal was first trained to locate the submarine without any sensory restrictions. In the final experimental procedure, a trial started with blindfolding the seal with a visually opaque stocking mask, supplying it with head phones for acoustical masking, and placing its head in a hoop station 40 cm above the water surface (11). The submarine was then started underwater from a platform close to the station (Fig. 1A). The seal learned that the trail always could be found ~1 m around its station. About 2 s after the submarine's engine had turned off (running time 3 to 5 s), the headphones were removed from the seal's head, which was the signal for the animal to start its search.

First, "linear hydrodynamic trails" were generated (Fig. 1, A and B). The submarine's heading was chosen pseudorandomly and counterbalanced over all trials. Because of its



**Fig. 1.** (A) Evaluation of the probability that the seal finds the submarine by mere chance. After the submarine's run in a pseudorandom direction (yellow line), it drifted somewhere on a semicircle (blue line; circumference, 12.57 m). With protracted vibrissae (span ~25 cm) and slight lateral head movements, the seal should detect an object in front of its head within a 50-cm span (1/25 length of the semicircle, white area). Thus, the seal's probability of finding the submarine by mere chance was  $P \leq 0.04$  (13 out of 326 trials) (13) when swimming an arbitrarily chosen search path (red line). (B) Single frames taken from video recordings showing a trial with a linear hydrodynamic trail. Yellow arrow, position of the submarine; red arrow, position of the seal. Colored lines are as in (A).

<sup>1</sup>Institut für Zoologie, Universität Bonn, Poppelsdorfer Schloss, D-53115 Bonn, Germany. <sup>2</sup>Ruhr-Universität Bochum, Allgemeine Zoologie und Neurobiologie, D-44780 Bochum, Germany.

\*To whom correspondence should be addressed. E-mail: dehnhardt@neurobiologie.ruhr-uni-bochum.de

## REPORTS

almost constant running distance, the submarine stopped somewhere on a semicircle (Fig. 1A). After leaving the hoop station, the seal immediately submerged and headed toward the center of the pool. Searching for the hydrodynamic trail was characterized by the seal protracting the vibrissae to the most forward position and performing slight lateral head movements. As soon as the seal intersected the hydrodynamic trail, the animal turned onto the submarine's course, thus indicating its detection of the trail, and followed the trail at a swim speed of  $\sim 2.0 \text{ m s}^{-1}$  (estimated from video recordings). As frame-by-frame analysis of video recordings revealed, the seal clung exactly to the submarine's trail. The seal located the submarine in 256 of 326 trials (78.5%). Location accuracy was independent of the submarine's position

on the semicircle. This location performance is highly significant (binomial distribution,  $P < 0.001$ ) (Fig. 1A) (15). In 59 of the 70 trials during which the seal failed to find the submarine, the animal seemed to have missed the beginning of the trail. In these cases, the seal stopped searching in the starting area after a few seconds. In only 11 trials (3.4%), failure to find the submarine was caused by the seal deviating from the previously correctly tracked hydrodynamic trail.

Increased delays between the start of the submarine and the start of the seal's search did not affect accuracy of trail detection and pursuit. In 24 of 30 trials with delays of 10, 15, and 20 s (10 trials each) the seal successfully located the submarine's final position (three failures after a delay of 10 s, one failure after 15 s, and two failures after 20 s). After 20 s, aging of the

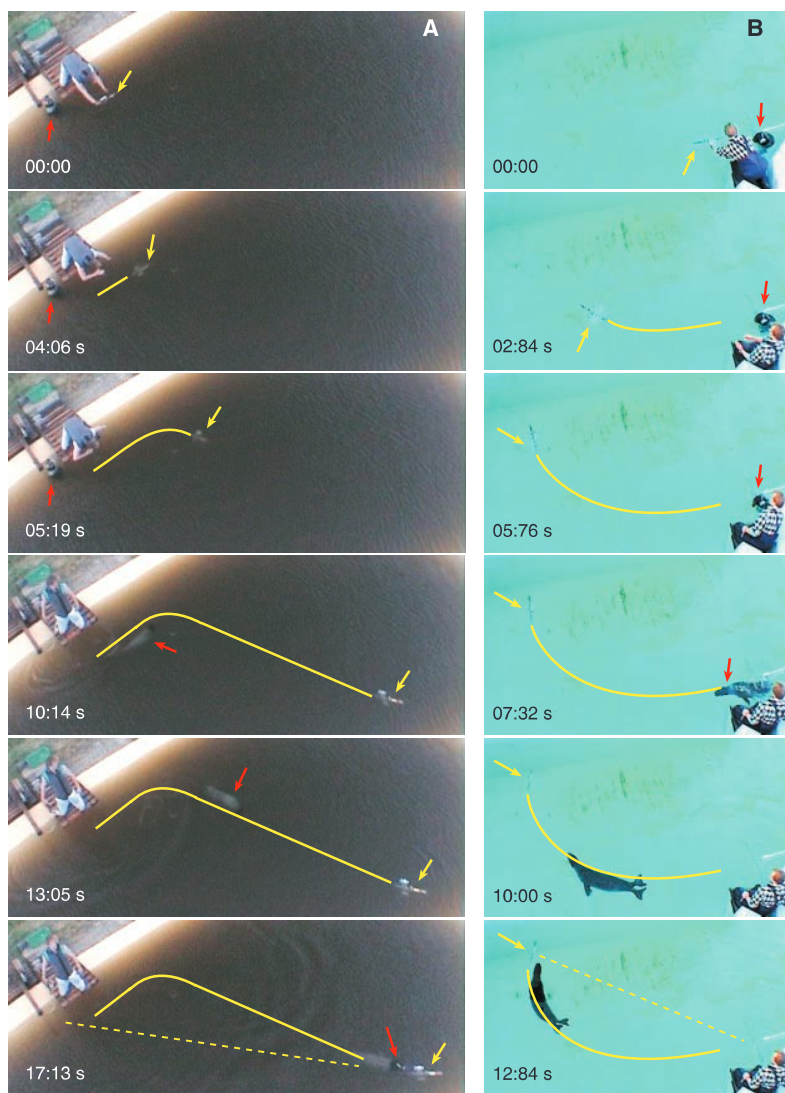
hydrodynamic trail in the seal's search area corresponded to that of a continuously running submarine that already covered a distance of  $\sim 40 \text{ m}$  (swim speed  $\sim 2 \text{ m s}^{-1}$  for 20 s).

Following a fish certainly requires detection of changes in the course of a trail. Therefore, we introduced an unpredictable change of course in the submarine's trail by using two lateral steering propellers (10). The seal spontaneously turned onto the new course when it met the submarine's turning point and successfully found the submarine in 26 of 30 trials (Fig. 2A). These results unequivocally show that the seal's location of the submarine was based on true trail-following. As in an echolocating animal, passive listening or the use of vision should have resulted in a straight approach to the submarine (Fig. 2A, yellow dashed line, last frame).

Under natural conditions, a seal may encounter a hydrodynamic trail not at its beginning but must be able to determine the swimming direction of a fish at any given point of the trail. Accordingly, we conducted 50 trials with the submarine running parallel to the long side of the pool, thereby passing the seal's hoop station at a distance of  $\sim 1 \text{ m}$ . In a pseudorandom sequence, the number of trials with the submarine running to the left or to the right was counter-balanced. In 46 trials the seal detected the trail, sharply turned into the correct direction, and followed the submarine's trail.

Thirty trials were randomly interspersed in the course of the experiments with a stocking mask that also covered the seal's muzzle. Whisker movements were impeded, but the seal was still able to open its mouth for the perception of potential chemosensory cues. In these trials, the seal started its search as usual but always failed to detect the hydrodynamic trail even when its head exactly met the submarine's starting point. These tests show that trail-following is only possible with unimpaired whiskers and is based on the detection and analysis of hydrodynamic information.

Experiments with hydrodynamic trails containing a change of course have been reproduced with a second experimentally naïve male harbor seal ("Nick"). These tests were conducted in an outdoor pool at "Zoo Köln" (Germany) filled with clear fresh water. Trail-following behavior of this seal corresponded to that described for the animal tested before (see Fig. 2B). The seal located the submarine in 37 out of 45 trials (82.2%). However, when the whiskers were covered by the stocking mask the seal never detected the trail. With this seal, we also tested the hypothesis that the use of acoustic cues should result in a straight approach to the submarine. During 10 trials randomly interspersed in the experiments, the seal was allowed to start its search right before the engine of the submarine stopped running, thus receiving



**Fig. 2.** (A) Sequence of single frames taken from video recordings showing a trial with a hydrodynamic trail containing a sharp change of course. (B) Sequence of single frames showing a trial with the submarine running a right-hand curve. Solid yellow lines indicate hydrodynamic trails. Arrows are as in Fig. 1. Broken yellow lines indicate the short-cuts the seal would have taken if using acoustic cues.



## REPORTS

ing a short acoustic cue from the submarine's final position. In these trials the seal directly approached the submarine's position in an unusually fast reaction (see Fig. 2B, last frame).

What might be the detection range of a trail-following seal for prey fish? Even after >3 min, the wake behind a swimming goldfish contains water velocities that are significantly higher than background noise (9) and exceed the sensitivity threshold of the whiskers of harbor seals (4). Given that a herring swimming at a sustained speed of  $\sim 1 \text{ m s}^{-1}$  (16) leaves a hydrodynamic trail just as stable as that of a goldfish, it might be detectable for a seal even when the herring is more than 180 m away. However, for a reliable estimate of the maximum detection range, we need to learn more about background noise in the wild as well as the aging of fish-generated trails under natural conditions.

Because a swimming seal itself produces considerable water movements that certainly affect the whiskers, the detection of fish-generated water movements was thought to be hardly possible (17). However, preliminary results from our laboratory suggest that seals may have overcome this problem by a simple mechanism. As a function of swim speed and their biomechanical properties, the whiskers of a swimming seal vibrate with characteristic frequencies. A hydrodynamic trail intersected by the seal will cause a modulation of this characteristic vibration that might be sensed by the seal.

Our results describe a system for spatial orientation in the aquatic environment that can explain successful feeding of pinnipeds in dark and turbid waters. The sensory ability of hydrodynamic trail-following may be also important to other species equipped with hydrodynamic receptor systems.

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- For the generation of linear hydrodynamic trails, the independently moving submarine was powered by a single propeller only. Two lateral steering propellers allowed the generation of curved trails. The submarine was always started with the steering propellers in the vertical plane, but rotated once around its longitudinal axis while running. Depending on the submarine's list, four inclination contacts switched on the steering propellers when these were in the almost horizontal plane after some meters of straight run. The new course was

not predictable, but if the submarine rotated fast, it changed its course sharply (Fig. 2A), if the rotation was slowly the resulting course was a left-hand or right-hand curve (Fig. 2B). The speed of the submarine was  $\sim 2 \text{ m s}^{-1}$  and  $\sim 1.5 \text{ m s}^{-1}$ , for linear and curved trails, respectively. Experiments were recorded by a camcorder installed  $\sim 5 \text{ m}$  above the pool. Video recordings were analyzed off-line frame by frame. The straight part of the hydrodynamic trail was described by measuring the direction and velocity of the particle movements (PIV) (9). A thin horizontal layer of laser light ( $\lambda = 650 \text{ nm}$ ) was laid about 30 cm below the water surface. A CCD-camera was installed 1 m from the edge of the pool, and neutrally buoyant seeding particles (Vetosint 1101, Hüls AG, Germany) were put into the water. The submarine was started in the depth of the laser plane at a distance of about 3 m. Several runs were performed with the submarine passing the camera in increasing lateral distances. Before each measurement, the direct current (DC) components of the water velocities were below  $10 \text{ mm s}^{-1}$ ; velocities of about  $5 \text{ mm s}^{-1}$  were typical. Particle movements were analyzed manually (Scion Image; Scion, Frederick, MD) or with a cross-correlation technique (MatLab; MathWorks, Natick, MA)

in order to describe direction, form and velocity of the water flow.

- Web fig. 1 is available on Science Online at [www.sciencemag.org/cgi/content/full/293/5527/102/DC1](http://www.sciencemag.org/cgi/content/full/293/5527/102/DC1).
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- The experimental animals were treated in accord with the official German regulations for research on animals. We thank D. Adelung, G. Nogge, S. Prange, and I. Röbbcke for their support during this study. Financed by grants of the Deutsche Forschungsgemeinschaft (G.D.).

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## Human Chromosome 19 and Related Regions in Mouse: Conservative and Lineage-Specific Evolution

Paramvir Dehal,<sup>1,2,4</sup> Paul Predki,<sup>1,5</sup> Anne S. Olsen,<sup>1,2</sup> Art Kobayashi,<sup>1,2</sup> Peg Folta,<sup>1,2</sup> Susan Lucas,<sup>1,2</sup> Miriam Land,<sup>1,8</sup> Astrid Terry,<sup>1,2</sup> Carol L. Ecale Zhou,<sup>1,2</sup> Sam Rash,<sup>1,2</sup> Qing Zhang,<sup>1,5</sup> Laurie Gordon,<sup>1,2</sup> Joomyeong Kim,<sup>1,2</sup> Christopher Elkin,<sup>1,3</sup> Martin J. Pollard,<sup>1,6</sup> Paul Richardson,<sup>1,5</sup> Dan Rokhsar,<sup>1,7</sup> Ed Uberbacher,<sup>1,8</sup> Trevor Hawkins,<sup>1,5</sup> Elbert Branscomb,<sup>1,2</sup> Lisa Stubbs<sup>1,2,\*</sup>

To illuminate the function and evolutionary history of both genomes, we sequenced mouse DNA related to human chromosome 19. Comparative sequence alignments yielded confirmatory evidence for hypothetical genes and identified exons, regulatory elements, and candidate genes that were missed by other predictive methods. Chromosome-wide comparisons revealed a difference between single-copy HSA19 genes, which are overwhelmingly conserved in mouse, and genes residing in tandem familial clusters, which differ extensively in number, coding capacity, and organization between the two species. Finally, we sequenced breakpoints of all 15 evolutionary rearrangements, providing a view of the forces that drive chromosome evolution in mammals.

Spanning 65 to 70 Mb and estimated to contain 1100 genes, human chromosome 19 (HSA19) is one of the smallest and most

gene-dense of human chromosomes (1, 2). A clone-based physical map spanning all but the centromeric regions of the chromosome with seven gaps (3) has provided the framework for HSA19 sequence, which to date includes 35 Mb of finished sequence and 22 Mb of high-quality draft. The solidly anchored clone framework and high percentage of ordered and oriented contigs generated through application of a plasmid paired-end sequencing strategy (4) have rendered unfinished portions of HSA19 draft sequence particularly amenable to annotation and analysis. Comparing human DNA sequence with that of other species has proved to be an especial-

<sup>1</sup>DOE Joint Genome Institute, Walnut Creek, CA 94598, USA. <sup>2</sup>Genomics and <sup>3</sup>Engineering Divisions, Lawrence Livermore National Laboratory, Livermore, CA 94550, USA. <sup>4</sup>Department of Genetics, University of California Davis, Davis, CA 95616, USA. <sup>5</sup>Genomics and <sup>6</sup>Engineering Divisions, Lawrence Berkeley National Laboratory, Berkeley, CA 94720, USA. <sup>7</sup>Physics Department, University of California Berkeley, Berkeley, CA 94720, USA. <sup>8</sup>Life Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831, USA.

\*To whom correspondence should be addressed. E-mail: stubbs5@llnl.gov



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